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Modeling species-rich ecosystems to understand community dynamics and structures emerging from individual plant interactions

Dissertation

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ABSTRACT

Grasslands cover 40% of the earth's land area and provide numerous valuable ecosystem services. However, climate change, global land use change and increasing intensive anthropogenic interventions make grasslands to one of the most endangered ecosystem types in the world. Effective protection in the future requires a fundamental understanding of the dynamics of grasslands and their major drivers. Field experiments have been conducted for impact analyses, for example, with different management intensities, plant community composition and altered climatic conditions. Complementary, ecological models allow to extend the analysis to long-term effects of changes as well as to a deeper understanding of the underlying ecological processes. In this thesis, an individual-based grassland model and network science were applied to understand the community structure and dynamics emerging from individual plant interactions – in relation to plant traits, ecological processes, environmental and anthropogenic impacts, and the small-scale spatial distribution of plants.

In the first study, an individual-based process-oriented grassland model was parameterized to simulate field data of a local biodiversity experiment using the concept of plant functional types. The influence of various functional plant traits and ecological processes on grassland productivity and functional composition were analyzed. Different functional plant traits showed partly contrasting effects on plant growth. With regard to the modeled ecological processes, competition for space between plants affected grassland productivity more than shading of plants.

In the second study, the parameterized grassland model was used to analyze the impact of functional diversity, mowing frequency and air temperature on ecological processes that lead to changes in grassland productivity. The model reproduced the increase of biomass yields with functional diversity as observed in the field experiment. Modeled plant competition for space showed to be the dominant process and was responsible for an increase in biomass yields in more frequently mown grasslands.

In the third study, an approach to generate a regionally transferable parameterization of the grassland model is presented. The impact of management, environment and climate change on productivity and functional composition of grasslands was analyzed within a German-wide scenario analysis. Management intensity had more influence on grassland productivity than environmental factors and correlations of productivity with environmental factors become stronger in less managed grasslands. Climate change showed to have only a minor influence on simulated vegetation attributes.

In the fourth study, network science was applied to forest megaplots to quantify the spatial neighborhood structure of species-rich ecosystems. Networks at the individual-tree and tree-species levels revealed similar structures at three investigated forest sites. Tropical tree species coexisted in small-scale networks and only up to 51% of all possible connections between species pairs were realized. A null community analysis showed that details on the tree position and tree size have no major influence on the network structures identified.

In summary, this thesis presents the development of advanced methods and analysis tools as well as their application to vegetation ecosystems with high diversity. Thereby, complex structures and dynamics of ecological systems could be systematically explored by combining ecological models with extensive field measurements.

ZUSAMMENFASSUNG

Grünland umfasst etwa 40% der Erdfläche und liefert zahlreiche wichtige Ökosystemleistungen. Klimawandel, globale Landnutzungsänderungen und eine zunehmend intensive Bewirtschaftung machen Grünland jedoch zu einem der am stärksten gefährdeten Ökosystemtypen der Welt. Zum wirksamen Schutz von Grünlandschaften, auch in Zukunft, ist ein grundlegendes Verständnis der Dynamik von Grünland und seiner Einflussfaktoren erforderlich. Feldexperimente untersuchen wie verschiedene Faktoren das Ökosystem beeinflussen (z.B. die Bewirtschaftungsintensität, die Zusammensetzung der Pflanzengemeinschaft oder veränderte klimatische Bedingungen). Ergänzend dazu ermöglichen ökologische Modelle auch langfristige Auswirkungen solcher Einflussfaktoren zu analysieren sowie ein tiefgehendes Verständnis der zugrunde liegenden ökologischen Prozesse zu erhalten. In dieser Arbeit wurde ein individuenbasiertes Grünlandmodell und Netzwerktheorie eingesetzt, um zu verstehen, wie Interaktionen zwischen einzelnen Pflanzen auf die Struktur und Dynamik von artenreichen Pflanzengemeinschaften wirken - bezüglich Pflanzenmerkmalen, ökologischen Prozessen, Umweltbedingungen und anthropogenen Einflüssen sowie der räumlichen Anordnung einzelner Pflanzen.

In der ersten Studie wurde ein individuenbasiertes, prozessorientiertes Grünlandmodell anhand von Felddaten eines lokalen Biodiversitätsexperiment parametrisiert und der Einfluss funktionaler Pflanzenmerkmale und ökologischer Prozesse auf das Grünland analysiert. Verschiedene Pflanzenmerkmale zeigten teilweise gegensätzliche Auswirkungen auf das Pflanzenwachstum. Raumkonkurrenz zwischen Pflanzen beeinflusste die Produktivität des Grünlands stärker als Beschattung von Pflanzen. In der zweiten Studie wurde das parametrisierte Grünlandmodell verwendet, um den Einfluss von funktioneller Diversität, Mahdhäufigkeit und Lufttemperatur auf ökologische Prozesse zu analysieren. Das Modell reproduzierte den im Feldexperiment beobachteten Anstieg der Biomasseerträge mit steigender funktioneller Diversität. Die Raumkonkurrenz zwischen Pflanzen zeigte sich als dominanter Prozess im Modell. Sie bewirkte einen Anstieg der simulierten Biomasseerträge mit erhöhter Mahdhäufigkeit. In der dritten Studie wurde eine regional übertragbare Parametrisierung des Grünlandmodells entwickelt. Anhand einer deutschlandweiten Szenarioanalyse wurde der Einfluss von Bewirtschaftung, Umweltfaktoren und Klimawandel auf das Grünland untersucht. Die Bewirtschaftungsintensität beeinflusste die Produktivität stärker als Umweltfaktoren. Klimawandel bewirkte nur kleine Veränderungen im Grünland. In der vierten Studie wurde Netzwerktheorie auf großflächige Waldinventuren von Megaplots angewandt, um räumliche Nachbarschaftsstrukturen von artenreichen Ökosystemen zu quantifizieren. Netzwerke auf Einzelbaum- und Baumarten-Ebene zeigten an drei untersuchten Waldstandorten ähnliche Strukturen. Tropische Baumarten koexistierten in Small-World-Netzwerken mit nur bis zu 51% aller möglichen paarweisen Verbindungen.

Zusammenfassend wurden in dieser Arbeit weiterentwickelte Methoden und Analysewerkzeuge sowie deren Anwendung auf Vegetationsökosysteme mit hohem Artenreichtum vorgestellt. Die Kombination ökologischer Modelle mit umfangreichen Feldmessungen erlaubte dabei eine systematische Analyse der komplexen Strukturen und Dynamik ökologischer Systeme.

PUBLICATIONS

PUBLISHED CHAPTERS OF THIS THESIS

Schmid, JS, Taubert, F, Wiegand, T, Sun, IF, and Huth, A (2020). “Network science applied to forest megaplots: tropical tree species coexist in small-world networks.” In: *Scientific Reports* 10.1, p. 13198. ISSN: 2045-2322. DOI: `10.1038/s41598-020-70052-8` ;

Schmid, JS, Huth, A, and Taubert, F (2021). “Influences of traits and processes on productivity and functional composition in grasslands: A modeling study.” In: *Ecological Modelling* 440, p. 109395. ISSN: 0304-3800. DOI: `https://doi.org/10.1016/j.ecolmodel.2020.109395` ;

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Taubert, F, Hetzer, J, Schmid, JS, and Huth, A (2020b). “Confronting an individual-based simulation model with empirical community patterns of grasslands.” In: *PLOS ONE* 15.7, e0236546. DOI: `10.1371/journal.pone.0236546` ;

CONTENTS

1

INTRODUCTION

1.1 GRASSLAND AND ITS RELEVANCE

1.1.1 *Definition, classification and distribution of grasslands*

Grassland covers 40% of the earth's land surface (corresponding to 52.5 million km^2) and occurs on each continent, most commonly in semi-arid zones (White, Murray, et al., 2000, Sala, Vivanco, et al., 2013). Its natural emergence is mainly determined by climate (mean annual temperature between 0 °C and 25 °C and annual precipitation between 150 and 1200 mm (Whittaker, 1975)), but also other factors such as disturbances by fire, the soil texture and the seasonality of precipitation can determine the occurrence and regional distribution of grasslands (Sala, Vivanco, et al., 2013). There exists a wide spectrum of grassland definitions (Dixon et al., 2014). One common definition describes grasslands as "terrestrial ecosystems dominated by herbaceous and shrub vegetation and maintained by fire, grazing, drought and/or freezing temperatures" (White, Murray, et al., 2000). Another definition for grassland by the UNESCO describes it as "land covered with herbaceous plants with less than 10 percent tree and shrub cover" (White, 1983). Grasslands are typically classified into two main types: temperate grasslands and savannas. Savannas are defined as "closed grass or other predominantly herbaceous vegetation with scattered or widely spaced woody plants" (Fosberg, 1961). They occur mainly in tropical and subtropical regions and are subject to rainfall variations from year to year and wildfires in the dry season. Temperate grasslands, covering up to 10% of the earth's land surface (13 million km^2) (White, Murray, et al., 2000, Dixon et al., 2014), in contrast to savannas, occur in temperate regions, are almost treeless, and exposed to seasonal climate variations (Choler, 2015).

In Europe, grassland covers about 8% of the total European land surface (corresponding to 2.5 million km^2) (Fig. 1.1) (Smit et al., 2008, FAOSTAT, 2019). The climatic conditions where grassland occurs range from semi-arid conditions in south-east Spain to humid conditions prevailing in north and north-west of Europe (Silva et al., 2008). The majority is temperate grassland, that can be further distinguished into natural, "semi-natural" and agriculturally improved grasslands (Bengtsson, Bullock et al. 2019). Natural grasslands mainly emerge by natural processes related to climate, fire and wildlife grazing without any anthropogenic influences (Bengtsson et al., 2019). Semi-natural grasslands are created and maintained depending upon human activities (e.g., livestock grazing or mowing) but their plant species pool and environmental conditions are given by nature (Silva et al., 2008). Thus, natural and semi-natural grasslands emerge from site-specific biotic and abiotic conditions and are composed of regional species pools (Dixon et al., 2014). Agriculturally improved grasslands are primarily built by humans via sowing agricultural varieties or non-native plant species and are usually intensively managed for agricultural reasons such as the production of hay or silage (Bengtsson et al., 2019).

In Germany, 47,500 km^2 is covered by permanent grassland (grassland that persists for at least five years (EU, 2013)), which corresponds to almost 30% of the total agricultural area and can be found in each federal state (FAOSTAT, 2019, Griffiths et al., 2020). Most grassland area can be found in Bavaria, Lower Saxony and Baden-Wuerttemberg (DESTATIS, 2020). Of this area, 40% is meadow (used for cutting), 55% is pasture (used for grazing and cutting), and less than 5% is low-yielding permanent grassland (not used for agriculture, e.g., nature conservation areas, areas in sparse forests or grassland areas with fruit trees) (DESTATIS, 2020).

Figure 1.1: Grasslands in Europe. Green areas in the land cover map correspond to grassland. The map is based on LUCAS (Land Use/Cover Area frame Survey) and Landsat-8 data of 2015 from Pflugmacher et al. (2018). Pictures show common grasslands in Scotland (top left), Spain (bottom left) and Germany (top right) (©Melanie Schmid).

1.1.2 *Biodiversity in grasslands*

Biodiversity describes the variety of living organisms within an ecosystem (Assessment, 2005) and can be assessed on different scales (i.e., genetic, population/species and community/ecosystem scale) (Redford and Richter, 1999). In grassland research, often the species scale is considered, as species diversity has shown to highly impact grassland dynamics and functioning such as stability. Species diversity can be distinguished into species richness, species composition and species abundance. Thereby, species richness corresponds to the number of species that can be found within the ecosystem, while species composition expresses the identity of the species present in the community. Species abundance corresponds to the relative representation of species in the ecosystem and can be measured by the number of individuals or proportional aboveground biomass per species. Additionally, a common approach in grassland research is to group plants with similar functional traits into plant functional types (Dyer et al., 2001, Schellberg and Pontes, 2012). Based on this approach, the functional richness, functional composition and the abundance of plant functional types in the grassland community can also be considered.

In semi-natural grasslands, up to 89 indigenous plant species per m^2 can be found (Heinz et al., 2020). This high species richness is comparable to tropical forests and thus gives semi-natural grasslands a high nature conservation value (Heinz et al., 2020). In temperate Europe, species diversity of grasslands evolved continuously over millions of years by speciation, extinction and migration of species from other biomes (Pärtel et al., 2005, Hejcman, Hejcmanová, et al., 2013). At smaller spatial scales, plant diversity in grasslands is often constrained by the regional plant species pool, which is a set of survivable species created through evolutionary processes (Pärtel et al., 2005).

Grasslands harbor not only numerous plant species, but also the survival of many animals depends directly or indirectly on the persistence of grassland areas. In Germany, 70 to 80% of more than 45,000 animal species, especially insects (Nickel, 2003) and butterflies (Swaay et al., 2006), inhabit such open biotopes like grasslands

(Gerowitt et al., 2013). Biodiversity in grasslands, among plants and other trophic levels, influences various other ecosystem functions and services directly and indirectly, which makes it an important topic in scientific research and for society (Turnbull et al., 2016).

1.1.3 *Grassland management*

The persistence of the vast majority of grasslands in Europe depends on anthropogenic management. Grassland management encompasses either mowing on meadows, grazing on pastures or a combination of both, with different intensities regarding frequency, mowing technique as well as stocking rate and duration. Fertilizer can be applied to offer enough nutrients for the plants (e.g., nitrogen and phosphorus). Cutting off plants through livestock grazing, regular mowing or a combination of both prevents afforestation and hence controls the successional change of the ecosystem (Isselstein et al., 2005, Pärtel et al., 2005). Further, regular low-intensity cutting is required to promote biodiversity in grasslands as light availability increases and nutrients are depleted (Oelmann et al., 2009). This offers plant species that are adapted, for example, to low nutrient levels and high light availability, to coexist with more competitive plant species that would otherwise dominate the grassland community (Knop et al., 2006).

There exists huge variation in management regimes depending, for example, on environmental conditions. Extensive management means little anthropogenic impact on natural grassland dynamics by mowing events (one to two events per year) and fertilization (no fertilizer or only moderate amounts) (BfN, 2014). This management is often conducted in areas with undesirable conditions such as low soil fertility (Pywell et al., 2002). In contrast, intensive management comprises up to eight mowing events per year and the application of larger amounts of fertilizer (Tallowin and Jefferson, 1999). In extensively managed grasslands a high biodiversity can generally be found, whereas intensive management often leads to the dominance of only a few plant species and less animal species (Marriott et al., 2004, D'Aniello et al., 2011). In addition, the cutting height can also influence the provided ecosystem services of grasslands (Zhang et al., 2015). Overall, management can strongly affect ecosystem functions and services in grasslands. Management intensification can lead to desired changes (e.g., higher yields) but often at the cost of other important ecosystem services (Taube et al., 2014, Sollenberger et al., 2019).

1.1.4 *Goods and services provided by grasslands*

Semi-natural grasslands belong to one of the most important ecosystems, as they provide various other ecosystem services besides the conservation of biodiversity. Anthropogenic management and biodiversity itself thereby affect the provided ecosystem services of grasslands.

1.1.4.1 *Sequestration and storage of carbon*

Grasslands store about 34% of the global carbon stock in terrestrial ecosystems, which is only 5% less than the amount that forests store (Silva et al., 2008, Ghosh and Mahanta, 2014). Thereby, the soil of grasslands constitutes the dominant carbon stock.

Plants sequester carbon dioxide (CO2) via photosynthesis from the atmosphere. Of this captured carbon, parts are released again to the atmosphere as gaseous carbon emissions through plant respiration, while the remaining captured carbon retains in the plant's living above- and belowground tissue. Another part of the organic carbon converts to soil organic matter and also partly releases to the atmosphere when plant parts die and are decomposed (Jones and Donnelly, 2004, Ghosh and Mahanta, 2014). Carbon storage in grasslands primarily happens through the growth and decomposition of plant roots, which is a cyclical process in perennial species, and especially occurs when plants are defoliated by grazing or mowing. Cutting a plant firstly reduces also root growth and causes relatively more parts of root biomass to die because the remaining plant leaves can no longer photosynthesize enough energy to support the entire root system of the plant. During a break in defoliation, the growth of the leaves and roots of the plants can recover again (Ghosh and Mahanta, 2014). With proper management, perennial plants can live and reproduce for many years in a continuous cycle of cutting, root death, and regeneration, thereby adding large amounts of carbon to the soil (Ghosh and Mahanta, 2014).

The amount of carbon that temperate grasslands can store varies greatly and depends on various factors such as the soil type, management and biodiversity (Conant et al., 2001, Jones and Donnelly, 2004, Soussana, Loiseau, et al., 2004, De Deyn et al., 2011, McSherry and Ritchie, 2013, Schierhorn et al., 2013, Yang, Tilman, et al., 2019). Conversion of forests or cropland to grasslands results in more carbon sequestered in soil organic matter (Hönigová et al., 2012). Furthermore, conversion of cropland to managed grasslands leads to more soil organic carbon sequestration than natural recovery of grassland from abandoned cropland (Li et al., 2018). However, anthropogenic management can also switch grasslands from carbon sinks to sources of greenhouse gases, dependent on management intensity and regional climatic conditions (Abdalla et al., 2018). For instance, low or moderate grazing rates, especially in warm and humid regions, have shown to increase soil organic carbon stocks and hence build carbon sinks. In turn, high grazing rates in cold and humid regions or in regions with low precipitation can result in lower carbon stocks and carbon sources compared to unmanaged grasslands (Abdalla et al., 2018, Sollenberger et al., 2019). Generally, intensively managed grasslands show an increased net ecosystem exchange and are often considered as a carbon dioxide sink (Ammann et al., 2007, Schmitt et al., 2010, Hörtnagl et al., 2018, Sollenberger et al., 2019), while nitrous oxide (N2O) and methane (CH4) emissions also increase due to organic fertilizer and manure from livestock (Hörtnagl et al., 2018, Sollenberger et al., 2019). Also, climate change can contribute to an increased carbon sequestration in soil organic matter due to increased carbon dioxide and nitrogen deposition (Jones and Donnelly, 2004, Chang, Ciais, Gasser, et al., 2021).

1.1.4.2 *Food, foraging and livestock*

Globally, the demand for agricultural products is increasing as human population grows, which has resulted in more than a doubling of domestic ruminants (from 1.4 billion to 3.4 billion) in the last century (Chang, Ciais, Gasser, et al., 2021). Cattles, sheep and goats offer meat and dairy products besides wool and leather. Worldwide, nearly 50% of the forage used for such livestock is provided by grasslands (Herrero et al., 2013). Forage quality and yield is substantially influenced by biodiversity and management (Tallowin and Jefferson, 1999, Schaub, Finger, et al., 2020). Semi-natural species-rich grasslands thereby offer significantly lower forage yield and quality than intensively managed grasslands (Tallowin and Jefferson, 1999, Isselstein et al., 2005), which in turn can provide largely increased biomass yields and forage quality (Isselstein et al., 2005, Schaub, Finger, et al., 2020).

1.1.4.3 *Cultural aspects and other ecosystem services*

Extensive grasslands with a high biodiversity can have a positive impact on human well-being including spiritual, aesthetic, educational and other cultural values (WRI, 2005, Tribot et al., 2018). In addition, grasslands with extensive use and traditional management (e.g., the use of dung instead of liquid manure) can preserve biodiversity and are considered as cultural heritage in some regions (e.g., in the Swiss Alps) (Fischer, Rudmann-Maurer, et al., 2008, Bengtsson et al., 2019). Furthermore, botanical gardens often engage for the conservation of rare or endangered grassland species (e.g., the botanical garden of the University of Marburg) (BMEL, 2017).

Many other ecosystem services are directly and indirectly supported by semi-natural grasslands, such as the provision of food (e.g., flowering habitat for bees and honey production), raw materials (e.g., for bioenergy production) and genetic resources (e.g., for medical purposes) (Hönigová et al., 2012). Regulating services comprise besides climate regulation by carbon sequestration and storage also the improvement of air quality, regulation of water flows, prevention of soil erosion, promotion of pollination, and the maintenance of soil fertility by grasslands (Bazzoffi, 2009, Cerdan et al., 2010, Hönigová et al., 2012, Bengtsson et al., 2019, Sollenberger et al., 2019).

1.1.5 *Threats of and future changes in grasslands*

Grasslands are among the most vulnerable ecosystem types in the world in terms of human impacts (Sala, Chapin, et al., 2000). Compared to other ecosystems, grasslands are particularly sensitive to the impacts of drivers on biodiversity and are located in parts of the world where ecosystems will be most affected by human activities (Sala, Chapin, et al., 2000).

The greatest threat is global land use change (Sala, Vivanco, et al., 2013). Grassland areas with ideal environmental conditions, favorable climate and soil, are often converted into cropland (White, Murray, et al., 2000, Sala, Vivanco, et al., 2013, Taube et al., 2014, IPBES et al., 2019). Since 1992, the global area covered by temperate grassland has declined by 2.5% (IPBES et al., 2019). The change of land cover and land use is mainly driven by an increasing food demand, human population growth, and the generally higher profitability (Silva et al., 2008, Taube et al., 2014). Besides the conversion into croplands, semi-natural grasslands disappear through management intensification and abandonment of agricultural land use, for example, the latter at sites with unfavorable environmental conditions (Isselstein et al., 2005, Gellrich et al., 2007, Aune et al., 2018). However, the continuation and intensity of management is crucial for the preservation and maintenance of grasslands and its biodiversity, and for the prevention of afforestation (Tallowin and Jefferson, 1999, Marriott et al., 2004).

Climate change is the second greatest threat to biodiversity in grasslands (Silva et al., 2008, Sala, Vivanco, et al., 2013). Global warming, more frequent and intense weather events, fires, floods and droughts associated with climate change impact many aspects of grassland biodiversity, for example, the regional species distribution, phenology and community structure (Walter et al., 2012, IPBES et al., 2019). For instance, rising temperatures have already led to an earlier timing of spring events and have shifted the ranges of plant and animal species toward the north as well as uphill (Silva et al., 2008).

Increased nitrogen deposition resulting from agricultural intensification and increased burning of fossil fuels by traffic and industry is the third greatest threat of biodiversity and other ecosystem functions of semi-natural grasslands (Silva et al., 2008, Stevens et al., 2010, Sala, Vivanco, et al., 2013). Enriched nitrogen soil content can lead to an increased plant growth and thus, can increase plant shading and competition for other resources. Such changed conditions are considered to result in a reduced number of species that can coexist (Hautier et al., 2009).

Furthermore, invasion by non-native exotic species induced by climate change, increased atmospheric carbon dioxide, nitrogen deposition and altered disturbances impacts ecosystem functions and services of grasslands and hence presents also considerable threats to grasslands (Ehrenfeld, 2010, Runyon et al., 2012, Teixeira et al., 2020).

In Germany, the area of permanent meadows and pastures decreased continuously from 1966 to 2013 (from 6.9 million ha to 4.6 million ha) and slightly increased to 4.75 million ha within the last years (FAOSTAT, 2019). As a result of political regulations, requirements to preserve grasslands have come into force in some German federal states (NABU, 2014). Agricultural farms in these states can generally continue to cultivate grasslands, given that they establish new grassland fields elsewhere on arable land (NABU, 2014). In addition, species-rich grasslands are more and more intensified in Germany besides conversion, afforestation, abandonment and overbuilding (NABU, 2014). Land use intensification and conversion affected the endangerment of almost 80% of the grassland habitat types listed in the German federal list of endangered biotopes (BfN, 2014). Grassland was converted to agricultural land for the production of, for example, maize as high-energy fodder for cattle and of energy crops for the production of biogas (BfN, 2014). Increasing grassland intensification, for example, overgrazing, is a further major threat in the Alps speeding up erosion rates (Hönigová et al., 2012).

Globally, the protection of temperate grassland is still low compared to other major terrestrial biomes (only 4%) (Hoekstra et al., 2005, Henwood, 2010). Hence, new strategies have to be found to conserve biodiversity and maintain other important ecosystem services of semi-natural grasslands. Besides the creation of nature reserves, a proper management might lead to high yields and simultaneously to the conservation of plants and animals (Dijk, 1991, WallisDeVries et al., 2002). For that, one fundamental task is to gain a deep knowledge on grassland dynamics – for example, how community dynamics emerge from the interactions of individual plants in managed grasslands or its influence by specific management regimes and environmental conditions. To answer such questions, scientific research thereby benefits from the combination of ecological modeling with knowledge gained from extensive field studies and experiments.

1.2 ANALYZING VEGETATION STRUCTURE, PROCESSES AND INTERACTIONS

Global change due to climate warming and human impacts makes it imperative to investigate how valuable ecosystems such as grasslands are changing in terms of ecosystem functions and services. The required basis for such an assessment can be provided by an in-depth analysis of the ecosystem vegetation structure and dynamics and their underlying processes and interactions.

1.2.1 *Environmental factors affecting ecosystems*

Plant species composition and plant growth in grassland ecosystems is influenced by multiple environmental components comprising biotic factors, abiotic factors such as soil and climate, and anthropogenic intervention like management actions (Borer, Grace, et al., 2017).

Abiotic environmental factors are nonliving aspects that influence ecological processes in grasslands and include factors related to soil and climate, for example, intensity of radiation, air temperature and soil water availability (Fig. 1.2). These factors can correlate with each other and can have various effects on grassland dynamics, which in turn can also feed back to the environment. For instance, a high intensity of radiation is associated with an increase of the near-surface air temperature, which can increase plant transpiration. This increased transpiration results in the closure of leave stomata and thus, in the restriction of plant photosynthesis (Bat-Oyun et al., 2012). Conversely, grassland and its growth can affect climatic factors, for example, through surface albedo (Wang and Davidson, 2007). Growth and the development of plants can be dependent on several of such abiotic factors. Thereby, the limiting factor that determines plant growth is often considered the one that is at the minimum (Liebig's law of the minimum (Sinclair, 1999)).

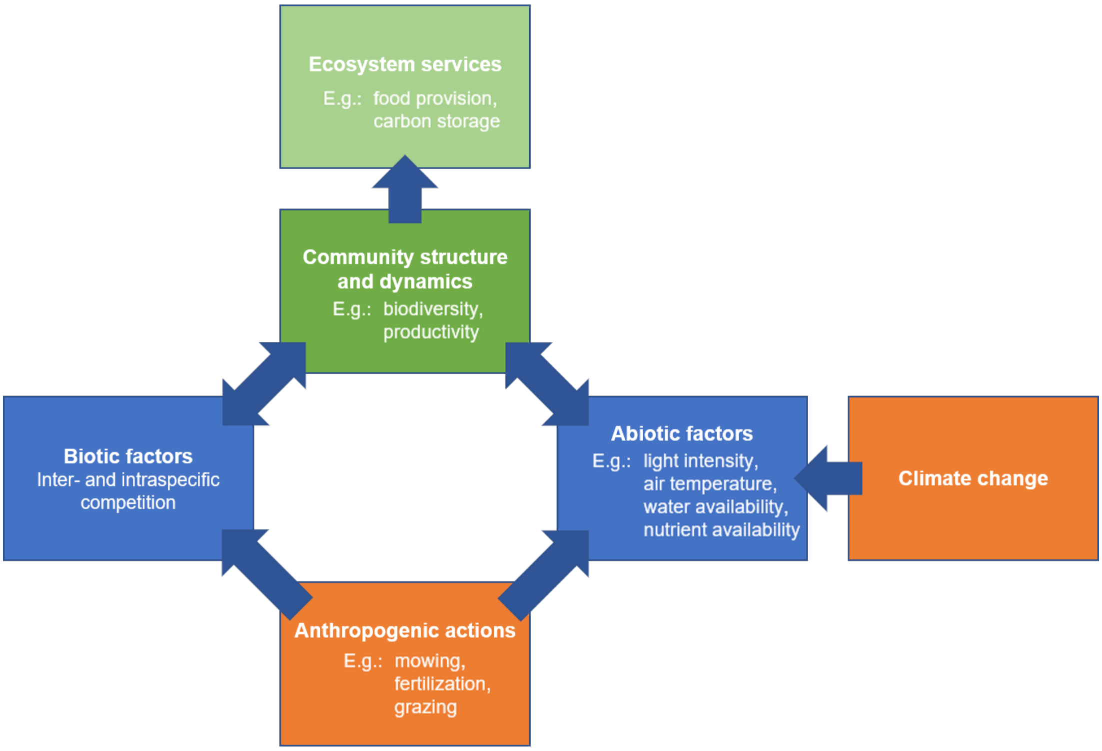

Figure 1.2: Interactions between vegetation community structure and dynamics, biotic factors, abiotic factors, anthropogenic actions climate change and ecosystem services.

Furthermore, biotic factors in terms of living organisms (e.g., plants and microbes) and their interactions influence the structure and dynamics of grasslands. Soil microbes can substantially increase grassland productivity by, for example, reducing plant diseases (Schnitzer et al., 2011). According to plant-plant interactions and to Lotka & Volterra, different plant species are supposed to coexist if intraspecific competition (i.e., competition between plants of the same species) is stronger than interspecific competition (i.e., competition between plants of different species) (Silvertown, 2004). Moreover, each plant species matches to specific biotic and abiotic environmental conditions – its so-called ecological niche (Polechová and Storch, 2019). Interspecific competition and intraspecific optimization can lead to niche differentiation to guarantee species coexistence over the course of evolution (Polechová and Storch, 2019). Overlapping niches can be narrowed over time within plant communities to shape differences by selection and phenotypic plasticity (Meilhac et al., 2020). These two mechanisms also allow plants to adapt to changing environmental conditions (Grenier et al., 2016). Thereby, trade-offs in plant traits and resource use prevent optimal adaptation to the environment, i.e., the emergence of a dominant "super-species".

Anthropogenic actions can cause substantial changes in abiotic and biotic factors and thus in the biotope as a whole (Borer, Grace, et al., 2017, Simons et al., 2017). For example, mowing or fertilizing can change the entire vegetation structure by changing light conditions or increasing the nutrient availability in soil in such a way that certain plants can no longer exist (Endels et al., 2007, Cleland and Harpole, 2010).

The interplay and importance of different environmental factors and anthropogenic actions influencing grassland structure and dynamics are still not well understood but crucial to derive predictions on, for example, biodiversity and grassland productivity under future global and climate change and to derive recommendations for mitigation and future management. For that, a detailed understanding of how ecological processes in grasslands are connected to environmental factors and anthropogenic actions is essential.

1.2.2 *Field studies and their importance*

The fast growth and manageable size of grasslands make it easy to analyze vegetation dynamics in field experiments. Field experiments are set up to investigate and validate ecological hypothesis, theories and other aspects of grasslands. One major topic addresses the question how biodiversity is related to grassland productivity and other ecosystem services (Hector, Schmid, et al., 1999, Tilman, Reich, et al., 2001, Adler et al., 2011, Tilman, Isbell, et al., 2014). Other topics for which field experiments of grasslands are set up relate to coexistence theory (Silvertown, 2004) and plant strategies (Grime, 1974). Also, experimental studies analyze grassland community responses to elevated carbon dioxide concentrations and other environmental changes driven by climate change (White, Carlyle, et al., 2012, Lei et al., 2016), and the impact of different management scenarios (Weigelt, Weisser, et al., 2009).

Field experiments are conducted at different spatial and temporal scales. The Nutrient Network (NutNet, `www.nutnet.org`) is a project that comprises more than 100 sites with a standardized experimental design distributed over the entire world and exists already for more than a decade (Borer, Grace, et al., 2017). It is used to deal with the question how nutrient excesses influence biodiversity and productivity of grasslands. Similarly, the International Drought-Net (IDE, `www.drought-net.org`), started in 2014, comprises more than 100 sites around the world where a controlled design is used to simulate different dimensions of drought (Knapp, Avolio, et al., 2017). The project was initiated to study the sensitivity of terrestrial ecosystems to climate change, i.e., more frequent and severe drought events. Further globally distributed, coordinated experiments are, for example, the Herbaceous Diversity Network (HerbDivNet, `www.herbdivnet.wordpress.com`) and the Disturbance and Resources Across Global Grasslands Network (DRAGNet, `www.nutnet.org/dragnet`). Other experiments are running rather locally over long periods of time to investigate long-term effects of changing impact factors (Lepš, 2014).

In Germany, regionally and locally established field experiments partially participate in the global networks. Two regional long-term German projects are (1) TERENO (Terrestrial Environmental Observations) (Bogena et al., 2016), which comprise four observatories for research studies on climate change and global change impacts, and (2) the Biodiversity Exploratories (Fischer, Bossdorf, et al., 2010), which comprise three different observatories across Germany established to analyze feedbacks between land use, biodiversity and ecosystem processes. In total, 34 long-term field experiments (minimum duration of 20 years) exist in Germany for the investigation of sustainable soil use and yield of grasslands (Grosse et al., 2020). One of the longest running biodiversity experiment, established in 2002, is the Jena Experiment (Weisser et al., 2017). Other local field experiments are, for example, the Global Change Experimental Facility (GCEF) (Schädler et al., 2019) and the University of Giessen Free-Air Carbon dioxide Enrichment study (GiFACE) (Jäger et al., 2003).

A common experimental design and setup is to establish replicates of small grassland plots (e.g., each with a size of 20 m^2) with varied plant compositions (e.g., in the Jena Experiment (Weisser et al., 2017)), management (e.g., in the Park Grass Experiment (Silvertown et al., 2006)) or manipulated environmental factors (e.g., in the Global Change Experimental Facility (GCEF) (Schädler et al., 2019)), and control plots with no modification for comparison. Vegetation measurements in field experiments often include aboveground biomass (in terms of yield), vegetation cover, vegetation height and leaf area index, either from the entire grassland community or from individual plant species, and at different time intervals (e.g., twice a year or prior to a mowing event). Soil properties such as soil moisture and nutrient contents are also often recorded (e.g., Volk et al., 2000, Carlyle et al., 2011). In contrast to experiments belonging to globally coordinated networks, measurements of local field experiments are often conducted with different methodologies (e.g., different techniques, spatial and temporal scales) and thus can also include variations in accuracy, frequency and effort (White, Carlyle, et al., 2012).

Field studies can provide huge amounts of data and are thus the basis for the majority of grassland research. However, based on field studies, it is still a challenge to disentangle the impact and importance of different treatments or variations in environmental factors and to analyze the validity of results on different spatial and temporal scales. For instance, a long-term grassland experiment established to investigate the impact of different management intensities on different scales revealed that the impact of management intensity on species richness depend on the combination of both, mowing frequencies and fertilization amounts, and lead to varying effects at different temporal and spatial scales (Lepš, 2014). To resolve this, for example, the challenge remains that either different field sites or even several plots at one field site can additionally differ in several other factors (e.g., regional or small-scale heterogeneous environmental conditions), and thus a high number of replications and further experiments would be necessary to disentangle the influence of multiple individual factors and their combinations. Field experiments of grasslands are thus primarily limited in space (and factorial study design), which makes it difficult to assess, for example, short- and long-term consequences of global change drivers for grasslands over larger spatial scales. In addition, long-term field data on the effects of climate change, particularly long-term changes in weather variables rather than increased atmospheric carbon dioxide, on grassland biodiversity and productivity are also still scarce (Oijen et al., 2018). Further, only the response of the vegetation to variations in manipulated factors can be measured, but the underlying process-based causes of these responses are often derived by statistical analyses based on specific assumptions (e.g., structural equation modeling (Grace, Anderson, et al., 2016)).

Besides the conventional methods to observe grassland dynamics, like field measurements, also other monitoring techniques such as remote sensing are more and more used to observe grassland dynamics (Liu, Cheng, et al., 2017, Schwieder et al., 2020). For example, remote optical sensors of satellites offer the ability to acquire information over large areas with little expense. Optical measurements allow to detect grassland cover and assess information on the greenness, vitality and density of grasslands (Pflugmacher et al., 2019, Preidl et al., 2020, Reinermann et al., 2020). These can be used to gain knowledge about the productivity and management of grasslands, for example, by the detection of cutting dates (Griffiths et al., 2020, Lobert et al., 2021).

1.2.3 *Ecological modeling*

Ecological modeling is an important tool to receive knowledge about the impact of different factors in environmental systems and thus, to overcome empirical limitations described in the previous section. Therefore, ecological models are used in combination with and complementary to field studies of grasslands.

A model is classically defined as a simplified abstract representation of a complex system. Models are used in ecology for a variety of purposes including the explanation of patterns observed in empirical data, making predictions on system development and guiding research (Jackson et al., 2000). Thereby, models can be deterministic or stochastic, static or dynamic and empirical or mechanistic (Thornley, 2001). While some model types evaluate only observation data using a particular method (e.g., statistical modeling like linear regression analysis), other model types such as process-based models integrate field data for model calibration and validation. Thus, ecological models often build on and depend on measurements in the field.

With the establishment of field experiments of grasslands, such as the grassland biodiversity experiment at Cedar Creek (Tilman, Knops, et al., 1997, Tilman, Reich, et al., 2001), models on grassland dynamics gained more and more popularity and relevance for scientists. Today, there exists extensive literature on grassland modeling ranging from empirical models to process-based models to integrated models (Oijen et al., 2018). Nevertheless, currently existing grassland models still fail in some aspects, for example, in reproducing the lower resistance of grasslands with lower biodiversity to climate change as observed in field studies, highlighting the ongoing need for further model development of grassland dynamics (Tilman and Downing, 1994, Oijen et al., 2018).

1.2.3.1 *Mechanistic models*

In mechanistic models, vegetation growth is driven by mathematical equations describing physiological processes such as photosynthesis or respiration. Mechanistic models have been developed for different temporal and spatial scales and can strongly vary in the degree of details regarding the modeled underlying processes. Some mechanistic models describe ecosystem processes at the community level (e.g., Dusseux et al., 2015), some models represent populations and distinguish between different plant species or plant functional types (e.g., Schapendonk et al., 1998, Thornley, 1998, Ma, Lardy, et al., 2015, and some models simulate the growth of each individual plant (e.g., Soussana, Maire, et al., 2012, Taubert, Frank, et al., 2012). The degree of complexity and focus of the model is thereby related to the aim of the study. In grassland modeling, models can be used (i) to estimate water, carbon or other greenhouse gas fluxes in grasslands at regional or global scales (Bondeau et al., 2007, Ma, Lardy, et al., 2015, Chang, Ciais, Gasser, et al., 2021), (ii) to analyze changes in vegetation attributes (Chen et al., 1996) or (iii) focus on appropriate future farm-level management in the face of climate change (Dusseux et al., 2015), while some models also focus explicitly on detailed soil processes such as soil temperature, soil moisture and nutrient content (Parton, Morgan, et al., 2007). Individual-based models are particularly suited for analyzing competition processes between plants and the role of different plant traits and their effect on grassland structures and attributes at the community level, such as functional composition or productivity (Soussana, Maire, et al., 2012, Taubert, Hetzer, et al., 2020a). However, individual-based models can be difficult to parameterize for larger heterogenous regions or species-rich grasslands because they may require a multitude of input parameters.

In order to make reliable statements with a model, sufficient field data are required for parameterization, and their availability often determines the chosen model complexity. Values of model input parameters, such as morphological plant traits of different species, are either obtained from direct plant measurements or require model calibration by comparing measured vegetation attributes to the model output. Many field studies provide time series of various vegetation attributes (e.g., aboveground biomass, leaf area index, or soil moisture). On the one hand, these data provide an excellent basis for estimating model parameters, specifically for model calibration using optimization algorithms and for model validation to assess model performance. On the other hand, the large amount of data can also pose a challenge for model parameterization, as the applied optimization to fit each observation becomes more complex.

Advantages of mechanistic models include the opportunity to analyze systems on different organizational levels (e.g., individual plants, species populations, community level or the entire ecosystem) to get a deep understanding of the role and interplay of plant traits, ecological processes and environmental factors. Sensitivity analyses, for example, allow to change input parameters (e.g., plant traits) to investigate their impact on vegetation dynamics and attributes (Saltelli, Aleksankina, et al., 2019). Robustness analyses allow to switch on and off or to modify entire processes (such as plant shading) to explore how the system depends on or reacts to such variations (Grimm and Berger, 2016). In addition, scenario analyses provide the opportunity to systematically change environmental factors (such as air temperature or management regime) to examine the dependence of community dynamics on such factors. Hence, mechanistic models are suited to analyze and understand in detail how ecological systems such as grasslands depend on certain plant traits, processes or factors, with much less effort compared to empirical studies in the field. Furthermore, additional vegetation attributes, for example, complementary to field measurements at the local scale, can be derived from process-based models, which also allow their large-scale estimation for entire regions based on developed regionalization concepts (Rödig et al., 2017).

Statistical methods commonly applied to measured field data, such as linear regression or structural equation modeling, can also be applied to model simulation results, for example, to relate statistically analyzed and explained empirical patterns to detected mechanisms and factors from process-based model simulations (Bai et al., 2007, Grace, Anderson, et al., 2016). In addition, advanced machine learning methods are more and more applied in scientific research. For example, decision trees are used in combination with process-based models and remote sensing to predict changes in aboveground biomass in tropical forests (Knapp, Fischer, et al., 2018) or are used for sensitivity analysis to determine the influence of different parameters in a model (Moulin, Perasso, and Gillet, 2018).

1.2.3.2 *Network science*

Another important methodological field is network science, which has been applied for various purposes in ecology (Poisot et al., 2016). Networks can be used to analyze the structure of dependencies, interactions or connections between different components in large complex systems. These models persist of nodes, the elements of the system, and edges that mark relations between the elements of the system. In ecology, nodes can be single individuals, species or communities, and edges can refer to dependencies or interactions between them. For instance, food webs (Montoya and Solé, 2002) or networks of plants and animal pollinators (Basilio et al., 2006) can be used to understand the performance of the system as a whole, like its resistance to perturbations, which can provoke extinction of species. Moreover, with respect to spatial networks, nodes can represent habitat patches and edges can refer to connections such as dispersal pathways – a model system that allows to analyze the dynamics of spatially explicit metapopulations in landscapes crucial for biodiversity conservation (Urban and Keitt, 2001, Moilanen, 2011). The mapping of complex ecological systems to networks and their evaluation makes them comparable to other systems. Network science revealed that common patterns such as the small world property (Watts and Strogatz, 1998) or scale freedom (Barabási, 2016) can be found in networks of systems across a wide variety of disciplines (Cancho and Solé, 2001, Liljeros et al., 2001, Eguíluz et al., 2005, Proulx et al., 2005).

In terms of vegetation ecosystems, connections that indicate potential interactions between individual plants can be represented and measured using network science. This requires spatial positions and interaction diameters of each plant. Such extensive data are available and regularly recorded, for example, in large field inventories of tropical rainforests. Protocols of CTFS-ForestGEO mega plots provide positions of thousands of trees growing on 25 to 50 ha forest plots, including further attributes like tree species and stem diameter at breast height for each tree (Condit, 1998). This data base represents a fundamental source of data on which spatial networks can be created using individual tree sizes and proximities.

1.3 OBJECTIVES OF THIS THESIS

The main objective of the thesis is to gain a deeper understanding by means of modeling on the effects of plant-plant interactions and the respective influence of plant traits, spatial structure, as well as abiotic and anthropogenic factors that lead to vegetation attributes and dynamics observed in field studies of vegetation systems.

From chapter to chapter, the spatial scale of the respective investigations and the considered interactions and influencing factors on vegetation dynamics increase (Fig. 1.3). Regarding temperate grasslands, Chapter 2 starts with the investigation of modeled plant-plant interactions for a local grassland experiment considering plant traits and different small-scale competition processes between plants. Chapter 3 then deals with a follow-up simulation study on the impact of anthropogenic actions (i.e., mowing frequency). In Chapter 4, the effect of regional differences in environmental factors and grassland management are modeled and analyzed based on German-wide field experiments. Lastly, in Chapter 5, tree-connection patterns within large tropical forest plots across different continents are analyzed in terms of network science.

Subsequent chapters address thereby the following main questions:

Chapter 2: Which plant traits and ecological processes are responsible for the structure and dynamics observed in temperate grasslands?

Chapter 3: Why and how do different anthropogenic management regimes and climate warming alter vegetation attributes of temperate grasslands?

Chapter 4: How do site-specific environmental factors and climate change alter grassland productivity and the proportion of herbs?

Chapter 5: Are there general patterns in the spatial connections of trees in tropical forests?

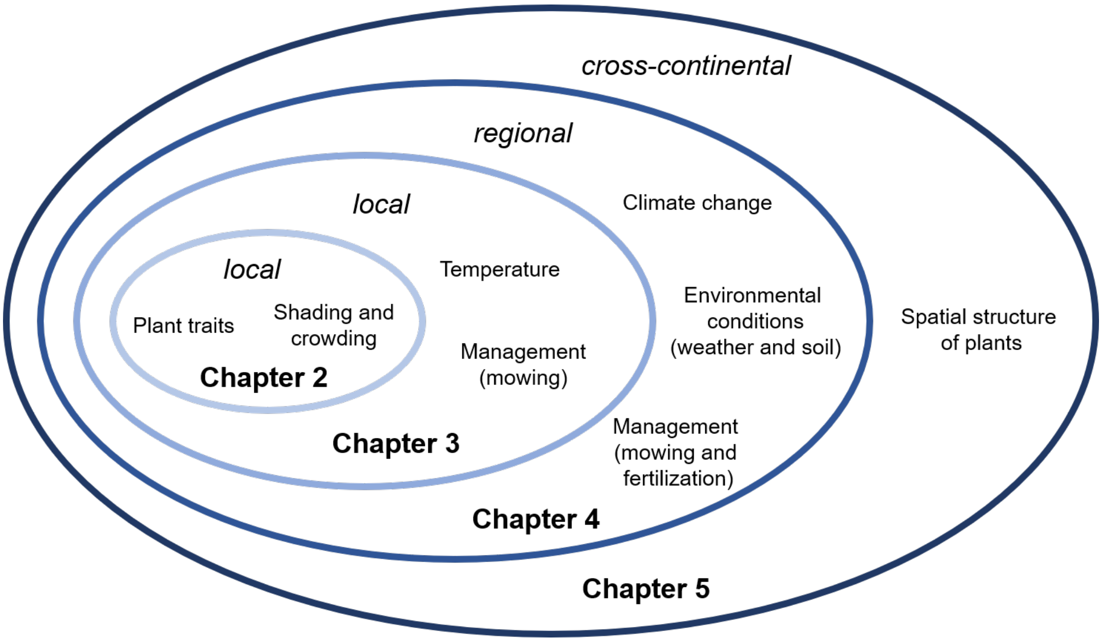

Figure 1.3: Content of the chapters of this thesis. Each chapter analyzes the influence of different biotic and abiotic factors on ecosystem attributes and dynamics. In Chapters 2 to 4, temperate grasslands are simulated and analyzed by means of an individual-based process-oriented simulation model. In Chapter 5, tropical forests are analyzed by means of network science.

Within this thesis, the main focus is on temperate grasslands, while the analysis of the fifth chapter is conducted with data of tropical forests. In the following Chapters 2 to 4 temperate grasslands are simulated using an individual-based process-oriented grassland model. For that, Chapter 2 describes the parameterization of a local field biodiversity experiment in Central Germany and evaluates its performance considering different vegetation attributes. Moreover, this chapter deals with the influences of specific plant traits and of shading and competition for space within plants and their effects on productivity and the abundances of plant functional types. In Chapter 3, anthropogenic and climate impacts, in terms of different mowing frequencies and air temperature increase, are analyzed on the simulated vegetation processes and structure. For testing whether those results apply also to other grassland sites and with the consideration of soil interactions, Chapter 4 presents a developed approach of a regional transferable model parameterization which takes also site-differences in soil type, climate conditions and regional species pool into account. With this generically parameterized grassland model, the importance of environmental factors and management intensity and the impact of climate change are analyzed considering several representative grassland sites across Germany. Finally, in Chapter 5, spatial tree and tree species locations within tropical forests at different field sites are compared by means of network theory. Thereby, the impact of tree location, tree size and tree species on the analyzed network measures in three tropical forest megaplots are analyzed. Chapter 6 summarizes the findings, discusses methodological aspects, gives an outlook on future developments and provides a final conclusion.

In summary, main objectives of this thesis are: 1) development of a local-scale and a regionally transferable parameterization of an individual-based simulation model (accounting for plant diversity) for managed grasslands; 2) exploration of how plant traits, ecological processes and environmental conditions affect vegetation attributes such as productivity and abundances of plant functional types; 3) understanding and projecting how anthropogenic management and climate change can alter ecological processes and vegetation attributes at the community level (e.g., productivity at short- and long-term scales); and 4) application of network science to tropical forests in order to assess the importance of the spatial distribution of plants in species-rich ecosystems.

2

INFLUENCES OF TRAITS AND PROCESSES ON PRODUCTIVITY AND FUNCTIONAL COMPOSITION IN GRASSLANDS: A MODELING STUDY

2.1 ABSTRACT

Grasslands are an important habitat for many plant species whose functional diversity and composition influences ecosystem functioning and services. Despite several field studies, still uncertainties remain about the interplay of species traits and ecosystem processes that lead to the functional diversity observed in grasslands. Here, we used an individual-based process-oriented model to simulate a biodiversity field experiment located in Central Europe. With the focus on plant functional types (PFT), the simulation model well reproduced vegetation attributes of grassland communities at different diversity levels (of up to four PFTs of grasses, small herbs, tall herbs and legumes). To understand how plant traits and competition between plants affects the functional composition of grasslands, we tested in a simulation study the impact of different ecosystem processes and detected sensitive plant traits. According to our model results, competition for space affects community productivity stronger than competition for light. While some traits increase and strengthen the growth of plants, other functional traits make plants stronger through advantages in demographic processes. Our model-based findings can be substantiated by several independent field studies in terms of relative yield, plant density, plant biomass and life span of plant functional types. The methods and analyses shown here represent a promising step for the development of grassland models to investigate the complex structures and dynamics of temperate grasslands in complement to field studies.

2.2 INTRODUCTION

More than a third of the European agricultural area is covered by grassland (Smit et al., 2008). Temperate grasslands provide a wide range of ecosystem services (Sala and Paruelo, 1997, Lemaire et al., 2011) and an important habitat for many plant species (Wilson et al., 2012). Increased anthropogenic interventions already have caused species loss and an altered functional composition in grasslands (Socher et al., 2012, Bernhardt-Römermann et al., 2011, Niu et al., 2014). For example, intensive management (high mowing and fertilizing frequencies) has led to increased biomass yields (Schaub, Finger, et al., 2020) by shifting species composition towards fast-growing acquisitive plant species. This may be at the expense of other ecosystem services such as stability (Allan et al., 2015, Schäfer et al., 2019, Tilman and Downing, 1994). In order to propose recommendations for future management of grasslands (e.g. adapted regimes or establishment of protected areas), it is necessary to understand the relationship between the biotic and abiotic components of the ecosystem (like species composition, soil, climate) and anthropogenic interventions.

For this purpose, field experiments offer, amongst others, the possibility to investigate the dynamics of different species compositions in grasslands. Various experiments have dealt with the relationship between productivity and biodiversity with different results (Adler et al., 2011, Wang, Cadotte, et al., 2019, Mittelbach et al., 2001), but only few of them also considered functional diversity (Díaz and Cabido, 2001). For instance, an experiment at Cedar Creek (Minnesota, USA) revealed that not only species diversity but also functional diversity and functional composition have a major impact on ecosystem processes such as productivity, plant nitrogen (Tilman, Knops, et al., 1997) and soil carbon and nitrogen (Fornara and Tilman, 2008). European-wide projects (e.g. BIODEPTH (Spehn et al., 2005)) showed that herbs and legumes are significant determinants of productivity (Hector, Schmid, et al., 1999). Experiments in Germany (Jena Biodiversity Experiment (Roscher, Schumacher, Baade, et al., 2004, Weisser et al., 2017)) with manipulated plant diversity and functional composition discovered that functional diversity has a positive effect not only on species diversity but also on community biomass (Marquard, Weigelt, Temperton, et al., 2009). Roscher, Schumacher, Gubsch, et al. (2012) further emphasized in this experiment that functional composition explains variation in community biomass to a greater extent than species richness. Field studies dealing also with land-use (e.g. Biodiversity Exploratories (Fischer, Bossdorf, et al., 2010)) showed that indirect land-use effects, mediated by biodiversity loss and shifts in functional composition, play a central role for multiple ecosystem services (Allan et al., 2015).

Besides field experiments, simulation models can be used to investigate and understand vegetation dynamics. Models can benefit from field experiments as measurement data can help to describe mechanisms and thus can serve as an excellent basis for the parameterization of the model. In particular, experiments manipulating biodiversity in a controlled design (such as the Jena Biodiversity Experiment) are well suited for this purpose since the combination of different monocultures and mixtures of species allows to analyze plant interactions in grasslands.

Grassland models have been developed for different purposes (Thornley, 1998, Taubert, Frank, et al., 2012, Ross et al., 1972, Moulin, Perasso, and Gillet, 2018, Johst, Drechsler, Mewes, et al., 2015, May et al., 2009). For the integration of different species into a model, it is common to use the concept of classifying species into plant functional types (PFT), since average functional properties are often sufficient to describe certain ecosystem functions (Lavorel et al., 1997, Roscher, Schumacher, Lipowsky, et al., 2018, Díaz and Cabido, 1997). Thereby, a PFT can be considered as a representative of a group of species with similar ecological and morphological traits. For instance, a population-based model used the concept of PFTs to predict the accumulation rate of forage under different management practices for a variety of plant communities (Duru et al., 2009).

Parameterizing PFTs, however, can be challenging, since field measurements often focus on populations of specific plant species. Grouping of species to PFTs and the determination of their traits (or model parameters) requires an understanding how modeled processes, PFT traits and the resulting simulated community dynamics interplay. In addition, simulation models are simplified representations of reality. Different degrees of detail in the description of processes are dependent on a detailed knowledge of species traits, which are not always measurable in the field and therefore require inverse parameterization of the model. Due to this, grassland models often focus on simulating a few measurable vegetation attributes at the population or community level (Moulin, Perasso, and Gillet, 2018, Duru et al., 2009), but the simulated dynamics still can include uncertainties about the underlying mechanisms at the individual plant level (e.g. a certain community biomass might be achieved by a few large plants or numerous small plants). Individual-based simulation models allow a closer and more extensive look on vegetation attributes at the community, population and individual plant level and enable to discover the impact of species traits on individual plant growth, inter- and intraspecific plant interactions and the resulting community dynamics.

Here, we test the individual-based process-oriented grassland model GRASSMIND for simulating the dynamics of different species mixtures using the concept of PFTs based on field measurements of the Jena Biodiversity Experiment located in Central

Europe, (Roscher, Schumacher, Baade, et al., 2004, Weisser et al., 2017). Field measurements of monocultures and mixtures in this field experiment include several vegetation attributes at the same time (aboveground biomass (AGB), leaf area index (LAI), vegetation height and cover), observed at the community and partly at the species level. We use measurements from different plots of different species diversity (monocultures and multi-species mixtures) aggregated according to four PFTs (grasses, small herbs, tall herbs and legumes) to represent functional diversity. Measured plant traits are only available for a few PFT traits (or model parameter). Remaining PFT traits therefore require inverse model parameterization in such a way that the four measured vegetation attributes (for four plots of one PFT and one mixture of PFTs) can be reproduced by consistent simulation results. Based on the model, we want to gain a deeper insight into key processes and plant traits that influence productivity and the functional composition in grasslands (here, proportional biomass of plant functional types). To put it more precisely, we want to answer the following questions:

1. Can we parameterize an individual-based grassland model for a biodiversity experiment based on four PFTs?
2. Which vegetation attributes of the community can be described best by the simulation model for grasslands of different functional diversities?
3. Which are the most influencing plant traits and processes regarding functional composition?

For this, we first inversely parameterized field plots consisting of one PFT only, transferred the parameters to a 4-PFT mixture and then tested this model parameterization for field plots of 2- and 3-PFT mixtures. By a robustness and sensitivity analysis we thereafter identified the impact of plant competition (for light and space) as well as different plant traits on functional composition.

2.3 MATERIALS AND METHODS

2.3.1 *The model – GRASSMIND*

GRASSMIND is a process-oriented grassland model which has the advantage of simulating each single plant on a daily basis. Since the model includes many detailed processes, we describe here only the most relevant processes for our study. Main processes are the photosynthesis, respiration, reproduction and mortality of individual plants. A detailed description of the GRASSMIND model can be found in Taubert, Hetzer, et al. (2020b), Taubert, Hetzer, et al. (2020a) and under `www.formind.org/downloads`. Note that in this study, we assume unlimited water and nitrogen supply for each plant in the model (therefore belowground processes in soil such as competition for water and nitrogen are excluded).

At the individual level, plants are established as seedlings and then grow in height and width based on the net primary productivity (NPP) calculated from photosynthesis and respiration. Individual plants may differ in their traits (PFT-specific model parameters) which affect plant growth. For example, physiological traits that influence photosynthesis are, amongst others, specific leaf area (SLA) and leaf life span (LLS). Plant growth is modeled according to a species-specific constant ratio (hw) of an individual plant's height to its width (or lateral extent). A mowing event causes all plants to be shortened to a certain height (e.g. to 10 cm) while maintaining the width of the plants (cut biomass is assumed to be removed). Subsequently, plants grow only in height until the PFT-specific ratio (hw) is reached again.

At the community level, plant growth can be limited due to shading by other plants (asymmetric competition for light). Competition for light is modeled implicitly for all plants (on a 1 m² plot). Tall plants shade smaller ones, which affects photosynthesis and can reduce growth. More precisely, the global radiation I_0 is reduced from the top to the floor in height layers (1 cm width) taking into account the leaf area LAI_i contributed by individual plants in each height layer i (Monsi and Saeki, 2005):

$$I_S = I_0 \cdot e^{-(\Sigma_{i>S} LAI_i)} \tag{2.1}$$

As a result, the global radiation is increasingly attenuated towards the lower end of the plot. The plant height determines which height layer S a plant can reach and thus, the irradiance the plant can receive. We evaluate a plant's light limitation with the light reduction factor $R_L = 1 - I_S/I_0$. Further influencing factors of plant growth include daily abiotic variables (like air temperature, global radiation and day length). Competition for space prevents too many plants growing into a simulated plot. This density-dependent mortality reduces plant density N (number of plants on the plot) if community cover exceeds plot area. If so, the number N_{crowd} [1/d] of dying plants is

$$N_{crowd} = N * \left(1 - \frac{1}{CC}\right), \tag{2.2}$$

where CC is the fraction of vegetation cover in the plot [-] (ranging between 0 and 1). Similarly, we assess space limitation by a competition factor $R_S = 1 - \frac{1}{CC}$.

Generally, light competition affects mainly the vertical community structure and space competition the horizontal grassland structure.

Reproduction is modeled by a PFT-specific seed ingrowth. This daily ingrowth encompasses also the constant incoming seed rain from the surrounding landscape. Simulated seed ingrowth starts from bare ground with the date of sowing the grassland. After a PFT-specific time (age_{rep}), growing seedlings turn into adult plants. Some plant characteristics then change, for instance, the allocation ($alloc_{shoot}$, investing partly energy in seed production) and the intrinsic mortality rate of plants (m_{seed} to m_{basic}).

Mortality of plants is included as stochastic events. Both mortality processes, base mortality and mortality due to space competition, select plants at random that die with their biomass being transferred to the litter pool. The random selection of dying plants can have a large impact on model results, as dead plants disappear immediately. For example, the death of the highest plant can lead to an immediate drastic decrease in vegetation height if it is by far the only large plant present in the community. In contrast, the death of a small plant usually does not cause markedly changes in vegetation attributes of a grassland community. To account for stochastic effects in our analyses, we calculated the average of results over ten simulation runs (corresponding to an area of 10 m², see A.2 Supplementary Results for effects of larger areas).

Simulation results of the model include daily vegetation attributes. We used the community and PFT-specific aboveground biomass (AGB) by summing up the AGB of all plants (or the AGB of plants belonging to a certain PFT). Leaf area index (LAI) is derived by calculating the leaf area from aboveground total AGB and the constant specific leaf area of a plant (PFT-specific model parameter). As vegetation height we used the height of the highest plant within the community. To obtain green vegetation cover (i.e. coverage by living plant parts) the sum of all plants' cover was multiplied by the ratio of green LAI to total LAI.

2.3.2 *Field data – the Jena Experiment*

As reference data for our model, we used measurements from the Jena Biodiversity Experiment. The Jena Experiment is one of the longest-running biodiversity experiments in Europe (Weigelt, Marquard, et al., 2010, Weisser et al., 2017). The main experiment, established in 2002, consists of 82 grassland plots (20 x 20 m^2) with up to 60 different species (Roscher, Schumacher, Baade, et al., 2004). It is located near Jena, Germany (50°55´N, 11°35´E), close to the river Saale. The climate measurements (see A.1 Supplementary Methods for details) show a mean temperature of 9.6°C and a mean annual precipitation of 539.6 mm (from 2002 to 2008). The field site was formerly used as arable land and therefore the soil type *Eutric Fluvisol* was highly fertilized in recent decades (Roscher, Temperton, et al., 2009, Fischer, Leimer, et al., 2019). Besides two mowing events per year (cutting height of 10 cm), regular weeding was carried out in spring and summer. Bi-annual field measurements include AGB and vegetation cover per species as well as the community LAI and vegetation height over seven consecutive years (2002 to 2008).

2.3.3 *Parameterization of the model – Species grouping, inverse parameterization, validation, evaluation*

2.3.3.1 *Species grouping*

For the parameterization of the model for the Jena Experiment we used plant functional types (PFTs). Roscher, Schumacher, Baade, et al. (2004) classified the existing species into four groups based on a multivariate cluster analysis of ecological and morphological traits. Hence, we parameterized four PFTs, which are trait-averaged typical representatives of grasses, small herbs, tall herbs and legumes including typical species occurring in Central Europe.

2.3.3.2 *Parameterization*

We used publicly available data over seven consecutive years (2002-2008) from the Jena Biodiversity Experiment (Heisse et al., 2007, Weigelt, Marquard, et al., 2010). Climate data were taken from two facilities in Jena and included daily air temperature, irradiance and day length. For details on the preparation of the climate data see A.1 Supplementary Methods.

The field data was used as follows: on each field plot, the AGB per species above 3 cm height, leaf area index (LAI), vegetation height and vegetation cover per species were measured bi-annually from 2003 to 2008, and once in 2002 (82 plots in total, (Weigelt, Marquard, et al., 2010)). We grouped the field plots according to their plant functional types (grasses (G), small herbs (S), tall herb (T) and legumes (L)) and functional diversity level (plots only of one PFT: G (9 plots), S (8 plots), T (9 plots) or L (8 plots); and the 4-PFT mixture: GSTL (16 plots)) and averaged each vegetation attribute for each measurement date. For AGB and vegetation cover also PFT proportions of each plot were available (except for one measurement in 2004). For missing proportions in 2004, we assumed the average AGB proportions of all other available AGB measurements in the respective plot. Since weeding (or the invasion of unknown species) is not considered in our model, but is carried out in the field plots, we corrected vegetation cover of the target species proportionally (i.e. sum of cover of target species, bare ground and dead material excluding weed cover equals 100 %). The calculated correction factors were also applied to measured AGB values (to exclude weed AGB). As a result, we obtained one time-series for each vegetation attribute (of the community and partly PFT-specific) per field plot for each single PFT (G, S, T, L) and the 4-PFT plot (GSTL).

To parameterize the grassland model GRASSMIND, 17 parameters for each PFT had to be specified. Six parameters per PFT were taken from field measurements and literature (Table A.1). The remaining parameters were determined by inverse parameterization (Table A.1).

The inverse parameterization of the grassland model comprised two steps (Fig. A.1). First, we inversely parameterized each PFT separately in 1-PFT plots (G, S, T, L). Second, we combined these four estimated parameter sets in the mixture of four PFTs (GSTL) and corrected only one parameter per PFT (i.e. the ingrowth of seeds N_{seed}) by inverse parameterization. The corrected values of N_{seed} were then also used in the parameter sets of 1-PFT plots (first step) when comparing simulation results and field measurements.

As reference data for the inverse parameterization, we used the measured vegetation attributes (for measurement dates see A.1 Supplementary Methods). A simulation run was performed over all seven years (2002 to 2008) and began on the day the field experiment was sown (in the field: 11 to 16 May 2002 (Weisser et al., 2017), in the model: 16 May 2002). Mowing height and mowing dates in the model correspond to those of the experiment (for exact dates see A.1 Supplementary Methods).

For further details on the parameterization, validation and evaluation see A.1 Supplementary Methods.

2.3.3.3 *Robustness analysis*

The advantage of process-based models is the possibility to switch on or off different processes. In this way, it is possible to analyze the effects of certain processes on model results – each process alone as well as their interaction (Ellner et al., 2019).

In this study, the role of competition for light and space has been analyzed. For this, the model's starting conditions, settings and parameter values remained similar to those used in the parameterization. Then, in addition to the standard run in which competition for light and space was switched on, we performed (a) a mode where competition for light was switched off and competition for space remained activated, (b) a mode where competition for space was switched off and competition for light remained activated, and (c) a mode where both competition processes were not activated.

Thereby switching off space competition means that plants do no longer die because of limited space on a plot ($N_{crowd} = 0$ for all time steps, see equation (2.2)). Thus, plants can unlimitedly overlap which in turn causes an increase in light competition. On the other site, switching off light competition means that plants do not shade each other anymore. Hence, small plants that grow below taller ones also receive the full daily global radiation, so their photosynthesis is not limited due to reduced light availability ($I_S = I_0$ for all height layers S and time steps, see equation (2.1)). This can cause an increase of space competition as plants grow faster.

To compare the different modes and detect which process has a high influence on the vegetation dynamics, we analyzed changes in the simulated vegetation attributes. For the calculation of plant density (number of plants per m^2), mean values were taken over the measurement dates of AGB (see A.1 Supplementary Methods).

2.3.3.4 *Sensitivity analysis*

A global sensitivity analysis was conducted to analyze the influence of various model parameters. For this, the Morris method allowed to investigate the effect of changes in a plant trait on simulated vegetation attributes (for details see A.1 Supplementary Methods)(Morris, 1991).

2.4 RESULTS

We analyzed vegetation attributes within the measured field plots and compared them with our simulations. Afterwards results of the robustness and sensitivity analysis are shown.

2.4.1 *Field data description*

Measured vegetation attributes showed large differences between the 1-PFT plots (Fig. 1A). Legumes were the most productive with on average twice as much aboveground biomass (AGB) and a 50 % higher leaf area index (LAI) but only slightly higher vegetation height and vegetation cover compared to grasses. Grasses had the second highest productivity. However, they were comparable to tall herbs (for AGB and LAI), and differed with regard to a larger height and a smaller degree of vegetation cover than tall herbs. Small herbs showed the lowest values - their AGB was only one fourth of legumes' AGB.

The grassland with four PFTs was on average less productive than plots of only legumes (average AGB of approx. 370 g/m^2 per measurement in 4-PFT mixture compared to the average AGB of approx. 385 g/m^2 in legume plots). Vegetation height and LAI were similar to those of the legume plot but cover of green leaves was higher in the mixture plot. Within the mixture, legumes were the dominant PFT with the highest biomass proportion (41 %).

Vegetation cover was similar between 1-PFT plots (70 to 81 %) as well as within the PFT proportions of the 4-PFT mixture (20 to 24 % per PFT). Variation of AGB between plots consisting of different species and richness levels was low in plots of small herbs and high in plots of legumes (Fig. A.2).

2.4.2 *Simulation results*

The grassland model could well reproduce the field measurements. Simulation and field measurements agreed in all vegetation attributes for each 1-PFT plot (averaged over time, Fig. 2.1B). Simulated AGB (average over 13 time points) deviated by a maximum of 6 % from mean measurements within the 1-PFT plots. AGB of the 4-PFT mixture was underestimated by 19 % in the model. Like in the field, simulated legumes were the most productive 1-PFT plot and dominate in the mixture. Although they showed a total biomass of only 2 % below the measurement in the field mixture

(150 g/m²), legumes in the simulations were much stronger than other PFTs (AGB proportion) compared to the observations (50 % in the simulation to 41 % in the measurements). AGB of other PFTs was underestimated in the simulated mixture (up to 54 % less AGB than in observations). The range of temporal variations of vegetation attributes in the simulation was mostly similar to the measured range of temporal variations (Fig. 2.1A-B).

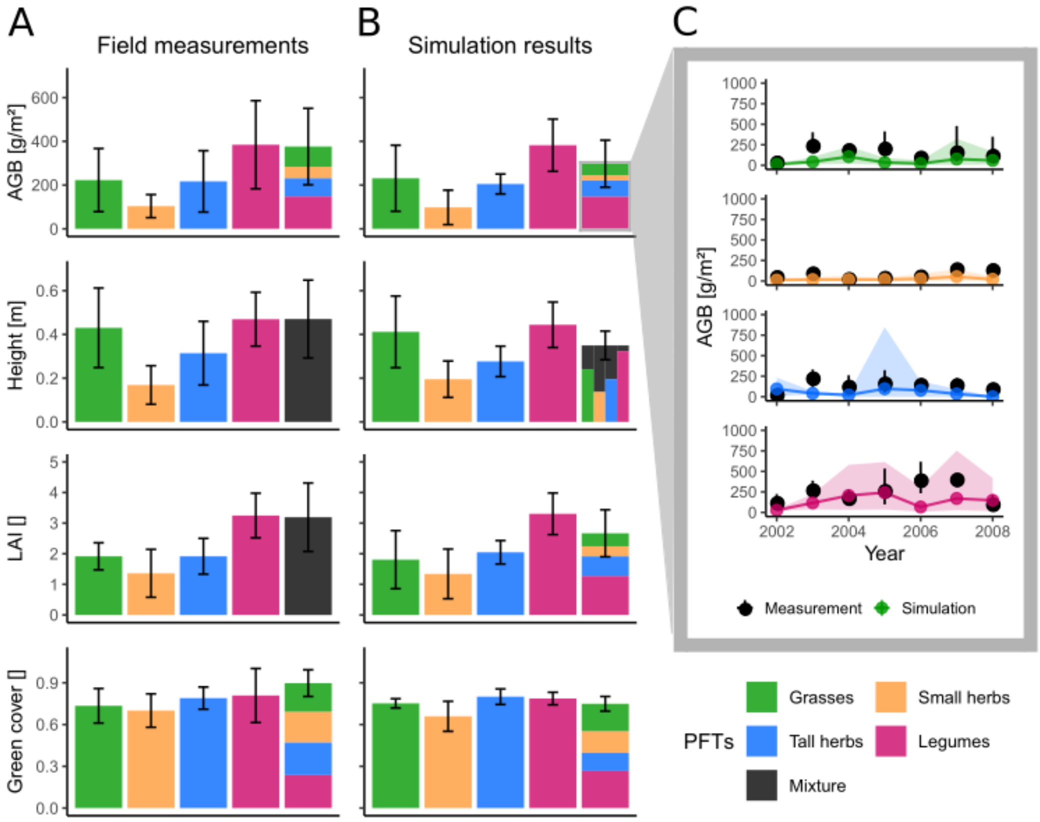

Figure 2.1: Comparison of field measurements and simulation results in plots of one plant functional type (PFT) and in the 4-PFT mixture. (A) Field data of the Jena Biodiversity Experiment – mean measurements of aboveground biomass (AGB), vegetation height, leaf area index (LAI) und green cover in 1-PFT plots and the 4-PFT mixture from 2002 to 2008 and (B) corresponding simulation results. Black lines show the standard deviation of temporal measurements (in the mixture regarding community vegetation attributes, see A.1 Supplementary Methods for measurement dates). In (B), the bar of simulated vegetation height (daily maximum height averaged over measurement dates) in the 4-PFT mixture show no proportions but the total height values of each plant functional type. For one missing measurement of proportional AGB in 2004 we assumed the average proportions of the existing measurements. (C) Yearly aggregated patterns of measured (black dots) and simulated (colored dots) AGB and their minimum and maximum values within the plots and simulation runs (black lines and shaded polygons).

Time-series of vegetation attributes were also in good agreement between simulations and field measurements (Figs. 2.1C and A.1). Surprisingly, both showed nearly equal temporal patterns for each vegetation attribute, although only the total sum over seven years was used for model calibration (Figs. A.2, A.3).

Overall, simulated vegetation cover and LAI showed small deviations from field measurements (average deviation of 6 % each with respect to mean community attributes over all measurements; averaged NRMSE = 0.16 (vegetation cover), averaged NRMSE = 0.52 (LAI); Fig. 2.1, Table A.3).

Validation of the parameterized grassland model was done by using independent data on grassland plots consisting of two and three PFTs. All simulated grasslands resulted in a slight to moderate underestimation and only one 2-PFT mixture (small herbs and legumes) showed an overestimation of AGB in the simulation results (Fig. A.4A). Again, legumes were often dominant with high AGB proportion in the simulated and measured mixtures and were partly overestimated by the model in two of the five mixtures in which legumes occurred (Fig. A.4B).

The validation analysis revealed that vegetation cover was the best fitted attribute of the simulation model (10.3 % deviation on average over all measurements and plots), though vegetation height was estimated slightly better in total than LAI (14.4 and 14.5 % deviation, see also Table A.4 for statistical measures including each measurement).

2.4.3 *Relationships to plant functional type richness*

For our analyses, we used averaged measured vegetation attributes over the years 2002 to 2008. By doing this, we found a higher productivity in plots of legumes than in functional mixtures, which at first sight seems to contradict previous studies Marquard, Weigelt, Temperton, et al., 2009. However, by calculating annual averages of all plots with a certain number of PFTs (one to four), we received a similar relationship in the simulations: the community AGB increased with higher PFT richness (Fig. A.5A). Our simulations reproduced this gradient well, but with a smaller slope (Fig. A.5A). Furthermore, annual averages of LAI also increased with PFT-richness, but opposite trends were detected for vegetation height and vegetation cover (Fig. A.5B-D).

2.4.4 *Mean relative yield, mean relative plant biomass and mean relative plant density*

We compared simulated AGB in grasslands of one PFT with its proportion in all mixtures (of 2 to 4 PFTs), defined as mean relative yield (RYI). Grasses and small herbs showed on average underyielding ($RYI < 1$, e.g., $RYI = 0.6$ for grasses), while tall herbs and legumes produced proportionally more AGB in mixtures ($RYI > 1$, e.g., $RYI = 1.2$ for tall herbs, Table A.5). Furthermore, legumes were the only plants that increased on average in mean plant biomass (AGB per plant) and simultaneously in mean plant density (number of plants per m^2) considering all mixtures ($RBI > 1$ and $RDI > 1$, similarly calculated as RYI, Table A.5). A stronger decrease of plant density (e.g. a lower RDI) from 1-PFT plots to mixtures while having a high RYI could be compensated by an increase in plant biomass (RBI) and thus, the establishment of taller plants, as is the case for tall herbs ($RDI = 0.5$, $RBI = 3.4$). PFTs with taller plants and larger plant AGB were more likely to shade other plants (also of other PFTs) which in turn could suffer from a lower light availability.

2.4.5 *Impact of light and space competition on productivity and functional composition*

To understand the importance of different processes for plant growth in plots consisting of one and four PFTs, the model could be used to analyze the impact of competition for light and space between plants. Overall, both processes affected productivity, but in different directions and dimensions within the plots. Competition for space caused much stronger changes in vegetation attributes than competition for light.

Between plots of one PFT, vegetation attributes were changed to different extents and with different causes by competition (Fig. 2.2A). In terms of AGB and vegetation cover, small herbs and legumes changed most whereas for vegetation height tall herbs were the most sensitive to space limitation. Less AGB and vegetation height with no light competition (Fig. 2.2A) was caused by an increased density of (smaller) plants (due to an increased mortality of few larger plants) and thus, higher vegetation cover. No space competition caused opposing effects in vegetation height whose decrease (e.g. in grasses) was the result of slower plant growth due to permanently strong light competition. An increase in vegetation height was related to a much lower plant density, so that only a few tall plants survived suffering less from light competition. This was observed for tall herbs, which indicated space competition to be the dominant process limiting their growth. Changes in the analyzed competition factors supported that competition for space is dominant in plots of grasses, tall herbs and legumes, whereas competition for light is dominant in plots of small herbs and the 4-PFT mixture (for details see A.2 Supplementary Results and Fig. A.6).

In grasslands with four PFTs, switching off light competition led to an AGB decrease of about 6 %, whereas no space competition between plants resulted in almost 40 times higher values. The other four attributes (LAI, vegetation height and green cover, plant density) were similarly affected (Fig. A.7). Within the mixture, changes of all vegetation attributes were mainly driven by changes of legumes' attributes. Interestingly, only the height of legumes increased immensely when space competition was switched off while that of grasses, small herbs and tall herbs decreased (Fig. 2.2B). This indicated that legumes prevent the growth of other PFTs and space competition made them less competitive. However, although competition for light and space reduced the growth of legumes and partially increased the productivity of other PFTs, the proportion of legumes always remained by far the highest (50 % with no light competition and 85 % with no space competition).

2.4.6 *Impact of plant traits on productivity and functional composition*

Plant traits with most impact on vegetation attributes were identified by a sensitivity analysis (see Methods for details). For 1-PFT plots, two geometric plant traits (height-width ratio of plants hw and specific leaf area SLA), two physiological traits (light extinction coefficient k and slope of the light response curve α) and one demographic trait (mortality of seedlings m_{seed}) caused the largest absolute changes in AGB (Fig. A.6A). Higher values of hw and α resulted clearly in an increase of biomass, whereas higher values of m_{seed} and k resulted in a decrease (Fig. 2.3A). The effect of these parameters on the simulation results was linear and additive (large mean and low standard deviation of elementary effect, lying outside the wedge of grey lines in the figure (Morris, 1991, Ruano et al., 2011)). On the other hand, a higher SLA could lead

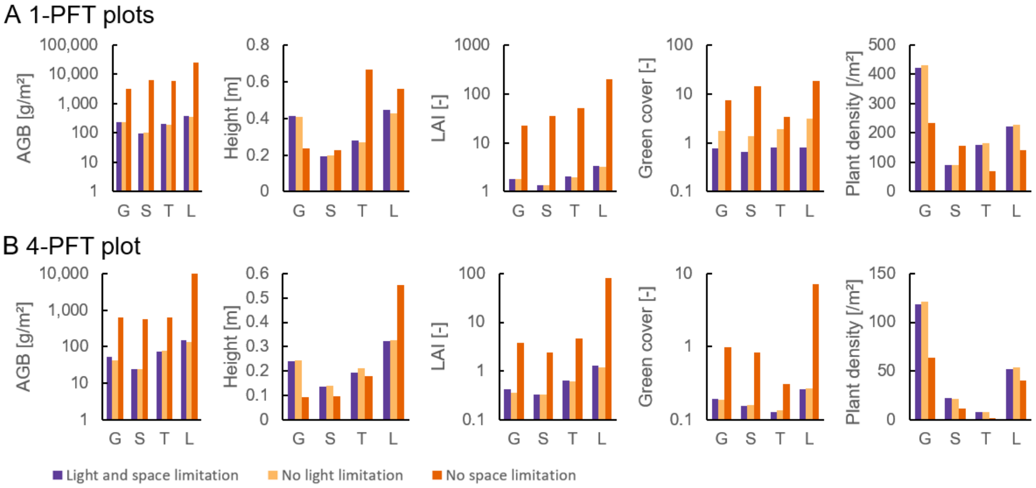

Figure 2.2: Impact of light and space competition on vegetation attributes in (A) plots of one plant functional type (PFT) and in (B) the 4-PFT mixture.Aboveground biomass (AGB), leaf area index (LAI), vegetation height, green vegetation cover and plant density were analyzed. Bluish bars show simulation results with light and space competition, yellowish bars with no light competition and reddish bars with no space competition of grasses (G), small herbs (S), tall herbs (T) and legumes (L). Values correspond to the mean value over the time-series of the corresponding vegetation attribute. Note that the axes of ABG, LAI and green vegetation cover are logarithmic. For results with no light and no space limitation and variation within the simulation runs see Fig. A.10.

to higher or lower AGB values (on average negative), because of interactions with other plant parameters or due to nonlinear effects.

To find out which traits affect the dominance of legumes, we varied trait parameters of legumes in the 4-PFT mixture. Two physiological traits (k and α), one demographic (m_{seed}) and one geometric trait (hw) belonged to the most influential traits of legumes concerning their AGB proportion (Fig. A.6B). Now, instead of SLA, two further demographic legume traits (seed ingrowth (N_{seed}) and germination rate of seeds ($germ_{\%}$)) were also relevant. The parameters k, α, m_{seed} and hw affected change in AGB of legumes similarly, except for hw whose higher values led in the mixture to a reduced AGB of legumes (Fig. 2.3B). The AGB of small herbs was least affected by changes in legume traits (low elementary effect; Fig. 2.3B). The reduced AGB of legumes due to its increased trait values of m_{seed} and hw increased AGB of the other PFTs. With α, N_{seed} and $germ_{\%}$ contrary results were observed – increased trait values of legumes led to more AGB of legumes and to less AGB of the other PFTs. The legume trait k had the weakest effect on the other PFTs (an increased value only led to a slightly higher AGB for grasses and small herbs and to a slightly lower AGB for tall herbs).

The analysis outlined diverse effects of traits on AGB of the different PFTs. Higher values of hw, α, SLA and $germ_{\%}$ and lower values of m_{seed} and k strengthened generally the productivity in plots of one PFT and weakened in the 4-PFT mixture the productivity of PFTs other than legumes due to increased competition. In turn, N_{seed} only made legumes more competitive in the 4-PFT mixture but did not considerably affect the productivity of 1-PFT plots. Despite the clear trend for the above-mentioned parameters (except for SLA, see Methods and Fig. 2.3), for almost none of the traits the mean elementary effect μ (of a varied trait on AGB) equaled the absolute mean elementary effect μ^*. This means that changes in trait parameter values in one direction increased or decreased the AGB depending on values of other parameters.

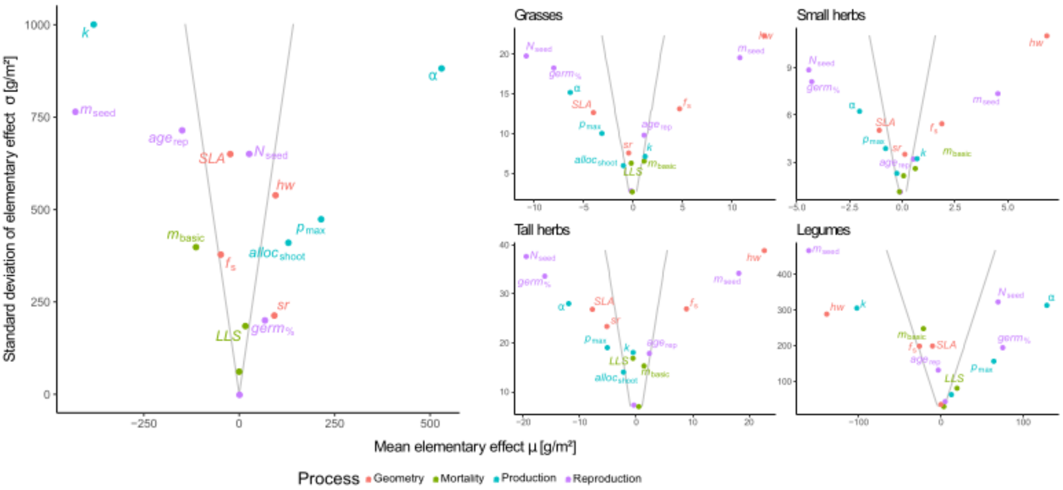

Figure 2.3: Results of the global sensitivity analysis (Morris method). Mean elementary effects (μ) on (A) aboveground biomass in a plot of one plant functional type (PFT) and on (B) aboveground biomass per PFT in a 4-PFT mixture (grasses, small herbs, tall herbs and legumes) and their standard deviations (σ). The grey lines correspond to $\mu = \pm 2\text{SEM}$ (see Methods for details). Labels are based on names of trait parameters in the model description of GRASSMIND (Taubert, Hetzer, et al., 2020a) (see Table A.1). Non-influential parameters are not labeled. In (B) only trait parameters of legumes were varied.

2.5 DISCUSSION

By using field measurements from a local biodiversity experiment, we showed that it is possible to simulate the growth and dynamics of grasslands with an individual-based model. We were able to cover four different vegetation attributes: aboveground biomass (AGB, in total and per PFT) and vegetation cover (in total and per PFT) as well as vegetation height and leaf area index (LAI). Model results revealed good fits (compared to field measurements) for plots of one PFT but showed an underestimation of vegetation attributes in mixtures (2 to 4 PFTs). Nevertheless, simulations also reproduced the observed positive relationship between productivity and PFT-richness. Annual dynamics of vegetation attributes matched well those measured in the field although only mean vegetation attributes over all years were used for calibration (Fig. A.2).

The parameterized grassland model enabled us to analyze the relative importance of specific processes and plant traits on the functional composition in grasslands. Competition for space had a much stronger impact on grassland AGB than competition for light. Increasing space competition led to a decreasing proportion of legumes and increased grasses, small herbs and tall herbs. Nevertheless, legumes always remained the dominant PFT.

A global sensitivity analysis revealed key trait parameters of different processes – geometry, productivity and reproduction of plants – with high influence on AGB in grasslands. Some traits differed in their sensitivity between plots of one PFT (with only intraspecific interactions between plants) and more PFTs (with additional interspecific interactions between plants). Some traits had a high impact on functional composition by generally increasing the growth of plants, while other traits made a PFT more competitive through advantages in demographic processes.

2.5.1 *Understanding the functional composition - trait and process influences in the model*

With a sensitivity analysis we obtained information on relevant plant traits that influence AGB and functional composition. A global sensitivity analysis enables to detect global trends, nonlinearity and interactions with other trait parameters in contrast to a local sensitivity analysis, for which changes of only one parameter are analyzed. Locally, changing one trait parameter can have opposite effects depending on the strengths of other processes. For example, if plants grow more in height than in width, it can result in more community AGB as there is more space for other plants. At the same time, however, larger plants increase light competition. This affects not only the growth of smaller plants through shading, but also the productivity of the plant itself through stronger self-shading. Thus, a global sensitivity analysis allowed us to explore, in the case of two interacting processes, which one is dominating when varying one specific trait.

The robustness analysis indicated that different processes dominated with respect to plant growth and interactions. Competition for light and space affected the PFTs differently (e.g. largest impacts on AGB of dominant legumes in the mixture). By the analysis of mean relative yield, mean plant biomass and mean plant density the individual-based model further allowed us to understand the mechanisms that led to the strength of legumes in mixtures. Extended model analysis on the trait variation of all four PFTs at the same time might reveal additional insights on the competitive advantages of each PFT in comparison to the other ones in the mixture.

2.5.2 *Comparison to field study results – plant densities and plant sizes*

Plant density (the number of plants per m^2) and mean biomass per plant for each PFT have many similarities when comparing our simulation results to those from field measurements of the Jena Experiment (Marquard, Weigelt, Roscher, et al., 2009). In the field, tall herbs generally produced large but few plants while grasses produced small but numerous plants, which is consistent with our model results (Table A.5). Marquard, Weigelt, Roscher, et al. (2009) revealed that legumes were often among the overyielding species, and grasses tend to underyield in mixtures which is also visible in our model results (Table A.5). Additionally, the discussed linkage between mean relative yield and mean relative density (if $RYI > 1$ then $RDI > 1$) as well as between mean relative yield and mean relative size (if $RYI < 1$ then $RBI < 1$) (Marquard, Weigelt, Roscher, et al., 2009) can be observed also in our simulation results (with the exception of tall herbs showing a $RYI = 1.2$ and a $RDI = 0.5$, Table A.5). An additional result of Marquard, Weigelt, Roscher, et al. (2009) has been that grassland biomass is positively related to plant density and to AGB per plant, and plant AGB increases with plant density. In our simulation, we obtained similar trends (Fig. A.9).

In the study of Marquard, Weigelt, Roscher, et al. (2009), plant density ranged approx. between 100 and 10,000 plants per m² and plant AGB ranged between about 0.1 g and 10 g (plots of different species richness, measured in May 2006), whereas our simulations showed a narrower range (100 to 500 plants per m² and 0.3 g to 2.2 g per plant, mean values over dates of AGB measurement, see A.1 Supplementary Methods).

We found further similarities of our simulations with an independent field study investigating life spans of plants of different PFTs (Lauenroth and Adler, 2008)(for details see A.2 Supplementary Results).

2.5.3 *Limitations of individual-based grassland models, possible enhancements and perspectives*

In this study, we demonstrated that an individual-based grassland model is able to simulate aggregated measured vegetation dynamics by including only a few abiotic variables (daily air temperature, irradiance and day length). Competition between plants focused on aboveground resources like light and space as we excluded information on precipitation and plant-soil interactions. We assumed sufficient water supply due to the field experiment's closeness to a river and sufficient nitrogen availability due to former land use (Roscher, Temperton, et al., 2009, Fischer, Leimer, et al., 2019). Strikingly, competition for light and space was sufficient to reproduce not only measured vegetation dynamics but also the positive relationship between functional richness and productivity (and its variation within each diversity level; with a less pronounced slope in the model compared to observations; Fig. A.5). At other sites, however, soil resource dynamics might influence community structure and functional composition stronger (Spehn et al., 2002, Pirhofer-Walzl et al., 2012, Fay et al., 2015). In this case, it is possible to couple grassland models with established soil models (e.g., DayCent (Parton, Hartman, et al., 1998)).

Although the vegetation attributes in plots of 1 PFT can be reproduced accurately by the model, larger deviations occur in the mixtures of different PFTs (Figs. 2.1, A.2). This can be due to different reasons. For example, species-specific influence of air temperature on plant productivity (Fig. A.5) or trait plasticity is currently not included in the model. However, plants could change their growth strategies, and thus their traits in response to management, climate, interactions with other plants and plant age (Abakumova et al., 2016, Lipowsky et al., 2015, Valladares et al., 2007). Further analyses and development in the modeling of interaction processes and their parameterization can provide additional insights, but also require specific measurements and experiments as well as suitable measures to compare them with individual-based models (e.g., measures describing the strengths of interaction and competition between plants (Burns and Strauss, 2012, Kraft et al., 2015).

With regard to the approach of grouping species to plant functional types, we were able to aggregate field observations to average plots of the assigned PFT. Derived attributes can thus be interpreted as dominant traits of the PFT. Species richness and composition as well as intraspecific trait variation within PFTs can also impact community productivity and functional composition (Marquard, Weigelt, Roscher, et al., 2009, Marquard, Weigelt, Temperton, et al., 2009, Moulin, Perasso, and Gillet, 2018, Tilman, Knops, et al., 1997, Buchmann et al., 2018). Combining trait distributions and grassland modeling allows to add trait variation to PFTs. Based on our sensitivity analysis, parameters with low influence (such as seed biomass or leaf life span) could remain constant at an average value while only trait parameters with higher influence on vegetation attributes could be varied among plants (e.g. by adding random fluctuations to traits of new seedlings). By this, not only interspecific diversity but also intraspecific diversity within the community (e.g., Crawford et al., 2019) which includes phenotypic and genetic variation (Wellstein et al., 2013, Garnier et al., 2007) could be considered. Thereby, plants could adapt to changing environmental conditions (due to higher mortality of individuals with poor suitability) which can enable to analyze intraspecific trait-environment relationships within habitats.

The use of a process-oriented model allows to investigate the influence of additional factors on vegetation dynamics. For instance, mowing frequencies or air temperature could be varied in order to conduct theoretical experiments that may not be feasible in the field (Völler et al., 2017, Gilhaus et al., 2017). Although field sites can differ in environmental factors, models provide the opportunity to analyze their effects separately and jointly, and in different intensities. In addition, models enable to analyze underlying processes structuring communities which are difficult to measure experimentally, such as the importance of competition for light versus space. Field measurements on the light climate and leaf area density in distinct height layers in a grassland mixture as well as mean characteristics of different PFTs could support such a model-based analysis. Such studies can build a first step towards deriving parameterizations that are regionally transferable. For this, abiotic factors such as climate and soil, and also management regimes differ regionally while traits of PFTs should remain unchanged. However, it is still an open question whether feedbacks between environmental changes and species traits need to be considered. Field experiments can support such future model developments. At the same time, confronting different modeling approaches with similar research questions can enable to identify decisive mechanistic processes, model strengths and model weaknesses. Then in turn, models can provide suggestions and recommendations for future field experiments as well as for the management or conservation of grassland communities.

2.6 CONCLUSION

In summary, our results show that an individual-based and process-oriented simulation model can reproduce aggregated dynamics of four vegetation attributes in grasslands. Not only the dynamics of plots along a gradient of functional diversity (with plant functional types of grasses, small herbs, tall herbs and legumes) can be simulated, but also the positive effect of functional richness on grassland productivity. Model analyses showed that competition for space has a stronger influence on functional composition than competition for light. Moreover, we identified specific traits that can make a plant functional type more productive and more competitive in mixtures. The methods and analyses shown represent a promising step for the development of grassland models and how to apply them to complement field experiments.

2.7 DATA AVAILABILITY

The data of the Jena experiment used for the calibration can be obtained from `http://esapubs.org/archive/ecol/E091/066/metadata.htm`. A detailed description of the simulation model GRASSMIND is available at `www.formind.org/downloads`, the code is available upon request.

2.8 ACKNOWLEDGMENTS

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3

IMPACT OF MOWING FREQUENCY AND TEMPERATURE ON PRODUCTIVITY OF TEMPERATE GRASSLANDS – EXPLANATIONS RECEIVED BY AN INDIVIDUAL-BASED MODEL

3.1 ABSTRACT

Grasslands represent an important ecosystem type as they provide numerous ecosystem services. Field studies have shown that temperate grasslands with high diversity can be highly productive. Management and changing environmental conditions can impact the diversity-productivity relationship. However, the specific mechanisms and role of biodiversity, environmental factors or anthropogenic interventions that lead to changes in productivity are not well understood. Here, we used the individual-based grassland model GRASSMIND parameterized for a field biodiversity experiment to analyze changes in the diversity-productivity relationship when varying the mowing frequency and increasing air temperature. Our results revealed that the positive diversity-productivity relationship persists with varied mowing frequency and temperature increase, with an increased proportion of herbs in more frequently mown grasslands. Using the model, we further investigated quantitatively how different processes (e.g., plant shading) affect grassland dynamics and productivity under varied mowing frequencies and air temperature. Although aboveground net primary productivity decreased in more frequently mown grasslands, biomass yields increased due to an even stronger decrease in space-dependent plant mortality. Plant mortality (intrinsic and by crowding) caused more biomass losses than caused by shading between plants or by a reduced productivity due to temperature increase. This study revealed how models, complementary to field experiments, can be used to analyze and quantify the importance of mechanisms and the role of environmental factors in grassland dynamics.

3.2 INTRODUCTION

Grasslands are a worldwide occurring ecosystem type (Smit et al., 2008) and can include a high species richness (e.g. 89 plant species per m^2) (Wilson et al., 2012). The biodiversity of grasslands is known to be linked to various ecosystem functions, such as resilience, robustness and also productivity (Hector, Hautier, et al., 2010). In terms of productivity, plant diversity can be considered as important as grassland management (Schaub, Buchmann, et al., 2020, Schaub, Finger, et al., 2020).

The relationship between biodiversity and grassland productivity ('diversity-productivity relationship') has already been analyzed in multiple field studies. Trends of the analyzed relationships thereby differ between experiments with manipulated levels of plant diversity and observational studies where the diversity emerges from natural and anthropogenic processes (Van Oijen et al., 2020). Experiments with manipulated species richness, for example, revealed that more plant diversity is connected with higher productivity (Hector, Schmid, et al., 1999, Weisser et al., 2017, Nyfeler et al., 2009, Schmid, 2002, Van Oijen et al., 2020). In contrast, in field observations species richness affects and responds to grassland productivity at the same time and thus, can show different patterns of diversity-productivity relations (Grace, Michael Anderson, et al., 2007, Grace, Anderson, et al., 2016, Mittelbach et al., 2001, Schmid, 2002, Van Oijen et al., 2020). High productivity values were thereby mostly associated with low species richness in intensively managed grasslands (Van Oijen et al., 2020), while natural grasslands showed only minor impacts of plant diversity on productivity (Grace, Michael Anderson, et al., 2007). In addition, explicit differences in management regime (in terms of frequency or intensity) can also result in contrasting effects (Yin et al., 2017, Weigelt, Weisser, et al., 2009, Walter et al., 2012). Depending on the experimental field site, increasing mowing frequency either caused higher productivity values irrespective of species richness or functional group richness (Weigelt, Weisser, et al., 2009), or caused marginally higher or lower productivity values related to the timing of mowing events (Walter et al., 2012), or even caused lower productivity values with reduced effects in more diverse grasslands (Yin et al., 2017).

Besides management, other environmental factors such as soil properties (Fay et al., 2015), climatic conditions, and the regional species pool and composition (Hector, Bazeley-White, et al., 2002) can play a role for the impact of plant diversity on productivity. For example, increased air temperature at different extensively managed experimental field sites led to lower (De Boeck et al., 2007), equal or higher productivity (Grant et al., 2017, Cowles et al., 2016) of grasslands, with significant effects of species diversity (De Boeck et al., 2007, Cowles et al., 2016). Grasslands under drought, which include besides warming also less precipitation, showed in turn equal to less biomass production, depending on management intensity (Vogel et al., 2012, Kahmen et al., 2005, Craine, Nippert, et al., 2012).

To gain a generalized understanding of how management intensity and environmental changes affect grassland diversity and productivity, a systematic analysis of single effects of the influencing factors - environment, management, plant diversity and vegetation dynamics, as well as their interplay and feedbacks is necessary. In combination with field experiments and observations, modeling allows expanding and thus complementing knowledge on the relative importance of different influencing factors for grassland dynamics. Grace, Anderson, et al. (2016) used structural equation modeling to identify important influencing factors on species richness and productivity based on observational grassland data around the world. For instance, they found that shading between plants is strongly tied to aboveground biomass and shading controls species richness on the plot-scale. To understand the detailed responsible mechanisms and to quantify the magnitude of influence of different factors, the use of process-based simulation models can be beneficial.

Process-based grassland models investigated, so far, the impact of different management with respect to mowing intensity and climate change (Kipling et al., 2016, Oijen et al., 2018). They often focused on consequences for other trophic levels, e.g., animals (Johst, Drechsler, Thomas, et al., 2006, Green et al., 1997), or on changes in grassland productivity (Rodriguez et al., 1999, Moulin, Perasso, Calanca, et al., 2021, Schippers and Joenje, 2002, Soussana, Maire, et al., 2012), but the detailed mechanisms in plant growth responsible for the varying results were not analyzed. Moreover, the models were mostly population-based and focused on modeling aboveground biomass (Duru et al., 2009, Schippers and Joenje, 2002); only few considered also explicit dynamics of other vegetation attributes such as functional composition or vegetation height (Moulin, Perasso, and Gillet, 2018). As a result, mowing events were often defined as the removal or as the retention of a certain amount of aboveground biomass (Schippers and Joenje, 2002, Rolinski et al., 2018, Puche et al., 2019, Schaphoff et al., 2018, Chang, Viovy, et al., 2013). For instance, Moulin, Perasso, Calanca, et al. (2021) examined the dynamics of functional composition under different management scenarios, considering mowing events as the removal of a certain proportion of each species, coupled to a species' mature plant height (i.e., maximum plant height). However, especially for mowing, the daily development of the height of each individual plant, and thus the explicit frequency of large and small plants per occurring species in the community on the day of mowing can play an important role. Individual-based models offer the possibility to track, among others, also the dynamics of plant height structure per species in grasslands. This allows to explicitly model mowing events defined by mowing height, and to analyze its impact (and feedback) on the size growth of each plant.

Here, we use an individual-based process-oriented model, parameterized for a field biodiversity experiment in Central Europe in which plant diversity is systematically manipulated and analyzed in terms of its effect on grassland productivity. The parameterized model already reproduces well the observed diversity-productivity relation for the diversity range of four plant functional types (Schmid, Huth, et al., 2021). Given this starting point, we investigated the following questions in this simulation study:

1. How do mowing frequency and air temperature influence the diversity–productivity relationship in grasslands?
2. How do demographic processes, plant shading and crowding as well as air temperature affect grassland dynamics?
3. Does mowing frequency change the relative abundances of plant functional types in grasslands?

We focused in our study on functional diversity by using plant functional types (PFTs). Each mixture of different functional richness (number of PFTs) was simulated in combination with different annual mowing frequencies (zero to five) and an increased air temperature (one and two degrees). Thereby, relative abundance of the considered PFTs could change in response to the modified climatic condition and management regime. On the example of the 4-PFT mixture, we systematically analyzed how the underlying vegetation processes that act on the individual plant level in the model led to differences in grassland productivity and abundances of plant functional types under the varied anthropogenic and environmental conditions. In order to take a first step in disentangling effects of environmental and management change, we focused here only on mowing frequencies (in terms of management) and air temperature increase (in terms of environmental change).

3.3 METHODS

3.3.1 *The grassland model*

We used here the individual-based grassland model GRASSMIND. The model is process-oriented and simulates the growth of individual plants on a daily basis. Main processes include plant photosynthesis, respiration, reproduction and mortality. Since the GRASSMIND model consists of many different processes, we describe here only those relevant for our study. A detailed description of the GRASSMIND model can be found in (Taubert, Hetzer, et al., 2020a), (Taubert, Hetzer, et al., 2020b) and under `www.formind.org/downloads`. Note that in this study, belowground processes in soil such as competition for water and nitrogen are excluded (assumption that soil water and nitrogen do not limit plant growth; see also (Schmid, Huth, et al., 2021)). In order to take a first step in disentangling effects of environmental and management change, we constrained our modeling study to vegetation processes acting aboveground only (e.g., plant shoot growth and mortality, shading of plants and crowding). By this, effects of changes in precipitation or soil resource dynamics (e.g., soil water and nitrogen content) on the dynamics of grasslands were excluded in this study first, but allow for extended impact analyses in follow-up studies (e.g., accounting also for effects of drought or fertilization regimes).

At the individual level, plants are established as seedlings and then grow in height and width based on a fraction of net primary productivity ($ANPP$ [g_{ODM}/d]), which is calculated from the balance of photosynthesis (GPP_{act} [g_{ODM}/d]) and respiration (R [g_{ODM}/d]) multiplied by the allocation rate to shoots $alloc_{\text{shoot}}$:

$$ANPP = alloc_{\text{shoot}} * (GPP_{\text{act}} - R) \tag{3.3}$$

whereby respiration is divided into cost for maintenance and plant growth:

$$R = R_{\text{main}} + R_{\text{growth}} \tag{3.4}$$

Individual plants may differ in their traits (PFT-specific model parameters) which affect plant growth. Plant growth is modeled according to a PFT-specific constant ratio of an individual plant's height to its width (or lateral extent). A mowing event causes all plants to be shortened to a certain height (e.g., to 10 cm) while maintaining the width of the plants (mown biomass is assumed to be removed). Subsequently, plants grow only in height until the PFT-specific ratio is reached again.

Reproduction is modeled by a PFT-specific seed ingrowth. This daily ingrowth encompasses the constant incoming seed rain from the surrounding landscape. Simulated seed ingrowth starts from bare ground with the date of sowing the grassland and is repeated each day. The amount of incoming seeds remains constant on each day, but seeds are constrained dependent on the available bare ground (reduction proportional to PFT-specific seed rain). Those (constrained) incoming seeds can germinate after a PFT-specific emergence time (dependent on a PFT-specific germination rate constant over time). After a PFT-specific time, growing seedlings turn into adult plants. Some plant characteristics then change, for instance, the allocation ($alloc_{\text{shoot}}$, investing partly energy in seed production) and the intrinsic mortality rate of plants (m_{seed} to m_{basic}).

Different limitation factors influence vegetation growth in the model (Fig. 3.1). At the community level, competition for space (crowding) prevents too many plants growing into a simulated plot. This density-dependent mortality reduces plant density (number of plants on the plot) if community cover exceeds plot area. Plant growth can be limited due to shading by other plants (asymmetric competition for light, modeled implicitly for all plants on a 1 m^2 plot). Tall plants shade smaller ones, which affects photosynthesis and can reduce growth. More precisely, the global radiation I_0 [$\mu mol_{photon}/m^2/s$] is reduced in horizontal layers (1 cm width) taking into account the total leaf area LAI_i [-] of all individuals in each height layer i to gain the irradiance I_S [$\mu mol_{photon}/m^2/s$] of the height layer S (Monsi and Saeki, 2005):

$$I_S = I_0 \cdot e^{-(\sum_{i>S} LAI_i)} \tag{3.5}$$

As a result, light intensity is reduced towards the ground of the plot. Plant height determines the height layer S a plant can reach and thus, the available irradiance of the plant. Light limitation is measured with the light reduction factor $R_L = I_S/I_0$.

Light reduction is considered in the calculation of the potential gross primary productivity GPP_{pot} [g_{ODM}/d] of each individual. GPP_{pot} is modeled via photosynthesis, and depends on different parameters such as the PFT-specific initial slope of the light response curve and the PFT-specific light extinction coefficient, as well as on plant-relating attributes such as the incoming irradiance on the leaf surface, the leaf area and the area of lateral extent of the plant.

Air temperature has an influence on plant photosynthesis and respiration. Potential gross primary productivity GPP_{pot} can be reduced by a temperature-dependent factor $R_T \in [0,1]$:

$$GPP_{\text{act}} = R_T * GPP_{\text{pot}} \tag{3.6}$$

and maintenance respiration R_{main} [g_{ODM}/d] and growth respiration R_{growth} [g_{ODM}/d] can be reduced or increased by a temperature-dependent factor $f_T \in [0,\infty)$:

$$R_{\text{main}} = f_T * r_m * B \tag{3.7}$$

$$R_{\text{growth}} = r_g \left(GPP_{\text{act}} - R_{\text{main}}\right) \tag{3.8}$$

whereby r_m [1/d] is a constant maintenance respiration rate, B [g_{ODM}/m^2] is the biomass of plant root and green shoot, r_g [-] is a constant parameter for growth respiratory costs and GPP_{act} [g_{ODM}/d] is the actual gross primary productivity. A temperature below 25°C causes a decrease in maintenance respiration R_{main} and a temperature above 25°C causes an increase.

Both, gross primary productivity and maintenance respiration, change with air temperatures, whereby gross primary productivity has its optimum at a temperature greater than or equal to 10 °C (Schippers and Kropff, 2001). Further abiotic variables (such as global radiation and day length) also influence plant growth.

Mortality of plants is included as stochastic events. Both mortality processes, intrinsic mortality and mortality by crowding, select plants at random to die. The intrinsic (PFT-specific) mortality rate can affect a plant at each day during its lifetime. Crowding mortality, instead, is only triggered if overall vegetation cover exceeds the simulated area (here one m^2). Note that, although each plant has generally the same chance to die due to crowding, smaller plants are more likely to die due to their higher frequency compared to larger plants (skewed plant size distribution).

To account for stochastic effects in our analyses, we calculated the average of results over twenty simulation runs (corresponding to an area of 20 m^2).

3.3.2 *Model settings*

In this study we used four plant functional types (PFTs) for representing functional diversity. Thereby, the traits of a PFT correspond to typical representatives of either grasses, small herbs, tall herbs or legumes (Roscher, Schumacher, Baade, et al., 2004). The parameterization of the PFTs is based on field measurements of the Jena Biodiversity Experiment in Central Europe (50°55´N, 11°35´E) (see Weigelt, Marquard, et al., 2010, Schmid, Huth, et al., 2021 for details). Plant species in the experiment were assigned to one of the four respective PFTs (Roscher, Schumacher, Baade, et al., 2004) and the originally set-up grassland plots (each 20 x 20 m^2) with different levels of plant species-richness (from monocultures to multi-species mixtures) collapsed into average plots consisting of (a) only one of the four PFTs, (b) all four PFTs and (c) different combinations of two or three of the respective PFTs. The aggregated grassland plots

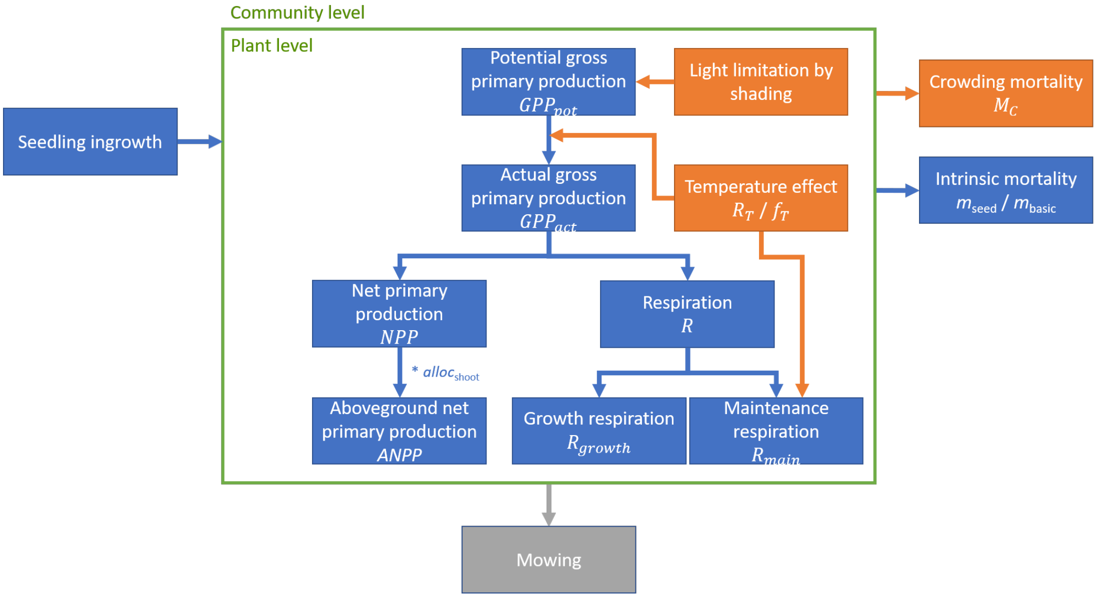

Figure 3.1: Model processes relevant for biomass dynamics in the model. Processes outside the green framed area take place on the community level, whereas processes inside happen for each individual plant. Orange boxes indicate competition processes leading to limiting growth. For a detailed description of variables and equations see Methods and `www.formind.org/downloads`.

of different functional diversities from (a) and (b) were then used to parameterize the grassland model in a stepwise manner (first, each average plot of one PFT, and second, the average plot including all four PFTs). The second step was only required for recalibration of the seed ingrowth per PFT and did not change any of the other PFT-specific model parameters calibrated before. The average 2-PFT and 3-PFT mixture plots were used for model validation. For model parameterization, calibration as well as validation, mean vegetation attributes over the entire measurement period from 2002 to 2008 were considered (Schmid, Huth, et al., 2021). Final parameter values of each of the four PFTs are shown in Table B.1. Methodological details of the calibration and a comparison of observed and calibrated grassland dynamics (in terms of different vegetation attributes and functional composition) are provided in Schmid, Huth, et al. (2021).

The model simulations started on the day of sowing (16^{th} of May, 2002) and ended six years later on 31^{st} of December. We simulated mixtures of all possible PFT combinations (of functional richness 1 to 4). In the model, the functional richness and diversity remained throughout the entire simulation time, and only the proportions of PFTs were variable.

The management regime in the first two simulation years corresponds to the setting in Schmid, Huth, et al. (2021) (first year mowing on 5^{th} of July and 10^{th} of September, second year mowing on 10^{th} of June 10 and 10^{th} of September). Climate data were taken from a weather station located near the Jena Experiment. To prevent different climatic conditions between years from influencing our results, climate data of 2002 were used for each year (average temperature $\overline{T} = 10.3°C$).

Temperature and mowing frequency were then varied from the third simulation year onwards (both described in the next section).

3.3.3 *Scenario analysis*

In the scenario analysis we investigated a range of annual mowing events for different temperatures. Those were applied for five consecutive years after two years of simulation with the same management and climate.

For the varied climate we considered three scenarios: (i) the daily temperature remained the same as in the first two years, (ii) temperature was increased by one degree on every day ($\overline{T} = 11.3°C$) and (iii) temperature was increased by two degrees on every day ($\overline{T} = 12.3°C$) while other climatic variables remained the same. For each climate scenario, management was altered according to Table 3.1. The dates of the varied mowing frequency (one to five times per year) were distributed evenly within each year (Table 3.1). Note that the dates for the scenario of two annual mowing events in our simulation study slightly differed from those mowing dates done in the Jena Experiment and used in a previous simulation study (Schmid, Huth, et al., 2021). Additionally, we simulated a management scenario with no mowing events from year 3 to 7.

Table 3.1: Dates of varied mowing frequency. Mowing dates were applied for five years after two years of simulation with the same management.

Mowing frequency	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
0												
1								10^{th}				
2						10^{th}			10^{th}			
3					10^{th}		10^{th}		10^{th}			
4				10^{th}		10^{th}		10^{th}		10^{th}		
5				10^{th}	10^{th}		10^{th}	10^{th}		10^{th}		

3.3.4 *Evaluation of model output*

The model output includes daily vegetation attributes of each plant. For our analysis, we considered different vegetation attributes over a period of five years (between 1^{st} of March and 31^{st} of October, 245 days per year, of the simulation years 3 to 7). We used the community and PFT-specific aboveground biomass (AGB) by summing up the AGB of all plants or the AGB of plants belonging to a certain PFT. AGB on day t results from AGB of the previous day, aboveground net primary productivity $ANPP$, the aboveground biomass of ingrowing seedlings (AGB_{seedling}) and plant mortality ($AGB_{mort_{\text{intrinsic}}}$ and $AGB_{mort_{\text{crowding}}}$) (see also Fig. 3.1):

$$AGB\,(t) = AGB\,(t-1) + ANPP + AGB_{\text{seedling}} - AGB_{mort_{\text{intrinsic}}} - AGB_{mort_{\text{crowding}}} \quad (3.9)$$

Total biomass change ΔAGB corresponds to the change of AGB at day t:

$$\Delta AGB(t) = AGB\,(t) - AGB(t-1) \quad (3.10)$$

We analyzed weekly and annual changes in total biomass by first, aggregating simulated daily values to weeks and years (using averages) and second, calculating changes based on these average values using equation (3.10).

Besides the total aboveground biomass, we also looked at the mown biomass, which corresponds to a fraction of the aboveground biomass above mowing height (here 10 cm). Leaf area index (LAI) is derived by calculating the leaf area from aboveground total AGB and the constant specific leaf area of a plant (PFT-specific model parameter). As vegetation height, we used the height of the highest plant within the community. To assess the abundances of PFTs, we regarded aboveground biomass proportions.

3.3.5 *Analysis of influencing processes*

To assess the impact of different influencing processes on the grassland dynamics, we analyzed which amounts of biomass would have grown without certain limiting processes on a day, respectively. For that, we computed (i) the *ANPP* that was produced in the standard setting, (ii) the AGB that got lost by crowding, (iii) the *ANPP* that would have been produced without shading between plants, (iv) the *ANPP* that would have resulted if there had been no temperature effects on photosynthesis (see equation (3.6), $R_T = 1$) and (v) the *ANPP* that would have resulted if there had been no temperature effects on respiration (see equation (3.7), $f_T = 1$) (Fig. 3.1, see also Table B.2). For each single day, the effect of a missing influencing process was always calculated based on the vegetation of the standard setting on the previous day, which means that for (iii) to (v), the effect of the missing process on one day had no influence on the result of the next day. Furthermore, a missing process had no impact on other (following) processes in the model (Table B.2). For instance, regarding the effect of shading, we do not consider a changed respiration that would have followed, but consider only the biomass that got lost due to less light availability.

3.4 RESULTS

3.4.1 *Impacts of mowing frequency and air temperature on the diversity-productivity relationship*

Overall, a higher mowing frequency led to increased mown biomass in the plots (Fig. 3.2, green dots and lines, Fig. B.1). For different mowing frequencies, plots of four PFTs showed the highest amount of mown biomass per year (up to 50% more than average plots of one PFT), while average plots of two and three PFTs were partly less productive than plots of one PFT. Nevertheless, we observed a positive trend with increasing functional group richness for all mowing frequencies. Functional group richness gained more influence on productivity with increasing mowing frequency, as the slope of trend lines in the relationship got steeper (on average 11 g/m^2yr more productivity per functional richness level when mowing once per year, and 53 g/m^2yr more productivity per functional richness level when mowing five times per year). A deeper analysis revealed that some low-diversity PFT compositions decreased productivity with increasing mowing frequency (1-PFT plot of grasses, and 2-PFT plot of grasses and small herbs, Fig. B.2). Productivity of PFT-mixtures strongly varied depending on their plant functional composition (Fig. B.2). Thereby, they mostly showed a dominance of PFTs that are highly productive in the corresponding 1-PFT plots (e.g., legumes, Fig. B.3).

With increasing air temperature, trends in the diversity-productivity relationships (in terms of functional richness) under different mowing frequencies still remained positive in our modeling study (Fig. 3.2, yellow and red dots and lines). Increased temperatures led to an overall increase of mown biomass (Fig. 3.2). Thereby, a 1°C increase of temperature affected a 5% increase in mown biomass, while a 2°C increase resulted in 10% more mown biomass (averages over all mowing frequencies and functional group richness levels). Remarkably, the higher the mowing frequency and the lower the functional group richness, the less change appeared according to biomass yield (Fig. 3.2) and other vegetation attributes (Table B.3).

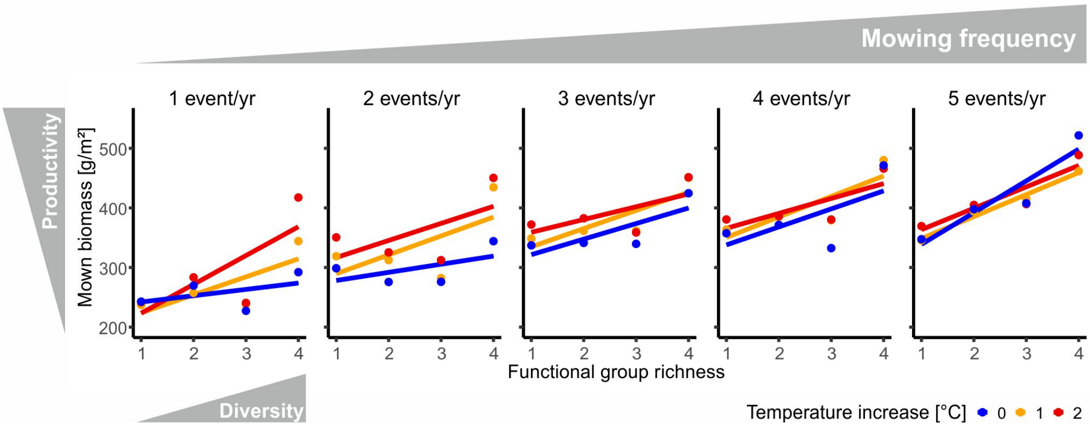

Figure 3.2: Impact of mowing frequency and air temperature on the diversity-productivity relationship. Productivity refers to the mean annual mown biomass (aboveground biomass above 10 cm height, mean over five simulation years), functional group richness refers to the number of plant functional types in the grassland. Daily temperature was increased by 0°C (blue color), 1°C (yellow color) or 2°C (red color), respectively. See Fig. B.1 for direct comparison of different mowing frequencies with no increased air temperature.

3.4.2 *Causes for changes in productivity*

To find an explanation for increased biomass yields with higher mowing frequencies and temperature increase, we analyzed the annual development of vegetation attributes and the influence of different model processes on each attribute with focus on the mixture of four PFTs.

3.4.2.1 *Annual development of AGB and ANPP in extensively managed grasslands*

When grasslands were mown once per year, simulations of annual aboveground biomass (AGB) showed more or less logistic growth until the mowing event affected a drastic decrease of AGB (Fig. 3.3A). Also, aboveground net primary productivity (ANPP) increased until the mid of the year, and decreased thereafter, whereby again the mowing event affected an abrupt change (Fig. 3.3B). Similar patterns were observed in simulated leaf area index and vegetation height (Fig. B.4A). In contrast, plant density decreased slightly until mid-year and remained stable thereafter, indicating an increase in average plant size (Fig. B.4A).

In the first months of the year, low temperatures (Fig. 3.3C) prevented a fast growth of plants which is reflected in a small increase of vegetation biomass and ANPP (Fig. 3.3A-B). As air temperatures became higher, plants accelerated in growth as especially taller plants increased their photosynthetic productivity (Fig. 3.3C). However, self-shading and mutual shading of plants (which increases with plant height) slowed down plant productivity again. Both, plant mortality by crowding and the intrinsic plant mortality, showed to have a greater influence on grassland productivity than the establishment of seedlings, shading between plants or temperature effects on photosynthesis and respiration (Fig. 3.3B-C). During the year, temperature decreased respiration costs and hence, increased grassland productivity in the model. These respiration-related biomass gains exceeded biomass losses due to temperature effects on plant photosynthesis at the end of the vegetation period. The mowing event caused less shading between plants, less plant mortality and increased seedling establishment (Fig. 3.3B-C).

3.4.2.2 *Changes in influencing processes at different mowing frequencies*

With higher mowing frequencies, plants became smaller which resulted in a decreasing ANPP (Figs. 3.4A-B, B.4B, Tables B.3, B.4). With this, shading of taller plants slightly decreased and biomass losses and gains due to temperature effects on photosynthesis and respiration became smaller (Fig. 3.4C, Table B.4). Since the modelled plants grew only in height after mowing and not in width anymore (until they had reached their previous height-width ratio again), biomass losses due to plant mortality by crowding decreased, while the impact of intrinsic mortality remained equal (Fig. 3.4B). As the decrease of biomass losses (crowding mortality and intrinsic mortality) was stronger than the decrease of biomass gain (ANPP and new seedlings) (Fig. 3.4B), higher mowing frequencies led in total to an increase in total annual AGB change and mown biomass (Fig. 3.4B).

3.4.2.3 *Changes in influencing processes at different air temperatures*

In the 4-PFT mixture, a 2°C increase in air temperature resulted in an increase of total AGB of grasslands for low mowing frequencies (up to 31% more) and remained similar for five mowing events per year (1% less) compared to no increase in temperature (Fig. B.6 and Table B.3). Main reasons for the increase of AGB at low mowing frequencies were a higher ANPP due to higher LAI, a weaker effect of temperature on photosynthesis (less loss compared to photosynthesis without temperature impact) and a stronger effect of temperature on respiration (more biomass gain compared to respiration without temperature impact), and less intrinsic plant mortality (Tables B.3 and B.4). However, ANPP loss due to shading slightly increased as plants grew taller in the simulations. Mowing grasslands more often led to reduced AGB and LAI and thus, the positive effect of an increased air temperature on photosynthesis was mitigated (Tables B.3 and B.4).

3.4.3 *Changes in abundances of plant functional types in grasslands*

To get an impression whether and how different mowing frequencies change grassland diversity, we looked at abundances of different PFTs in the simulations. Different mowing frequencies resulted in small changes in the relative abundances of PFTs in the grassland mixture of four PFTs. The proportion of grasses in total AGB decreased with increasing mowing frequency from 22% (no mowing) to 15% (five times per year), thus herbs proportionally increased (Fig. 3.4A, Table B.5). Within the herbs, AGB was dominated by legumes (39-57% of total biomass). When more frequently

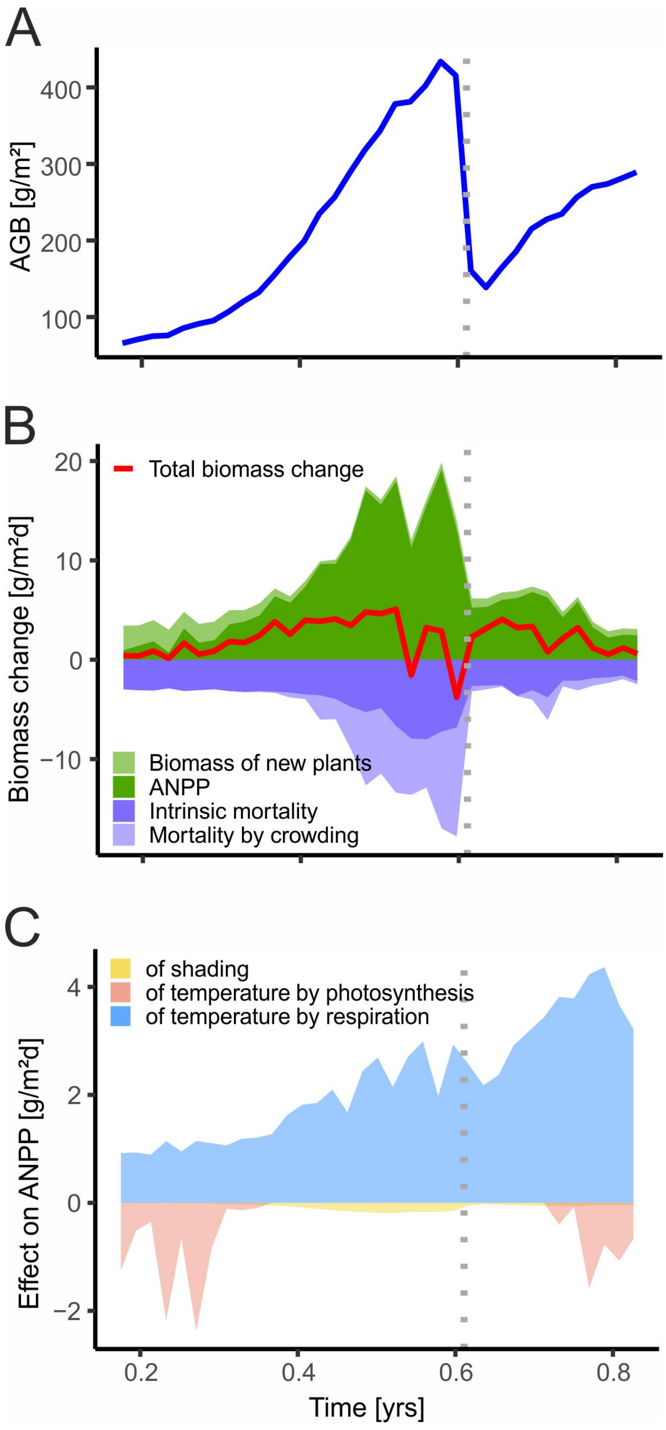

Figure 3.3: Annual courses of vegetation attributes in the grassland mixture of four plant functional types with one mowing event per year (marked by the gray dotted line). Vegetation attributes are weekly means and correspond to averages over the vegetation periods of five simulation years. In (A) the annual developments of aboveground biomass (AGB) is shown. In (B) total biomass changes (red line) and the leading influence of different processes in the model are shown. In (C) the colored areas show the amount of aboveground biomass that would have been additionally produced without activating certain processes in the grassland model (shading and temperature effects on plant photosynthesis and respiration, see Methods). For annual courses of further vegetation attributes see Fig. B.4A.

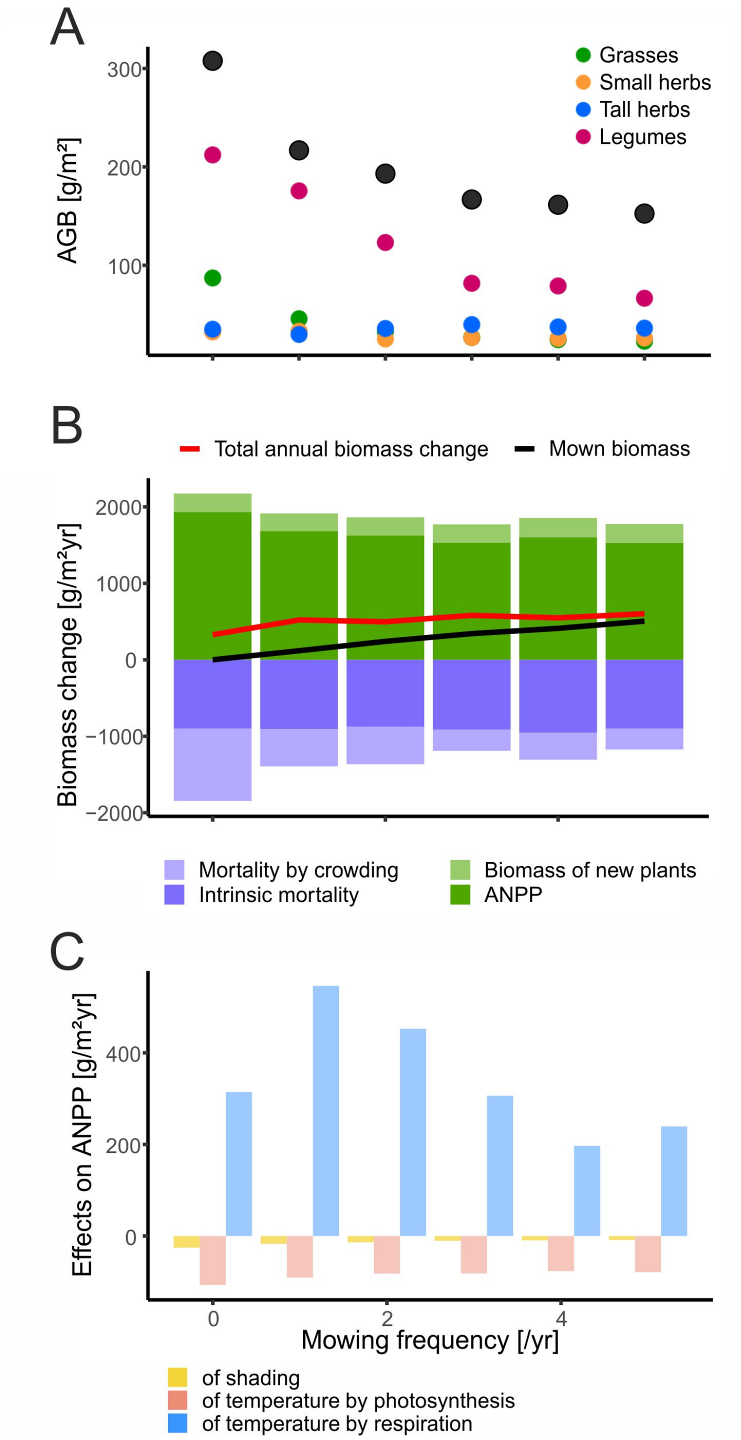

Figure 3.4: Influence of different mowing frequencies (4-PFT mixture). Annual aggregations were taken over the vegetation periods of five simulation years. (A) shows annual mean aboveground biomass (AGB) for different mowing frequencies of the total community (black dots) and of different plant functional types (colored dots). In (B) average annual sums of aboveground net primary productivity (ANPP), biomass gain due to new plants, biomass loss due to intrinsic mortality and by crowding are shown. The difference of those gains and losses corresponds to the total annual biomass change (red line). The black line is the average of the annual total mown biomass. In (C) colored bars show the amount of biomass that would have been produced without activating certain processes in the model (shading and temperature effects on photosynthesis or respiration, see Methods). For annual courses of AGB and changes in further vegetation attributes see Figs. B.6 and B.4B.

mown, grasslands showed a decrease in the proportion of legumes and an increase in the proportion of small and tall herbs. Small herbs always maintained a low biomass proportion with 9-16%. When considering only mown biomass (at mowing dates above 10 cm height) the results slightly differed (see B.1 Supplementary Results and Fig. B.7).

Quantitatively, higher mowing frequencies led to a decrease in the AGB of legumes and grasses, an increase in the AGB of tall herbs and no remarkable changes in small herbs (Fig. 3.4A). LAI and vegetation height showed similar trends, while plant density remained stable regardless of mowing frequency (Fig. B.5).

Generally, the PFTs showed different growth strategies in the mixture. Tall herbs and legumes had highest ANPP, whereas small herbs produced the highest amount of seedling biomass among the PFTs, especially in the beginning of the growth period (Figs. 3.5A-B, B.8). However, small herbs also had, together with tall herbs, high biomasses losses due to intrinsic mortality (Fig. 3.5A), which is certainly connected to their low plant densities (Fig. B.5). Remarkably, ANPP of legumes was still high, although they had high losses due to shading and temperature effects (Fig. 3.5B).

An impact of different mowing frequencies was visible in ANPP and crowding mortality of the PFTs (Fig. 3.5A). Higher mowing frequencies led to less ANPP and crowding mortality of grasses and legumes, but increased productivity of tall herbs. The decreasing impact of shading between plants with higher mowing frequency was visible in all PFTs (Fig. 3.5B). In contrast, temperature effects increased for tall herbs, decreased for grasses and legumes and remained stable for small herbs (Fig. 3.5B).

Increased air temperature caused only minor changes in relative abundances of PFTs in the modeled grassland (Fig. B.7B and Table B.5). Overall, legumes and small herbs became slightly more dominant, which was mainly at the expense of the biomass proportion of tall herbs (i.e., by maximum 9 percentage points). For example, the proportion of legumes increased from 53% to 62% in the scenario of two mowing events per year, or the proportion of tall herbs decreased from 31% to 22% in the scenario of four mowing events per year).

3.5 DISCUSSION

In this study, we used an individual-based process-oriented model parameterized for a local field biodiversity experiment to investigate the effect of different mowing frequencies and air temperature on the productivity and the abundances of plant functional types in temperate grasslands. We studied in detail the role of different influencing processes and temperature on vegetation productivity and revealed the following insights: (i) The positive diversity-productivity relationship persisted with increasing mowing frequency, with an increased proportion of herbs in more frequently mown grasslands. Although higher mowing frequencies led to a lower overall aboveground net primary productivity, biomass yields increased. Effects of increased air temperature were greatest in grasslands with high functional richness and low mowing frequency. (ii) Among the vegetation processes considered, plant mortality (intrinsic and by crowding) had the greatest impact, and shading between plants the least impact on grassland productivity in diverse mixtures. (iii) The analyzed diverse grassland mixture was dominated by herbs, especially by legumes. The proportion of grasses and legumes decreased in the model simulations under more frequent mowing.

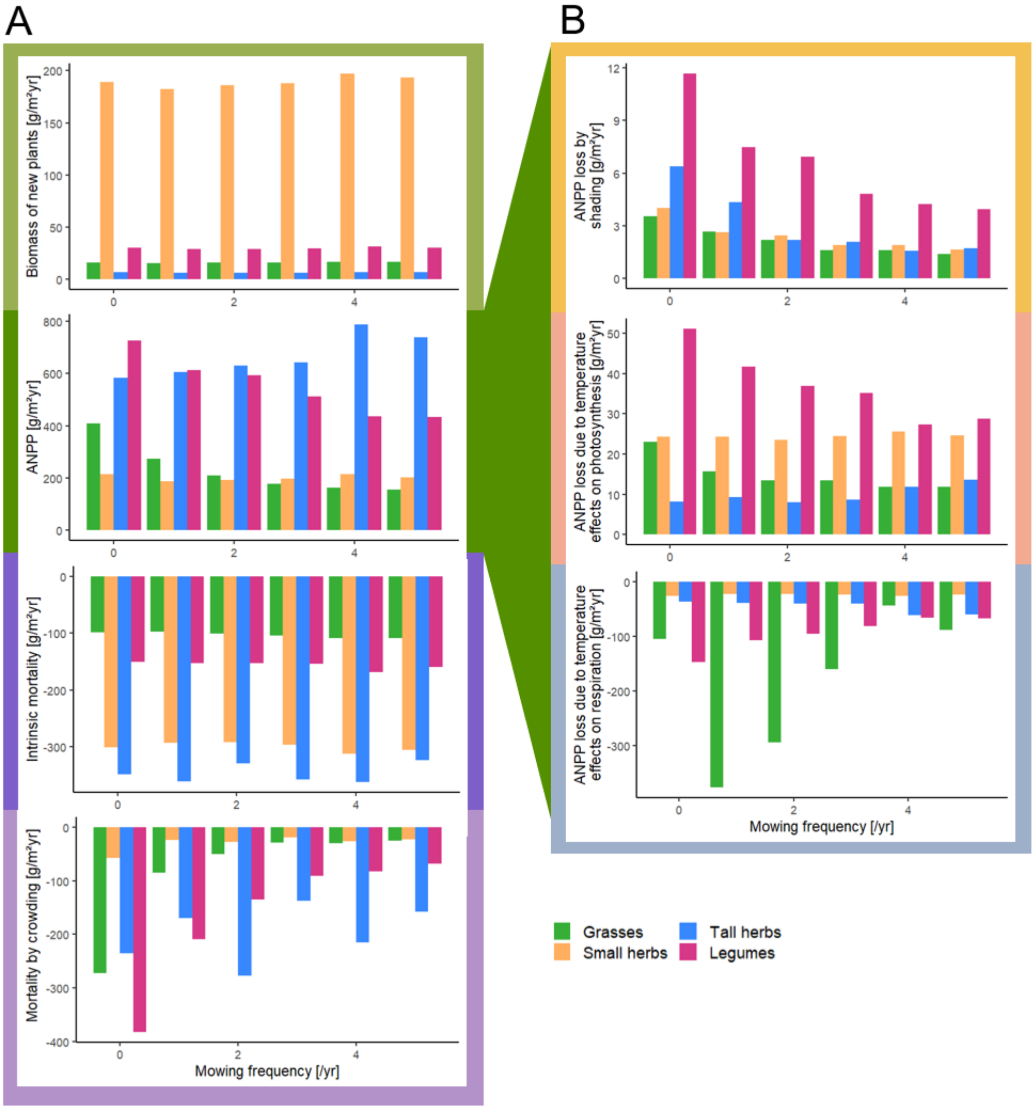

Figure 3.5: Influence of different mowing frequencies on PFT-specific grassland dynamics (plant functional types: grasses, small herbs, tall herbs and legumes) in the 4-PFT mixture. (A) Impacts on aboveground biomass gains and losses (biomass of new plants, aboveground net primary productivity (ANPP), intrinsic mortality and mortality by crowding) and (B) impacts on the strength of limiting processes affecting ANPP (by shading and temperature effects).

3.5.1 *Impacts of mowing frequency and air temperature on the diversity-productivity relationship*

The increase of biomass yields with diversity and under more frequent mowing (or when temperature rises) was also observed in field experiments in which the level of plant diversity has been manipulated (Weigelt, Weisser, et al., 2009, Cowles et al., 2016). Our model results indicate that the positive diversity-productivity relationships may be driven by the dominance of PFTs in the mixtures, that strongly increase productivity with mowing frequency. Higher mowing frequencies allow fast-growing plants (e.g., tall herbs) to regrow more often before reaching its saturation at the maximum height, thus making them more productive and dominant. More frequently mown grasslands not only achieved higher biomass yields in our model simulations, but also showed less reaction to temperature increase. In modeled grasslands with low mowing frequency, air temperature stimulated vegetation growth. In contrast, vegetation growth did not change remarkably at high mowing frequencies as overall less aboveground biomass and shorter recovery times between mowing events resulted in a lower plant photosynthesis and thus, less stimulation by increased temperature.

The conducted analysis of changes in management regime and temperature increase and its impacts on the diversity-productivity relationship can be extended. Some studies already emphasized that, besides plant diversity and air temperature, the effects of management can also interact with other local and regional environmental conditions (e.g., soil conditions or precipitation). This complex interplay of management and various site-specific environmental factors makes it difficult to give general recommendations, for example for increasing biodiversity in grasslands (Gilhaus et al., 2017, Michaud, Plantureux, Amiaud, et al., 2012). In order to progress insight, process-based models can be applied for systematic variations of multiple environmental factors for analyzing separate and combined effects and disentangling their overall impact on grassland growth (e.g., extension of this study to additional changes in precipitation and fertilization and the resulting soil resource dynamics) – by this, supporting the synthesis of biodiversity effects on grassland productivity along an environmental gradient (Wang, Cadotte, et al., 2019).

3.5.2 *Quantifying effects of different processes on vegetation growth*

The effects of different processes on growth, such as shading between plants or the influence of temperature, are difficult to measure and to quantify in field experiments. For instance, measuring light availability using a light meter (Borer, Seabloom, et al., 2014) or determining temperature on different vegetation heights by using a sensor network (Schädler et al., 2019) are costly, but can indirectly provide information about plant size structure and corresponding plant interactions, e.g., shading within the grassland. Although controlled experiments (Roscher, Kutsch, et al., 2011) can offer more insight on such plant interactions and vegetation processes, it still remains difficult in the field to disentangle and directly measure individual plants. This, however, would be required to estimate how different plant species are vertically distributed in the size structure of grasslands (especially in species-rich semi-natural grasslands) and to understand which effect comes into play for plant growth and to what extent.

Our study is a well example of how models can be used to gain a deeper understanding of vegetation dynamics in complementing field studies. Specifically, our simulation analysis revealed that plant mortality has a major impact on vegetation dynamics. Model parameters of the responsible processes, namely intrinsic mortality and mortality by crowding, have therefore been quantified using inverse calibration methods due to lack of observation data (Schmid, Huth, et al., 2021). Thereby, calibrated demographic model parameters on plant mortality and seed ingrowth might mediate each other in our simulations and could be responsible for the observed high impact of plant mortality by crowding and high ANPP (i.e., high turnover of small seedlings). Sensitivity analyses of previous simulation studies using the GRASSMIND model already detected a strong influence of parameters regarding plant geometry, photosynthesis and demography (Schmid, Huth, et al., 2021, Hetzer et al., 2021, Taubert, Hetzer, et al., 2020a), but also with high (non-linear) interactions to other model parameters. Thus, future observations of field studies that explicitly measure plant mortality rates or plant life spans, and plant densities (Lauenroth and Adler, 2008, Hovenden et al., 2017, Wilcox et al., 2020) could support a robust estimation of such model parameters. Nevertheless, plant mortality can have multiple reasons (e.g., age- or stress-related) underpinning the need for detailed field experiments and measurements under various (controlled) conditions.

The here determined influences of different vegetation processes and air temperature are based on model simulations. Analyzing those influences using other similar mechanistic models could validate our results. For instance, the model of Schippers, Groenendael, et al. (2001) did not include the removal of plants due to crowding, but by an intrinsic mortality or external disturbance events (like mowing, which lets a certain percentage of adult plants die). In other models, intrinsic plant mortality depends on air temperature (Soussana, Maire, et al., 2012) or on annual growth efficiencies (Schaphoff et al., 2018). Such model inter-comparisons (e.g., Bugmann et al., 2019) can not only help to assess the sensitivity of different model formulation for similar vegetation processes, but also support the development of up- and downscaling approaches between models of different complexity and level of detail. For example, statistical relations between plant density and aggregated grassland attributes at the community level can be derived from individual-based models (including variations of environmental factors) and can support the formulation of density-dependent plant mortality in less detailed models.

3.5.3 *Changes in relative abundances of plant functional types in grasslands*

Increased abundances of fast-growing acquisitive species are known to occur with intensive management (i.e., high mowing frequencies) (Allan et al., 2015). Like in our simulation results, experimental field studies showed an increase in herbs and a decrease in grasses when grassland was mown once per year compared to no mowing (Maron and Jefferies, 2001) and temperature increase had only minor effects on the functional composition of grasslands (Grant et al., 2017). Note that grassland intensification often combines frequent mowing with fertilization whereby fertilization amounts can change functional species composition in an opposite direction than presented in this simulation study (in which plant growth was only limited by shading or crowding but not limited by soil resources).

3.5.4 *Possible model extensions*

Our study provides possible extensions in several directions. In our analysis, we only considered fixed mowing dates and a constant mowing height. Shifting mowing dates within a year or changing mowing height could result in different outcomes of vegetation dynamics. For example, the day of the first mowing event within a year is known to influence species diversity, composition and hence also productivity (Socher et al., 2012, Knop et al., 2006). Earlier first mowing events can promote lower species richness and higher proportions of grasses (Socher et al., 2012). The mowing dates in our study are rather theoretical, as we chose evenly distributed dates over a year independent from the developmental stage of particularly selected grassland attributes. In contrast, agri-environmental management often provide recommendations to preserve biodiversity of plants and animals (Kleijn, Baquero, et al., 2006, Kleijn, Schekkerman, et al., 2010, Tälle et al., 2018, Johst, Drechsler, Mewes, et al., 2015, Green et al., 1997). For instance, temporal heterogeneity of mowing events is required for conserving multiple grassland species in the landscape (Johst, Drechsler, Mewes, et al., 2015). In future studies, mowing events can be modeled as a function of the climatic condition (e.g., triggered when reaching specific thresholds of aboveground biomass). In addition to mowing, the model can be extended to simulate additional disturbances such as grazing (Thornley, 1998, López-Mársico et al., 2015), or extreme events (e.g., drought or flooding).

Furthermore, we focused our study on aboveground processes. Plant-soil interactions were not included in this analysis, which corresponds to the assumption of no limitations in water and nutrient supply. Soil interactions are, however, especially interesting when simulating increased temperatures, which can also result in a decreased water availability as potential evaporation increases (Wetherald and Manabe, 1995, Bates et al., 2008). The here presented simple approach is useful to study the influence of temperature only on vegetation, i.e., it represents a scenario in which soil could be watered (and cooled down) at rising temperature. Field studies investigating the impact of climate change often include both, increased temperature and less precipitation (Schädler et al., 2019, Hossain and Beierkuhnlein, 2018) or only consider less precipitation (drought) (Craine, Nippert, et al., 2012, Loik et al., 2019). An experimental study indicated that both changes of the environment, temperature and soil water, can have different influences on grassland growth (Hoeppner and Dukes, 2012). In field observations, biomass of herbs increased under warming with ambient precipitation conditions, but decreased with a combination of warming and doubled precipitation (Hoeppner and Dukes, 2012). Further, semi-natural grasslands often include a considerable number of drought-tolerant species (Craine, Ocheltree, et al., 2013), which are important components determining their resilience.

Simulation models can serve as an important tool to analyze the influence of different environmental settings. As demonstrated in this study, extrinsic factors (like mowing frequency and air temperature) and functional diversity (e.g., mixtures of any combination of plant functional types) can be rapidly varied in simulation models and analyzed over long time periods. Despite this, also the influence of intrinsic factors on grassland dynamics can be tested with models, like the variation, adaptation or evolution of plant traits or the role of plant and population plasticity (Schmid, Huth, et al., 2021, Maire et al., 2013). For example, management and plant interactions can alter growth strategies of plants. Trait variation in response to growth conditions under different species richness levels, community compositions and management scenarios has already been observed in the field (Roscher, Schumacher, Gubsch, et al., 2018, Silveira Pontes et al., 2010) and has also shown to be necessary in an individual-centered vegetation model simulating trends in productivity (Maire et al., 2013). Including trait distributions instead of fixed trait values might enhance the adaption of the plant community to certain environmental influences.

3.6 CONCLUSION

In summary, the individual-based grassland model applied here enabled us to quantify the impact of different climatic and management scenarios on vegetation attributes like productivity or abundances of plant functional types. It further allowed us to identify the importance and change of different processes and factors influencing vegetation dynamics. Our simulation study demonstrates how models, complementary to field experiments, can help to understand vegetation growth and its responses to human impacts and climate change.

3.7 ACKNOWLEDGMENTS

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4

IMPACT OF MANAGEMENT, ENVIRONMENT AND CLIMATE CHANGE ON PRODUCTIVITY AND THE PROPORTION OF HERBS IN GRASSLANDS: A SIMULATION STUDY ACROSS GERMANY

IMPACT OF MANAGEMENT, ENVIRONMENT AND CLIMATE CHANGE ON PRODUCTIVITY AND PLANT FUNCTIONAL COMPOSITION OF GRASSLANDS

4.1 ABSTRACT

Temperate grasslands are important ecosystems as they provide various ecosystem services (e.g., biodiversity and biomass production). Environmental conditions and management intensity affect productivity plant functional composition and relative abundances of plant functional types in grasslands; however, the importance of different factors and quantitative impacts are still largely unexplored. Here, we used an individual-based grassland model and created a generic regionally transferable parameterization by accounting for six different grassland observational sites along a gradient of climatic, management and soil conditions for calibration and validation. In a scenario analysis for 24 representative regions across Germany, we then analyzed how grassland productivity and the biomass proportion of herbs depend on management intensity and various environmental factors in combination with climate change. The model-based scenario analysis revealed that intensive management generally leads to high grassland productivity and low herb proportions. Correlations with environmental factors decreased with management intensity (i.e., mowing frequency and fertilization amount). Precipitation and irradiance belonged to the most influential environmental factors. Climate change had only a minor influence on the analyzed vegetation attributes. Our study shows how process-based grassland models can be used to gain a general understanding of how environmental factors and anthropogenic interventions impact grassland dynamics – knowledge which is especially crucial with regard to climate change.

4.2 INTRODUCTION

Natural and semi-natural grasslands can be home for more than 80 different plant species (WallisDeVries et al., 2002). Biodiversity (e.g., species richness or functional richness of species grouped to plant functional types (PFTs), the composition and relative abundances of species or plant functional types) can vary in grasslands, depending on management intensity and environmental factors (e.g., soil type and climatic conditions) which all together interact with ecosystem functions such as productivity. On the one hand, intensive management of high mowing frequencies and fertilization leads mostly to more productive grasslands with less diversity and altered functional composition and abundances of PFTs (Plantureux et al., 2005, Socher et al., 2012, Allan et al., 2015). The application of fertilizer can lead to the absence of legumes and the dominance of highly productive tall-growing grasses (Gałka et al., 2005, Hejcman, Klaudisová, et al., 2007) which can prevent the establishment of other plant species due to increased competition for light and hence lead to low species diversity (Maron and Jefferies, 2001, Hejcman, Klaudisová, et al., 2007, Boch et al., 2021). On the other hand, abandonment of grasslands can lead to loss of diversity and shifts in functional composition as the conservation of plant species is mainly driven by extensive management (Maron and Jefferies, 2001, Moog et al., 2002). Extensive management gives plants more access to light due to regular mowing events. That enhances seedling germination and, e.g., the establishment of different herb species and therefore promotes diversity (Foster and Gross, 1998, Maron and Jefferies, 2001). Management intensity, functional richness, composition and abundances of PFTs can have a strong impact on ecosystem functions and services like ecosystem stability, carbon storage or the cultural value of grasslands (Tilman, Knops, et al., 1997, Allan et al., 2015, Weisser et al., 2017). For that, finding an appropriate management that maintains and restores a high level of diversity in grasslands is crucial (Plantureux et al., 2005).

Field studies showed that the effects of management are substantially influenced by local and regional abiotic conditions (e.g., soil properties or weather), and the interplay of management and site-specific environmental factors makes it difficult to formulate general recommendations specifically for increasing biodiversity in grasslands (Adler et al., 2011, Michaud, Plantureux, Amiaud, et al., 2012, Socher et al., 2012, Fraser, Pither, et al., 2015, Gilhaus et al., 2017, Mayel et al., 2021). Management and environmental conditions affect plant functional composition and relative abundances of PFTs, and all together determine grassland productivity (which in turn can change plant functional composition and relative abundances). In a local field experiment, management intensity partly mitigated or amplified the impact of weather conditions and plant diversity on productivity, whereby intermediate management maximized biomass yields (Bernhardt-Römermann et al., 2011). Observations of permanent grasslands from different region types in France revealed that vegetation characteristics including functional composition and weather conditions explained up to 40% of productivity variability (Michaud, Plantureux, Pottier, et al., 2015).

Environmental changes, like climate change and resulting drought events, can alter the dynamics of grasslands (Korell et al., 2021). In order to maintain ecosystem functions like stability during drought events, plant diversity plays an important role for mitigation (Frank and McNaughton, 1991, Isbell et al., 2011, Craine, Ocheltree, et al., 2013). Hence, it is crucial to understand how different environmental factors contribute quantitatively under certain management to grassland diversity, in terms of functional composition and relative abundances of PFTs, at different sites.

Simulation models allow to analyze the interplay of plant diversity, environmental factors, management and vegetation dynamics with regard to climate change (Kipling et al., 2016, Oijen et al., 2018). Process-based simulation models are particularly helpful to determine the impact of different external influences on grassland dynamics. When modeling different grassland regions, site-specific model parameterizations of plant traits are often created by calibration with local field measurements (Schmid, Huth, et al., 2021). However, these locally derived parameter sets, which are only valid for a certain location with fixed environmental conditions, could lead to inconsistencies and uncertainties when simulating the local site under environmental conditions of different regions (e.g., weather and soil type) and analyzing their influence on mechanisms like plant growth. Following a regional modeling approach, the creation of a multi-site common parameter set that simulates site-specific vegetation dynamics only by exchanging environmental conditions and management can overcome this limitation (Chang, Viovy, et al., 2013, Ma, Lardy, et al., 2015). Such a generic, regional transferable model parameterization further allows to project grassland dynamics for sites with so far (partly) missing observations of specific vegetation attributes. More generally valid conclusions can be drawn about how environmental factors and management impact grassland dynamics with regard to climate change. This, in turn, can be used in the future to provide regional management recommendations, e.g., to preserve biodiversity.

Here, we used the individual-based process-oriented model GRASSMIND to create a regional parameterization for investigating grassland dynamics in Germany with regard to the following questions:

1. Is it possible to create a generic, regional transferable parameterization of GRASSMIND for grasslands in Germany?
2. How do site-specific environmental factors such as soil properties and weather variables influence productivity and the proportion of herbs (in terms of aboveground biomass) under different management intensity?
3. How does climate change influence grassland attributes and the proportion of herbs?

We created a generic parameterization of the model using grassland measurements of six field sites which allowed to apply one set of growth characteristics (of four PFTs) to locations at different regions across Germany with differences in grassland dynamics, only driven by environmental conditions and management. Secondly, in a scenario analysis by simulating 24 representative locations across Germany differing in their environment in combination with a gradient of management scenarios, the model enabled us to investigate the importance and relative effects of management intensity, soil and climatic conditions on grassland productivity and the proportion of herbs. This analysis also included the consideration of various climate change scenarios (i.e., RCP scenarios) and their impact on changes in grassland dynamics.

4.3 MATERIALS AND METHODS

4.3.1 *The grassland model GRASSMIND*

4.3.1.1 *Model description*

We used the individual-based grassland model GRASSMIND. The model is process-oriented and simulates the growth of individual plants on a daily basis. Main processes include plant photosynthesis, respiration, reproduction and mortality. Since the GRASSMIND model consists of many different processes, we describe here only those relevant for our study. A detailed description of the GRASSMIND model can be found in (Taubert, Hetzer, et al., 2020a, Taubert, Hetzer, et al., 2020b) and under `www.formind.org/downloads`. Details of the modeled belowground processes in soil, such as competition for water and nitrogen, are explained in Supplementary Methods and Fig. C.1.

At the individual level, plants are established as seedlings and then grow in height and width based on the balance of photosynthesis and respiration. For expressing diversity in the model, different species or plant functional types (groups of species, PFTs) can be simulated. Individual plants may differ in their traits (species-specific or PFT-specific model parameters) which affect several processes. For example, the growth of a plant is influenced by a PFT-specific constant ratio of the plant's height to its width (or lateral extent).

Reproduction is modeled only by a PFT-specific seed ingrowth which represents a daily constant seed rain from the surrounding landscape. The simulation starts with bare ground, and the seed application starts with the sowing date, which is repeated every following day, whereby the establishment of seedlings depends on available bare soil. After a PFT-specific time, growing seedlings turn into adult plants. Some plant characteristics then change, for instance, the allocation rates and the intrinsic mortality rate of plants. Note that only perennial plants are modeled in this study (maximum life span of an individual plant was set to 20 years).

Different limitation factors influence vegetation growth in the model. At the community level, competition for space prevents too many plants growing within a simulated plot. This density-dependent mortality reduces plant density (number of plants on the plot) if community cover exceeds plot area (1 m^2). Tall plants shade smaller ones by reducing the available irradiance (asymmetric competition for light, weighted by 1/9 of the plot area), which affects photosynthesis and can reduce growth.

Mortality of plants is included as stochastic events. Both mortality processes, intrinsic mortality and mortality due to space competition, select plants at random that die with their biomass being transferred to the litter pool. To account for stochastic effects in our analyses, we calculated the average of results over multiple simulation runs.

4.3.1.2 *Impact of soil and weather in the model*

Site-specific factors such as weather and soil type influence the growth of the vegetation in the model. All factors can limit the net primary production (NPP) of individual plants. Thereby air temperature, daylength and global radiation impact directly the amount of photosynthesis and respiration of each individual plant.

For instance, air temperature has an influence on both, plant photosynthesis and respiration. A temperature below 25°C causes a decrease in respiration and a temperature above 25°C causes an increase, whereby photosynthesis has its optimum at a temperature greater than or equal to 10°C (Schippers and Kropff, 2001). Details on the influence of other abiotic variables (such as global radiation and daylength) on the growth of individual plants can be found under `www.formind.org/downloads`.

In contrast, plants compete belowground for soil water (depending on precipitation) and soil nitrogen. Both, insufficient water and nitrogen availability can lead to reduced plant growth, expressed by reduction factors in the model (ratio of supply to demand, ranging between zero and one). Thereby, water and nitrogen demand are calculated dependent from the potential (non-reduced) NPP. The growth of legumes is not limited by insufficient nitrogen availability, but they have to provide each time step a proportion of their NPP for symbiosis with rhizobia bacteria. Water reduction is determined before nitrogen reduction. Soil was modeled using 20 horizontal layers with two meter depth in total (10 cm depth each layer). For a detailed description of the modeled soil processes see C.1 Supplementary Methods and Fig. C.1.

4.3.1.3 *Impact of management in the model*

Two management events are implemented in the model: the conduction of a mowing event and the addition of fertilizer to the soil. Both management events take place on predefined days. A mowing event affects a cut of all plants to a predefined height (if the plant's height is greater) while maintaining the width of the plants (mown biomass is assumed to be removed). Thereafter, cut plants grow only in height, until they have reached their previous height-width ratio again (PFT-specific trait). Fertilization causes an increase of available nitrogen for plants which could favor the growth of especially non-legume plants.

4.3.1.4 *Typical model output*

The model output comprises daily vegetation attributes of each individual plant belonging to a certain PFT. Typical vegetation attributes are, e.g., aboveground biomass, leaf area index and vegetation cover. The attributes can be aggregated to the population level (e.g., aboveground biomass of each PFT) or to the community level (aggregation of all existing individuals).

4.3.2 *Generic parameterization of the model*

Instead of simulating each plant species we used the approach of PFTs (Schellberg and Pontes, 2012). For that, existing species were classified in groups oriented on the multivariate cluster analysis of Roscher, Schumacher, Baade, et al. (2004). Based on 18 functional traits the latter distinguished between grasses, small herbs, tall herbs and legumes. Hence, we parameterized trait-averaged typical representatives of those groups describing common plants occurring in Germany.

In the first part of our study, we created a generic, regional transferable parameterization of the grassland model. This parameterization contained fixed plant traits of the four PFTs and should simulate measured vegetation attributes of different grassland sites in Germany by only exchanging management, climatic conditions and soil properties (Table C.1). For gaining the generic parameterization of the four PFTs, we initially used the parameter values received in a previous study based on a local field experiment (Schmid, Huth, et al., 2021). We then recalibrated parameters that were sensitive in a global sensitivity analysis (Schmid, Huth, et al., 2021) and parameters that were related to soil interactions. For that, three grasslands in Germany differing in management and environmental conditions were considered (two different land use types from the Global Change Experimental Facility (GCEF) (Schädler et al., 2019) and one site from the University of Giessen long-term Free Air Carbon dioxide Enrichment Experiment (GiFACE) (Jäger et al., 2003), Fig. 4.1A). Besides the environmental conditions, also one plant parameter (PFT-specific constant seed ingrowth, encompassing incoming seeds from the surrounding and the reproduction by existing plants) were site-specific. Validation was conducted using three further temperate grassland sites in Germany (regions of the Biodiversity Exploratories: SEG, HEG and AEG (Fischer, Bossdorf, et al., 2010), Fig. 4.1A) with seed ingrowth parameter value of GiFACE. See C.1 Supplementary Methods and Tables C.2-C.4 for details on the different sites and vegetation measurements used.

At each site, the model simulated an area of 10 m² to account for stochasticity. All simulations began with bare soil and sowing seeds. For the simulation of the sites at GiFACE and the Biodiversity Exploratories we included a spin-up time before the first measurement in the field as these are permanent grasslands with no available sowing dates. See C.1 Supplementary Methods for details on the calibration and validation.

4.3.3 *Scenario analysis*

4.3.3.1 *Simulation settings*

With the scenario analysis, we investigated how environmental factors, management and climate change influence grassland productivity and the proportion of herbs in the model. Thereby, productivity refers to the mean annual sum of aboveground biomass that exists one day before a mowing event on the plot, respectively. The mean proportion of herbs corresponds to the fraction of the PFTs small herbs, tall herbs and legumes in total aboveground biomass on these days. The average over several years was taken to gain one value for the productivity and one value of the proportion of herbs for one specific scenario. We used the proportion of herbs as a simple measure for diversity in the grasslands in our analysis.

We divided the scenario analysis into two parts: (i) the analysis of ambient grasslands, with ambient climatic conditions on 24 different locations representing different natural areas in Germany (Fig. 4.1B, for details see C.1 Supplementary Methods, Table C.5-C.6) and varied management intensity at each location (1-5, for details see C.1 Supplementary Methods and Table C.7) and (ii) the analysis of future grasslands, regarding the same regions and respective management variations, now also considering climate change scenarios.

Climate data and simulation time periods differed between both parts of the scenarios. For the analysis of ambient grasslands, we used measured climate data at all considered locations (see C.1 Supplementary Methods). Simulations of 20 m^2 started in year 1990 (sowing date 16th of May) and run until 2019. The first two simulation years were considered as transient states for the establishment of the plant community and were not included in the evaluation of the proportions of herbs (in total we considered an average productivity and proportion of herbs over 28 years).

For the analysis of future grasslands, we used simulated climate data at all considered locations (for details see C.1 Supplementary Methods). We used three different RCP-scenarios (RCP2.6, RCP4.5, RCP8.5) simulated by six different climate models (Table C.8). Simulations of 20 m^2 plots also started in year 1990 (sowing date 16th of May) and ended in 2099. We then compared the time period 1990-2019 to the time period 2070-2099 by analyzing the change in grassland productivity and the proportion of herbs (change of attributes in two time periods of 30 years, respectively).

4.3.3.2 *Impact of management and environmental factors*

To analyze the relative impact of management and environmental factors on vegetation attributes we used random forest models. These models can be applied for non-linear relationships between predictors and model output. We used the method of conditional inference forests that provides unbiased variable selection in the individual trees since predictor variables varied in their scales (Hothorn et al., 2004, Strobl, Boulesteix, Zeileis, et al., 2007). Predictor variables in the model comprised six soil variables (saturated conductivity, porosity, permanent wilting point, clay content, silt content, sand content), five weather variables (temperature, precipitation, irradiance, potential evapotranspiration (daily means over entire simulation time, respectively) and latitude (proxy for variation in daylength)) and the discrete variable "management intensity" (ranging from 1 to 5). Two random forest models were set up to predict (i) the productivity of the grassland and (ii) the proportion of herbs (in terms of biomass). After training the model with a training set of 80 random samples, model performance was tested on 40 test samples (data comprised in total five management intensities x 24 grassland locations). Then, variable importance was measured by permutations of the variables, using a conditional permutation scheme to account for correlations between predictor variables (Strobl, Boulesteix, Kneib, et al., 2008). The analysis was conducted in R (version 4.0.5, Team, 2019) with the party package (version 1.3-7, Strobl, Hothorn, et al., 2009).

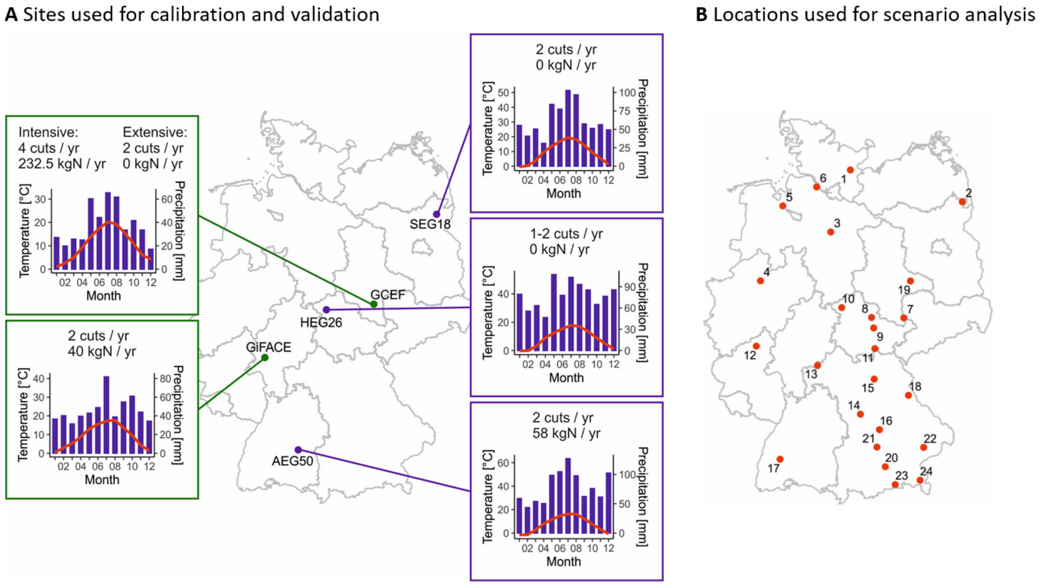

Figure 4.1: Map with (A) sites used for calibration (green) and validation (purple) of the grassland model and (B) 24 grassland locations used for the scenario analyses. Monthly precipitation sums are marked with blue bars and the annual cycle of monthly mean temperatures is shown in red. At GCEF, plots with different management intensity (extensive and intensive management) were considered.

Regression was done by constructing 500 conditional inference trees with six features tried at each tree split using the cforest() function. For all other hyperparameters of cforest() default settings were used. We received an accuracy of R^2 = 0.86 and rmse = 183 g/m²yr for the productivity on the test set (training set: R^2 = 0.854, rmse = 182 g/m^{2}yr) and an accuracy of R^2 = 0.741 and rmse = 0.06 for the biomass proportion of herbs on the test set (training set: R^2 = 0.814, rmse = 0.05) (Fig. C.2).

To determine the importance of different environmental variables, conditional variable importance was conducted which follows the permutation principle of the "mean decrease in accuracy" importance in random forests (Strobl, Boulesteix, Kneib, et al., 2008). "Mean decrease in accuracy" importance scores are the differences in the prediction accuracy of the random forest before and after permuting the predictor variable. Predictor variables were permutated in each tree following the conditional permutation scheme which adjusts for correlations between predictor variables (Strobl, Boulesteix, Kneib, et al., 2008) (see Fig. C.3 for correlations between predictor variables). We used the default settings of the varimp() function with conditional permutation in the party package.

Linear correlations between the predictor variables were tested by computing Pearson's correlation coefficients (Fig. C.3). Additionally, linear correlations between vegetation attributes and predictor variables were tested for each management scenario (Fig. C.4). For the most important variables, we used simple linear regressions to complement the complex random forest models and get insights on preferred environmental conditions.

4.4 RESULTS

4.4.1 *Generic model parameterization*

The calibration for a generic parameterization of the grassland model resulted in good agreements of various vegetation attributes (Fig. 4.2A, Tables C.9-C.10). Within the three field plots used for calibration (GCEF intensive, GCEF extensive and GiFACE), the best fitted attribute was total vegetation cover with a slight mean overestimation in the model (12%), followed by total aboveground biomass with a mean underestimation of 32% in the model across all sites. Vegetation height was underestimated by 58% on average at GCEF intensive and GiFACE. Leaf area index agreed well at GiFACE (7% less), was underestimated at GCEF intensive (42% less) and overestimated at GCEF extensive (21% more). Regarding the abundances of PFTs, management intensity at GCEF had only a minor impact in the model (Fig. 4.2A). For instance, the biomass proportion of grasses in intensively managed grassland was as high as in extensively managed grassland (87%), but total aboveground biomass and vegetation cover in grasslands differed.

The comparisons of the grassland plots used for validation show similar results (Fig. 4.2B). Simulation of vegetation cover and proportions of PFTs agreed very well with field measurements at SEG18 and differed by a maximum of 46% from the mean measurement at the other sites. The amount of total aboveground biomass agreed at HEG26 and was underestimated at the other two sites (AEG50 and SEG18). As at the sites used for calibration, vegetation height was also underestimated at the sites used for validation.

4.4.2 *Germany-wide scenario analysis*

4.4.2.1 *Impact of management intensity*

With higher management intensity grassland productivity increased and the proportion of herbs decreased (Fig. 4.3). Management intensity had more impact on productivity compared to environmental factors. Increasing management intensity from 1 to 5 caused on average an increase of 900 g/m^{2}yr (from 510 g/m^{2}yr to 1420 g/m^{2}yr), whereas for a certain management intensity productivity varied on average by 700 g/m^{2}yr among the locations (mean of total range over all management intensities, Fig. 4.3A). Regarding the simulated proportion of herbs, management intensity and environmental factors revealed similar impacts (maximal variation of about 21% among management intensities and locations, Fig. 4.3B). However, when looking at mean aboveground biomass over all days one day before a mowing event, respectively (instead of productivity corresponding to the annual sum of biomass one day before the mowing events) management intensity and environmental factors have almost equal impacts (average increase of 225 g/m^2 by management intensity versus average variation of 263 g/m^2 among locations, Fig. C.5).

4.4.2.2 *Impact of climate change scenarios*

Climate change generally caused an increase in grassland productivity (Fig. 4.3C). The more intensively grasslands are managed, the greater the change in productivity and the greater also the differences between RCP scenarios (with RCP4.5 always

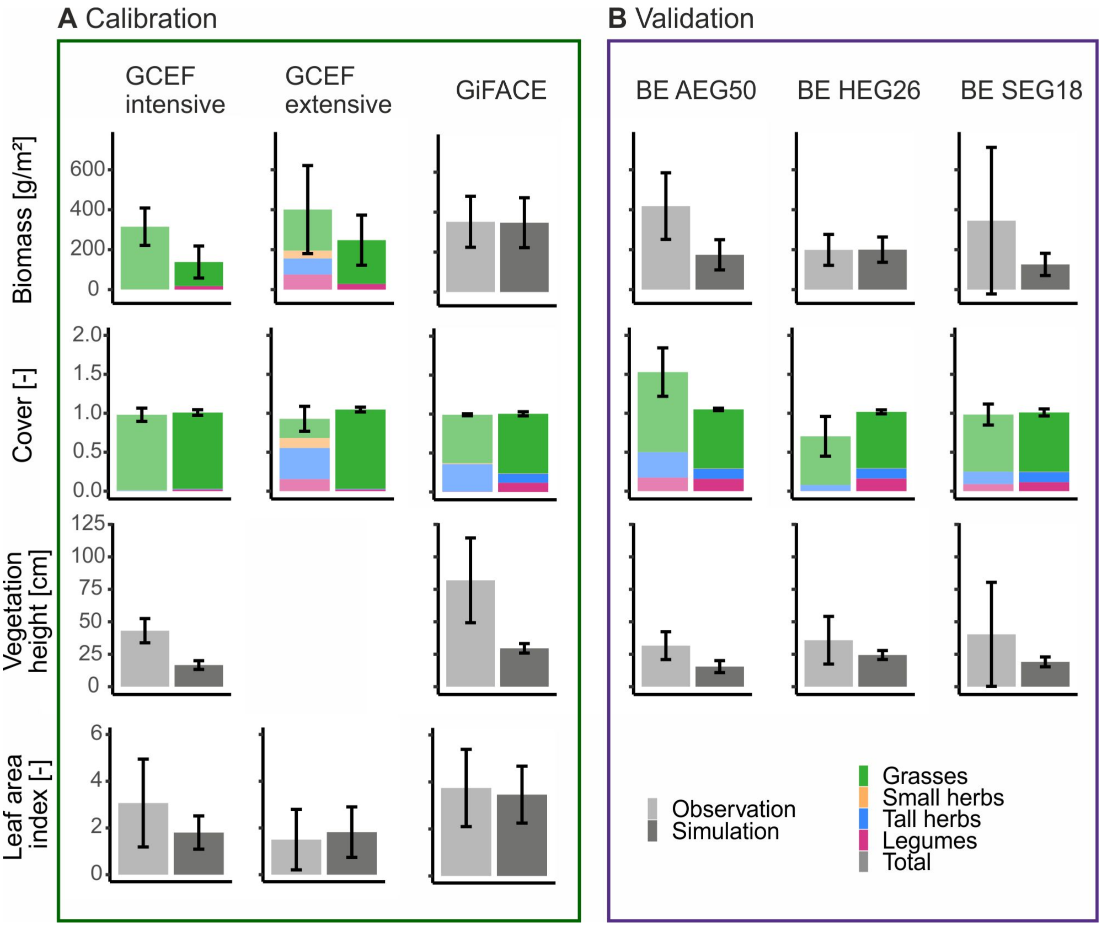

Figure 4.2: Comparison of field measurements and simulation results at different sites in Germany used for the (A) calibration and (B) validation of the grassland model GRASSMIND. Bars correspond to the mean attribute over all measurement days, respectively. Black error bars show the temporal variation in the measurements. At sites used for validation, tall herbs correspond to all herbs in the plots (no differentiation between small and tall herbs).

showing highest productivity change). The biomass proportion of herbs increased due to climate change only for intermediate management intensities, and otherwise remained stable (Fig. 4.3D), whereby the simulations with different RCP scenarios scarcely differed. The biggest change between the two considered time periods (1990-2019 and 2070-2099) was 180 g/m^{2}yr in productivity and 6 percentage points in the biomass proportion of herbs, indicating a small effect of climate change in the model.

4.4.2.3 *Impact of environmental variables*

We used conditional inference forests to assess the conditional importance of management intensity and environmental variables on grassland productivity and biomass proportion of herbs. For important variables we applied linear regression to analyze trends and quantitative impacts. Within the constructed forests, management intensity had the highest effect on the grassland attributes (Fig. 4.4A). Regarding grassland productivity under ambient climatic conditions, only precipitation and saturated conductivity in soil (KS) showed high importance, whereby locations with high precipitation and low KS in soil revealed more productive grasslands (Fig. 4.5A).

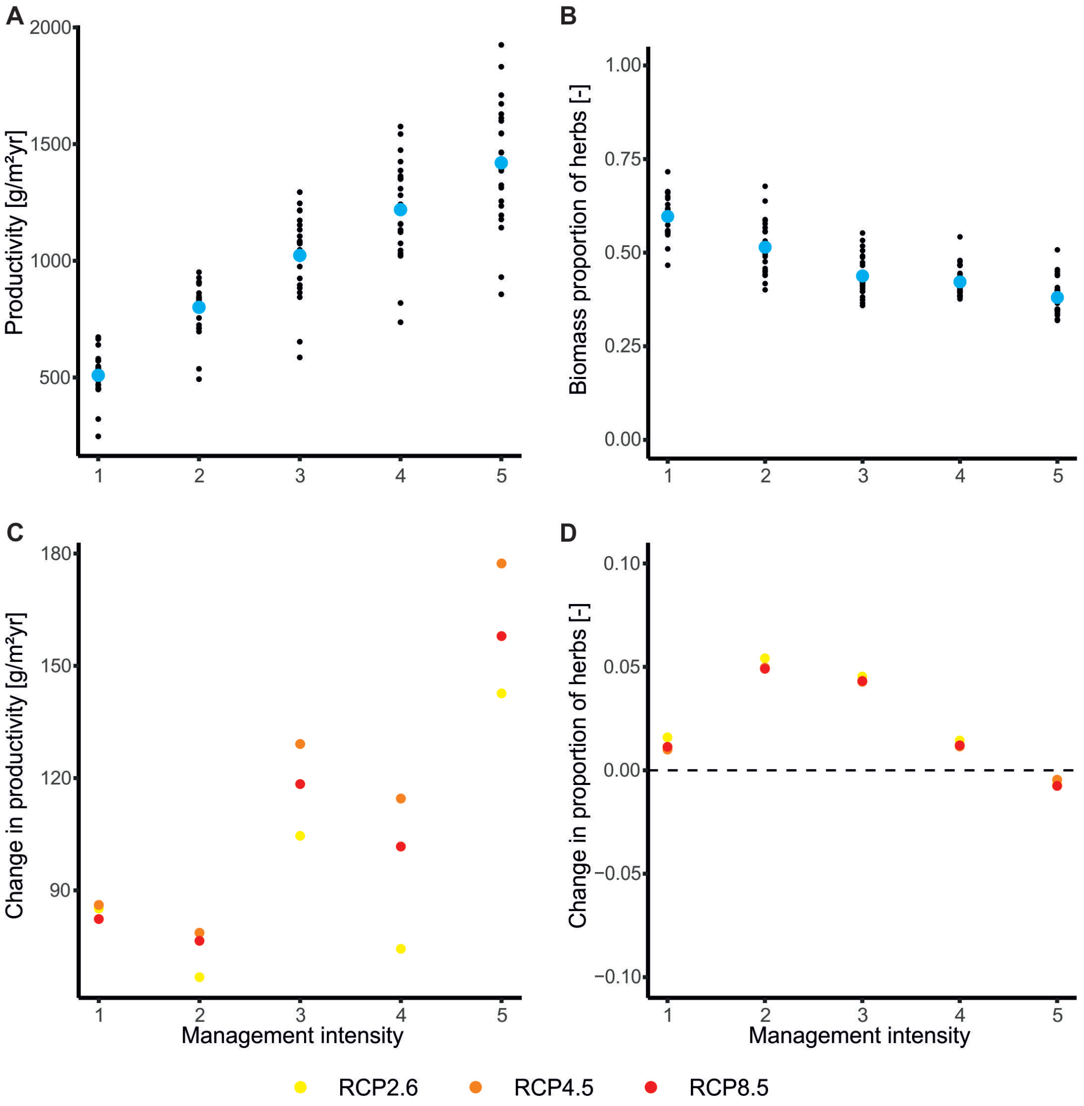

Figure 4.3: Impact of management intensity on (A) grassland productivity and (B) biomass proportion of herbs in the model. Black dots depict the different locations in Germany, blue dots are means over all locations. Changes in (C) productivity and (D) the biomass proportion of herbs due to climate change. Grassland attributes in the time periods 1990-2019 and 2070-2099 were compared. Dots show means over the 24 locations in Germany.

Intensive management strengthened the impacts as the slopes of regression lines increased. For the change in grassland productivity under future climate conditions, air temperature, irradiance, precipitation and latitude belonged to the most important variables. Temperature showed a weakly negative, significant linear correlation only for the highest analyzed management intensity (Figs. 4.5C and C.4B). In turn, we observe a strong positive correlation for irradiance and a strong negative correlation for latitude with the change in productivity for lower management intensities (note that irradiance and latitude are strongly positively correlated to each other, Fig. C.3).

For the biomass proportion of herbs under ambient climate, irradiance and potential evapotranspiration (PET) belonged to the most important variables (Fig. 4.4B), which are both also significantly correlated to each other (Fig. C.3). Both have a positive effect on the proportion of herbs, especially in extensively managed grasslands (Fig. 4.5B). The change in biomass proportion of herbs under future climate was, besides irradiance and PET, also influenced by precipitation and latitude. The positive effect of precipitation was visible for almost all management intensities, whereby the effects from the other variables were only significant in extensively managed grasslands.

Overall, environmental variables affecting aboveground growth limitations (e.g., temperature, irradiance, latitude) showed similar importance as variables affecting belowground limitations due to, e.g., limited water content (e.g., precipitation, PET, KS).

The correlation analyses revealed that fewer environmental variables were significantly correlated with grassland productivity and the biomass proportion of herbs in intensively managed grasslands, except for productivity under ambient climatic environmental conditions, where the number of significantly correlated variables remained almost equal for all management intensities (Fig. C.4). Remarkably, locations with high annual precipitation showed the greatest grassland productivity, though at these locations productivity was again reduced by climate change in the future.

4.5 DISCUSSION

In this study, we took a first step towards a generic, regional transferable parameterization of an individual-based grassland model and analyzed the impact of management and environmental factors on grassland attributes. The model results showed moderate to good agreements to field measurements of aboveground biomass production, leaf area index, vegetation cover, vegetation height and abundances of PFTs (in terms of proportional biomass and cover) for six differently managed and located grasslands in Germany. A followed scenario analysis of 24 simulated locations representing different natural areas in Germany revealed a higher impact of management than environmental factors on grassland productivity and herb proportion (in terms of biomass). Within the environmental factors, climatic variables (e.g., precipitation and irradiance) showed higher importance in comparison to soil properties in the model (e.g., saturated conductivity and silt content). The importance of environmental factors decreased with more intensive management. Similar results occurred for scenarios including climate change, whereby climate change had only a minor overall influence on simulated vegetation attributes in the grassland model.

4.5.1 *Parameterization of the model and possible model adaptations*

Although the individual-based process-oriented model reduces complex interactions in grasslands by, e.g., the use of plant functional types with static plant traits, good agreements of model simulations with observation were received for most of the observed vegetation attributes. Accounting for several vegetation attributes in the calibration process (e.g., vegetation height, cover and biomass) instead of only using attributes related to productivity (e.g., PaSim (Ma, Lardy, et al., 2015)) made the model parameterization challenging. Comparing the grassland sites used for calibration of the model, it is noticeable that the simulated relative abundances of PFTs in GCEF are quite consistent for both management scenarios (intensive and extensive). A key determinant of the abundance of a PFT could be the seed ingrowth, which is assumed to be equal for both plots at GCEF (of different management types), and similar

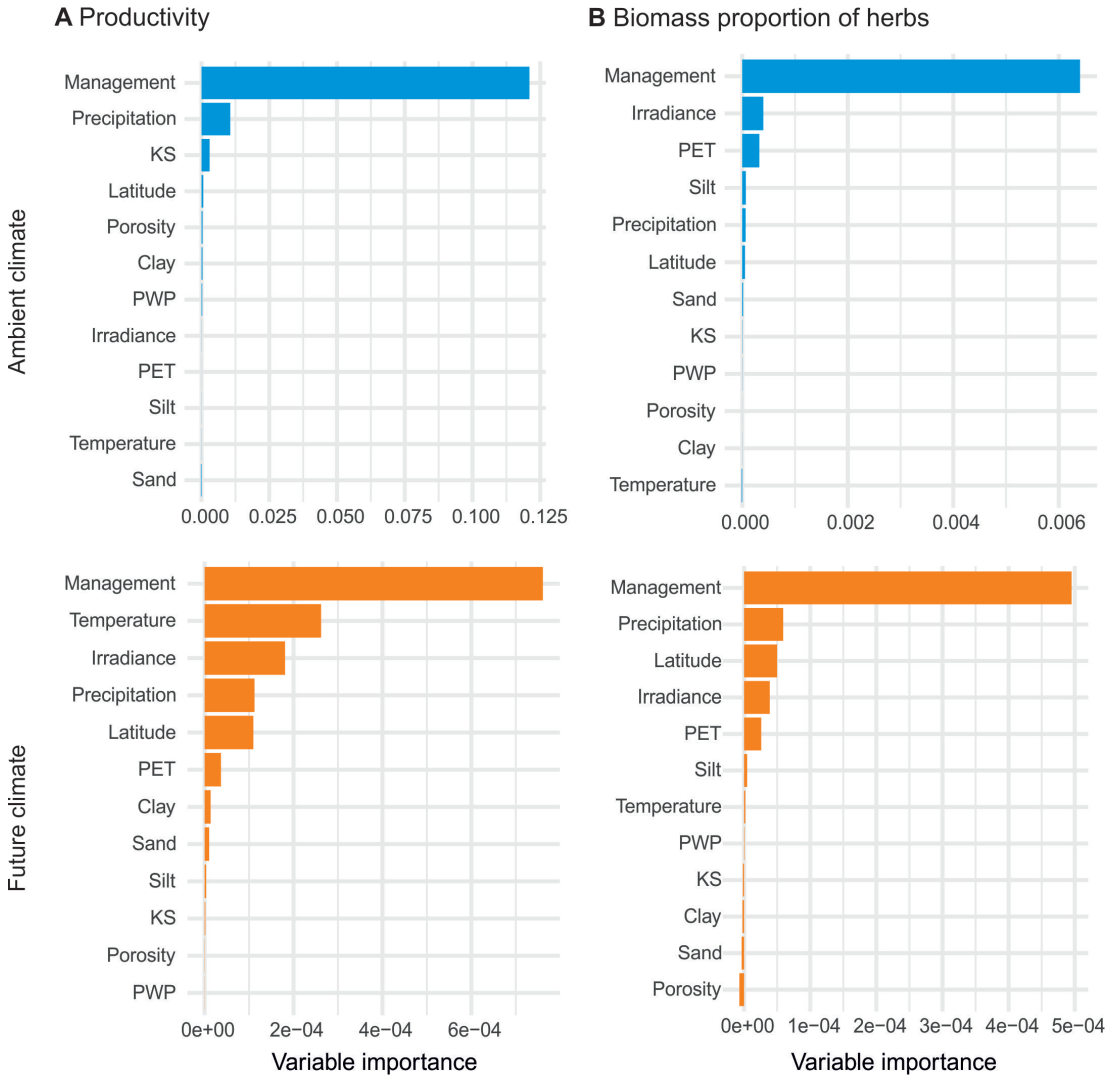

Figure 4.4: Importance of different variables in the conditional inference forests for (A) productivity and (B) the biomass proportion of herbs of the simulated grasslands. The panels on the top show the importance for the ambient vegetation attributes (1990-2019), the panels on the bottom for the change in the vegetation attributes due to climate change (difference 1990-2019 and 2070-2099, RCP4.5). Note that the absolute values of the scores should not be interpreted (Strobl, Boulesteix et al. 2008). Abbreviations: PET – potential evapotranspiration, KS – saturated conductivity in soil, PWP – permanent wilting point.

to GiFACE at the sites used for validation (sites of Biodiversity Exploratories). The constant seed ingrowth, which encompasses both, the reproduction by mother plants and the income of seeds from the surrounding landscape, might reduce complexity of grassland processes too much, as recruitment capacity can vary between PFTs over the year (e.g., after droughts (Zeiter et al., 2016)) and with different management intensity (depending on existing plants). Further, in a drought field experiment recruitment capacity of different PFTs mainly explained changed community composition after re-colonization (Stampfli and Zeiter, 2004).

Another concept that might improve our first basic regional approach is to vary model parameters, i.e., PFT-specific plant traits, at different sites in relation to environmental factors as certain plant traits might adopt to the environment. For instance,

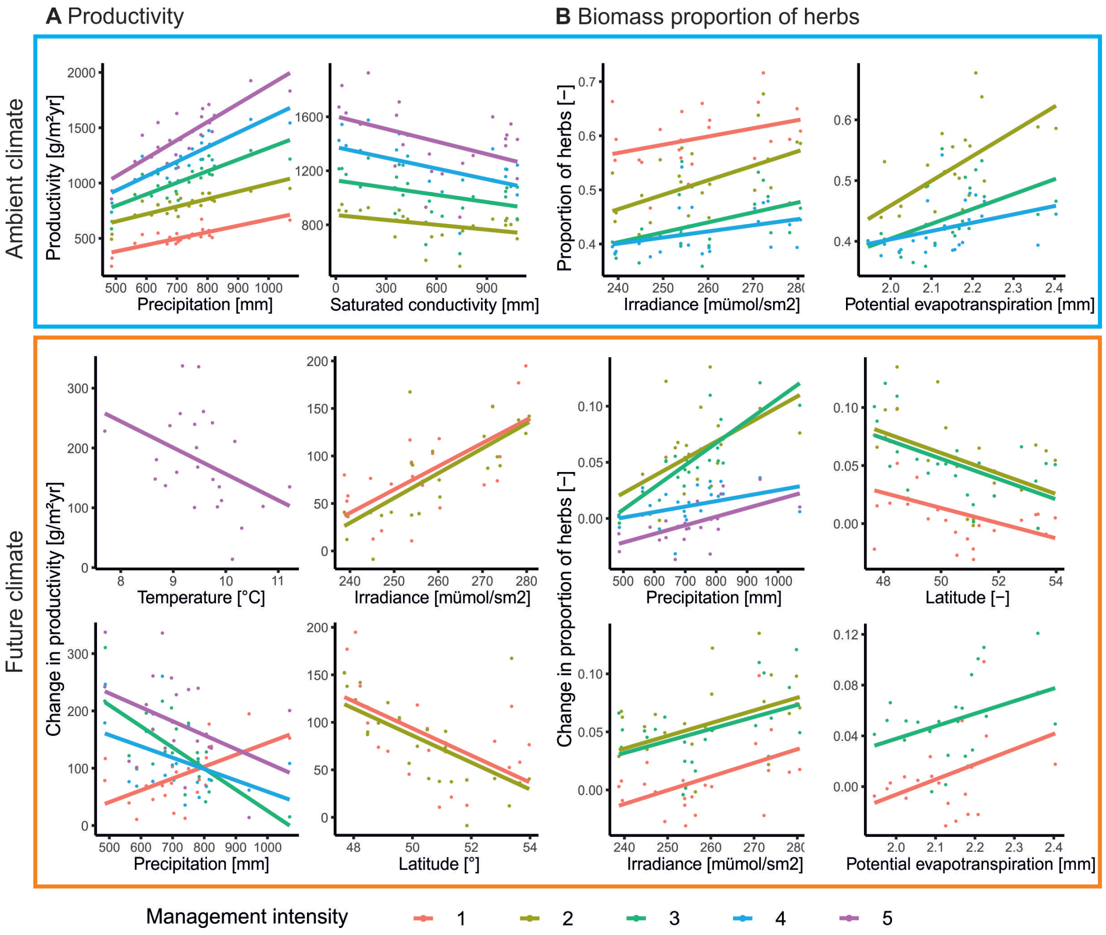

Figure 4.5: Linear regressions between environmental variables and (A) productivity, (B) biomass proportion of herbs, (C) change in productivity and (D) change in biomass proportion of herbs for different management intensities. Dots depict the different locations of the scenario analysis. The changes in (C) and (D) correspond to differences due to climate change (difference 1990-2019 and 2070-2099, RCP4.5) in the simulation model. Only important environmental variables (Fig. 4.4) and significant (p-value < 0.1, Fig. C.4) correlations are shown.

highly sensitive parameters such as the seed ingrowth or intrinsic mortality of plants (Schmid, Huth, et al., 2021) could be used to find correlations with environmental variables at different sites (Rödig et al., 2017) or management intensity (Chang, Viovy, et al., 2013). Phenology of plants is not included in the model, but the date of flowering seemed to be important in an analysis of Michaud, Plantureux, Amiaud, et al. (2012), as mowing could substantially influence the production of seeds. Correlating seed ingrowth with the timing of management events or adding further processes could integrate this fact in the simulation model.

Overall, discrepancies (especially in cover) in our model results should not be overevaluated, as uncertainties exist in field measurements. For instance, slightly varied measuring methods were used at the different study sites, e.g., distances to the edge of the grassland plots (Knop et al., 2006), and grassland plot sizes differed. Using field experiments with consistent methodology over different sites (both with different environmental conditions and with regard to climate change) would be beneficial for more reliable model parameterization ((White, Carlyle, et al., 2012), e.g., coordinated field experiments like HerbDivNet (Fraser, Jentsch, et al., 2014), the Nutrient Network

(Borer, Harpole, et al., 2014) or the BIODEPTH experiment (Minns et al., 2001)). In our modeling analysis, we related simulated grassland attributes to the field measurements at the respective dates of each measurement to make our modeling results comparable to field studies. However, different ways of aggregation could play a role in the overall results and trends identified (e.g., whether vegetation attributes are considered at dates one day prior to mowing or mean vegetation attributes over the entire growing season).

In this basic modeling approach, the static traits of the PFTs prevent plants from adapting their morphology and physiology to environmental changes (Völler et al., 2017, Weisser et al., 2017). Frequent mowing events can induce, e.g., a changed height-width ratio or plants with deeper roots might occur after more frequent drought events caused by climate change (Walter et al., 2012, Zeiter et al., 2016, Liu, Mi, et al., 2018, Kirschbaum et al., 2021). This trait plasticity, which could also be interpreted as a changed species composition within a PFT, could be reached by the use of trait distributions. Such plant trait distributions were already used in Dynamic Global Vegetation Models (Pavlick et al., 2013, Scheiter et al., 2013, Sakschewski et al., 2016), mostly with focus on trees in forests.

Moreover, trait distributions could also be used to express species richness within our four modeled PFTs. Grassland productivity has also been shown to be connected to species richness in multiple field studies (Mittelbach et al., 2001). The relation depends on different environmental parameters as investigated by the population-based simulation model DynaGram (Moulin, Perasso, and Gillet, 2018). In the model, species richness was expressed by up to 21 species in different simulation versions, whereby species could become extinct during the simulation time. In our modeling study, species richness is represented only by four PFTs that were always present in our scenario analysis only differing in their respective proportions.

4.5.2 *Impact of management and environment on productivity and abundances of plant functional types*

The conclusions received by our Germany-wide scenario analysis show similarities to existing field studies that investigated the impact of management and environmental factors. A study of Michaud, Plantureux, Amiaud, et al. (2012) revealed that management, weather and soil properties together affect plant functional composition of permanent grasslands in France. Management belonged to the most important factors determining productivity and the abundances of PFTs (based on the biomass proportion of herbs) in our model, whereby productivity monotonously increased with management intensity. This is in contrast to many field studies, that showed a peak of productivity for intermediate management, i.e., two mowing events per year (Weigelt, Weisser, et al., 2009, Bernhardt-Römermann et al., 2011, Boch et al., 2021). Besides management, precipitation was one of the environmental factors with high importance and leaded to higher productivity in intensively managed grassland, which was also observed in field experiments (Knapp and Smith, 2001, Bernhardt-Römermann et al., 2011, Byrne et al., 2017).

The impact of environmental factors on grassland attributes was also analyzed in comparable simulation studies using other process-based simulation models. In these modeling studies, soil water (besides nutrient availability) belonged to the major limiting environmental factors of productivity (Moulin, Perasso, and Gillet, 2018).

Comparing results of our study with those of a previous study (using the model GRASSMIND with the assumption of optimal water and nutrient supply), management intensity resulted in contradictory effects on the proportion of herbs (Schmid et al., under review) which highlights the major impact of soil dynamics on grassland attributes. The availability of other nutrients than nitrogen can limit grassland productivity (Fay et al., 2015). Further, soil biodiversity has shown to influence multiple ecosystem functions such as productivity and functional composition (Wagg et al., 2014) whereby their relation depends on climate and environmental conditions (Jing et al., 2015). More detailed soil processes and properties, e.g., belowground biodiversity, can also be included in the GRASSMIND model by coupling a more complex soil model in future studies (Sándor et al., 2017).

Due to warming induced by climate change, meta-analyses concluded that grassland productivity is expected to increase if soil water availability is not limiting (Dellar et al., 2018, Wang, Quesada, et al., 2019), similar to what we received with the GRASSMIND model in this and in a previous study (with the assumption of no water limitation) (Schmid et al., under review). The increasing productivity in the model GRASSMIND might be related to higher temperature and increased precipitation in the future scenarios. Also other mechanistic population-based models such as ORCHIDEE-GM predicted increased grassland productivity for Europe, mainly caused by rising CO2 (Chang, Ciais, Viovy, et al., 2017). The model LandscapeDNDC predicted strongly increased, only slightly increased or even decreased productivity depending on the management strategy (Petersen et al., 2021). In addition to fixed management dates, the models also considered dynamic management adopted to grassland productivity that can prospectively also be included in the GRASSMIND model.

Regarding the effect of climate change on the abundance of PFTs, our simulation results show agreements to field studies, namely an increase in the proportion of herbs and especially legumes (Soussana and Lüscher, 2007). These findings are again explained by an elevated atmospheric CO_2 concentration in field experiments, that is not accounted for in our model. However, management and seasonal climatic effects on plant communities can be stronger than effects of elevated CO_2 concentration (Lüscher et al., 2005). Also the simulation model CoSMo predicted a changed plant composition in grasslands caused by increasing temperatures (Confalonieri, 2014).

Many analyses concluded that the impact of climate change on productivity depends on grassland biodiversity (e.g., stability and resilience) (Hector, Hautier, et al., 2010). In field experiments, single species with specific functional traits might compensate the loss of unsuitable species to changed environmental conditions which leads to higher stability (Cardinale et al., 2007). The limited representation of biodiversity with four PFTs in our model approach might prevent this behavior in the simulations of this study. Again, the approach of trait distributions (which allow for plant adaptation to changed environmental conditions (Lavergne et al., 2010) and the expression of species richness within a plant functional type) could be used to receive the increasing stability with biodiversity in the model. However, the creation of a regional parameterization using this approach can be very challenging, as trade-offs between functional traits have to be determined. Moreover, biodiversity in terms of species richness was not the focus of our study and seemed to have a poor effect on productivity in managed grasslands (Assaf et al., 2011).

4.5.3 *Conclusion*

In conclusion, our study shows how process-based grassland models can be used to gain a general understanding of how environmental factors and anthropogenic interventions impact grassland dynamics. It presents a basic approach for creating a regional transferable parameterization which can be extended by a larger data base of field measurements and model adaptations. In perspective, such modeling results can be used to determine how management and environmental conditions should be chosen to mitigate the effects of climate change on productivity, functional composition and the abundances of plant functional types. This approach can further be used as a basis for the analysis of changes in biodiversity-productivity relationship along an environmental gradient to maintain biodiversity in grasslands (Wang, Quesada, et al., 2019).

4.6 DATA AVAILABILITY

Weather data at the field site of GCEF were provided by the UFZ: "Meteorological data of Bad Lauchstädt, Helmholtz Centre for Environmental Research - UFZ, Department of Soil System Science"

Weather data at the field sites of the Biodiversity Exploratories and at the locations of the scenario analysis and the different climate change scenarios were received from the German national meteorological service (Deutscher Wetterdienst, DWD) (national climate database of the Climate Data Center (CDC): `https://opendata.dwd.de/climate_environment/`).

Vegetation and soil measurements at the sites of the Biodiversity Exploratories were received from:

- Prati, Daniel; Stephanie Socher; Steffen Boch; Jörg Müller; Markus Fischer (2017): Vegetation Records for Grassland EPs in 2008, Header Data without Species Identities. Version 2. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/5400`
- Prati, Daniel; Stephanie Socher; Steffen Boch; Joerg Mueller; Markus Fischer (2017): Vegetation Records for Grassland EPs in 2009, Header Data without Species Identities. Version 2. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/6340`
- Schmitt, Barbara; Daniel Prati; Markus Fischer; Stefan Blaser (2017): Vegetation Records for Grassland EPs in 2010, Header Data without Species Identities. Version 2. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/13486`
- Schmitt, Barbara; Daniel Prati; Markus Fischer (2017): Measurement of biomass (2010, all grassland EPs). Version 2. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/12706`
- Schmitt, Barbara; Daniel Prati; Markus Fischer (2018): Vegetation Records for Grassland EPs in 2011, Header Data without Species Identities. Version 2. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/14326`

- Schmitt, Barbara; Daniel Prati; Markus Fischer; Judith Minker (2018): Measurement of biomass (2011, all grassland EPs). Version 3. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/14346`
- Schmitt, Barbara; Markus Fischer (2018): Vegetation Records for Grassland EPs in 2012, Header Data without Species Identities. Version 2. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/15588`
- Schmitt, Barbara; Daniel Prati; Markus Fischer (2018): Vegetation Records for Grassland EPs in 2013, Header Data without Species Identities. Version 4. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/16826`
- Prati, Daniel; Markus Fischer; Judith Minker; Barbara Schmitt (2018): Measurement of biomass (2013, all grassland EPs). Version 2. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/16786`
- Schöning, Ingo; Emily Solly; Theresa Klötzing; Susan Trumbore; Marion Schrumpf (2018): MinSoil 2011 - Soil Bulk Density and Carbon and Nitrogen stocks. Version 4. Biodiversity Exploratories Information System. Dataset. `https://www.bexis.uni-jena.de/ddm/data/Showdata/17086`

4.7 ACKNOWLEDGMENTS

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5

NETWORK SCIENCE APPLIED TO FOREST MEGAPLOTS: TROPICAL TREE SPECIES COEXIST IN SMALL-WORLD NETWORKS

5.1 ABSTRACT

Network analysis is an important tool to analyze the structure of complex systems such as tropical forests. Here, we infer spatial proximity networks in tropical forests by using network science. First, we focus on tree neighborhoods to derive spatial tree networks from forest inventory data. In a second step, we construct species networks to describe the potential for interactions between species. We find remarkably similar tree and species networks among tropical forests in Panama, Sri Lanka and Taiwan. Across these sites only 32 to 51 % of all possible connections between species pairs were realized in the species networks. The species networks show the common small-world property and constant node degree distributions not yet described and explained by network science. Our application of network analysis to forest ecology provides a new approach in biodiversity research to quantify spatial neighborhood structures for better understanding interactions between tree species. Our analyses show that details of tree positions and sizes have no important influence on the detected network structures. This suggests existence of simple principles underlying the complex interactions in tropical forests.

5.2 INTRODUCTION

Tropical forests are ecosystems of global relevance. Besides their important role in the global carbon cycle (Le Quéré et al., 2016, Bonan, 2008), they are known for their high species richness (Wright, 2002). Several hundreds of tree species, often with similar resource requirements, are able to coexist at a local scale over centuries (John et al., 2007, Uriarte, Condit, et al., 2004). To better understand the mechanisms that allow for coexistence of tree species in tropical forests, a closer examination of tree interactions is essential (Levine et al., 2017) as the species interaction structure is closely linked to the dynamics and structure of the forest community. Various approaches – ranging from theoretical (Chesson, 2000a, Chesson, 2000b) over statistical (Clark, Dietze, et al., 2007, Uriarte, Swenson, et al., 2010, Volkov et al., 2009) and pattern-based (Wiegand, Huth, et al., 2012, Wang, Wiegand, Hao, et al., 2010, Wang, Wiegand, Kraft, et al., 2016) to mechanistic modeling (Tilman, 1994, Hubbell, 2001, Lotka, 1925, Volterra, 1926) – have been used to describe interactions between individual trees and species in ecosystems. Trees compete for light, space or nutrients within their local neighborhoods (Lorimer and Krug, 1983, Berger and Hildenbrandt, 2000, Uriarte, Canham, et al., 2004, Bella, 1971) and thus tend to interact primarily with nearby neighbors. Thus, the spatial proximity network of trees contains key information on the potential of trees to interact.

Long-term monitoring plots (e.g., of the CTFS–ForestGEO network (Hubbell, Condit, et al., 2005, Condit, 1998, Hubbell, Foster, et al., 1999, Anderson-Teixeira et al., 2015)) facilitate the in-depth analysis of the interaction structure in tropical forests. Besides tree species and stem diameter, also the position of trees within the forest plot is recorded, which allows to study individual trees in their local neighborhoods. We follow here the long tradition of distance-dependent analyses of species interactions in forests mediated by neighborhood competition for nutrients, space or light (Lorimer and Krug, 1983, Berger and Hildenbrandt, 2000, Uriarte, Canham, et al., 2004, Bella, 1971). A potentially powerful and natural approach to analyze proximity and potential interactions between neighboring trees in such data sets is network analysis that has already been applied in numerous disciplines such as computer science (Albert et al., 1999), sociology and psychology (Cancho and Solé, 2001, Newman, 2001, Liljeros et al., 2001), neurosciences (Eguíluz et al., 2005) and ecology (Proulx et al., 2005, Montoya, Pimm, et al., 2006, Bansal et al., 2007). Fuller et al. (2008) conducted network analyses for small plots in a tropical forest to assess the impact of tree size on the species composition of its neighborhood in the understory. Here, we apply network analysis for the first time to CTFS–ForestGEO mega plots (25-50ha), using all trees with diameter at breast height (dbh) larger than 10 cm for the analysis of the spatial proximity networks of trees and tree species to assess the potential for species interactions.

In network analysis, systems are characterized by nodes (here, trees or species) and edges (which represent connections between nodes). Thus, for a tropical forest we can construct a spatial tree network by analyzing the overlapping of the 'interaction zone' of individual trees, given as a multiple of their crown size derived from allometric relationships. Symmetric neighborhood interactions (e.g., competition for space or nutrients) result in undirected networks where an interaction occurs if the interaction zones of two trees overlap. In contrast, suppression of trees due to asymmetric competition (e.g., competition for light) leads to directed networks where an edge links the larger 'overtopping' tree with the smaller 'overtopped' one. However, our focus here is on the non-spatial species networks that are constructed on top of the marked tree networks (with the mark "species") by combining trees (nodes) of the same species. With this approach a species pair is connected if the interaction zones of at least one pair (or a larger number of pairs) of trees overlap. For example, while point pattern approaches (Wiegand, Huth, et al., 2012, Wang, Wiegand, Hao, et al., 2010, Wang, Wiegand, Kraft, et al., 2016) to quantify species interactions rely on mean neighborhood densities, here we focus on proximity of individuals which is the precondition for interactions to occur. The tree and species networks should capture essential features of the interaction structure in tropical forests, given that competition for space and light are main driving forces of forest structure and dynamics (Pretzsch, 2009, Shugart, 1984, Taubert, Jahn, et al., 2015, Farrior et al., 2016).

Of special biological interest is the node degree distribution $P_s(k)$ of the species network that tells us in detail how many connections (k) the different species maintain with other species. However, it is difficult to derive a priori biological hypotheses on the shape of $P_s(k)$ because the species network emerges from the marked spatial tree network in possibly complex ways through the interacting effects of the distribution of species abundances, tree sizes, and the small-scale placement of trees. Frequently encountered network structures include scale-free networks that show a power law node degree distribution (Barabási, 2016). Such networks show typically few nodes (i.e., species) with many connections to other species, many nodes with few connections and maintain its structural attributes independently of network size. Another property of numerous real-world networks is the 'small-world' attribute, which means that there is always a short connection between two randomly chosen nodes (i.e. species), although most nodes are not connected to each other (Watts and Strogatz, 1998).

By applying network analysis to trees in tropical forests, fundamental questions can be raised: 1. Which type of network structures emerge in tropical forests? 2. Which attributes of the forest drive the observed network properties (species abundance, species identity, tree size, and spatial location)? To answer these questions, we translated forest inventory data into proximity networks of trees and species from three large tropical forest sites in Panama, Sri Lanka and Taiwan. The results will help us to better understand the factors that govern the interaction structure of tropical forests and thereby its assembly and dynamics.

5.3 RESULTS

For each forest we constructed networks of trees (with individual trees as nodes, Fig. 5.1a-c) and species (with tree species as nodes, see Methods and Fig. D.1 for details). In the following we present mostly results of undirected networks (for results of the directed networks see D.2 Supplementary Results). Tree networks were about factor 50 to 250 larger than their corresponding species network (Table 5.1, Fig. 5.1d-e). The main component (largest connected part) of the tree network at the 50-ha plot of Barro Colorado Island (BCI) in Panama included 20730 out of 20735 trees (nodes) which means that almost all trees of the forest were connected (in the following the term 'network' refers to the main component). Similarly, all nodes of the species network build one component.

5.3.1 *Basic characteristics of the tree networks*

Tree networks represent spatial (or geometric) networks which are well known in the literature (Dall and Christensen, 2002, Barthélemy, 2011, Gilbert, 1961). However, in contrast to two-dimensional random geometric networks, where all circles have equal radii and random positions (Dall and Christensen, 2002), our tree networks consider different disk sizes (interaction zones) depending on tree crown sizes. A tree individual at the BCI plot was connected on average with approximately $\langle k \rangle = 9.6$ other trees (i.e. the average node degree $\langle k \rangle$; Table 5.1). Hence, network density D was low ($D \approx 0.001$ is the observed number of connections divided by the maximal possible number of connections). Almost two thirds of all trees that were connected with a specific tree were also connected with each other ($C = 0.631$ is the clustering coefficient describing the local connectivity, which is close to the value of $C = 0.587$ for random geometric networks (Barthélemy, 2011)). The shortest path between two randomly selected trees passed on average 22.6 other trees (average path length L) and no pair of trees required more than 56 other trees to pass (network diameter d) (Table D.1). Most network characteristics (i.e. D, C, L and d) were similar between all three tropical sites (Tables 5.1, Table D.1). However, tree networks at Sinharaja (Sri Lanka) and Fushan (Taiwan) showed almost the double number of nodes compared to BCI (i.e. they hosted more trees per 25 ha; Table 5.1). As the mean radius of the interactions zones was similar among all three forests (Fig. D.2), the higher tree density at Fushan and Sinharaja led also to higher average node degrees $\langle k \rangle$. Note that the tree size and the species abundance distributions of the three forests were different (Fig. D.2).

5.3.2 *Node degree distribution of the tree networks*

We found similar patterns of the node degree distribution $P_{\mathrm{t}}(k)$ in the tree networks regardless of the tropical forest site considered. They can be described well by Gamma distributions with a pronounced peak at low node degrees of $k = 7$ (BCI) and $k = 14$ (Sinharaja and Fushan), followed by a decaying tail (Fig. 5.2a). By assigning either shade-tolerance or light-demanding attributes to each tree individual (node in the

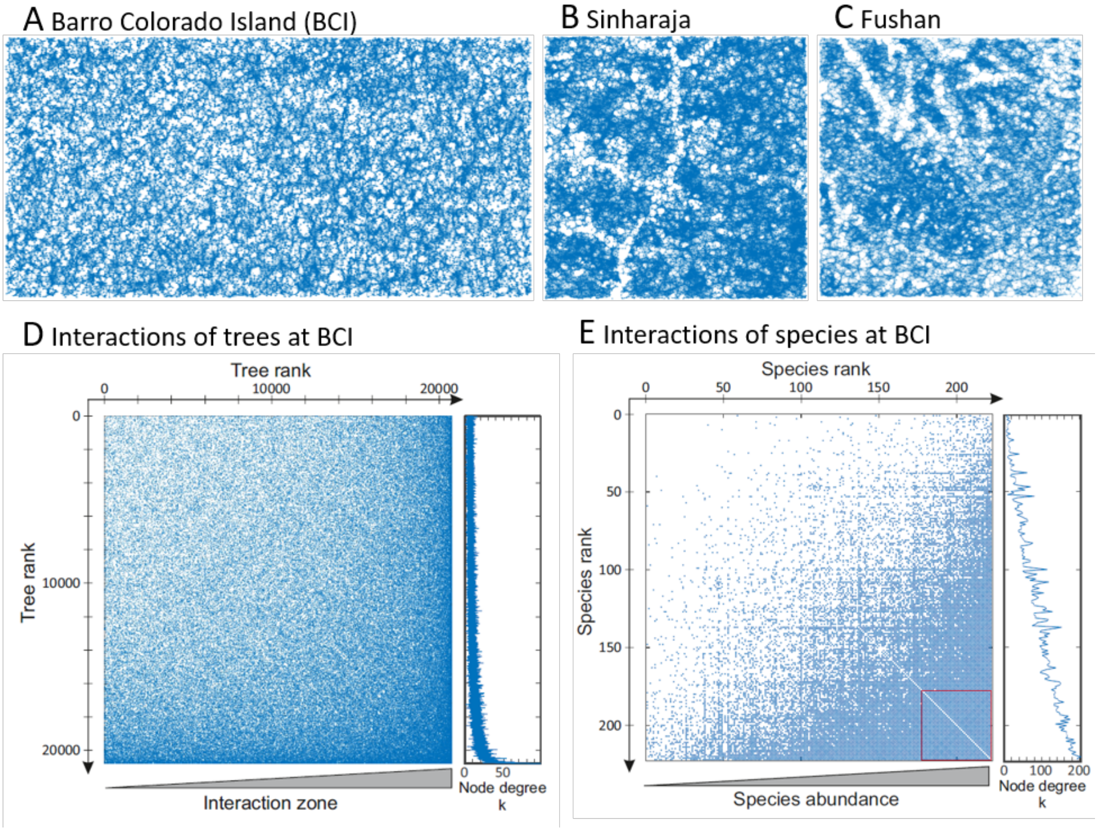

Figure 5.1: Visualization of the spatial tree networks for the tropical forest plots of (A) BCI in Panama, (B) Sinharaja in Sri Lanka and c Fushan in Taiwan. The positions of the visualized nodes correspond to the spatial positions of the trees. Connections in the networks are represented by adjacency matrices: in (D) for the tree network and in (E) for the species network (50ha plot). Rows and columns show existing nodes. Nodes are ordered in the tree network by their interaction zone (tree rank shows low values for the tree with the smallest zone to high rank values for the tree with the tallest zone). In the species network nodes are ordered by their abundance (observed number of trees of a species; species rank shows low values for the species with lowest abundance to high values for the species with highest abundance). A blue dot reflects an existing connection (edge) between a pair of trees or species (the specific node in the row and the node in the column). The small panels along the y-axis show the node degrees of d individual trees and (E) species. The adjacency matrices of symmetric connections are symmetric. The adjacency matrix of the tree network reveals 0.5 % existing tree connections, while the adjacency matrix of the species network shows that 38 % species connections of all possible connections (edges) occur at BCI. In e the red rectangle highlights that the 50 most abundant species all interact with each other.

tree network; classification based on (Knapp, Fischer, et al., 2018)), we found that the proportion of light-demanding trees increased with increasing node degree (Fig. 5.2c).

The node degree distributions $P_t(k)$ showed similarities to that known from random geometric networks (with a constant distance threshold between two nodes (Dall and Christensen, 2002)). However, the distributions of the three forests were somewhat more fat-tailed (Figs. D.1, D.3), probably due to large trees with many connections. Indeed, larger trees (with larger interaction zones) had a substantially higher node degree and interacted mainly with individual trees having high node degrees as well (Fig. 5.1d, Fig. D.4).

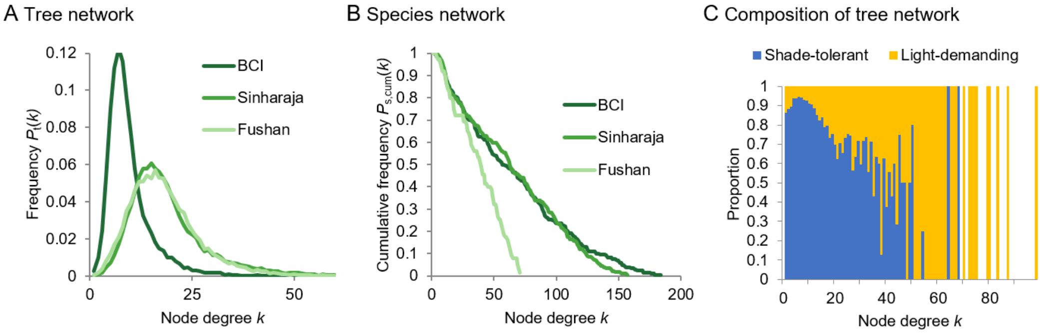

Figure 5.2: Node degree distributions of the networks and classification of node degrees. (A) The node degree distribution of the tree networks $P_t(k)$ with $\langle k \rangle = 9.6$, 19.2, 18.3 and $k_{max} = 83$, 136, 88 for BCI (left 25-ha subplot), Sinharaja and Fushan, respectively. (B) The node degree distribution of the species networks $P_{s,cum}(k)$ (cumulative distribution) with $\langle k \rangle = 65$, 65, 37 for BCI (left 25-ha subplot), Sinharaja and Fushan, respectively. (C) Node degrees of the tree network are classified according to shade-tolerant (blue) and light-demanding (yellow) trees (forest site at BCI, entire 50-ha plot).

5.3.3 *Node degree distribution of the species networks*

Only 32 to 51 % of all species pairs were connected at the three tropical sites (i.e. network density D; Table 5.1) when assuming conservatively that a species connection existed if at least one pair of trees was connected. These figures dropped substantially when requiring up to ten connected pairs for defining a species connection, but stabilized afterwards at roughly 15 % for BCI (Table D.2). The forest with the lowest number of species (Fushan) showed the highest amount of connections (51 %), but still half of all possible species connections were missing. Most other characteristics of the species networks were remarkably similar among the three tropical forests (Table 5.1, Table D.1).

The node degree distributions $P_s(k)$ of the species networks showed for all three forests the same shape: the $P_s(k)$'s were evenly distributed, as indicated by an almost linear decline of their respective cumulative frequencies $P_{s,cum}(k)$ (Fig. 5.2b). This result is surprising because, to the best of our knowledge, constant node degree distributions have not yet been described and explained by network science (see e.g., Albert et al., 1999, Cancho and Solé, 2001, Newman, 2001, Liljeros et al., 2001, Eguíluz et al., 2005, Proulx et al., 2005, Montoya, Pimm, et al., 2006, Bansal et al., 2007, Amaral et al., 2000). There is also no a priori reason that the node degree distributions should be structurally similar among forests. The forests show very different species richness, species abundance distributions and ecological characteristics that were crucial for the construction of the networks (see D.1 Supplementary Methods, Fig. D.2).

Figure 5.1e gives insight into the connection structure of species at BCI based upon their abundance (adjacency matrices). As expected, more abundant species had a substantially higher node degree (see also Fig. D.5) and connected mainly to species

Table 5.1: Network characteristics of tree and species networks at three tropical forest sites. To obtain comparable network characteristics among plots we report here results from the left 25-ha subplot of BCI. The characteristics of the other 25-ha subplot and entire 50-ha plot of BCI are similar (see Table D.1, Fig. D.14). For the results of directed networks see Table D.10.

					Local connectivity		Global connectivity		
	Forest site	N	$\langle k \rangle$	D	C	C_{ER}	L	L_{ER}	Type
Tree network	BCI	10161	9.6	0.00095	0.631		22.6		
	Sinharaja	17015	19.2	0.00113	0.635		21.3		
	Fushan	17647	18.3	0.00104	0.630		22.6		
Species network	BCI	208	65.4	0.316	0.772	0.314	1.69	1.68	SW
	Sinharaja	177	64.7	0.368	0.810	0.367	1.64	1.63	SW
	Fushan	75	37.4	0.506	0.856	0.513	1.50	1.49	SW

N: number of nodes, $\langle k \rangle$: mean node degree, D: network density, C: clustering coefficient, L: average path length, SW: small-world property. *Clustering coefficient and average path length of random graphs following the Erdős–Rényi (ER) model of the same size (C_{ER} and L_{ER}) for testing the small-world property. See (Watts and Strogatz, 1998) and 5.5 Methods for definition of the small-world property.

having high node degrees as well. Focusing on the 50 most abundant species reveals that all of them connected with each other (Fig. 5.1e). In contrast, the adjacency matrix of the directed species network (Fig. D.4) shows that some species exist (a few of them even with low abundance) which compete asymmetrically with almost all other species (herein referred to as 'overshadow').

5.3.4 *Small-world property*

Geometric networks such as the here presented tree networks are known a priori not to be small-world (Dall and Christensen, 2002, Watts, 2003). In contrast, the species networks of the three forest sites are small-world networks. In agreement with the definition of the small-world property, they have approximately the same average path length L and higher clustering coefficients C than random networks of the same size (Watts and Strogatz, 1998) (Table 5.1, see Methods). This result was robust against more restrictive criteria for occurrence of a connection between two species (e.g., at least eight instead of a single pair of trees must be connected; Table D.2). Thus, the small-world phenomenon can be observed in tropical forests between species, but not between trees.

Clearly, the species networks are not scale free as they show uniform node degree distributions. Neither a different plot size nor species-specific deviations of interaction zones influenced these conclusions (D.2 Supplementary Results). For the analysis of tree networks see D.2 Supplementary Results.

5.3.5 *Which factors drive network structures*

To determine the degree to which small-scale spatial neighborhood effects influence the observed network properties, we assembled four different types of null communities (Wiegand, Uriarte, et al., 2017, Wiegand, May, et al., 2017) that randomize certain elements of the observed data. Differences in network properties emerging in the null communities hint to an important role of the randomized elements in structuring the tree community. Our null communities include (i) relocating trees to random positions in the plot (Complete Spatial Randomness - CSR null community), (ii) randomly shuffling the species identity among trees (Random Labeling – RL null community), (iii) using a fixed tree size for all trees (Equal interaction Diameter – ED null community) and (iv) combining CSR and ED to obtain a random geometric network (RGN null community) (see Methods and Table D.3).

All null communities of the three forests showed species network characteristics that resembled their observed characteristics very closely, including the small-world property (Table 5.1, Table D.4), but only with moderate departures due to spatial effects (e.g., intraspecific aggregation and interspecific co-occurrence) present in the observed communities and not in the null communities (Table D.4, Fig.D.6). The randomized communities tended to be slightly more connected with larger mean ($\langle k \rangle$) and maximal ($k_{\max}$) node degrees, larger clustering coefficients C and smaller average path lengths L. Interestingly, even the null community based on a random geometric network (RGN) showed only minor deviations from the observed networks, with similarities to the RL communities.

The null communities also approximated the characteristics of the tree networks (Table D.5), but not as closely as the characteristics of the species networks. Especially the ED and RGN null communities (with constant tree size) showed larger differences to the observed node degree distributions that were more fat-tailed (Fig. D.6).

5.4 DISCUSSION

In this study, we applied network science to tropical forests by developing a new methodology that translates the size and spatial position of trees into a tree network that measures potential neighborhood interactions between tree individuals by its proximity, and aggregates the tree network into a species network. Our network approach quantifies the complex spatial neighborhood structures occurring in forest communities for better understanding the determinants of interactions among tree individuals and among tree species.

Our first question focused on the types of network structures that develop in tropical forests. We found remarkably similar network structures among forests. One tree was on average connected with ten to twenty other trees. A few tall trees were connected with even more than a hundred other trees. The node degree distributions of all three tree networks followed Gamma distributions, similar to the network of contacts between neighboring linguistic groups (Capitán et al., 2015). The species networks showed the small-world property with evenly distributed node degree distributions across the three different forest sites; a pattern not described before in network science. The similar structures of the tree and species networks of the analyzed forests (Fig. 5.2a-b) and the temporal constancy of network characteristics (over up to 30 years of observations, Fig. D.7) let us hypothesize that the type of networks found here are typical for tropical forests in general.

Only 32 to 51 % of all potential pairwise connections between tree species were realized in our most conservative estimates (Table D.2), which means that not all tree species have the opportunity to interact with each other in the forests simply because they do not meet each other. This result is in agreement with previous studies assessing species interaction strength in tropical forests based on the principle of maximum entropy, stochastic dynamics and spatial point pattern analysis (e.g., Volkov et al., 2009, Wiegand, Huth, et al., 2012, Lieberman and Lieberman, 2007).

Interestingly, the Fushan forest with highest tree density and the lowest number of species showed the highest proportion of species pair connections. We can explain this finding on the basis of the results of our null model analyses, which showed that the species abundance distribution drives most characteristics of the species network (Table D.4). Fushan had the lowest proportion of rare species (Fig. D.2), species with higher abundance tended to have a higher node degree k (Fig. 5.1e, Fig. D.5), and therefore a higher proportion of the species pairs were connected at Fushan. Nevertheless, 50 species had less than 100 individuals at Fushan, which explains that still half of the species pairs are not connected.

The lower number of species and the lower proportion of rare species at Fushan have predictable influences on the other network properties of the species networks. First, it causes a higher network density D at Fushan, compared to that of BCI and Sinharaja. Additionally, the number N of species influences the mean node degree $\langle k \rangle$ (see equation (5.14) in 5.5 Methods) which is lower at Fushan compared with the two other forests. The maximal node degree $k_{\max}$ is more strongly driven by the number of species since the most connected species is connected to almost all other species. Still, the local clustering coefficient C shows relatively little variation among forests, with a tendency to be higher in forests with lower number of species.

Additionally, species that interact only with few others are as frequent as species that interact with nearly all other species. The observed constant node degree distribution of the species networks is a very particular distribution that differs from the power laws and peaked distributions usually observed in network science46. We suspect that this non-standard network type together with the small-world architecture reflect a combination of constraints in forests and a biologically optimal way of species assembly. Potential constraints include tree packing38 due to tree architecture together with competition for space and mechanism such as stochastic population dynamics that can generate the typical species abundance distributions of tropical forests with many rare and a few abundant species (McGill et al., 2007). The constant node degree distribution is an intriguing pattern, and the consequences of such particular interaction structures for community stability need to be explored. Clearly, the number and type of interactions strongly influences community dynamics and stability, and fewer and weaker interactions can imply more stability (May, 1973, May, 2001, May, 1971, Mccann, 2000). Although previous methods required to focus on abundant tree species (Volkov et al., 2009) or on the understory (Fuller et al., 2008), we point here to missing interactions that might be highly relevant for understanding species coexistence.

Additional information can be obtained by the distribution of out-degrees ('shadow indices') and in-degrees ('overshadow indices') (Figs. D.8, D.9, see Methods for details). We found that some species, not necessarily those with the highest abundance, overshadowed many other species. Pioneer species are less likely to be shaded compared to shade-tolerant tree species, but tend to shade other trees (Fig. D.9). One further feature, especially of the BCI forest, is that the network of light demanding trees fragmented into some 500 isolated components, probably re-colonized canopy gaps (Hubbell, Foster, et al., 1999), whereas the network of shade-tolerant trees consisted basically of one large component (Fig. **??**).

Secondly, we investigated which properties of the forest drive the observed network properties. Shuffling species identity among trees, assigning random positions to trees, or setting a constant tree size for all trees resulted in the persistence of the basic characteristics of the species networks, including the small-world property. For example, shuffling the species identities among trees removes species aggregation and the species-specific size distribution and allows each species in principle to have large trees with many connections to other trees. Randomizing tree positions removes effects of species aggregation and small-scale species interactions. Nevertheless, almost all null communities resulted only in a slightly higher network density and average node degree of the species network (Table D.4). These results suggest that species abundances (together with mean tree size) are the main biological ingredients that determine the overall structure of the species proximity networks (see also Fig. 5.1e, Figs. D.5, D.11), whereas spatial small-scale patterns of tree placement and tree sizes had only a minor influence on the structure of the species networks (Table D.4, Fig. D.6). However, small-scale patterns of tree placement and tree sizes together with the niche overlap between species are important drivers of the performance (e.g., survival, growth) of individual trees (e.g., Uriarte, Swenson, et al., 2010, Wiegand, Uriarte, et al., 2017, Fortunel et al., 2016). It is interesting that these effects do not scale up into patterns of the species networks. Thus, it should be possible in principle to derive fundamental aspects of the proximity networks of tropical forests without spatially explicit information of tree positions, only based on species abundance and tree size distributions. This is good news for ecological theory because it tells us that fundamental aspects of forest structure do not depend too much on the idiosyncrasies of the particular local spatial structure.

In this study, we laid an essential foundation for the connection of forest ecology and network science. Our study contributes to the question of determining the interaction structure in ecosystems (e.g., Volkov et al., 2009, Wiegand, Huth, et al., 2012, Wang, Wiegand, Hao, et al., 2010) by taking advantage of powerful methods developed in network science. Tree network analysis thereby allows an in-depth mapping of proximity of trees and tree species. The strong similarities in network structures among different tropical forests is an intriguing pattern that calls for explanation and suggests existence of simple principles structuring fundamental aspects of tropical forests. Perspective applications of our approach further allows to support progress in tropical forest ecology, for example by understanding spread patterns of tree diseases (e.g., Lambert et al., 2018) or the general impact of forest disturbances (e.g., logging, forest fires, or droughts). Linking network science and ecology has a large potential to understand species coexistence and forest ecosystems' resilience in a globally changing world.

5.5 METHODS

5.5.1 *Study sites and tree geometry*

We included three field inventories of old-growth tropical forests located on Barro Colorado Island (BCI, Panama), Sinharaja (Sri Lanka) and Fushan (Taiwan) that have plot sizes of 50 ha, 25 ha and 25 ha, respectively (Losos and Leigh, 2004). To enable a better comparison of the larger BCI plot with the other sites, we considered in some analyses only the left 25-ha subplot of the BCI plot.

All three plots belong to the CTFS-ForestGEO network (Anderson-Teixeira et al., 2015) of long-term forest dynamics research sites where all trees are measured in diameter at breast height (dbh) are identified to species, mapped, and recensused every five years according to a standardized protocol detailed in Condit (1998). The books Su et al. (2007) and Gunatilleke et al. (2004) provide further specific detail about the inventories at Fushan and Sinharaja, respectively. In the main analysis, we used the data of the 2010 census of BCI (Condit et al., 2019), the 2001 census of Sinharaja and the 2013/2014 census of Fushan. To check the generality of our results, we analyzed the node degree distribution of additional censuses of these sites (Fig. D.7). To derive tree height $h(dbh)$ in m, we used the allometric relationship (dbh in cm):

$$h(dbh) = h_1 \cdot dbh^{h_2} \tag{5.11}$$

The parameters h_1 and h_2 in equation (5.11) were derived from independent datasets (Bohlman and O'Brien, 2006, Kohyama et al., 2003, see D.1 Supplementary Methods for details). We used for our main analyses the same parameters h_1 and h_2 for all individual trees, independent on species identity. For building the tree and species network, we examined only trees with stem diameters $\geq$ 10 cm and main stems (in case of multiple stems per tree).

5.5.2 *The network analysis*

For building the networks, we considered trees as planar disks located at a certain height in a three-dimensional space. The positions of the disks are given by the x- and y-coordinates of the trees, and the z-coordinate is equal to the height of the tree (Fig. D.1, equation (5.11)). The dimension (or diameter) of a disk d_{int} in m, which represents the interaction zone of a tree, is related to the measured stem diameter dbh in cm by the allometric relationship (see Figs. D.1, D.8, Table D.6 for details):

$$d_{\text{int}}(dbh) = f \cdot i_1 \cdot dbh^{i_2} \tag{5.12}$$

with parameters i_1 and i_2 derived from tree crown measurements in the field (Bohlman and O'Brien, 2006, Kohyama et al., 2003) and f being a proportionality factor (see D.1 Supplementary Methods, Fig. D.12, Table D.7 for a sensitivity analysis of the factor f). Again, we used the same parameters f, i_1 and i_2 for all individual trees.

We tested the sensitivity of the constructed networks to species-specific variations of the parameters in the allometric relationships for tree crowns and tree heights (equations (5.11) and (5.12)). Details and results can be found in D.1 Supplementary Methods, Fig. D.13, and Tables D.8 and D.9.

5.5.3 *Constructing tree networks (TN)*

For the construction of the tree network (TN), we used all trees which are present within the forest plot as nodes. A network can be either undirected or directed. To construct an undirected tree network, we neglected tree height (height of the disks) and if the interaction zones of two trees (disks) overlap, the corresponding trees were linked through an edge (connection).

In a directed tree network, tree heights are decisive for the direction of the connections (edges). Therefore, we analyzed the forest from a top view and considered shading of each tree (disk) by the interaction zone of larger trees (overtopping disks). Larger trees (higher disks) always have larger interaction zones due to larger tree crowns (granted by the assumed tree allometries, equation (5.11) and (5.12)). Hence, if the interaction zones of two trees (disks) overlap, a directed edge links the larger tree with the smaller one (Fig. D.1). If two trees with the same size (or height) overlap, a random direction of the connecting edge is chosen.

The node degree distribution $P_{\mathrm{t}}(k)$ of the tree network quantifies the proportion of nodes with a given node degree k (number of connected edges to the node). For a directed tree network, we obtain two different node degrees for each tree (node): the in-degree and the out-degree. As a result, two separate node degree distributions can be calculated. The out-degree of one node reflects the number of trees which are overlapped (or shaded) by the respective tree. The in-degree of one node reflects the number of trees who are overlapping (or shading) the respective tree. The in- and out-degrees can be interpreted as competition indices. We refer to the out-degree as 'shadow index' and to the in-degree as 'overshadow index' (Fig. D.8).

The constructed tree networks are geometric networks as their connections arise from geometric rules. However, as we assume different interaction radii (depending on the tree size), the analyzed tree networks differ from classical geometric networks (Barthélemy, 2011).

5.5.4 *Constructing species networks (SN)*

In the tree species network nodes represent all tree species that occur at the tropical forest plot. The species network is obtained from the marked tree network (where the mark represents a species identity) by condensing all nodes of trees which belong to the same species into one species node. That means, at least one overlap between two trees of different species identity results in an edge (connection) in the species network. Again, undirected and directed species networks can be built (Fig. D.1). If some tree of species A overlaps with trees of species B and vice versa, the emerging species network includes two directed connection (edges) between species A and B (one edge from A to B and the other edge from B to A). Note that the species networks do not belong to spatial networks as their construction does not depend on space anymore. More precisely, species networks (SN) emerge from marked spatial tree networks (TN) by aggregation methods using the additional information of the marks.

5.5.5 *Network characteristics*

We used several measures to describe the properties of the analyzed networks. The size of the network is in general expressed by the number of nodes N and the number of edges E. The density D of the network is built upon those values by dividing the number of existing edges by the maximum possible number of edges in the network:

$$D = \frac{2}{N(N-1)}E \tag{5.13}$$

whereby factor 2 arises for undirected networks, but is dropped for directed networks. The network density is the species network is of special interest because it gives the proportion of species that are connected.

The average node degree $\langle k \rangle$ can be computed by:

$$\langle k \rangle = \frac{1}{N} \sum_{i=1}^{N} k_i = \frac{2E}{N} \tag{5.14}$$

where k_i is the number of edges of node i and factor 2 is dropped again for directed networks. The average node degree is the average number of trees a tree is connected with (tree network), or the average number of other species a species is connected with (species network).

The average path length L is a global property of the network and indicates the mean of the shortest path lengths d_{ij} between all pairs $i - j$ of nodes of the network65:

$$L = \frac{2}{N(N-1)} \sum_{i \geq j} d_{ij} \tag{5.15}$$

whereby factor 2 drops again for directed networks. The longest shortest path length $d = max(d_{ij})$ is defined as the diameter d of the network66. The average path length L is used to test for the small-world property of a network.

The clustering coefficient C is a local property of the network and computed according to Watts and Strogatz (Watts and Strogatz, 1998) as the average of the local clustering coefficients C_i of all nodes i as:

$$C = \frac{1}{N} \sum_{i=1}^{N} C_i \tag{5.16}$$

where C_i is estimated in analogy to the density D of the network as $C_i = (2e_i)/(k_i(k_i - 1))$ with k_i being the number of neighbors of node i, e_i the number of existing edges between the neighbors of node i, and $k_i(k_i\breve{\ }1)$ being the maximum possible edges between them. Factor 2 drops again for directed networks. For nodes with a node degree of $k_i = 1$, we defined their local clustering coefficient as $C_i = 0$. The clustering coefficient is of special interest for local topology of the tree network, because it gives information on the degree of connections among trees that are connected to a specific tree. For the influence of plot size on network characteristics see D.2 Supplementary Results.

5.5.6 *Testing for the small-world property of the species networks*

For testing the small-world property (Cancho and Solé, 2001, Watts and Strogatz, 1998, Montoya and Solé, 2002), we constructed random graphs that had the same number of nodes and edges as the observed species networks (Erdős and Rényi, 1959), and compared the clustering coefficient C and average path length L of the random graphs with those observed. The random graphs were constructed with the Erdős–Rényi (ER) model (Erdős and Rényi, 1959). A random graph has a node degree distribution that follows a Poisson distribution with expected value being the observed average node degree $\langle k \rangle$. Furthermore, it generally shows a small average path length L and a low clustering coefficient $C = \langle k \rangle / N$.

Small-word networks are networks with properties ranging between regular networks and random graphs (Watts and Strogatz, 1998). They follow two independent structural features, namely their clustering coefficients are higher than that of a corresponding random graph, while their average path lengths are similar.

In addition to the small-world property, networks can also be 'scale-free' if they show a power law node degree distribution. Here, we tested only tree networks for the scale-free property (see D.2 Supplementary Results for details) as the constant node degree distribution of the species networks clearly rejects this property.

5.5.7 *Construction and analysis of null communities*

We constructed four types of null communities by randomizing one or several of the following elements of the census data: (i) tree positions, (ii) species identities, (iii) tree size distribution (species-specific), but we maintained the observed species abundance distribution (see Table D.3 for details).

First, in the Complete Spatial Randomness (CSR) null community (Wiegand, Uriarte, et al., 2017), trees were assigned new positions within the forest plot (randomly and evenly distributed). This null model removed the observed species aggregation and co-occurrence patterns, while maintaining the observed identities and the species abundance and species-specific size distributions.

Second, in the Random Labeling (RL) null community, only the existing species identities were randomly redistributed among the trees while keeping the spatial positions of trees, the species abundances and the tree size distribution within the plot. This null model removed the observed species aggregation and co-occurrence patterns as well as the species-specific size distributions, while maintaining the observed species abundances and the overall size distribution.

Third, in the Equal interaction Diameter (ED) null community the observed variable tree sizes were replaced by the constant mean tree size. This null model removed only the observed species-specific size distributions, while maintaining all other properties of the data.

Finally, the Random Geometric Network (RGN) null community combines the CSR and ED null communities by replacing tree sizes by a mean value and by randomizing tree locations.

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6

SYNTHESIS AND OUTLOOK

6.1 MAIN RESULTS

Grasslands are valuable ecosystems as they provide numerous ecosystem services. Among others, grasslands support the security of the world's food supply and show potential to mitigate negative consequences of climate change. However, climate change, global land use change and increasing intensive anthropogenic interventions make grassland to one of the most endangered ecosystem types in the world and point to the urgent need for their protection. To effectively protect grasslands in the future, a fundamental understanding of grassland dynamics and its major drivers is of utmost importance. For this, the influence of external factors and their changes, such as management intensification or climate change, on grassland dynamics have to be assessed both quantitatively and in relation to intrinsic processes, and also at different organizational levels (entire ecosystem, grassland community, species populations and individual plants). In this context, various field experiments have been conducted worldwide for an impact analysis, for example with different management intensities, plant community composition and modified climate variables. Complementary, ecological models enable to extend the analysis towards long-term effects of changes as well as towards a deeper understanding of the underlying ecological processes. In this thesis, an individual-based process-oriented grassland model and network science were used to understand the community dynamics emerging from individual plant interactions in two representative ecosystem types (temperate grasslands and tropical forests) – in relation to plant traits, ecological processes, environmental and anthropogenic conditions and the small-scale spatial distributions of plants.

The following objectives were addressed in this thesis: 1) development of a local-scale and a regionally transferable parameterization of an individual-based simulation model (accounting for plant diversity) for managed grasslands; 2) exploration of how plant traits, ecological processes and environmental conditions affect vegetation attributes such as productivity and abundances of plant functional types; 3) understanding and projecting how anthropogenic management and climate change can alter ecological processes and vegetation attributes at the community level (e.g., productivity at short- and long-term scales); and 4) application of network science to tropical forests in order to assess the importance of the spatial distribution of plants in species-rich ecosystems. The following sections summarize and discuss key findings of each objective.

6.1.1 *Local-scale and regionally transferable model parameterizations*

In this thesis two parameterizations of the grassland model (GRASSMIND) were developed: i) a local-scale parameterization for a field biodiversity experiment located in Central Germany, whereby plant species diversity was represented by four plant functional types (PFTs) and optimal soil conditions were assumed (i.e., sufficient soil water and nutrient supply for plant growth) (Chapter 2), and ii) a generic regionally transferable parameterization of the four PFTs by accounting for six different grassland sites in Germany along a gradient of climatic, management and soil conditions (Chapter 4). The focus of the local-scale model parameterization was to accurately represent functional diversity in grasslands in the simulation model based on field experimental plots with varying levels of functional composition and richness. For calibration, a two-step approach was devised: first, all morphological plant traits of the four PFTs were determined separately based on field plots including plant species of one PFT only to cover interactions between plants of the same PFT, and second, one trait per PFT was updated were updated based on field plots with higher PFT richness to account for interactions between plants of different PFTs in grassland communities. Complementary, the generic regionally transferable parameterization was then focused to account for different environmental conditions and management regimes typical across Germany. Three of the six included grassland sites were used at the same time for model calibration of the plant trait parameters while the other field sites were used for validation.

For both concepts of the model parameterization, the calibration was done using optimization algorithms (Lehmann and Huth, 2015). The corresponding model simulations resulted in moderate to good agreements with the measured vegetation attributes, although aggregated objective functions were used for calibration (i.e., averages over time instead of the time series of measured vegetation attributes). However, deviations between measurements and simulations still existed in some vegetation attributes, especially regarding the generic regionally transferable parameterization. Simulations based on the local-scale parameterization showed a mean deviation of 8% from the measured vegetation attributes (mean over deviations for aboveground biomass, vegetation height, leaf area index and vegetation cover of the total community, at plots used for calibration). Simulations based on the generic regionally transferable parameterization deviated by around 29% from field measurements of the three grassland sites used for calibration. These differences in deviations between both concepts of model parameterization can be traced back to the number of considered factors influencing vegetation dynamics (i.e., local vs. regionally different climate, soil type and management regime) but also to the measurement protocols of the grassland sites. Field data varied between 1 to 15 measurements per year with differing measurement methods for the grassland sites included in the regionally transferable parameterization. In contrast, measured information used for the local-scale parameterization followed a consistent protocol aligned with the management regime (e.g., two measurements per year prior to mowing).

6.1.2 *Impact of plant traits, ecological processes and environmental conditions on vegetation attributes*

Both, the local-scale and regionally transferable parameterization were the basis for obtaining a deeper process understanding of the modeled grassland ecosystems and for investigating the impact of environmental change on grasslands. Therefore, a variety of methods were used ranging from global sensitivity analyses and a robustness analysis in Chapter 2 and a process analysis in Chapter 3 (each based on the local-scale parameterization), to an extended analysis on the importance of regionally differing environmental factors by applying a machine learning model in Chapter 4 (based on the regionally transferable parameterization). The analyses focused on exploring the impacts of plant traits, plant competition, ecosystem processes and environmental conditions on grassland productivity, functional composition and relative abundances of PFTs.

Regarding plant traits, our analysis revealed that no single plant trait parameter of the grassland model but rather multiple trait parameters (and their interactions) had a large influence on aboveground biomass. Some traits increased and strengthened the growth of plants (e.g., height-width ratio and specific leaf area), while other traits made plants stronger through advantages in demographic processes (e.g., seed ingrowth and germination rate of seeds) (Chapter 2). Plant traits included in this analysis were restricted to those traits related to aboveground plant processes (e.g., photosynthesis or plant mortality). Traits related to belowground processes (e.g., plant rooting depth for determining access to soil resources) were not considered as an optimal soil water and nutrient supply was assumed at the grassland site (local-scale parameterization).

Regarding plant competition and ecosystem processes, plant mortality had a stronger impact on vegetation attributes of grasslands compared to shading between plants (Chapters 2 and 3). Plant mortality was thereby induced by aboveground competition for space (crowding) and an intrinsic plant mortality rate in the model while shading between plants rather affected the photosynthesis and respiration of plants in the model. Belowground competition for soil water and nutrients were neglected in the analyses as adequate water and nutrient supply was assumed at the considered grassland site (local-scale parameterization).

Regarding environmental conditions, only a few of the considered factors had a large importance for the modeled vegetation attributes (based on the regionally transferable parameterization and including belowground soil and plant processes and related plant traits in the model, Chapter 4). Precipitation and saturated conductivity had both a high importance for grassland productivity, while irradiance and potential evapotranspiration were more important for the biomass proportion of herbs in grasslands. Air temperature had a rather low influence compared to other environmental factors and ecological processes (Chapters 3 and 4).

6.1.3 *Impact of management and climate change on ecological processes and vegetation attributes*

Scenarios reflecting different management intensities were used to assess the impact of anthropogenic management on different ecological processes and vegetation attributes of grasslands (Chapters 3 and 4). More intensive management (in terms of mowing and fertilization frequency as well as fertilizer amount) led to a higher productivity (especially in grasslands with high plant functional diversity). A detailed process analysis thereby revealed that rather a decreasing plant mortality by crowding was responsible for the higher biomass yields (instead of an increased net primary productivity). More frequently mown grasslands showed an increase of herbs when assuming optimal soil conditions and no belowground plant competition (based on the local-scale parameterization) (Chapter 3) and a decrease of herbs when integrating different soil properties, belowground plant competition and fertilization in management regimes (based on the regionally transferable parameterization) (Chapter 4). For the latter, correlations with environmental factors further decreased with management intensity.

Impacts of climate change were analyzed with the grassland model by simulating an increase in air temperature (Chapter 3) and based on different RCP scenarios (Chapter 4). Both impact analyses resulted in slight increases of grassland productivity and changes in the abundances of PFTs. The magnitude of climate change impacts was thereby dependent on plant functional diversity and management intensity. Based on the local-scale parameterization (assuming optimal soil conditions), more intensive management (i.e., higher mowing frequencies) led to smaller effects of warming on grassland productivity (Chapter 3). In turn, simulations of climate change impacts based on RCP scenarios using the regionally transferable parameterization (accounting also for soil dynamics) led to stronger effects of climate change on productivity for more intensive management (i.e., mowing and fertilization) (Chapter 4). In terms of abundances of PFTs, both impact analyses came to similar results, namely smaller changes in more intensively managed grasslands than in extensively managed grasslands.

Compared to management, climate change had only little effect on the analyzed vegetation attributes in grasslands. Among the environmental factors, climatic variables (e.g., precipitation and irradiance) showed higher importance for productivity and proportion of herbs in the grassland model than soil properties (e.g., saturated conductivity and silt content) (Chapter 4).

6.1.4 *Assessment of spatial proximities and community structures of plants in ecosystems*

In this thesis, also network science was applied to real-world ecosystems in order to assess spatial proximities and community structures of plants (Chapter 5). This was conducted on the example of tropical forests using data of three forest megaplots located on different continents. Measures of network science allowed to quantify potential neighborhood interactions between trees and tree species and to compare the spatial structure of tree and tree species positions among the three analyzed forest sites. Network structures and the analyzed corresponding network measures of the three sites were remarkably similar. A creation of different null communities (e.g., assigning new random tree positions) revealed that neither the tree positions nor the tree sizes had an influence on the detected network structures. The study revealed that network science has a large potential to better understand interactions between plants and plant species.

6.2 LIMITATIONS IN THE STUDIES AND PERSPECTIVES FOR FUTURE RESEARCH

The methods and results presented in this thesis show some limitations which point to potential future extensions of the research studies in various directions. The following sections discuss those limitations and provide perspectives for future research with respect to (i) model parameterization, (ii) model analyses and (iii) model extensions and applications.

6.2.1 *Model parameterization*

Directly measured plant traits and time-series measurements of several vegetation attributes were available from field studies and used for the parameterization of the grassland model GRASSMIND (Taubert, Hetzer, et al., 2020b). However, the parameterization of such an individual-based grassland model, which combines matter fluxes (e.g., carbon fluxes by photosynthesis and respiration) with plant diversity, was still challenging when compared to other model types (e.g., population-based models) or other ecosystems (e.g., forests). A large set of trait parameters describing characteristics of individual plants for each PFT had to be determined (in total 17 parameters per PFT for the local-scale parameterization excluding soil processes, and 27 parameters per PFT for the regionally transferable parameterization including soil processes). Such information at the individual plant level is more demanding and time-consuming to measure in dense grasslands compared to, for example, forest ecosystems (where single trees can be recorded (Condit et al., 2019) and is not required for models of reduced complexity (like population-based models, e.g., Siehoff et al., 2011).

Further, the resolution of available field measurements for model calibration and validation was rather scarce (in time and with respect to different organizational levels (e.g., community, population and individual plant level), site locations, plant diversity levels and management regimes). The additional aggregation of field measurements over time (e.g., aboveground biomass, leaf area index and vegetation height) in the objective function used for model calibration resulted in an even lower required accuracy when simulating the considered attributes, but still reproduced the temporal patterns of the measurements. Future calibrations, however, could benefit from higher temporal resolution of field observations, as uncertainties in single field measurements (e.g., measurement errors or day-specific external influences) can be reduced and the accuracy of model processes can be verified. Not only a higher temporal resolution, but also more detailed measurements at the individual plant level would be beneficial for model calibration (Taubert, Hetzer, et al., 2020b). For instance, besides community attributes and species-specific biomass and cover, also species-specific plant height or plant density could be sampled from the field (Marquard, Weigelt, Roscher, et al., 2009). However, more information could also pose a challenge for model calibration because not all vegetation attributes can be fitted equally well at the same time (see Chapter 3, (Taubert, Hetzer, et al., 2020b)) and overfitting could occur (Hawkins, 2004, Clark, Ann Turnbull, et al., 2020). To cover several grassland types and locations through a regional parameterization, observational data of networks such as the Nutrient Network (`www.nutnet.org`) or the Drought-Network (`www.drought-net.org`) with consistent measurement protocols across multiple grassland sites could be used for future model parameterizations. Moreover, field experiments excluding certain processes or environmental factors could be useful to parameterize grassland communities. For example, experiments measuring growth of individual plants without any competition can be used, as standalone plants can also be simulated in the individual-based model (Hetzer et al., 2021). Again, a larger data base with higher resolution of observations could be a greater challenge for robust model calibration.

Besides, other optimization methods than used in this thesis, like approximate Bayesian computation, could be tested for model calibration (Reichert and Omlin, 1997, Hartig et al., 2012). The optimization algorithms used (dynamically dimensioned search algorithm and adaptive simulated annealing) only provide a parameter set for which the objective function reaches a (local) minimum. Approximate Bayesian computation would also provide uncertainty areas of each parameter (Hartig et al., 2012).

Major discrepancies with measured field data could indicate that either processes are missing or processes already included should be adjusted in further model developments. For example, the abundances of PFTs in grasslands simulated in Chapter 3 showed an inadequate response to different management intensities (at the GCEF site with intensive and extensive management). However, according to the principle of parsimony (Reichert and Omlin, 1997, Coelho et al., 2019), a model should be kept as simple as possible. In this context, it may be possible to reduce model complexity elsewhere for other objectives. For example, future analyses could test whether a “mean-species” approach would be sufficient for simulating large-scale grasslands (thereby immensely reducing the number of model parameters). Such a parameterization might be sufficient to analyze productivity at different grassland sites, but information in terms of plant diversity would get lost. The approach of PFTs used in this thesis, in turn, incorporated this aspect; however, the adaptation of plant traits to changing environmental conditions is not yet possible in the GRASSMIND model with this approach. Future model development might account for specific traits within each PFT to be adjusted according to site-specific conditions or incorporates the concept of trait distributions. By this, the distribution of plant traits, rather than species of functional groups, is modeled, allowing adaptation of plant traits to a changing environment (e.g., due to more intensive management or climate change). However, for both knowledge on the respective response functions of specific traits to the environment and on trade-offs between plant traits is required (Mitchell and Bakker, 2016).

6.2.2 *Model analyses*

The analyses conducted in this thesis show a selection of possible methodologies applied to the individual-based process-oriented grassland model GRASSMIND and related to network science with the purposes to explore the sensitivity and importance of plant traits, plant and species interactions and ecological processes in vegetation ecosystems. The following section describes further potential analyses in an extended context.

The sensitivity and robustness analysis as well as the scenario analyses in Chapters 2 and 3 are based on the local-scale model parameterization that assumes optimal soil conditions (no limitations in soil water or nutrient availability). Soil resource dynamics and plant-soil interactions were excluded in this model parameterization because vegetation growth was not shown to be limited by soil resources in the measured data used for parameterization (local grassland site). This complexity reduction enabled to obtain a detailed understanding of the ecological processes acting aboveground in grasslands. Future studies revisiting the objectives of Chapter 2 and 3 may account for variable soil resource dynamics and supply, for example by applying the same methods (global sensitivity analysis, robustness analysis, process analysis) using the regionally transferable parameterization from Chapter 4. Knowledge already gained before, such as the sensitivity of plant trait parameters influencing aboveground grassland dynamics, can then be extended to soil-related plant parameters influencing plant-soil interactions (e.g., plant rooting depth or soil water demand). Other methods than the Morris method applied in this thesis might therefore be more informative, for example, the Sobol method, which allows to also quantitatively determine the influence of parameters in addition to the order of sensitivity and nonlinear effects (Saltelli, Tarantola, et al., 1999, Saltelli, Aleksankina, et al., 2019). Furthermore, the process analysis presented in Chapter 3 (with focus on plant shading or the influence of air temperature) could be extended to additional processes like limitations in soil water and nitrogen availability for plant growth and grassland productivity. Both methodologies applied to the regionally transferable parameterization and scenario analysis framework of Chapter 4 have the potential to provide more insights on the vulnerability of extensively and intensively managed grasslands under climate change.

The analyses presented in this thesis mainly focused on the productivity at the community-level and population-level (i.e., biomass proportions of different PFT populations). More in-depth analysis, for example, following the development of a single plant within a grassland community (surrounded by conspecific or heterospecific plants) could be compared to the growth of a standalone plant with no inter- or intraspecific competition to analyze interaction strengths and the role of different plant traits (Taubert, Hetzer, et al., 2020a), plant size structures (Hara, 1988, Schwinning and Weiner, 1998) as well as other plant-specific vegetation attributes such as plant ages (Lauenroth and Adler, 2008). Such simulations would allow for an investigation of the relative importance of competition for plant growth (e.g., root and shoot competition (Kiær et al., 2013)), identification of differences in plant traits that favor coexistence (Kraft et al., 2015), plant invasions (Vilà and Weiner, 2004) or plant survival (Lauenroth and Adler, 2008).

The analysis presented in Chapter 5, specifically applying network science to forest megaplots, can also be extended. Interaction strengths, for example, measured by the overlapping crown area of larger trees, could be used to represent weighted network edges between trees and tree species. Connections between tree species would then be represented not only by the number of adjacencies to trees of other species, but also by the strength of interaction, for example, in terms of shading or competition for space. In this way, interactions between trees and tree species can also be measured quantitatively and could provide insights on whether individual trees or tree species play a key role by suppressing the growth of many other trees or tree species standing nearby or not. Integrating network science into mechanistic individual-based models (e.g., the forest model FORMIND, (Fischer, Bohn, et al., 2016)) could further provide the opportunity to simulate and analyze dynamic network structures and to estimate interaction strengths by additional simulated measures (e.g., soil water competition between trees). Thereby, forest megaplots, which are censused over several decades, provide an extensive and informative basis for such a dynamic network model and analysis (Condit, 1998).

6.2.3 *Model extensions and applications*

Further development of the grassland model GRASSMIND opens up opportunities for model application in various directions of future research.

Firstly, phenology could be extended in the model, for example, by distinguishing between vegetative reproduction (via rhizomes or stolons) of plants and sexual reproduction of flowering plants (including the date of flowering) (Yang and Kim, 2016, Klinerová et al., 2018). The date of flowering is specifically decisive with regard to plant reproduction after mowing events (Michaud, Plantureux, Amiaud, et al., 2012).

Secondly, the model could also consider variations in the date of management events besides the management intensity (e.g., mowing frequency). The timing of specific management regimes plays a decisive role regarding the impact on different ecosystem services, for example, the conservation of species richness, and depends on site-specific factors (Eriksson et al., 2015, Johst, Drechsler, Mewes, et al., 2015, Leins et al., 2021). For instance, mowing during the reproductive period (flowering and fruiting period) can lead to reduced genetic diversity and reproduction, whereas mowing before this period enhances reproductive success (Bissels et al., 2006, Nakahama et al., 2016). Further, birds are affected by management dates and intensity as they use this habitat for breeding and feeding (Chamberlain et al., 2000, Benton et al., 2002, Marriott et al., 2004). Instead of setting fixed dates (and intensities) prior to the model simulation, flexible management regimes could be designed, which are aligned with current day-specific conditions and are particularly needed with respect to climate change. Therefore, concepts for dynamic management regimes have to be developed and tested, for example, by implementing management rules related to actual plant development influenced by air temperature and soil moisture (Chang, Ciais, Viovy, et al., 2017, Petersen et al., 2021).

Thirdly, management regimes could be extended in the model towards pastures and mown pastures (Ma, Derner, et al., 2019). The GRASSMIND model so far focuses on meadows. Grazing could prospectively be integrated into the model to investigate the importance of vegetation processes and the influence of environmental factors also for pastures and to explore differences between meadows and pastures (e.g. whether plant mortality and management also dominate vegetation dynamics, Chapters 2 and 3).

Fourthly, the network analysis performed in Chapter 5 could also be applied to grassland ecosystems. Compared to forest inventory data, observation data on the spatial position of plants in grassland communities are rare and were not available for an analysis in this thesis. Monitoring individual plants in grasslands is challenging because measurements could destroy the root system, and the definition and identification of individual plants in grasslands is difficult (Lauenroth and Adler, 2008). Individual-based models such as the GRASSMIND model, which are parameterized based on field measurements, can be used to simulate plant size distributions and potential plant positions explicitly and can thus provide information for network analyses. Analyzing grasslands by network science allows to quantify spatial plant and plant species proximities and to detect changes in spatial structures (e.g., caused by mowing or climate change).

Fifthly, grassland ecosystems at other sites in Europe and worldwide could be modeled and simulated by the grassland model GRASSMIND in the future, which, however, may require the integration of additional processes in the model. Besides testing GRASSMIND for simulating semi-arid grasslands, whose growth is primarily determined by more frequent but small rainfall events (Heisler-White et al., 2008, Cherwin and Knapp, 2012), fire events can be incorporated into the model (Aragón et al., 2006). Simulating grasslands in the US requires a mechanistically adaptation of plant photosynthesis for C4 grasses (Chen et al., 1996) and grasslands in alpine regions can be exposed to landslides (Tasser et al., 2003). Such extended model applications would allow to compare grassland dynamics and the importance of different environmental and anthropogenic factors among these different grassland ecosystems.

Lastly, large-scale simulations of grassland dynamics by the GRASSMIND model, for example, of all grassland areas within Germany, can be feasible in the future by further improving the developed regionally transferable parameterization and by integrating remote sensing information on land cover (Griffiths et al., 2020, Preidl et al., 2020). Such large-scale application of GRASSMIND to Germany could allow, among others, to identify potential risks of plant diversity loss and related declines of ecosystem services under scenarios of future climate change combined with different management regimes.

6.3 VISION

This thesis has laid a foundation for analyzing, understanding and predicting vegetation dynamics and interactions using an individual-based grassland model and network science.

Ecological models have a great potential to predict shifts in vegetation dynamics due to environmental change. This aspect makes them prospectively an important tool for decision support of farmers and policy makers. Farmers can benefit from information systems (especially the connection of process-based models with remote sensing) which can forecast vegetation dynamics for a local grassland site with high temporal resolution and which can provide management recommendations to increase profits while still managing the land sustainably. A main worldwide challenge is sustainable intensification, which means raising productivity while reducing environmental impacts (Taube et al., 2014). Therefore, the preservation of biodiversity (flora and fauna) and the protection of grassland areas are important issues in politics (e.g., supported through subsidies to change farmer behavior in desirable directions). In this context, process-based grassland modeling (such as presented in this thesis) could support in future the identification of suitable grassland sites (in relation to environmental conditions) for corresponding appropriate management regimes, also under projected climate change.

The scope of recommendations that ecological models can provide to farmers and policy makers is not limited to vegetation dynamics. Coupling vegetation models such as the grassland model GRASSMIND with other mechanistic models, for example, hydrological models (e.g., Samaniego et al., 2010), economic or socioeconomic agent-based models regarding policy instruments and subsidies (e.g., Ziv et al., 2020) or models on animal movement (e.g., Leins et al., 2021), could expand potential applications in order to tackle a variety of environmental and societal challenges. Coupling multiple models can provide a system for simulating ecological and socioeconomic dynamics to produce high-resolution forecasts for the conservation of multifunctional landscapes. However, consideration should always be given to the extent to which a larger model system complexity can provide an advantage for the respective research question and corresponding analysis.

The ability to assess the consequences of policy decisions and management actions through modeling would enable biodiversity conservation, food security, and targeted mitigation of negative impacts by climate change on the Earth system. This is essential to prevent major environmental disasters such as floods and droughts and the associated consequences such as poverty and famine.

A

APPENDIX OF CHAPTER 2: INFLUENCES OF TRAITS AND PROCESSES ON PRODUCTIVITY AND FUNCTIONAL COMPOSITION IN GRASSLANDS: A MODELING STUDY

A.1 SUPPLEMENTARY METHODS

A.1.1 *Preparation of climate data*

Daily climatic conditions were received from two weather stations located near the experiment. Data from January 2004 onwards were supplied by the weather station of the Max Planck Institute (MPI) for Biogeochemistry in Jena, Germany. Missing climate data for the years 2002 and 2003 were substituted by data from the weather station of the University of Applied Science Jena (FH Jena). Gaps of missing data at three days were filled with the mean value of the previous and following day. Day length was calculated based on the latitude (Forsythe et al., 1995).

A.1.2 *Dates of mowing and vegetation measurements*

The grassland model used the same mowing and vegetation measurement dates as carried out in the field. Both was done twice per year (mowing: early June and early September, aboveground biomass (AGB) harvest: prior to mowing events (Weisser et al., 2017, Weigelt, Marquard, et al., 2010)) so that we set the following dates:

Year	Date	Mowing events	Vegetation measurements			
			AGB, vegetation cover, plant density*	AGB proportions in mixtures	Leaf area index (LAI)	Vegetation height
2002	05.07.	x				
	05.09.		x	x		x
	10.09.	x				
2003	09.06.		x	x	x	
	10.06.	x				
	08.09.		x	x	x	x
	10.09.	x				
2004	08.06.		x	x	x	x
	10.06.	x				
	07.09.		x		x	
	10.09.	x				
2005, 2007	08.06.		x	x	x	x
	10.06.	x				
	07.09.		x	x	x	x
	10.09.	x				
2006	08.07.		x	x	x	x
	10.07.	x				
	07.09.		x	x	x	x
	10.09.	x				
2008	07.06.		x	x	x	x
	10.06.	x				
	06.09.		x	x	x	x
	10.09.	x				

*Dates of plant density are only used for the analysis of model results and do not correspond to measurements in the field.

A.1.3 *Details on parameterization*

The inverse parameterization was done with an optimization tool, using two algorithms (each with maximum 10,000 evaluations) (Lehmann and Huth, 2015). In the first step, we used the dynamically dimensioned search algorithm to minimize our goal function that included the mean absolute percentage errors of the four summed vegetation attributes (AGB, LAI, vegetation height and vegetation cover) in plots of one PFT:

$$C_{1PFT} = \frac{1}{4} \sum_{i=1}^{4} \frac{\left|\sum_t x_{i,t} - \sum_t \hat{x}_{i,t}\right|}{\sum_t \hat{x}_{i,t}} \tag{A.17}$$

where $x_{i,t}$ are simulated and $\hat{x}_{i,t}$ are measured values which are summed for each vegetation attribute i over all measurement points at time t. To prevent that too many small and only one tall plant establishes in our model (which would cause large jumps in vegetation attributes if a tall plant randomly dies), we included a condition. We considered time intervals between mowing events or the turn of the year (since at the turn of the year in our model brown biomass is immediately transferred to the litter). In each time interval, we summed up the negative changes in vegetation height (due to random death of the tallest plant) and considered the time interval with the largest negative height change. If the amount of this change in height was greater than one third of the total height change in this time interval (maximum height minus minimum height), the set of parameters was not considered in the inverse parameterization. After checking our results of the inverse parameterization for plausibility, we introduced further restrictions, namely a maximum plant density (maximum number of plants on the plot, for grasses 4000 plants, for small herbs and legumes 2500 plants and for tall herbs 1000 plants) and reran the algorithm.

In the second step, we inversely estimated parameters of the mixture consisting of four PFTs. We used the adaptive simulated annealing algorithm to minimize the extended goal function C_{4PFT} of community attributes by including the functional proportions of AGB and vegetation cover:

$$C_{4PFT} = \frac{1}{6}\left(\sum_{i=1}^{4} \frac{\left|\sum_t x_{i,t} - \sum_t \hat{x}_{i,t}\right|}{\sum_t \hat{x}_{i,t}} + \frac{1}{4}\sum_{PFT=1}^{4} \frac{\left|\sum_t b_{PFT,t} - \sum_t \hat{b}_{PFT,t}\right|}{\sum_t \hat{b}_{PFT,t}} + \frac{1}{4}\sum_{PFT=1}^{4} \frac{\left|\sum_t c_{PFT,t} - \sum_t \hat{c}_{PFT,t}\right|}{\sum_t \hat{c}_{PFT,t}}\right) \tag{A.18}$$

where $b_{PFT,t}$ stands for the simulated proportional AGB of a PFT, $c_{PFT,t}$ stands for the simulated proportional cover of a PFT and $x_{i,t}$ are community vegetation attributes (AGB, LAI, vegetation height and vegetation cover) at time t. Respective variables with hat denote the corresponding measured data, whereby the first year of measurement was excluded.

The corrected values of N_{seed} determined in the second step showed no major changes in the simulation results of 1-PFT plots.

A.1.4 *Validation*

The validation of the model parameterization was done by using independent additional data from the field experiment. This data comprised plots consisting of two and three PFTs. Analogous to the parameterization, we prepared the field data by aggregating vegetation attributes (four combinations in 2-PFT mixtures: GS, GT, SL, TL, aggregations over five field plots each, and four combinations in 3-PFT mixtures: GST, GSL, GTL, STL, three field plots each). By using the same simulation settings as described in the parameterization section (in terms of climate, starting conditions and simulation time) and the previously determined parameter sets for each PFT, we simulated mixtures of each PFT combination and compared simulation results with the respective field observations (see next paragraph on evaluation).

A.1.5 *Evaluation*

To evaluate the accuracy of our simulation results (parameterization and validation), we calculated in addition to graphical comparisons three statistical criteria: the mean absolute percentage error ($MAPE$), the normalized root mean square error ($NRMSE$) and sample Pearson's correlation coefficient (r_{SM}) for each vegetation attribute i, including each field measurement:

$$MAPE = \frac{1}{n}\sum_{i=1}^{n}\left|\frac{M_i - S_i}{M_i}\right| \tag{A.19}$$

$$NRMSE = \frac{\sqrt{\sum_{i=1}^{n}\left(M_i - S_i\right)^2}}{\overline{M}} \tag{A.20}$$

$$r_{SM} = \frac{\sum_{i=1}^{n}\left(S_i - \overline{S}\right)\left(M_i - \overline{M}\right)}{\sqrt{\sum_{i=1}^{n}\left(S_i - \overline{S}\right)^2}\sqrt{\sum_{i=1}^{n}\left(M_i - \overline{M}\right)^2}} \tag{A.21}$$

where S_i and M_i are the i-th simulated and measured values, $\overline{S}$ and $\overline{M}$ are the means of simulated and measured values and n is the number of data points.

A.1.6 *Sensitivity analysis*

In the Morris method, elementary effects $EE_i(\boldsymbol{x})$ describe the effect that the change of a model input parameter value x_i (e.g. SLA) has on the simulation result y (e.g. AGB). We used the function *morris()* of the package 'sensitivity' in R (version 1.16.1) (Iooss et al., 2020). Elementary effects of each model parameter were calculated using the one-factor-at-a-time (OAT) method, i.e. only one parameter x_i was varied at a time (Morris, 1991):

$$EE_i(\boldsymbol{x}) = \frac{y\left(x_1, x_2, \ldots, x_i + \Delta, \ldots, x_k\right) - y(\boldsymbol{x})}{\Delta} \tag{A.22}$$

Each input parameter had eight possible realizations within its range (see Table S2). The variation of one parameter in one step was $\Delta = \frac{5}{7}(\max\left(range\left(x_i\right)\right) - \min\left(range\left(x_i\right)\right)$, respectively (with jump over five realizations in one step, see (Iooss et al., 2020) for details). Elementary effects were calculated r times for random trajectories through the parameter space. To identify the number of trajectories needed, we used the method proposed by Menberg et al. (2016). Then, for each parameter i we determined the mean elementary effect μ, the standard deviation σ and the mean absolute effect μ^* (Morris, 1991):

$$\mu_i = \frac{\sum_{n=1}^{r} EE_n\left(x\right)}{r} \tag{A.23}$$

$$\sigma_i = \sqrt{\frac{1}{r}\sum_{n=1}^{r}\left(EE_n\left(x\right) - \mu_i\right)^2} \tag{A.24}$$

$${\mu^*}_i = \frac{\sum_{n=1}^{r} \left|EE_n\left(x\right)\right|}{r} \tag{A.25}$$

Thereby, parameters with low mean elementary effect μ and low standard deviation σ are considered unimportant. The effect of parameters lying outside of a wedge built by $\mu = \pm 2SEM$ (with $SEM = \sigma/\sqrt{r}$) in the $\mu - \sigma$ figure is expected to be linear and additive, while the effect of parameters inside the wedge indicates dependence on values of other parameters or non-linearity. The output y is most sensitive to parameters with high μ^* (Campolongo et al., 2007).

We have tested the sensitivity of 16 trait parameters of the model (see Table S2). Thereby, we considered as output y the AGB in a 1-PFT plot and PFT-proportional AGB in the 4-PFT mixture (whereby only trait parameters of legumes were varied), averaged over measurement dates, respectively. We used r = 200 trajectories.

A.1.7 *Calculation of mean relative yield*

Similar to the study by Marquard et al. (2009), we determined mean relative yields (RYI) for each plant functional type (PFT). Instead of species richness, we considered only plant functional group richness in our formula:

$$RYI = \frac{1}{N_i}\sum\left(RY_i * \#PFTs\right) \tag{A.26}$$

where N_i is the number of mixtures including PFT i, $\#PFTs$ is the total number of PFTs in the respective mixture and RY_i is the relative yield (here, aboveground biomass (AGB)) of PFT i:

$$RY_i = \frac{AGB\ of\ PFT\ i\ in\ mixture}{AGB\ of\ PFT\ i\ in\ plot\ of\ 1\ PFT} \tag{A.27}$$

Thereby, $RYI > 0$ represents overyielding which means that a PFT is more productive in mixtures than in the 1-PFT plot. Conversely, $RYI < 0$ indicates underyielding, meaning that the PFT is more productive in 1-PFT plots than in mixtures. Analogous to RYI, mean relative plant biomass (*RBI*, excluding the factor *#PFTs*) and mean relative density (*RDI*) was computed (Marquard, Weigelt, Temperton, et al., 2009).

A.2 SUPPLEMENTARY RESULTS

A.2.1 *Impact of stochasticity on the simulation*

We tested for differences between 10 and 100 simulation runs. We observed only on average 12% of deviations between 10 and 100 simulation runs in the AGB of 1-PFT and 4-PFT plots (maximum 18.5%) and a mean deviation of 11% in LAI, of 12% in vegetation height and of 1% in vegetation cover.

A.2.2 *Changes of competition factors in the robustness analysis*

It is expected that competition for space increases if competition for light is deactivated. However, this is not the case for small herbs and the 4-PFT mixture (Fig. A.6) which indicates that competition for light influences their dynamics stronger than competition for space. The same applies to the light reduction factor when competition for space is deactivated. As expected, the light reduction factor increases for small herbs and for the mixture, but decreases in the other plots. Hence, competition for space seems to be the dominant process for grasses and legumes in the 1-PFT plots.

The factors influence productivity in different dimensions. This can also be seen in the plots of small herbs and the mixture: although the light reduction factor increases (in case of no competition for space) productivity still increases (Fig. 2).

In the mixture, the light reduction factors of the PFTs show the same direction of change as in the 1-PFT plots, with the exception of grasses, whose light reduction factor now also increases in case of no competition for space. This may be related to the high plant density of grasses, and the overall lower vegetation height compared to tall herbs and legumes (Fig. 2).

Note that the values of the competition factors strongly depend on plant density and the size distribution of plants (e.g., in terms of height or width). Here, both factors show arithmetic means over all plants and simulated days.

A.2.3 *Comparison to field studies - Life spans*

Annual measurements of perennial plants in Kansas, USA, revealed maximum lifetimes of 3 to 39 years (Lauenroth and Adler, 2008), whereas compared to our model results we observed a maximum lifetime of only about 3 years (Fig. A.11). Herbs tend to have on average a much shorter life span than grasses ((Lauenroth and Adler, 2008); 3 to 25 years for forbs and 5 to 39 years for grasses). This is consistent with our model results as life spans of the PFTs in the modeled mixture ranges from one day to 3.1 years for grasses and to 1.9 years for forbs (mean of maximal life spans over small herbs, tall herbs and legumes). Note that it is often challenging to identify individual plants in grasslands, which is why Lauenroth and Adler (2008) defines genets and grass polygons (overlapping grass plants share one identity) as one plant each.

A.3 SUPPLEMENTARY FIGURES

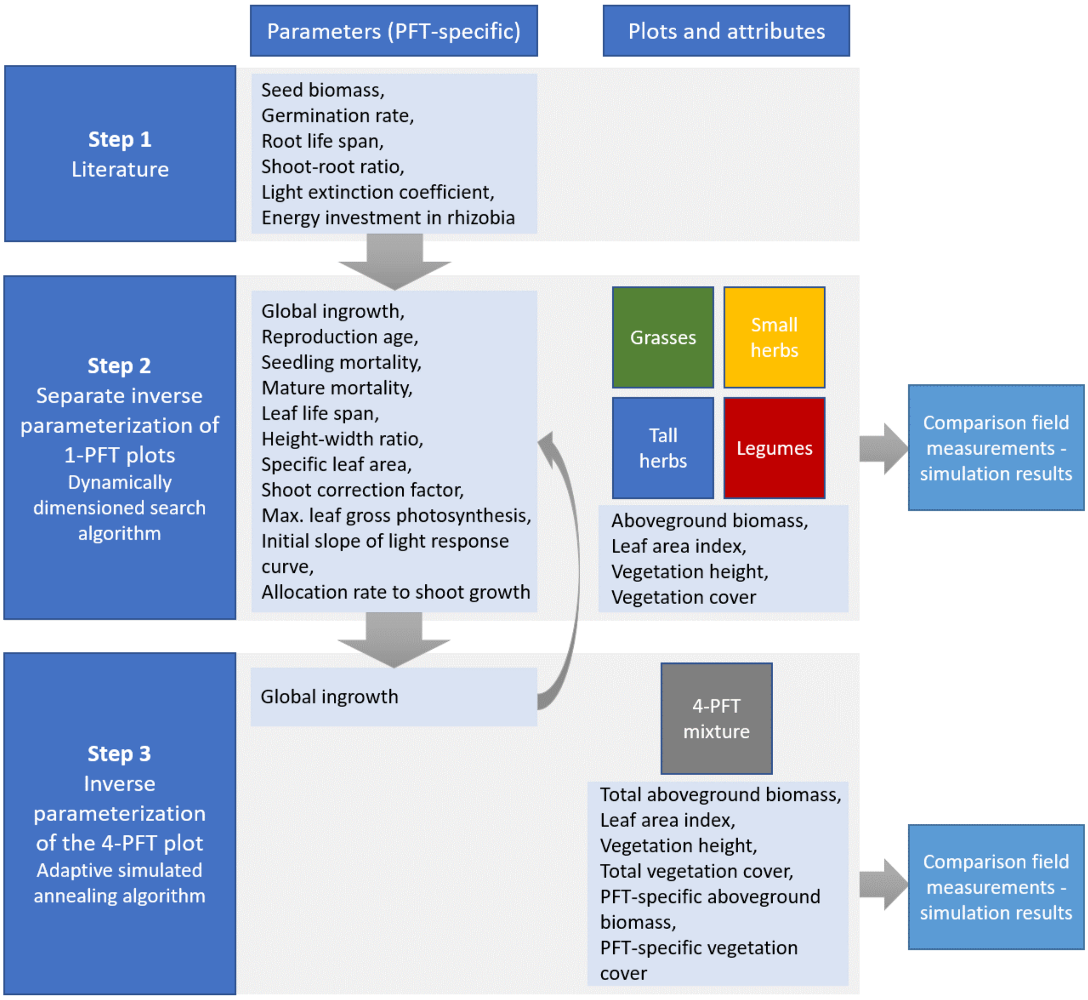


Figure A.1: Flow chart showing the steps of the inverse parameterization of the model.

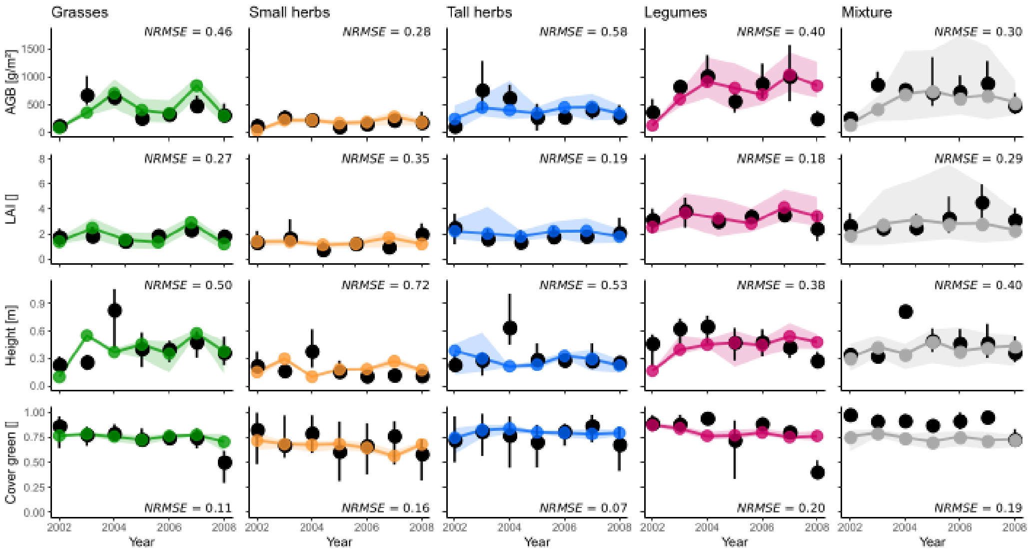


Figure A.2: Annual means of field measurements (black) in comparison to corresponding simulation results (colored) in plots of one plant functional type (PFT) and the 4-PFT plot. Black lines and shaded polygons show maximum and minimum annual values within the field plots and simulation runs. The normalized root mean square errors (*NRMSE*) were calculated using the annual aggregated measurements (seven data points).

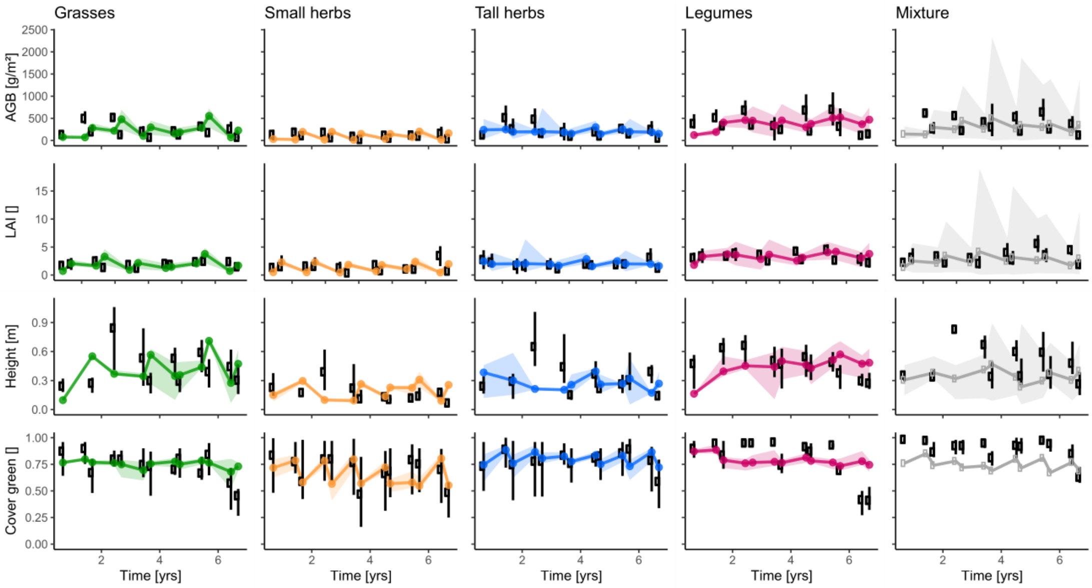


Figure A.3: Field measurements (black) in comparison to corresponding simulation results (colored) in plots of one plant functional type (PFT) and the 4-PFT plot. Black lines and shaded polygons show maximum and minimum values within the field plots and simulation runs (spatial variation).

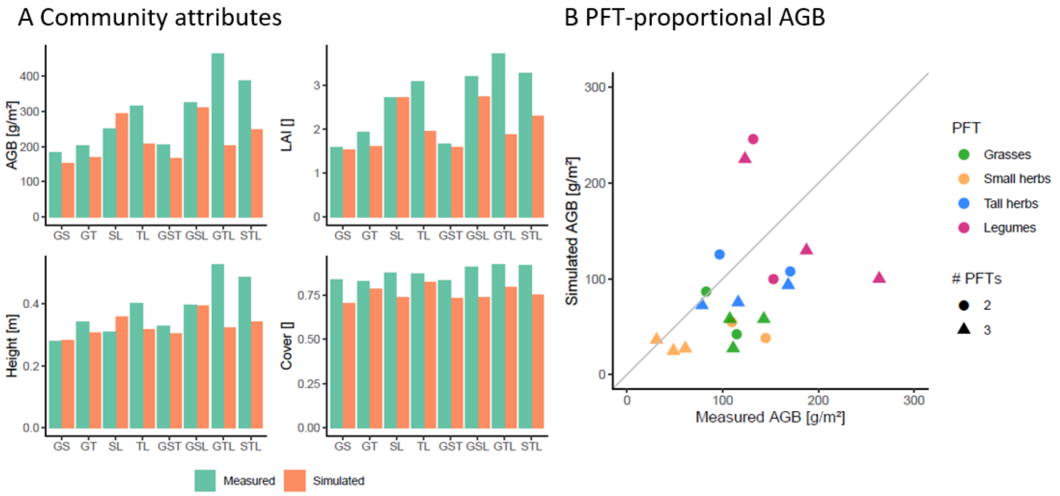


Figure A.4: Validation results of the model parameterization. (A) Mean measured vegetation community attributes in different plots of the Jena Main Experiment (green) and corresponding simulated attributes (orange). The letters show the occurring plant functional types (PFTs) in the plots (G: grasses, S: small herbs, T: tall herbs, L: legumes). In (B) mean proportional aboveground biomass (AGB) of the PFTs in 2-PFT and 3-PFT mixtures are shown in a 1:1 plot.

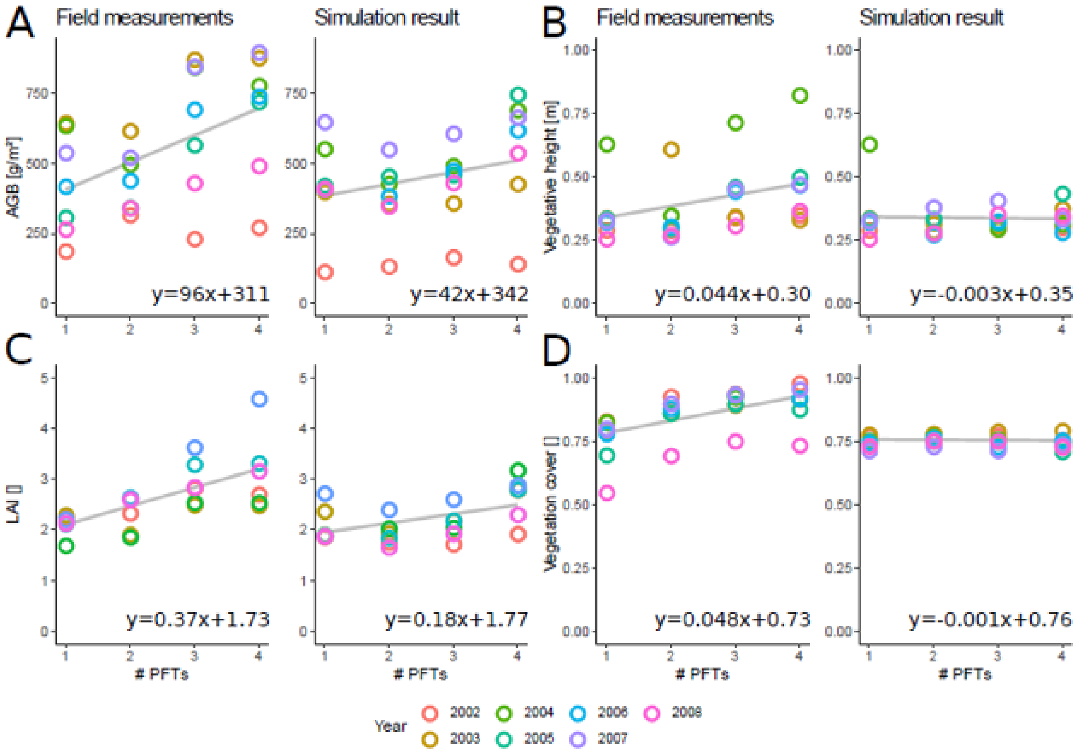


Figure A.5: Vegetation patterns of different plant functional type (PFT) richness in years 2002 to 2008. In (A) aboveground biomass (AGB) of measurement dates per year was summed up (two per year in 2003-2008, one measurement only in 2002), in (B)-(D) averages over the measurements per year were taken, of the field measurements and the associated simulation results, respectively. Grey lines show linear regressions.

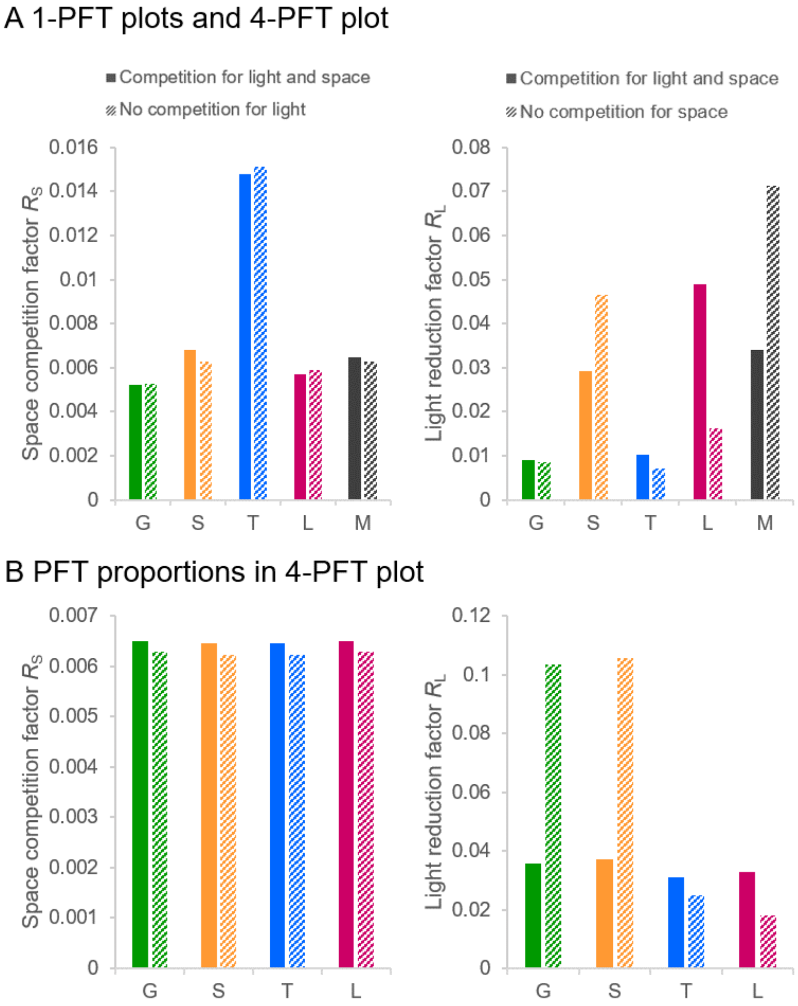


Figure A.6: Space competition factor R_S and light reduction factor R_L of the simulated (A) 1-PFT plots of grasses (G), small herbs (S), tall herbs (T) and legumes (L) and the 4-PFT mixture (M) and (B) PFT proportions in the mixture in different scenarios (the standard setting with competition for light and space, and respectively no competition for light or space). Note that R_S is averaged over all days of the seven simulation days (the same for all plant on one day) and R_L is averaged over all days and all plants in the plot (larger for smaller plants). Note that for the scenario of no space and no light competition, both factors are zero.

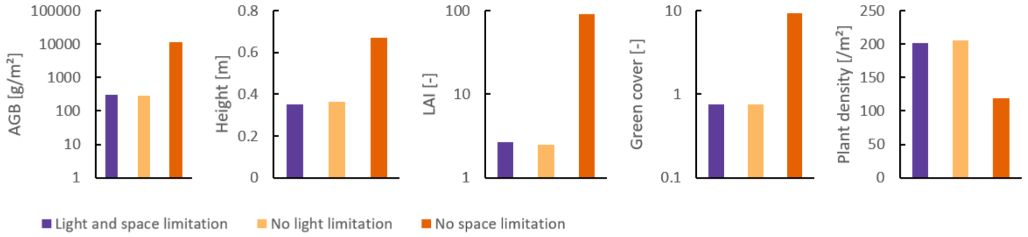


Figure A.7: Impact of light and space limitation on vegetation community attributes in the mixture of four plant functional types. Bluish bars show simulation outputs with light and space limitation, yellowish bars with no light limitation and reddish bars with no space limitation. Values correspond to the mean value over the measurement dates (see A.1 Supplementary Methods) averaged over ten simulation runs. Note that the axes of ABG, LAI and green vegetation cover are logarithmic.

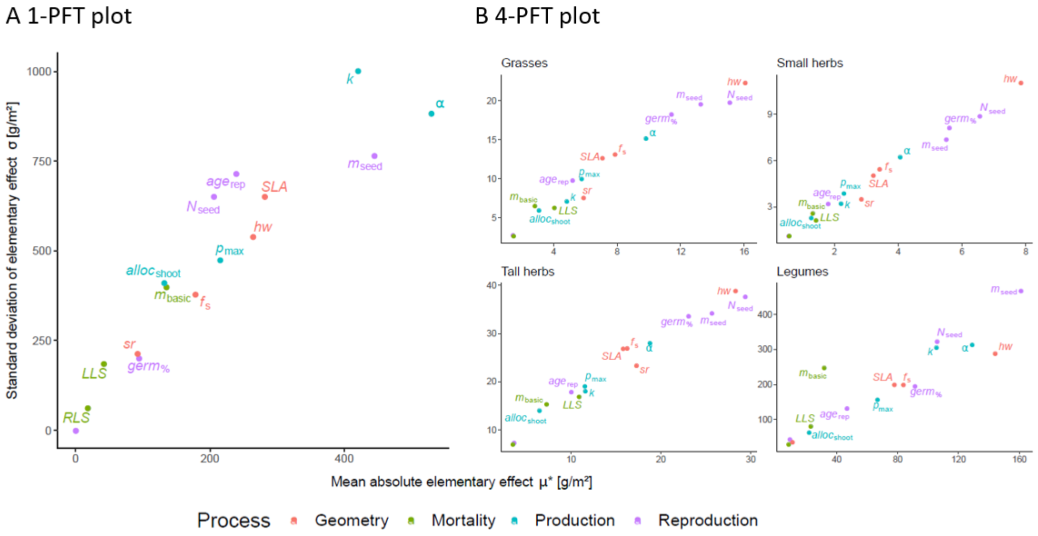


Figure A.8: Absolute elementary effects μ^* on aboveground biomass (A) in a plot of one plant functional type (PFT) and (B) in a mixture of four PFTs. In (B) only the trait parameters of legumes were varied, but affected also changes in the aboveground attributes of the remaining PFTs. Non-influential parameters are not labeled.

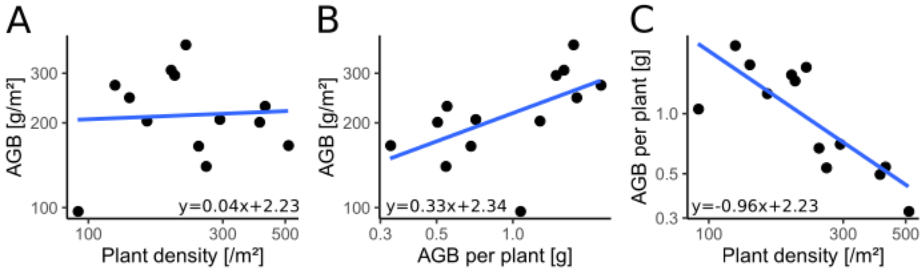


Figure A.9: Relationship between (A) plant density and community aboveground biomass (AGB), (B) plant biomass and community AGB and (C) plant density and AGB per plant. Points correspond to mean values at dates of AGB measurement (see A.1 Supplementary Methods) of four simulated plots of one plant functional type (PFT), four simulated plots of two PFTs, four simulated plots of three PFTs and one simulated plot of four PFTs. Blue lines show linear regressions. Note that all axes are logarithmic.

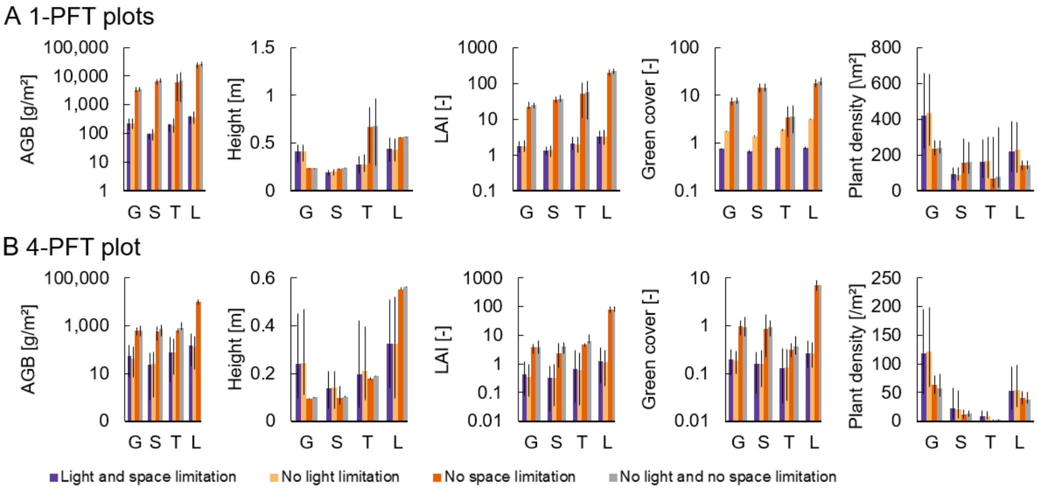


Figure A.10: Impact of light and space competition on vegetation attributes in (A) plots of one plant functional type (PFT) and in (B) the 4-PFT mixture. Aboveground biomass (AGB), leaf area index (LAI), vegetation height, green vegetation cover and plant density were analyzed. Bluish bars show simulation results with light and space competition, yellowish bars with no light competition and reddish bars with no space competition of grasses (G), small herbs (S), tall herbs (T) and legumes (L). Values correspond to the mean value over the time-series of the corresponding vegetation attribute. Black lines indicate maximum and minimum values in the simulation runs (spatial variation). Note that the axes of ABG, LAI and green vegetation cover are logarithmic.

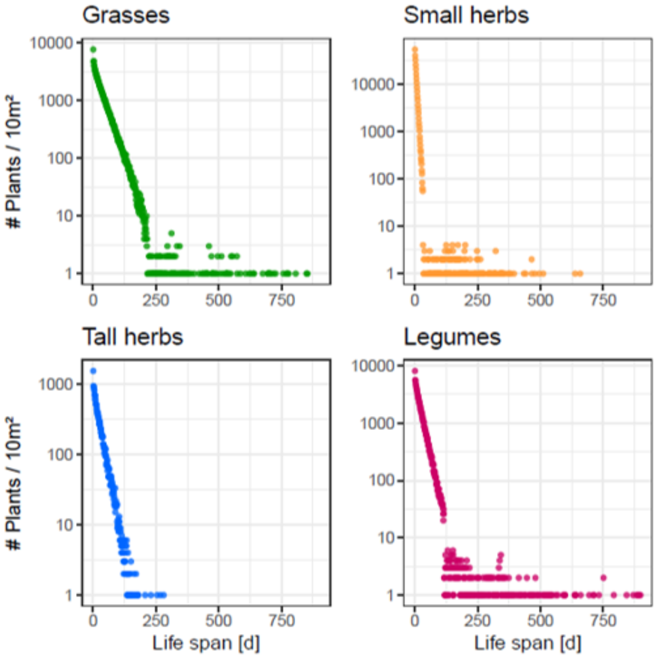


Figure A.11: Life spans of plants of different plant functional types in the 4-PFT mixture. Individual plants that established on 10 m² are shown.

A.4 SUPPLEMENTARY TABLES

Table A.1: Parameter values of the grassland model. 11 parameters were inversely parameterized relating to model processes of plant reproduction, mortality, geometry and production. For detailed descriptions of the parameters and processes in the model see Taubert, Hetzer, et al. (2020a). Means over species belonging to one plant functional type were taken from measurements of the Jena experiment in Heisse et al. (2007).

Process	**Parameter**	**Shortcut**	**Grass**	**Small herbs**	**Tall herbs**	**Legumes**	**Source**
Reproduction	Global ingrowth of seeds [1/day]	N_{seed}	3,215	4,809	659	2,241	inversely parameterized
	Reproduction age [yrs]	age_{rep}	0.59	0.09	0.48	0.32	inversely parameterized
	Seed biomass [g_{ODM}]	B_{seed}	1.38	0.88	1.75	5.68	(Heisse et al., 2007)
	Germination rate of seeds [-]	$germ_{\%}$	0.66	0.75	0.62	0.78	(Heisse et al., 2007)
	Seedling mortality [1/yr]	m_{seed}	9.0	68.6	13.9	15.1	inversely parameterized
Mortality	Mature mortality [1/yr]	m_{basic}	0.03	0.03	4.01	0.03	inversely parameterized
	Leaf life span [days]	LLS	90	42	33	114	inversely parameterized
	Root life span [days]	RLS	709	241	241	709	(Tjoelker et al., 2005) and estimated
Geometry	Height-width ratio [-]	hw	1.2	0.4	0.7	0.9	inversely parameterized
	Specific leaf area of a single plant [cm^2/g_{ODM}]	SLA	63.12	100.98	81.61	72.16	inversely parameterized
	Shoot correction factor [t/m^3]	f_s	0.0011	0.0008	0.0012	0.0014	inversely parameterized
	Shoot-root ratio [-]	sr	2.35	4.05	3.99	13.01	(Heisse et al., 2007)
Production	Max. leaf gross photosynthesis [$\mu mol_{CO2}/m^2/s$]	p_{max}	14.47	17.51	29.69	24.22	inversely parameterized
	Initial slope of light response curve [$\mu mol_{CO2}/\mu mol_{photon}$]	α	0.30	0.10	0.24	0.07	inversely parameterized
	Light extinction coefficient of leaves [-]	k	0.215	0.7	0.26	0.5	estimated, (Thornley and France, 2007)
	Allocation rate (fraction of NPP) to shoot growth [-]	$alloc_{shoot}$	0.79	0.44	0.89	0.71	inversely parameterized
	Energy investment in rhizobia (fraction of NPP) [-]	$rhiz_{\%}$	0	0	0	0.2	(Minchin et al., 1981)

Table A.2: Ranges of input trait parameters in the Morris Method and the corresponding output values (including output range; other parameters were set to mean values within their ranges) in model simulations with one plant functional type.

Process	**Parameter**	**Shortcut**	**Input range**	**Output vegetation attribute**	**Lower output**	**Upper output**	**Output range**
Reproduction	Global ingrowth of seeds [1/day]	N_{seed}	0 – 3,000	AGB [g/m^2]	0	289	289
				Height [m]	0.00	0.32	0.32
				LAI []	0.00	75.67	75.67
				Cover []	0.00	0.95	0.95
	Reproduction age [yrs]	age_{rep}	0.04 – 0.99	AGB [g/m^2]	1,645	242	1,402
				Height [m]	0.49	0.32	0.17
				LAI []	281.42	59.81	221.62
				Cover []	0.68	0.69	0.00
	Seed biomass [g$_{ODM}$]	B_{seed}	0.1 – 10	AGB [g/m^2]	242	242	0
				Height [m]	0.32	0.32	0.00
				LAI []	59.81	59.81	0.00
				Cover []	0.69	0.69	0.00
	Germination rate of seeds [-]	$germ_{\%}$	0.01 – 0.99	AGB [g/m^2]	19	287	268
				Height [m]	0.24	0.32	0.08
				LAI []	3.91	75.35	71.44
				Cover []	0.03	0.95	0.92
	Seedling mortality [%/yr]	m_{seed}	5 – 90	AGB [g/m^2]	1,810	79	1,730
				Height [m]	0.55	0.19	0.36
				LAI []	301.75	23.26	278.49
				Cover []	0.68	0.34	0.34
Mortality	Mature mortality [1/yr]	m_{basic}	0 – 10	AGB [g/m^2]	242	242	0
				Height [m]	0.32	0.32	0.00
				LAI []	59.81	59.81	0.00
				Cover []	0.69	0.69	0.00
	Leaf life span [days]	LLS	30 – 150	AGB [g/m^2]	244	242	1
				Height [m]	0.32	0.31	0.00
				LAI []	59.98	59.77	0.21
				Cover []	0.60	0.70	0.10
	Root life span [days]	RLS	100 – 1,000	AGB [g/m^2]	242	242	0
				Height [m]	0.32	0.32	0.00
				LAI []	59.81	59.81	0.01
				Cover []	0.68	0.69	0.00
Geometry	Height-width ratio [-]	hw	0.1 – 8.5	AGB [g/m^2]	324	131	193
				Height [m]	0.08	0.35	0.27
				LAI []	86.52	28.67	57.85
				Cover []	1.14	0.26	0.88
	Specific leaf area of a single plant [cm^2/g$_{ODM}$]	SLA	30.00 – 3,000.00	AGB [g/m^2]	18	153	135
				Height [m]	0.10	0.29	0.19
				LAI []	0.27	82.64	82.37
				Cover []	0.32	0.55	0.23
	Shoot correction factor [t/m^3]	f_s	0.001 – 0.1	AGB [g/m^2]	402	4	398
				Height [m]	0.84	0.04	0.80
				LAI []	66.42	139.56	73.15
				Cover []	1.09	0.22	0.87
	Shoot-root ratio [-]	sr	1 – 20	AGB [g/m^2]	131	251	119
				Height [m]	0.20	0.32	0.12
				LAI []	39.30	61.30	22.00
				Cover []	0.57	0.69	0.12

Production	Max. leaf gross photosynthesis $[\mu mol_{CO2}/m^2/s]$	p_{max}	5 – 60	AGB [g/m²] Height [m] LAI [] Cover []	71 0.14 26.94 0.48	272 0.37 64.16 0.69	201 0.23 37.23 0.21
	Initial slope of light response curve $[\mu mol_{CO2}/\mu mol_{photon}]$	α	0.01 – 0.6	AGB [g/m²] Height [m] LAI [] Cover []	6 0.05 9.79 0.26	340 0.38 76.81 0.75	335 0.33 67.02 0.49
	Light extinction coefficient of leaves [-]	k	0.1 – 0.9	AGB [g/m²] Height [m] LAI [] Cover []	782 0.51 151.48 0.99	142 0.24 40.42 0.56	640 0.26 111.06 0.43
	Allocation rate (fraction of NPP) to shoot growth [-]	$alloc_{shoot}$	0.3 – 0.99	AGB [g/m²] Height [m] LAI [] Cover []	242 0.32 59.81 0.69	242 0.32 59.81 0.69	0 0.00 0.00 0.00

Table A.3: Values of evaluation criteria (mean absolute percentage error $MAPE$, normalized root mean square error $NRMSE$, sample Pearson's correlation coefficient r_{MS}) in plots of one plant functional type (PFT) and in the 4-PFT plot (PFTs: grasses (G), small herbs (S), tall herbs (T) and legumes (L)). Criteria are calculated based on biannual measurements of the vegetation attributes.

Vegetation attribute	**Statistical measure**	**1-PFT plot**				**4-PFT plot**					**Community mean**
		G	**S**	**T**	**L**	**Total**	**G**	**S**	**T**	**L**	
Above-ground biomass	$MAPE$	0.80	0.82	0.79	0.80	0.65	0.90	0.56	0.98	1.27	0.77
	$NRMSE$	1.03	1.14	0.58	0.60	0.66	0.94	0.83	0.94	0.86	0.80
	r_{MS}	-0.29	-0.71	0.39	-0.07	-0.48	-0.30	0.06	-0.17	-0.26	-0.23
Leaf area index	$MAPE$	0.76	0.84	0.64	0.70	0.44	-	-	-	-	0.68
	$NRMSE$	0.54	0.97	0.30	0.31	0.50	-	-	-	-	0.52
	r_{MS}	-0.06	-0.50	0.34	-0.09	-0.35	-	-	-	-	-0.13
Vegetation height	$MAPE$	1.57	3.46	1.96	1.39	0.35	-	-	-	-	1.75
	$NRMSE$	0.57	0.88	0.56	0.37	0.48	-	-	-	-	0.57
	r_{MS}	-0.08	-0.60	-0.34	-0.23	-0.18	-	-	-	-	-0.29
Green vegetation cover	$MAPE$	0.75	0.81	0.69	0.79	0.17	0.21	0.29	0.48	0.44	0.64
	$NRMSE$	0.15	0.18	0.09	0.22	0.19	0.23	0.33	0.58	0.45	0.16
	r_{MS}	0.49	0.43	0.46	0.38	0.49	0.68	0.68	0.07	-0.29	0.45

Table A.4: Values of evaluation criteria (mean absolute percentage error $MAPE$, normalized root mean square error $NRMSE$, sample Pearson's correlation coefficient r_{MS}) in mixtures of two and three plant functional types (PFTs: grasses (G), small herbs (S), tall herbs (T) and legumes (L)). Criteria are calculated based on biannual measurements of the vegetation attributes.

Vegetation attribute	**Statistical measure**	**2-PFT mixtures**				**3-PFT mixtures**				**Mean**
		GS	**GT**	**SL**	**TL**	**GST**	**GSL**	**GTL**	**STL**	
Above-ground biomass	$MAPE$	1.29	0.85	1.27	0.37	0.61	0.67	0.59	0.54	0.77
	$NRMSE$	1.09	0.74	0.99	0.52	0.76	0.61	0.72	0.69	0.77
	r_{MS}	-0.55	-0.18	-0.50	0.13	-0.09	-0.19	0.09	-0.50	-0.22
Leaf area index	$MAPE$	0.81	0.38	0.57	0.35	0.41	0.41	0.45	0.30	0.46
	$NRMSE$	0.77	0.47	0.65	0.45	0.52	0.42	0.58	0.46	0.54
	r_{MS}	-0.32	-0.12	-0.43	0.25	-0.29	-0.11	0.27	-0.05	-0.10
Vegetation height	$MAPE$	0.64	0.44	0.61	0.31	0.41	0.58	0.37	0.37	0.47
	$NRMSE$	0.66	0.51	0.56	0.47	0.57	0.47	0.47	0.49	0.53
	r_{MS}	-0.13	-0.40	-0.20	-0.23	-0.39	-0.07	0.00	-0.36	-0.22
Green vegetation cover	$MAPE$	0.17	0.12	0.17	0.09	0.13	0.18	0.18	0.18	0.15
	$NRMSE$	0.20	0.14	0.20	0.11	0.17	0.20	0.18	0.21	0.18
	r_{MS}	0.31	0.13	0.32	0.32	-0.02	0.43	0.27	-0.03	0.22

Table A.5: Plant density, mean biomass per plant on plots of one plant functional type (PFT) and on the 4-PFT mixture (PFTs: grasses, small herbs, tall herbs and legumes), and mean relative yields RYI, mean relative AGB per plant RBI and mean relative densities RDI including all mixtures (2-PFT mixtures, 3-PFT mixtures and the 4-PFT mixture, see A.1 Supplementary Methods for formula). Means were taken over plants present at the dates of aboveground biomass measurements (AGB; see A.1 Supplementary Methods).

	# PFTs on plot	**Grasses**	**Small herbs**	**Tall herbs**	**Legumes**
Plant density (number of plants per m^2)	1 PFT	422	92	161	221
	4 PFTs	119	22	9	52
AGB per plant [g]	1 PFT	0.547	1.068	1.274	1.730
	4 PFTs	0.445	1.094	8.549	2.819
Mean relative yield RYI	2-4 PFTs	0.648	0.933	1.206	1.154
Mean relative size RBI	2-4 PFTs	0.835	0.665	3.402	1.506
Mean relative density RDI	2-4 PFTs	1.386	0.951	0.455	1.258

B

APPENDIX OF CHAPTER 3: IMPACT OF MOWING FREQUENCY AND TEMPERATURE ON PRODUCTIVITY OF TEMPERATE GRASSLANDS – EXPLANATIONS RECEIVED BY AN INDIVIDUAL-BASED MODEL

B.1 SUPPLEMENTARY RESULTS

B.1.1 *Changes of PFT proportions in mown biomass with different mowing frequencies*

Mown biomass (AGB above 10 cm height at mowing dates) showed a slightly different functional composition than total AGB. Compared to total AGB, the proportion of grasses is greater when mown once per year, und smaller for the other mowing frequencies (Fig. B.7A, Table B.4). Small herbs showed overall smaller proportions in mown biomass und tall herbs increased in their proportion (especially for high mowing frequencies). The proportion of tall herbs became even higher than the one of legumes when mown four or five times per year. A 2°C increase in temperature caused similar changes in relative abundances of PFTs as observed in total AGB (Fig. B.7B).

B.2 SUPPLEMENTARY FIGURES

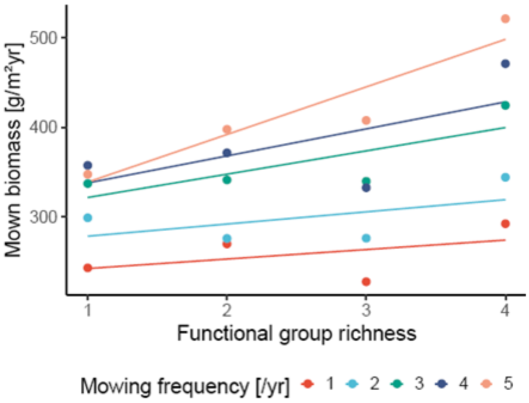


Figure B.1: Impact of mowing frequency on the diversity-productivity relationship. Productivity refers to the mean annual mown biomass (aboveground biomass above 10 cm height, mean over five simulation years), functional group richness refers to the number of plant functional types in the grassland (no air temperature increase).

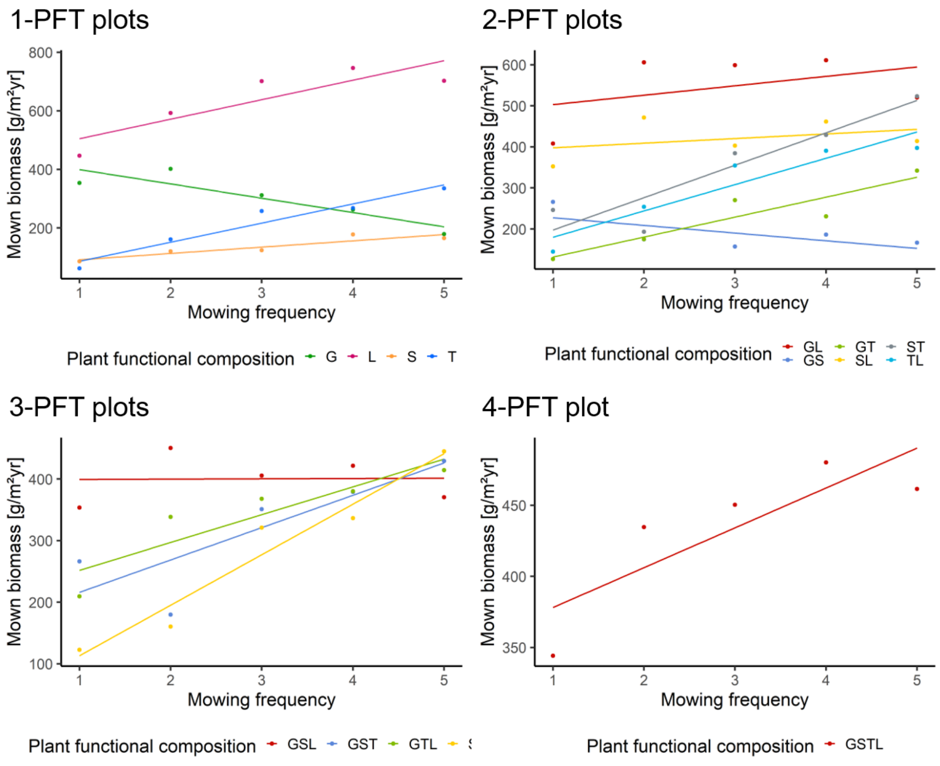


Figure B.2: Mown biomass of the plant functional type (PFT) combinations at different mowing frequencies (no air temperature increase). Abbreviations: G – grasses, S – small herbs, T – tall herbs, L – legumes..

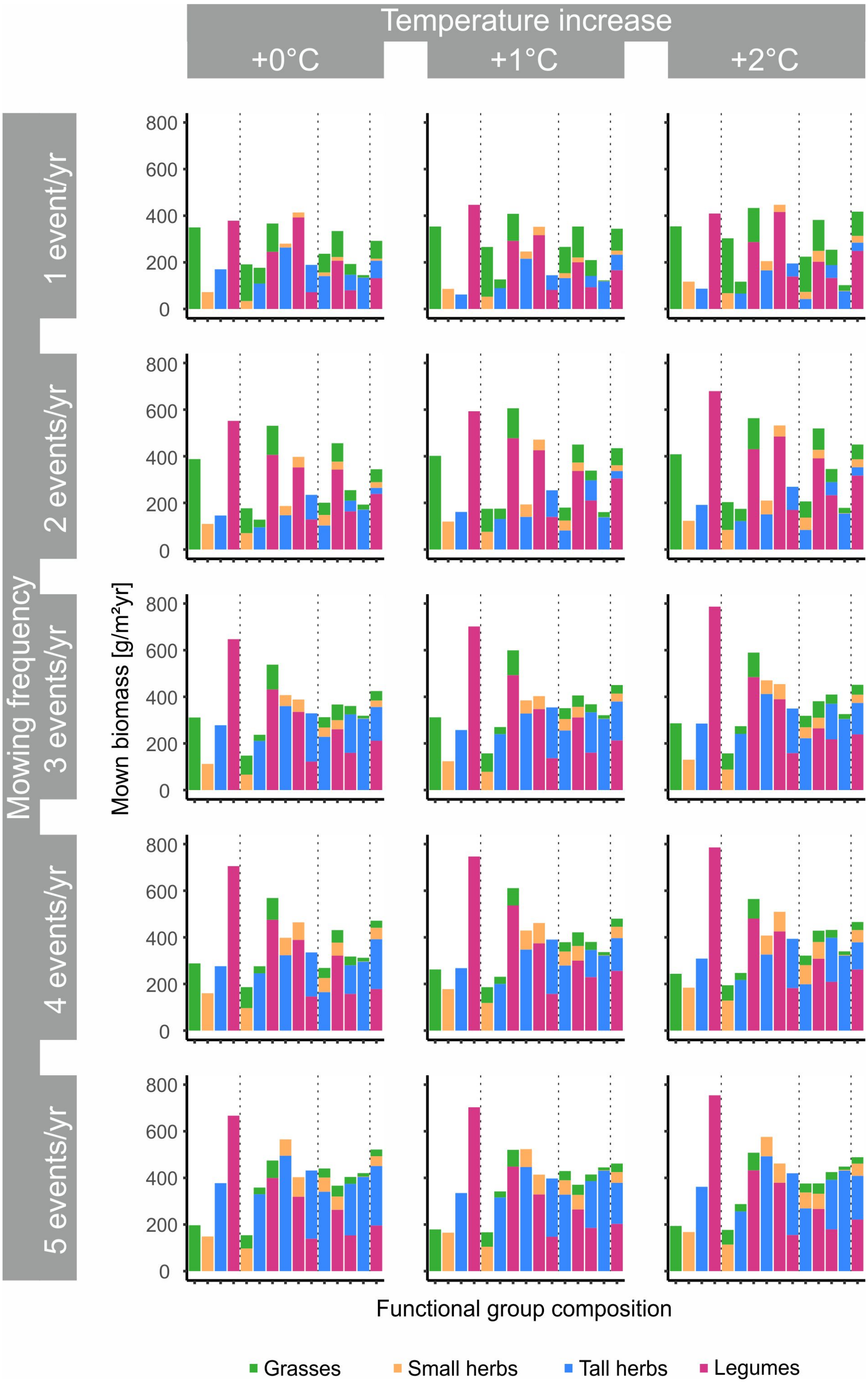


Figure B.3: PFT proportions in mean annually mown biomass of all PFT combinations with different mowing frequencies and air temperature increase. In each panel all PFT combinations at different levels of functional group richness were simulated (from left to right): the first four bars denote each 1-PFT simulation, next six bars denote the 2-PFT mixtures, next four bars show the 3-PFT mixture and the last bar represents the 4-PFT mixture.

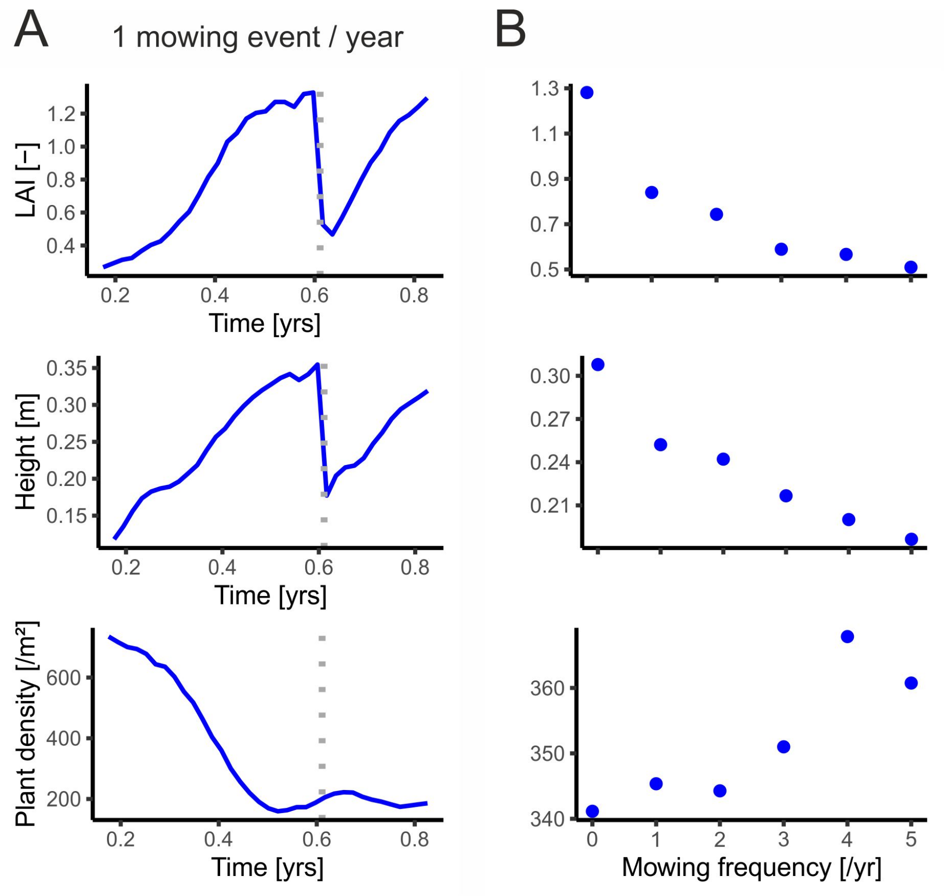


Figure B.4: Vegetation attributes in the mixture of four plant functional types over time and with different mowing frequencies. (A) Development of leaf area index (LAI), vegetation height and plant density with one mowing event per year (marked by the grey dotted line) are shown. Vegetation attributes are weekly means and correspond to averages over the vegetation periods of five simulation years. (B) shows annual mean LAI, vegetation height and plant density for different mowing frequencies.

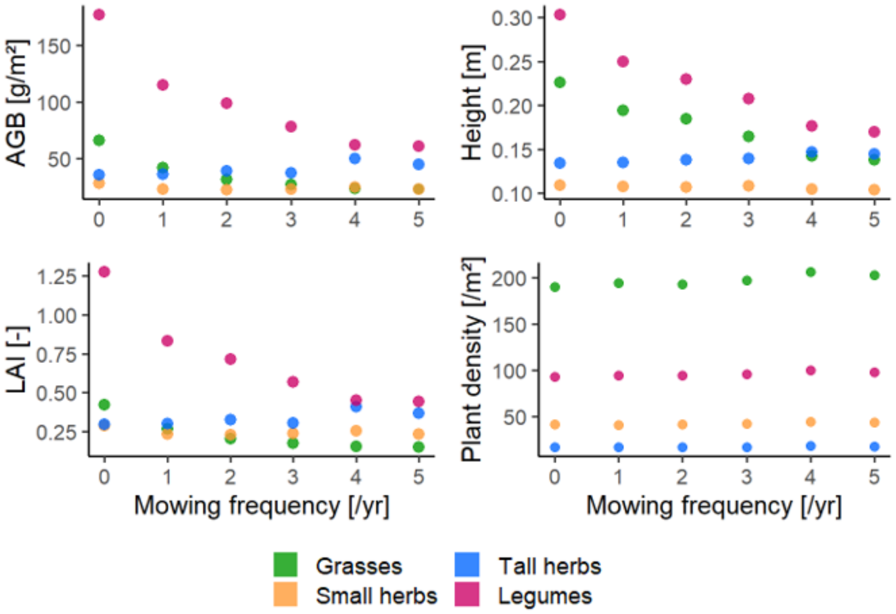


Figure B.5: Influences of different mowing frequencies on PFT-specific vegetation attributes in the 4-PFT mixture. Annual aggregations were taken over the vegetation periods from five simulation years.

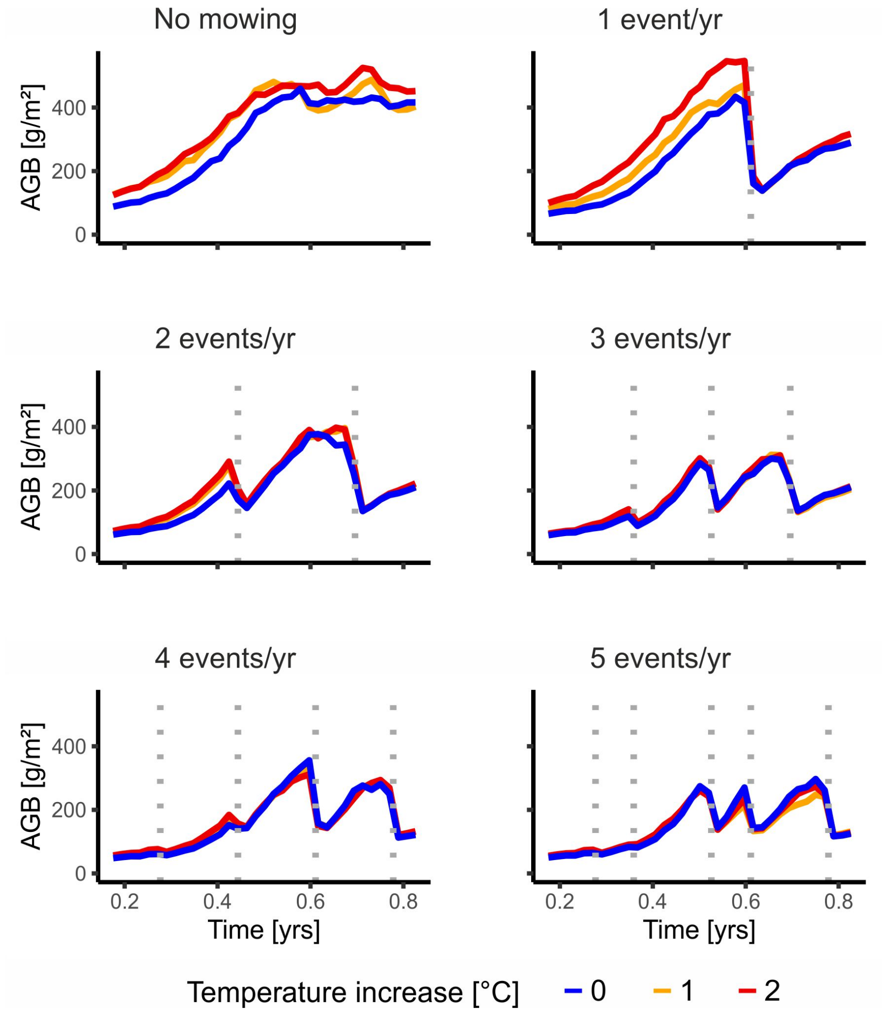


Figure B.6: Aboveground biomass (AGB) in the mixture of four plant functional types over time for different mowing frequencies and air temperature increase. Grey dotted lines mark each mowing event. Weekly means of averages over the vegetation periods of five simulation years are shown.

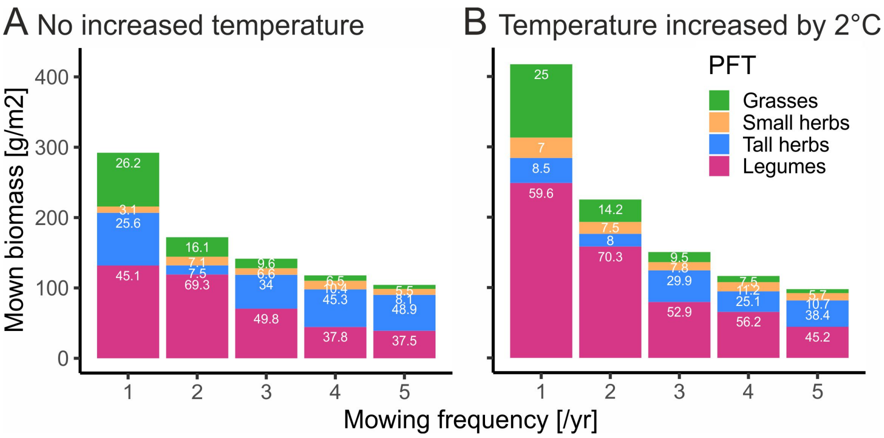


Figure B.7: Influences of different mowing frequencies on the relative and absolute abundances of plant functional types (PFTs) in mown biomass (aboveground biomass above 10 cm height) with (A) ambient climatic conditions and (B) with an increased temperature of 2°C in the 4-PFT mixture. Mown biomass corresponds to the average biomass amount removed per mowing event. Numbers are percentages of the total amount.

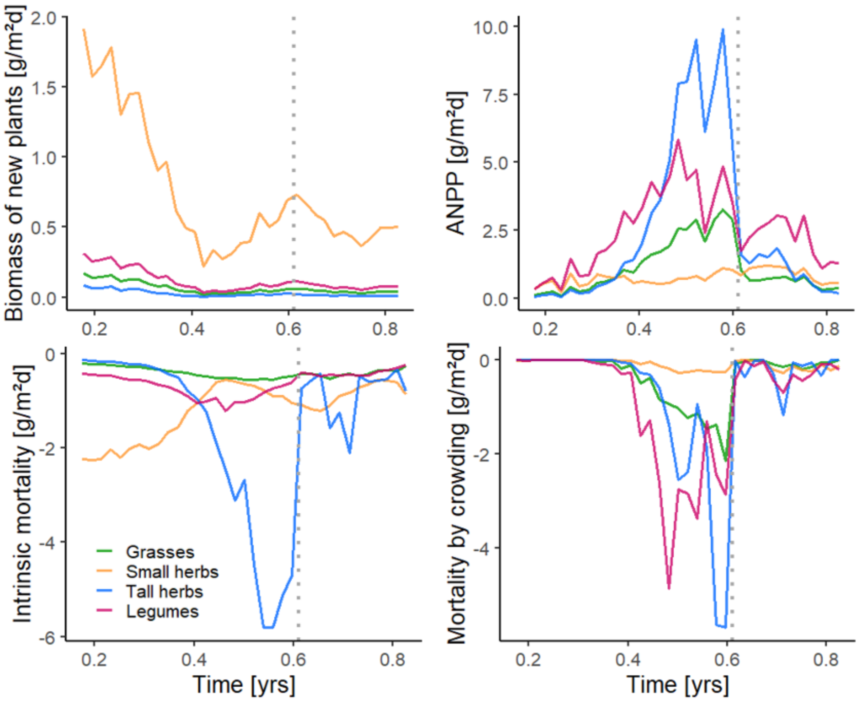


Figure B.8: Different productivity sources and losses of the PFTs in the 4-PFT mixture with one mowing event per year (marked by the gray dotted line). Mean courses over a year (averages were taken over simulation years 3 to 7, weekly means).

B.3 SUPPLEMENTARY TABLES

Table B.1: Parameter values of the grassland model GRASSMIND. For detailed descriptions of the parameters and processes in the model see Taubert, Hetzer, et al. (2020a). For a detailed description of the parameterization of the model see Schmid, Huth, et al. (2021).

Process	**Parameter**	**Shortcut**	**Grass**	**Small herbs**	**Tall herbs**	**Legumes**
Reproduction	Global ingrowth of seeds [1/day]	N_{seed}	3,215	4,809	659	2,241
	Reproduction age [yrs]	age_{rep}	0.59	0.09	0.48	0.32
	Seed biomass [g_{ODM}]	B_{seed}	1.38	0.88	1.75	5.68
	Germination rate of seeds [-]	$germ_{\%}$	0.66	0.75	0.62	0.78
	Seedling mortality [1/yr]	m_{seed}	9.0	68.6	13.9	15.1
Mortality	Mature mortality [1/yr]	m_{basic}	0.03	0.03	4.01	0.03
	Leaf life span [days]	LLS	90	42	33	114
	Root life span [days]	RLS	709	241	241	709
Geometry	Height-width ratio [-]	hw	1.2	0.4	0.7	0.9
	Specific leaf area of a single plant [cm^2/g_{ODM}]	SLA	63.12	100.98	81.61	72.16
	Shoot correction factor [t/m^3]	f_s	0.0011	0.0008	0.0012	0.0014
	Shoot-root ratio [-]	sr	2.35	4.05	3.99	13.01
Production	Max. leaf gross photosynthesis [$\mu mol_{CO2}/m^2/s$]	p_{max}	14.47	17.51	29.69	24.22
	Initial slope of light response curve [$\mu mol_{CO2}/\mu mol_{photon}$]	α	0.30	0.10	0.24	0.07
	Light extinction coefficient of leaves [-]	k	0.215	0.7	0.26	0.5
	Allocation rate (fraction of NPP) to shoot growth [-]	$alloc_{shoot}$	0.79	0.44	0.89	0.71
	Energy investment in rhizobia (fraction of NPP) [-]	$rhiz_{\%}$	0	0	0	0.2

Table B.2: Different scenarios for the analysis of influencing processes on aboveground net primary productivity ($ANPP$). Changes in equations of the model. In all scenarios, the actual gross primary production of the standard setting $GPP_{act}^{standard}$ was used for the calculation of the growth respiration R_{growth}.

Scenario	$\boldsymbol{ANPP = alloc_{\text{shoot}} * \left(GPP_{act} - (R_{main} + R_{growth})\right)}$		
	$\boldsymbol{GPP_{act}}$	$\boldsymbol{R_{main}}$	$\boldsymbol{R_{growth}}$
Standard	$GPP_{act}^{standard} = R_T * GPP_{pot}$ with $R_L = I_S / I_0$	$r_m * f_T * B$	$r_g \left(GPP_{act}^{standard} - r_m * f_T * B\right)$
No space competition	$R_T * GPP_{pot}$ with $R_L = I_S / I_0$	$r_m * f_T * B$	$r_g \left(GPP_{act}^{standard} - r_m * f_T * B\right)$
No shading	$R_T * GPP_{pot}$ with $R_L = 1$	$r_m * f_T * B$	$r_g \left(GPP_{act}^{standard} - r_m * f_T * B\right)$
No temperature effect on photosynthesis	$1 * GPP_{pot}$ with $R_L = I_S / I_0$	$r_m * f_T * B$	$r_g \left(GPP_{act}^{standard} - r_m * f_T * B\right)$
No temperature effect on respiration	$R_T * GPP_{pot}$ with $R_L = I_S / I_0$	$r_m * 1 * B$	$r_g \left(GPP_{act}^{standard} - r_m * 1 * B\right)$

Table B.3: Vegetation attributes of the 4-PFT mixture for different scenarios. Averages were taken over the vegetation periods from five simulation years. Abbreviations: AGB – aboveground biomass, LAI – leaf area index.

Temperature increase	**Mowing frequency**	**AGB [g/m^2]**	**LAI [-]**	**Height [m]**	**Plant density [/m^2]**
0°C	0	307.8	1.28	0.31	341
	1	216.8	0.84	0.25	345
	2	193.1	0.74	0.24	344
	3	166.9	0.59	0.22	351
	4	161.5	0.57	0.20	368
	5	152.6	0.51	0.19	361
2°C	0	366.6	1.57	0.35	304
	1	284.1	1.27	0.30	271
	2	216.5	0.89	0.26	303
	3	174.7	0.62	0.23	327
	4	166.4	0.58	0.21	331
	5	151.5	0.51	0.19	339

Table B.4: Productivity measures of the 4-PFT mixture for different scenarios (all in g/m²yr). Annual sums were taken over the vegetation periods from five simulation years. Abbreviations: ANPP – aboveground net primary productivity, phot – photosynthesis, resp – respiration.

Temperature increase	**Mowing frequency**	**ANPP**	**Seedling biomass**	**Intrinsic mortality**	**Mortality by crowding**	**ANPP loss by shading**	**ANPP loss due to temp (phot)**	**ANPP loss due to temp (resp)**
0°C	0	1931.9	242.7	898.6	948.0	25.6	106.9	-314.3
	1	1681.3	233.4	905.3	488.5	17.2	90.9	-546.3
	2	1625.9	237.9	875.4	490.7	13.8	82.1	-452.7
	3	1530.9	240.6	913.1	277.3	10.5	81.8	-306.2
	4	1602.4	252.7	952.7	353.8	9.4	76.7	-196.9
	5	1528.5	247.4	899.4	273.8	8.7	79.0	-239.3
2°C	0	2086.2	225.0	770.5	1213.0	31.8	62.6	-313.5
	1	1769.8	190.2	655.6	668.8	24.5	53.0	-534.9
	2	1661.6	205.3	797.8	462.2	16.5	45.3	-650.0
	3	1570.0	224.2	851.6	336.6	11.3	43.2	-275.4
	4	1491.6	224.3	865.9	301.4	10.7	40.7	-290.3
	5	1441.2	231.8	867.2	238.8	8.7	40.1	-348.0

Table B.5: Percentual proportions of plant functional types in aboveground biomass of the 4-PFT mixture for different scenarios.

Temperature increase	**Mowing frequency**	**Grasses**	**Small herbs**	**Tall herbs**	**Legumes**
0°C	0	0.22	0.09	0.12	0.57
	1	0.19	0.11	0.17	0.53
	2	0.17	0.12	0.20	0.51
	3	0.16	0.14	0.22	0.47
	4	0.15	0.16	0.31	0.39
	5	0.15	0.15	0.29	0.40
2°C	0	0.24	0.09	0.10	0.58
	1	0.16	0.12	0.10	0.62
	2	0.15	0.12	0.17	0.57
	3	0.15	0.15	0.23	0.47
	4	0.15	0.15	0.22	0.47
	5	0.15	0.17	0.24	0.44

C

APPENDIX OF CHAPTER 4: IMPACT OF MANAGEMENT, ENVIRONMENT AND CLIMATE CHANGE ON PRODUCTIVITY AND THE PROPORTION OF HERBS IN GRASSLANDS: A SIMULATION STUDY ACROSS GERMANY

C.1 SUPPLEMENTARY METHODS

C.1.1 *Soil module in GRASSMIND*

The soil module used in this study consists of carbon-nitrogen dynamics and soil water dynamics and is operated on a daily time scale. The modeled carbon-nitrogen dynamics were used from the CENTURY model version 4.0 (weekly dynamics scaled to daily dynamics with parameter adaptions according to the DAYCENT model version 4.5, (Parton, Hartman, et al., 1998, Parton, Stewart, et al., 1988). For modeling the soil water dynamics, processes were adopted from different soil models: CENTURY (Parton, Scurlock, et al., 1993), DAYCENT (Parton, Hartman, et al., 1998), BOWET (Mirschel et al., 1995) and CANDY (Franko et al., 1995). The following subsections describe the modeled soil water processes in detail with an overview shown in Fig. C.1. Plant-soil interactions (nitrogen and water uptake by plants) are described in the GRASSMIND model description provided under `https://formind.org/downloads/`.

C.1.1.1 *Snow*

Two snow pools are considered according to the CENTURY model: a solid snow pool and a liquid snow pool. Given daily measurements, precipitation is converted to solid snow if air temperature is below or equal to 0 °C, and subsequently accumulated in the solid snow pool (process 1 in Fig. C.1). If air temperature rises above 0 °C, the solid snow pool starts to melt and is partly or completely transferred to the liquid snow pool (amount dependent on air temperature and available solid snow, process 2 in Fig. C.1)(Parton, Hartman, et al., 1998). Under such temperature conditions, daily precipitation is not freezing and either added to the liquid snow pool (in case of a non-empty solid snow still exists in the snow pool; process 3 in Fig. C.1) or added to the liquid water flux (which is able to percolate into soil). If non-empty, some amount of the liquid snow pool is transferred to the liquid water flux (the content of the liquid snow pool should not exceed 5% of the water stored in the solid snow pool; process 4 in Fig. C.1). Water stored in the solid snow pool and the liquid snow pool partly sublimates each day (processes 5 and 6 in Fig. C.1), whereby the maximum amount sublimating is 0.87 times the daily potential evapotranspiration and proportionally subtracted from both pools.

C.1.1.2 *Interception and aboveground runoff*

If the solid snow pool is empty and air temperature is above 0 °C, the daily input of precipitation can be intercepted by the vegetation (process 7 in Fig. C.1). Intercepted water partly evaporates if it exceeds 1.3 times of the daily potential evapotranspiration (Mirschel et al., 1995). Some amount of the remaining water goes into the aboveground runoff (process 9 in Fig. C.1). Thus, liquid water flux WFl [mm/d] in soil corresponds to:

$$WF_l = P - I - R_a \tag{C.28}$$

with P being the daily precipitation, I the interception and R_a being the aboveground surface runoff (processes 7 and 9 in Fig. C.1).

C.1.1.3 *Vertical runoff*

Precipitation minus interception and aboveground runoff (processes 7 and 9 in Fig. C.1) or the melted liquid snow (process 4 in Fig. C.1) is added from top to bottom to the soil. Therefore, the soil profile is divided into 20 vertical water layers, each 10 cm thick (2 m depth in total). The amount of water transferred from one soil layer down to the next layer is determined by layer-specific soil properties such as field capacity and saturated conductivity (process 10 in Fig. C.1). Remaining water in the lowest soil layer is considered as belowground runoff.

C.1.1.4 *Evapotranspiration*

The soil water content in each soil layer is reduced by plant water uptake (here equivalent to plant transpiration) and evaporation. Soil evaporation thereby occurs only in the upper four soil layers (process 12, Fig. C.1)(Mirschel et al., 1995). As restriction, soil water content cannot fall below the layer-specific permanent wilting point (process 11, Fig. C.1).

C.1.2 *Study sites for reference data for the generic parameterization of the grassland model*

For the calibration and validation of the model, we used field measurements of five different field sites in Germany. At one of those sites, two different management regimes (intensive and extensive) were conducted resulting in six different grassland field plots considered.

C.1.2.1 *Sites used for model calibration*

The Global Change Experimental Facility (GCEF) was established in 2014 to investigate how climate change influences ecosystem services of different land-use types (Schädler et al., 2019). Different land use types were established on ten blocks of five plots each (26x24 m) under ambient and future climate conditions (five replicates for each type and condition). We used measurements of ten plots consisting of intensive and extensive grassland under ambient climate conditions (five plots, respectively). The field site is located in Bad Lauchstädt, Saxony-Anhalt, Germany (51°23’30 N, 11°52’49 E, 116 m a.s.l.) and shows a relatively low mean annual precipitation of 454 mm and a mean temperature of 10.5°C (2013–2017). The present soil type is highly fertile Chernozem and the field site is a former arable field. The five plots of intensive grassland were mown four times and fertilized three to four times per year (except for 2014). In the five extensive grassland plots, only moderate mowing (two events per year) was conducted and no fertilizer was applied.

The University of Giessen long-term Free Air Carbon dioxide Enrichment Experiment (GiFACE) studies the response of a semi-natural grassland to elevated CO_2 since 1998 and is located near Giessen, Hesse, Germany (50°32’ N, 8°41’3 E) (Jäger et al., 2003). With a mean temperature of 9.2°C and a mean annual rainfall of 554 mm (from 1995 to 2000), the site is colder and wetter than GCEF. The field has been managed as a meadow and fertilized with 50-80 kg N / (ha a) for at least 50 years. The soil is a Fluvic Gleysol with a texture of sandy clay loam over a clay layer. Three control rings with no enrichment of CO_2 included 10.3 m^2 harvest area each which consisted of up to almost 60 species and were mown twice per year and once fertilized in spring.

C.1.2.2 *Sites used for model validation*

The Biodiversity Exploratories are a large-scale long-term project to investigate the impact of land use on biodiversity and the modifying role of biodiversity change for land-use effects on ecosystem processes (Fischer, Bossdorf, et al., 2010). They comprise standardized field plots in three geographical regions of Germany with diverse management types and intensities in grassland and forest. We selected one experimental plot (50 x 50 m) from each region: one located in Schorfheide-Chorin (SEG) in North-eastern Germany (53°08’24 N, 13°52’48 E, BE SEG18), one located in Hainich-Dün (HEG) in Central Germany (51°16’48 N, 10°22’12 E, BE HEG26) and one located in Schwäbische Alb (AEG) in South-western Germany (48°24’36 N, 9°28’12 E, BE AEG50). The sites differ in their environmental conditions and management intensity. In the considered time period, SEG was the warmest and driest site (mean temperature 9.3 °C, mean annual precipitation 564 mm), AEG was the coldest and wettest site (7.4 °C, 935 mm) and HEG was in between (8.6 °C, 703 mm). In AEG, the soil types Cambisols and Leptosols were dominant in the selected experimental grassland plots. In HEG, Cambisols, Vertic Stagnosols and a few Stagnic Vertisols were chosen and in SEG, the characteristic soil type was mostly Cambisol.

C.1.3 *Data preparation*

C.1.3.1 *Vegetation attributes*

As reference data for the calibration and validation of the grassland model, temporal observation patterns of vegetation attributes were acquired.

At the GCEF, all vegetation patterns are averages over five replicate plots of intensively (plotcodes 1-5, 3-3, 5-2, 8-1, 10-4) and extensively (plots 1-1, 3-4, 5-5, 8-3, 10-2) managed grassland, respectively

(Schädler et al., 2019). Measured data was available from 2015 to 2017 in different temporal resolutions. Aboveground biomass was measured four times per year in the intensive and twice per year in the extensive grassland. Leaf area index (LAI) was measured about 15 times per year in both grassland types. Vegetation height was measured four times per year in the intensive grassland. Vegetation cover was measured three to four times in the intensive grassland and two times in the extensive grassland. For biomass and vegetation cover, species-specific data was available which were aggregated into four PFTs (grasses, small herbs, tall herbs, legumes) by taking sums over the species belonging to a PFT. We took the summed up biomass over species-specific biomasses as total biomass (as the amounts differed between the measurements).

At GiFACE, we used measurements over four consecutive years (1997-2000) (plotcode K2) from the Department of Plant Ecology, Justus-Liebig-University Gießen (Jäger et al., 2003). Aboveground biomass, vegetation height and vegetation cover were measured twice per year in spring and summer from 1997 to 2000. For vegetation cover, also species-specific measurements were taken. LAI was measured 15 to 22 times per year from 1998 to 2000.

From the Biodiversity Exploratories, we used measurements from 2008-2013 of the region Schorfheide Chorin (plotcode ID SEG18), from 2008-2013 of the region Hainich Dün (plotcode ID HEG26,) and from 2009-2013 of the region Schwäbische Alb (plotcode ID AEG50) (Fischer, Bossdorf, et al., 2010). At all sites, aboveground biomass, vegetation height and vegetation cover were measured once per year in spring. For cover, PFT-specific measurements were available.

All sites included in this study were mown and partly fertilized in the considered time periods, and no grazing took place. An overview of available measurements and detailed management is given in Table C.2.

C.1.3.2 *Soil, weather and management data*

In GCEF, the available measurement data for block 3 from the initial soil survey were complemented with soil data from Altermann et al. (2005) for the model simulations (Tables C.3 and C.4). Weather data was provided by the Department of Soil System Science at the UFZ. Potential evapotranspiration was computed according to the extended formula of Blaney-Criddle with parameters a = -1.55 and b = 0.96 (Weiss et al., 2019).

In GiFACE, soil texture was taken from measurements of the experimental control ring A2 (Jäger et al., 2003). Based on the texture, we classified the soil as loam and received missing soil properties of field capacity, permanent wilting point and porosity from Maidment (1993), as no depth-specific measurements were available. Weather measurements by the Department of Plant Ecology, Justus-Liebig-University Gießen included daily precipitation, mean temperature and irradiance. Daylength was computed according to Forsythe et al. (1995). Potential evapotranspiration was computed according to Turc with parameters $a = 0.31$, $b = 2.094$ (Diouf et al., 2016). Management data were provided by the Department of Plant Ecology, Justus-Liebig-University Gießen.

From the Biodiversity Exploratories, we used the experimental plots AEG50, HEG25 and SEG18. Soil texture was estimated based on the soil classification using BOART1000OB Version 2.0 (*TRIANET Soil* n.d.) (HEG26: Ut3, SEG18: Sl3, AEG50: Ut3). Saturated hydraulic conductivity was computed according to Saxton et al. (1986). Porosity was computed out of the measured bulk density (Maidment, 1993). Field capacity and permanent wilting point were taken from Maidment (1993) based on the soil classification. Measured weather was received from near weather stations provided in the national climate database by the Climate Data Center (CDC) of the German national meteorological service (Deutscher Wetterdienst, DWD) (`https://opendata.dwd.de/climate_environment/`) (AEG50: station ID 3402 Münsingen-Apfelstetten, HEG25: station ID 2925 Leinefelde, SEG18: station ID 164 Angermünde). These included the daily precipitation, mean daily temperature, sunshine duration and air humidity in the considered time periods, respectively. Daylength was computed according to Forsythe et al. (1995). For the computation of daily global irradiance, the approach of Angström was used with parameters a = 0.25, b = 0.5 based on Julian day, latitude, sunshine duration and daylength (Şen, 1998). Potential evapotranspiration was computed according to Turc with parameters a = 0.31, b = 2.094 (Diouf et al., 2016). Management data were received from Vogt et al. (2019).

Starting values for relative water content [-] and mineral nitrogen content [g/m^2] in soil were initially set to 1 for each soil layer. For a summary of soil parameter values used in the model see Tables C.3 and C.4.

C.1.3.3 *Calibration and validation*

For the parameterization, the model parameters were initially set to values of a parameter set received in a previous study for a local biodiversity experiment in Central Germany (Schmid, Huth, et al., 2021). To obtain a generic, regionally transferable parameterization, we selected 15 plant parameters with either high sensitivity on vegetation attributes in the model or correspondence to soil interactions and recalibrated them for each of the four PFTs (Table C.1). Thereby, only the parameters for the global ingrowth of seeds were site-specific. Calibration was done by using the dynamically dimensioned search algorithm within an optimization tool (Lehmann and Huth, 2015) with 10 simulation runs per plot (corresponds to 10 m²) per step.

All three study sites ($GCEF\_ext$, $GCEF\_int$ and $GiFACE$) were considered simultaneously by including the differences of simulation results from field measurements of vegetation attributes over all three measured plots in the objective function C_{Total} of the optimization algorithm:

$$C_{Total} = C_{GCEF\_ext} + C_{GCEF\_int} + C_{GiFACE} \tag{C.29}$$

For each study site, we considered all available measurements of aboveground biomass (AGB), leaf area index (LAI), vegetation height and cover within the selected time spans (Table C.2). Hence, the specific objective functions were:

$$C_{GCEF\_ext} = \sum_{i=1}^{3} \frac{\left|\sum_t x_{i,t} - \sum_t \hat{x}_{i,t}\right|}{\sum_t \hat{x}_{i,t}} + \frac{\sum_{PFT=1}^{4} \left|\sum_t b_{PFT,t} - \sum_t \hat{b}_{PFT,t}\right|}{\sum_{PFT=1}^{4} \sum_t \hat{b}_{PFT,t}} + \frac{\sum_{PFT=1}^{4} \left|\sum_t c_{PFT,t} - \sum_t \hat{c}_{PFT,t}\right|}{\sum_{PFT=1}^{4} \sum_t \hat{c}_{PFT,t}} \tag{C.30}$$

$$C_{GCEF\_int} = \sum_{i=1}^{4} \frac{\left|\sum_t x_{i,t} - \sum_t \hat{x}_{i,t}\right|}{\sum_t \hat{x}_{i,t}} + \frac{\sum_{PFT=1}^{4} \left|\sum_t b_{PFT,t} - \sum_t \hat{b}_{PFT,t}\right|}{\sum_{PFT=1}^{4} \sum_t \hat{b}_{PFT,t}} + \frac{\sum_{PFT=1}^{4} \left|\sum_t c_{PFT,t} - \sum_t \hat{c}_{PFT,t}\right|}{\sum_{PFT=1}^{4} \sum_t \hat{c}_{PFT,t}} \tag{C.31}$$

$$C_{GiFACE} = \sum_{i=1}^{4} \frac{\left|\sum_t x_{i,t} - \sum_t \hat{x}_{i,t}\right|}{\sum_t \hat{x}_{i,t}} + \frac{\sum_{PFT=1}^{4} \left|\sum_t c_{PFT,t} - \sum_t \hat{c}_{PFT,t}\right|}{\sum_{PFT=1}^{4} \sum_t \hat{c}_{PFT,t}} \tag{C.32}$$

where $b_{PFT,t}$ stands for the simulated proportional AGB of a PFT, $c_{PFT,t}$ stands for the simulated proportional cover of a PFT and $x_{i,t}$ are community vegetation attributes (total AGB, LAI, total vegetation cover and vegetation height) at time t. Respective variables with hat denote the corresponding measured data.

The validation of the resulting regional parameterization was done using field measurements of three further grassland sites in Germany. Like in the calibration step, deviations between simulated and measured grassland attributes were calculated for validation as described in the objective functions above.

For values of the objective function of the final parameter set see Table C.11.

C.1.3.4 *Scenario analysis: Grassland regions in Germany*

We used 24 locations representing different soil regions and natural areas in Germany in order to ensure a sufficient national representativeness (determined based on a natural area map and BÜK200 in Filipiak et al. (2022)). Five locations are distributed in the northern part, nine locations in the middle part and ten locations in the southern part of Germany (Fig. 4.1B). All locations were continuously used as grassland. Each soil region in Germany was represented by two locations. SeeFilipiak et al. (2022) for details.

Soil textures (silt, clay, sand), bulk densities and soil horizon thicknesses of the 24 representative locations were received from the soil map BÜK200 (BGR, 2018). Therein, texture and bulk density were provided as classes with an upper and lower delimiter, in accordance to the classification system of the KA5 soil mapping guideline used across Germany (Sponagel, 2005). Quantitative input values for the model were acquired by using the median of the upper and lower delimiter of a given interval. Initial relative water content [-] and mineral nitrogen content [g/m²] were again assumed to be 1 at the beginning of simulations. Field capacity [V%] and permanent wilting point [V%] were determined based on soil texture and bulk density (Wessolek et al., 2009). Soil porosity [V%] was calculated from bulk density (Maidment, 1993) and particle density was assumed to be 2.6 g/cm^3, based on the predominance of quartz in soil minerals. Saturated conductivity [mm/d] was computed according to (Saxton et al., 1986).

Measured climate data was received from weather stations provided in the national climate database by the Climate Data Center (CDC) of the German national meteorological service (Deutscher Wetterdienst, DWD) (`https://opendata.dwd.de/climate_environment/`). These included daily precipitation, mean daily air temperature, sunshine duration and air humidity from 1990 to 2019. Daylength was computed according to Forsythe et al. (1995). For the computation of daily global irradiance, the approach of Angström was used with parameters $a = 0.19$ and $b = 0.55$ (Şen, 1998. Potential evapotranspiration was computed according to Turc (1961) (Diouf et al., 2016) with a correction factor of 1.1 (DVWK, 1996) and correction for values from November to February according to Turc/Inovav with differentiation for temperatures (KLIWA, 2008).

Since measured climate data was not available for the entire time span at the locations Grünow (station ID 1869) and Weimar-Schöndorf (station ID 5424), we completed time gaps with data of Angermuende (station ID 164) and Jena (station ID 2444), respectively. Gaps in specific climate factors (especially air humidity, precipitation and sunshine duration; small time periods of 1 to 9 days) were filled by specific routines at the DWD.

c.1.3.5 *Management scenarios*

We used five different management scenarios representing different management intensities. The number of mowing and fertilization events per year and the amount of applied fertilizer per year increased with management intensity (Table C.7). The specific dates of mowing and fertilization events and fertilization amounts were determined by analyzing the real management of the 24 locations and the German Fertilizer Ordinance (DüV – Düngeverordnung – (DüV, 2017), number of cuts and dates detected by remote sensing (Griffiths et al., 2020, Filipiak et al., 2022). According to the real management, all 24 locations were mowed no more than three times per year, with only one location having three cuts in a year. Thus, real management (or near-real management) is represented by management intensity 1-3, while the remaining scenarios represent an intensification of use. We assumed a mowing height of 10 cm for each mowing event in the simulation model.

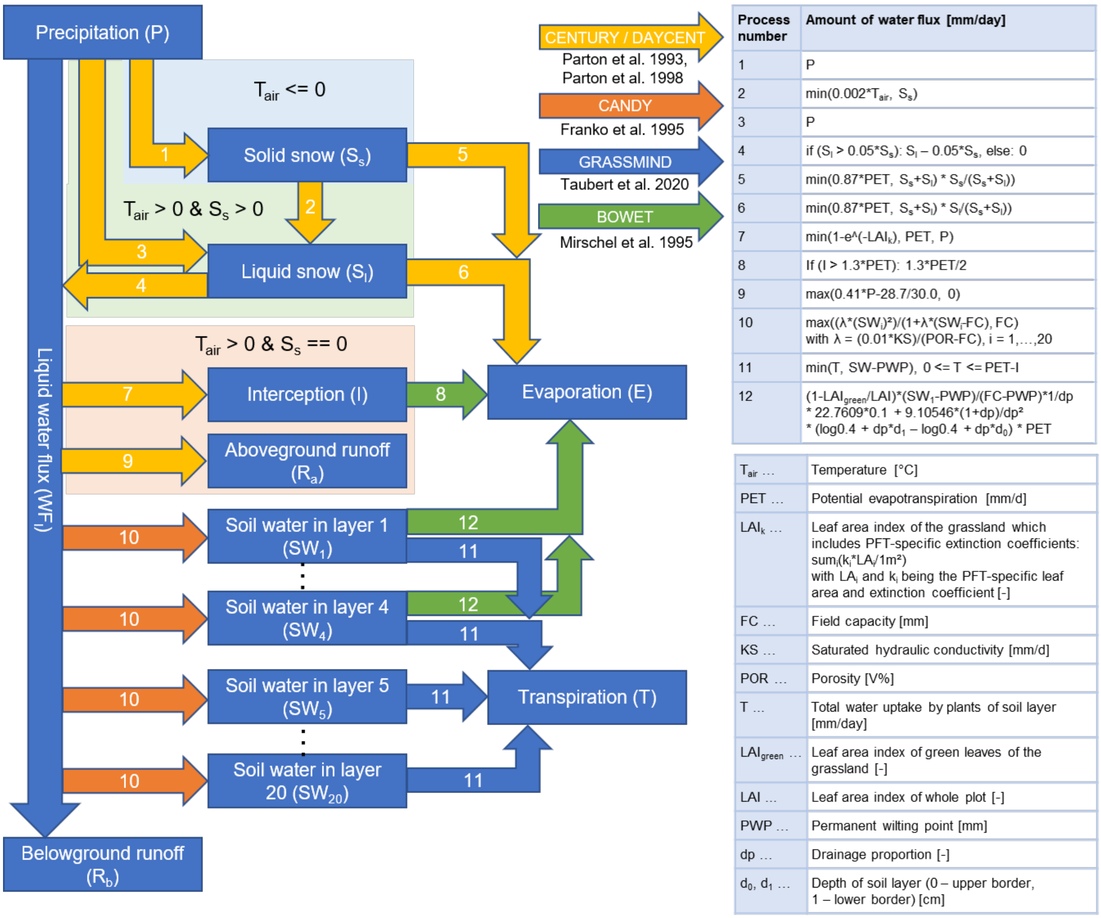
Management dates remained static for the climate change scenarios.

c.1.3.6 *Climate change scenarios*

We used three different climate change scenarios (RCP2.6, RCP4.5 and RCP8.5) to evaluate the impact of climate change (Moss et al., 2010). For each scenario, climate projections of only six different models were used (Table C.8) from the reference ensemble (same model projections for each scenario), provided by the German national meteorological service (Deutscher Wetterdienst, DWD) (Brienen et al., 2020). Hence, we conducted six simulations per RCP scenario per location and management scenario. The simulation output (productivity and biomass proportion of herbs) was then averaged over the six models for the respective RCP scenario and location. In leap years, the day with the date 29th of February was excluded in the simulation.

The simulated climate data included daily precipitation, mean daily air temperature and global irradiance that were directly used as input for the grassland model. Daily potential evapotranspiration was computed based on the method of Hargereaves and Samni using extraterrestrial radiation, maximal temperature, minimal temperature and mean temperature per day (Hargreaves and Samani, 1985). The required extraterrestrial radiation was computed according to Iqbal (1983). Daylength was computed according to Forsythe et al. (1995).

C.2 SUPPLEMENTARY FIGURES



Process number	Amount of water flux [mm/day]
1	P
2	$\min(0.002*T_{air}, S_s)$
3	P
4	if ($S_l > 0.05*S_s$): $S_l - 0.05*S_s$, else: 0
5	$\min(0.87*PET, S_s+S_l) * S_s/(S_s+S_l))$
6	$\min(0.87*PET, S_s+S_l) * S_l/(S_s+S_l))$
7	$\min(1-e$^$(-LAI_k), PET, P)$
8	If ($I > 1.3*PET$): $1.3*PET/2$
9	$\max(0.41*P-28.7/30.0, 0)$
10	$\max((\lambda*(SW_i)^2)/(1+\lambda*(SW_i-FC), FC)$ with $\lambda = (0.01*KS)/(POR-FC)$, $i = 1,\dots,20$
11	$\min(T, SW-PWP)$, $0 <= T <= PET-I$
12	$(1-LAI_{green}/LAI)*(SW_1-PWP)/(FC-PWP)*1/dp$ $* 22.7609*0.1 + 9.10546*(1+dp)/dp^2$ $* (\log0.4 + dp*d_1 - \log0.4 + dp*d_0) * PET$

T_{air} …	Temperature [°C]
PET …	Potential evapotranspiration [mm/d]
LAI_k …	Leaf area index of the grassland which includes PFT-specific extinction coefficients: $\mathrm{sum}_i(k_i*LA_i/1m^2)$ with LA_i and k_i being the PFT-specific leaf area and extinction coefficient [-]
FC …	Field capacity [mm]
KS …	Saturated hydraulic conductivity [mm/d]
POR …	Porosity [V%]
T …	Total water uptake by plants of soil layer [mm/day]
LAI_{green} …	Leaf area index of green leaves of the grassland [-]
LAI …	Leaf area index of whole plot [-]
PWP …	Permanent wilting point [mm]
dp …	Drainage proportion [-]
d_0, d_1 …	Depth of soil layer (0 – upper border, 1 – lower border) [cm]

Figure C.1: Soil water processes included in the simulation model. The numbers of the processes correspond to the order in which the processes take place in the model. The different colors of the arrows indicate from which soil model processes were taken.

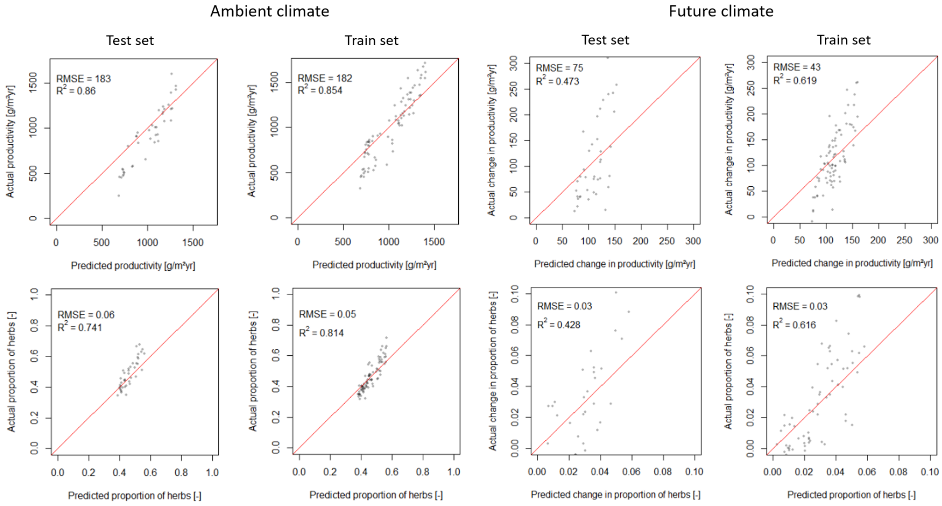


Figure C.2: Results of the conditional inference forests predicting productivity and the proportion of herbs in biomass of the simulated grasslands.

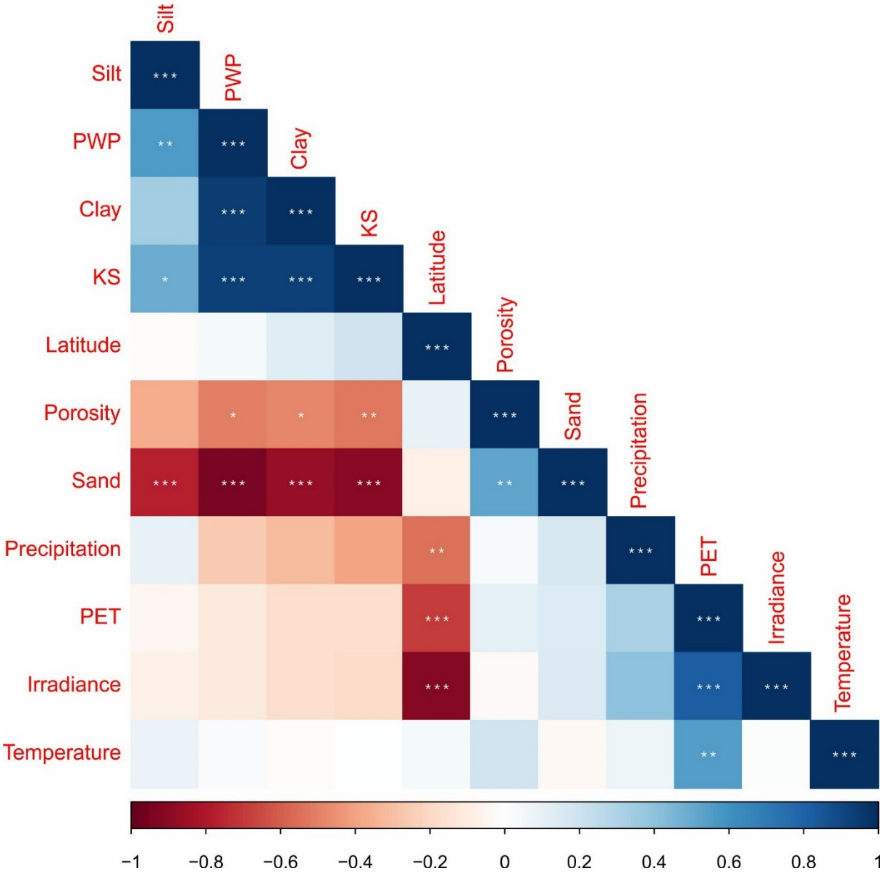


Figure C.3: Pearson correlation coefficients between different environmental variables of the 24 representative grassland sites across Germany. Color denotes the sign and degree of the relations. Asterisks denote statistical significance of the coefficient (***: $p < 0.001$, **: $p < 0.01$ and *: $p < 0.05$). $N = 24$ samples were used. Abbreviations: PET – potential evapotranspiration, KS – saturated conductivity in soil, PWP – permanent wilting point.

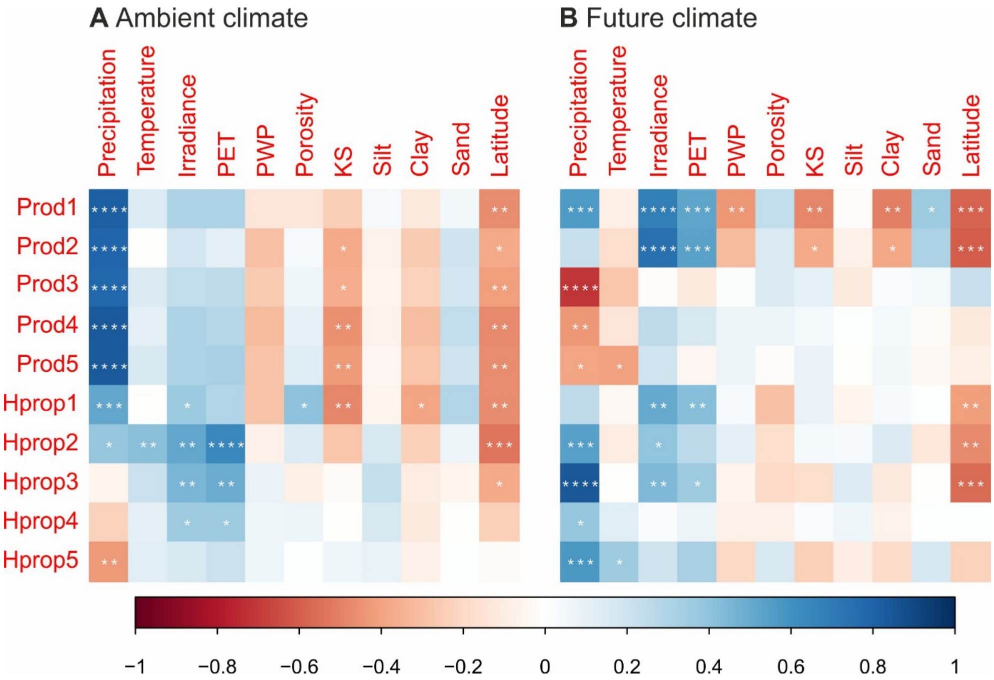


Figure C.4: Pearson correlation coefficients between productivity (Prod) and biomass proportion of herbs (Hprop) and different environmental variables for different management intensities (1-5). (A) shows correlation to the total vegetation attributes, (B) shows correlations to the changes in the correlation attributes. Color denotes the sign and degree of the relations. Asterisks denote statistical significance of the coefficient (****: $p < 0.001$, ***: $p < 0.01$, **: $p < 0.05$ and *: $p < 0.1$). $N = 24$ samples were used for each management intensity. Abbreviations: PET – potential evapotranspiration, KS – saturated conductivity in soil, PWP – permanent wilting point.

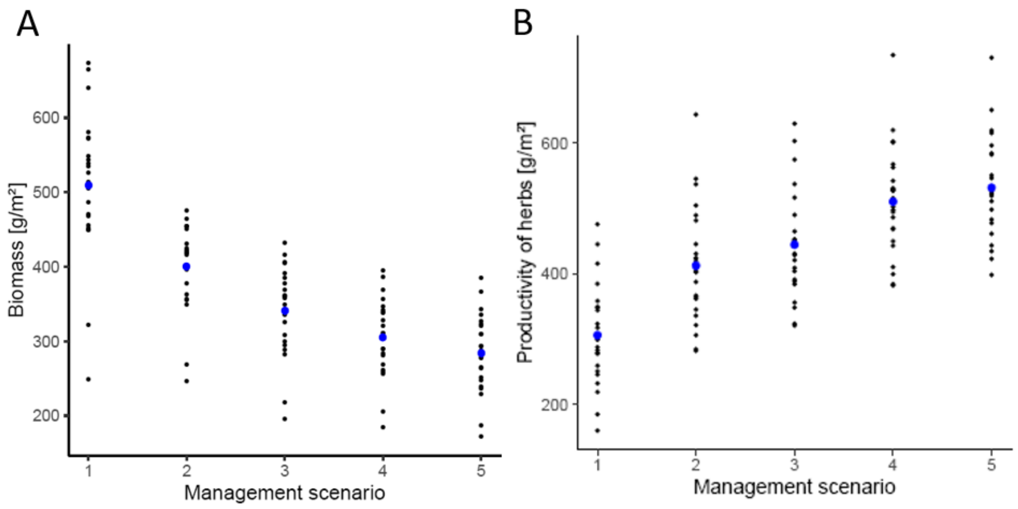


Figure C.5: Impact of management intensity on (A) grassland biomass and (B) productivity of herbs in the model. Grassland biomass corresponds to mean aboveground biomass on day before a mowing event. Black dots depict the different sites in Germany, blue dots are means over all sites.

C.3 SUPPLEMENTARY TABLES

Table C.1: Parameter values of the final generic parameterization of the grassland model GRASSMIND.

Process	Parameter	Shortcut	Grass	Small herbs	Tall herbs	Legumes	Reference
Reproduction	Global ingrowth of seeds* [1/day]	N_{seed}	361 (3,353)	753 (3,543)	3,755 (1,695)	2346 (1776)	calibrated
	Reproduction age [yrs]	age_{rep}	0.27	0.17	0.45	0.40	calibrated
	Seed biomass [g_{ODM}]	B_{seed}	1.38	0.88	1.75	5.68	Heisse et al. (2007)
	Germination rate of seeds [-]	$germ_{\%}$	0.79	0.39	0.87	0.72	Heisse et al. (2007) and calibrated
	Seedling mortality [1/yr]	m_{seed}	31.2	58.6	31.9	23.0	calibrated
Mortality	Mature mortality [1/yr]	m_{basic}	0.03	0.03	4.01	0.03	Schmid, Huth, et al. (2021)
	Leaf life span [days]	LLS	90	42	33	114	Schmid, Huth, et al. (2021)
	Root life span [days]	RLS	159	311	130	741	Tjoelker et al. (2005) and calibrated
	Plant life span [yrs]	$life$	20	20	20	20	Predefined
Geometry	Height-width ratio [-]	hw	0.5	3.1	3.4	5.7	calibrated
	Specific leaf area of a single plant [cm^2/g_{ODM}]	SLA	111.79	47.25	51.50	83.14	calibrated
	Shoot correction factor [t_{ODM}/m^3]	f_s	0.0014	0.0061	0.0014	0.0034	calibrated
	Shoot-root ratio [-]	sr	16.09	2.72	6.07	15.91	(Heisse et al. (2007)) and calibrated
Production	Max. leaf gross photosynthesis [$\mu mol_{CO_2}/m^2/s$]	p_{max}	14.47	17.51	29.69	24.22	Schmid, Huth, et al. (2021)
	Initial slope of light response curve [$\mu mol_{CO_2}/\mu mol_{photon}$]	α	0.18	0.37	0.38	0.59	calibrated
	Light extinction coefficient of leaves [-]	k	0.215	0.7	0.26	0.5	Thornley and France (2007) and estimated
	Transmission coefficient of leaves [-]	m	0.1	0.1	0.1	0.1	Thornley and France (2007)

	Maintenance respiration rate [1/day]	r_m	0.02	0.02	0.02	0.02	Amthor (1984)
	Fraction of gross productivity attributed to respiratory costs for growth [-]	r_g	0.2	0.2	0.2	0.2	Fixed
	Allocation rate (fraction of NPP) to shoot growth [-]	$alloc_{shoot}$	0.79	0.44	0.89	0.71	Schmid, Huth, et al. (2021)
	Energy investment in rhizobia (fraction of NPP) [-]	$rhiz_{\%}$	0	0	0	0.17	Minchin et al. (1981)
Soil	Water use efficiency $[g_{ODM}/kg_{H_2O}]$	wue	14.6	4.5	10.6	12.4	calibrated
	C-N ratio of green material [-]	CN_{green}	5.7	17.9	0.4	36.2	calibrated
	C-N ration of brown material [-]	CN_{brown}	74.3	79.6	44.1	40.0	calibrated
	Shoot biomass – rooting depth relation parameters [-]	r_1 / r_2	5.881 / 0.336	4.804 / 0.379	5.212 / 0.371	4.414 / 0.313	calibrated
	Specific root length $[m/g_{ODM}]$	SRL	360,965,518	365,914,781	248,684,774	183,212,952	calibrated

*Value corresponds to ingrowth received for the site GiFACE, value for GCEF is shown in brackets.

Table C.2: Available measurements of the used grasslands sites for the calibration and validation of the grassland model.

		GCEF, extensive	GCEF, intensive	GiFACE	BE HEG26	BE SEG18	BE AEG50
Measured community vegetation attributes	AGB	x	x	x	x	x	x
	LAI	x	x	x			
	Height		x	x	x	x	x
	Cover	x	x	x	x	x	x
Measured PFT-specific vegetation attributes	AGB	x	x				
	Cover	x	x	x	x	x	x
Simulation time span for calibration		2014 - 2017	2013 - 2017	1995 - 2000	2006-2013	2006-2013	2008-2013
Spin up time* [yrs]		0	0	2	2	2	1
Date of sowing †		04.03.2014	24.09.2013	NA – 15.05.1995 in the model	NA – 15.05.2006 in the model	NA – 15.05.2006 in the model	NA – 14.05.2008 in the model
Mowing events per year		2	4	2	1-2	2	2
Mowing height [cm]		5	5	10	4	10	7
Fertilization events per year		0	3-4	1	0	0	1
Mean fertilization amount per year (kg N / ha)		-	232.5	40	-	-	58

*Spin up time corresponds to additional simulation years in permanent grasslands prior to the time span with available field measurements for calibration. †If no sowing date was available (permanent grasslands) we assumed the 15th May as sowing date in the spin up time

Table C.3: Soil texture at different field sites used for the calibration and validation of the grassland model. Values marked with (M) were measured at the site, values marked with (R1) were taken from (*TRIANET Soil* n.d.) based on the soil type received by the soil map BOART1000OB Version 2.0 and marks with (R2) were taken from Altermann et al. (2005).

	GCEF	GiFACE	BE HEG26	BE SEG18	BE AEG50
Silt content [%]	56 (M, R2)	40 (M)	76 (R1)	25 (R1)	76 (R1)
Clay content [%]	14 (M, R2)	28 (M)	14 (R1)	10 (R1)	14 (R1)
Sand content [%]	30 (M, R2)	32 (M)	10 (R1)	65 (R1)	10 (R1)

Table C.4: Soil properties at different sites used for the calibration and validation of the grassland model. The mark (M) means that the value was measured in the field, (C) denotes calculations using pedotransfer functions (Maidment, 1993, Saxton et al., 1986), (A) represents a model assumption, and values marked with (R1) were taken from Maidment (1993) and with (R2) from Altermann et al. (2005).

Site	**Soil depth [m]**	**Field capacity [V%]**	**Permanent wilting point [V%]**	**Porosity [V%]**	**Saturated hydraulic conductivity [mm/d]**
GCEF	0.0 – 0.3	38.4 (R2)	15.5 (R2)	48.46 (R2, C)	604 (R2)
	0.3 – 0.5	38.5 (R2)	15.1 (R2)	49.05 (R2, C)	280 (R2)
	0.5 – 0.6	37.7 (R2)	15.0 (R2)	50.75 (R2, C)	277 (R2)
	0.6 – 1.3	38.2 (R2)	9.5 (R2)	46.82 (R2, C)	108 (R2)
	1.3 – 1.7	15.6 (R2)	7.0 (R2)	31.95 (R2, C)	1243 (R2)
	1.7 – 2.0	20.2 (R2)	8.4 (R2)	35.36 (R2, C)	625 (R2)
GiFACE	0.0 – 2.0	27.0 (R1)	12.0 (R1)	46.00 (R1)	317 (R1)
BE HEG26	0.0 – 2.0	33.0 (R1)	13.0 (R1)	72.10 (C)	386 (C)
BE SEG18	0.0 – 2.0	12.5 (R1)	5.5 (R1)	47.40 (C)	244 (C)
BE AEG50	0.0 – 2.0	33.0 (R1)	13.0 (R1)	71.20 (C)	386 (C)

Table C.5: Climate stations of Germany's national meteorological service (DWD) and coordinates of the 24 locations used for the Germany-wide scenario analysis.

	DWD climate station		**Coordinates of the simulation site (UTM)**	
	Station ID	City	Latitude	Longitude
1	4625	Schwerin	5981232.791	600632.6635
2	1869	Grünow	5925692.302	838739.8694
3	4745	Soltau	5850022.054	561354.6638
4	1766	Münster/Osnabrück	5745383.778	408576.8236
5	691	Bremen	5905259.737	458924.1372
6	1975	Hamburg-Fuhlsbüttel	5944929.404	530520.4968
7	2928	Leipzig-Holzhausen	5668108.189	726361.7216
8	198	Artern	5666391.157	654474.1205
9	5424	Weimar-Schöndorf	5643160.975	659905.5265
10	2925	Leinefelde	5686619.661	587667.7663
11	2261	Hof	5597247.988	664123.618
12	2667	Köln-Bonn	5601235.436	396621.051
13	3287	Michelstadt-Vielbrunn	5557178.958	534909.6763
14	5440	Weißenburg-Emetzheim	5447302.341	635079.6951
15	282	Bamberg	5528471.917	664595.09
16	2700	Kösching	5412865.008	680353.7853
17	2812	Lahr	5341255.83	447780.0085
18	5397	Weiden	5494562.014	744560.497
19	5629	Wittenberg	5749759.486	737313.01
20	3379	München-Stadt	5326602.602	696929.7147
21	232	Augsburg	5372124.357	675712.8542
22	73	Aldersbach-Kriestorf	5375855.28	785682.9702
23	4261	Rosenheim	5285367.136	722233.555
24	3366	Mühldorf	5298301.368	780954.5959

Table C.6: Soil properties of the different sites used for the Germany-wide scenario analysis.

	Silt / clay / sand [%]	**Soil depth [m]**	**Field capacity [V%]**	**Permanent wilting point [V%]**	**Porosity [V%]**	**Saturated hydraulic conductivity [mm/d]**
1	26 / 19 / 55	0.0 – 0.4	23	10	42.3	244
		0.4 – 0.7	25	16	26.9	632
		0.7 – 2.0	26	15	34.6	636
2	34 / 18 / 47	0.0 – 0.3	21	8	42.3	114
		0.3 – 0.4	22	10	34.6	244
		0.4 – 0.8	26	16	26.9	632
		0.8 – 2.0	27	16	34.6	634
3	13 / 3 / 84	0.0 – 0.6	24	7	42.3	37
		0.6 – 2.0	12	3	34.6	11
4	31 / 36 / 33	0.0 – 0.7	24	13	34.6	417
		0.7 – 1.2	25	16	26.9	938
		1.2 – 2.0	34	29	34.6	1094
5	58 / 40 / 2	0.0 – 0.2	36	24	42.3	1012
		0.2 – 2.0	33	23	34.6	1012
6	58 / 40 / 2	0.0 – 0.2	36	24	42.3	1012
		0.2 – 2.0	33	23	34.6	1012
7	46 / 13 / 41	0.0 – 0.2	29	11	42.3	332
		0.2 – 0.9	27	11	34.6	332
		0.9 – 1.4	30	19	34.6	675
		1.4 – 2.0	19	8	34.6	114
8	46 / 27 / 27	0.0 – 0.6	33	17	42.3	629
		0.6 – 0.7	31	17	34.6	639
		0.7 – 1.0	27	11	34.6	332
		1.0 – 2.0	30	21	34.6	938
9	45 / 53 / 2	0.0 – 0.3	33	23	34.6	1012
		0.3 – 2.0	34	29	34.6	1094
10	42 / 53 / 5	0.0 – 0.3	31	24	34.6	1004
		0.3 – 2.0	34	29	34.6	1094
11	43 / 15 / 43	0.0 – 0.3	27	11	34.6	332
		0.3 – 0.9	30	19	34.6	675
		0.9 – 1.2	25	12	26.9	336
		1.2 – 2.0	20	10	26.9	244
12	60 / 14 / 26	0.0 – 0.1	31	14	42.3	404
		0.1 – 0.5	30	19	34.6	675
		0.5 – 2.0	27	11	34.6	332
13	19 / 7 / 73	0.0 – 0.3	23	10	42.3	244
		0.3 – 0.5	22	10	34.6	244
		0.5 – 2.0	19	8	34.6	114
14	33 / 23 / 44	0.0 – 0.3	21	8	42.3	114
		0.3 – 0.6	19	8	34.6	114
		0.6 – 2.0	26	20	26.9	856
15	25 / 69 / 6	0.0 – 0.3	33	23	34.6	1012
		0.3 – 0.4	34	29	34.6	1094
		0.4 – 2.0	41	34	42.3	1046
16	34 / 28 / 38	0.0 – 0.4	30	11	50.0	332
		0.4 – 0.8	28	16	34.6	632
		0.8 – 2.0	30	21	34.6	938

17	24 / 13 / 62	0.0 – 0.2	27	15	42.3	636
		0.2 – 0.6	26	15	34.6	636
		0.6 – 2.0	22	10	34.6	244
18	19 / 4 / 77	0.0 – 0.3	23	12	50.0	114
		0.3 – 0.6	23	10	42.3	244
		0.6 – 0.8	20	5	42.3	10
		0.8 – 2.0	18	5	34.6	10
19	23 / 19 / 58	0.0 – 0.6	25	13	42.3	417
		0.6 – 1.3	26	15	34.6	636
		1.3 – 2.0	24	15	26.9	636
20	35 / 9 / 56	0.0 – 0.2	30	16	42.3	632
		0.2 – 0.4	31	24	34.6	1004
		0.4 – 2.0	22	7	34.6	37
21	31 / 15 / 54	0.0 – 0.3	28	16	34.6	632
		0.3 – 0.9	27	16	34.6	634
		0.9 – 1.0	24	13	34.6	417
		1.0 – 2.0	22	10	34.6	243
22	59 / 35 / 6	0.0 – 0.2	28	10	34.6	856
		0.2 – 0.4	31	24	34.6	1004
		0.4 – 1.2	33	23	34.6	1012
		1.2 – 2.0	31	20	34.6	860
23	44 / 4 / 52	0.0 – 0.1	24	7	42.3	37
		0.1 – 2.0	24	7	34.6	36
24	53 / 42 / 5	0.0 – 0.1	35	24	50.0	1004
		0.1 – 0.3	33	24	42.3	1004
		0.3 – 0.5	39	30	42.3	1094
		0.5 – 2.0	30	22	34.6	1012

Table C.7: Management regimes used for the scenario analysis.

Management intensity (Number of mowing and fertilization events per year)	**Mowing dates**	**Fertilization dates**	**Amounts of applied fertilizer [kg N/ha]**
1	01.08.	01.04.	55
2	01.06., 01.09.	01.04., 15.06.	65, 35
3	01.05., 01.07, 01.09.	15.03., 15.05., 15.07.	125, 32.5, 32.5
4	15.04., 15.06., 01.08., 01.10.	01.03., 01.05., 01.07., 15.08.	165, 40, 20, 20
5	01.04., 15.05., 01.07., 15.08., 15.10.	01.03., 15.04., 01.06., 15.07., 01.09.	210, 25, 25, 25, 25

Table C.8: Climate projections used for the scenario analyses. [rcp] has to be replaced by "rcp26", "rcp45" and "rcp85" for the corresponding RCP scenario.

Climate projections	ICHEC-EC-EARTH_[rcp]_r12i1p1_CLMcom-CCLM4-8-17_v1 ICHEC-EC-EARTH_[rcp]_r12i1p1_KNMI-RACMO22E_v1 ICHEC-EC-EARTH_[rcp]_r12i1p1_SMHI-RCA4_v1 ICHEC-EC-EARTH_[rcp]_r3i1p1_DMI-HIRHAM5_v1 MPI-M-MPI-ESM-LR_[rcp]_r1i1p1_MPI-CSC-REMO2009_v1 MPI-M-MPI-ESM-LR_[rcp]_r2i1p1_MPI-CSC-REMO2009_v1

Table C.9: Comparison of vegetation attributes observed in the field and simulated at experimental sites used for model calibration and validation. The values given correspond to an averaged measurement over the measurement days.

Study site	**Attribute**	**Observation**	**Simulation**
GCEF intensive	Biomass [g/m²]	315.0	138.1
	Leaf area index [-]	3.07	1.80
	Vegetation height [cm]	31.6	15.5
	Vegetation cover [-]	0.98	1.01
GCEF extensive	Biomass [g/m²]	400.8	247.6
	Leaf area index [-]	1.50	1.82
	Vegetation cover [-]	0.93	1.05
GiFACE	Biomass [g/m²]	351.7	347.1
	Leaf area index [-]	3.74	3.46
	Vegetation height [cm]	81.9	29.6
	Vegetation cover [-]	0.82	1.00
AEG50	Biomass [g/m²]	418.1	174.3
	Vegetation height [cm]	43.1	16.7
	Vegetation cover [-]	1.53	1.05
HEG26	Biomass [g/m²]	199.0	200.1
	Vegetation height [cm]	35.8	24.4
	Vegetation cover [-]	0.70	1.02
SEG18	Biomass [g/m²]	345.2	126.1
	Vegetation height [cm]	40.3	19.1
	Vegetation cover [-]	0.98	1.01

Table C.10: Comparison of herb proportion in field observations and simulation results at experimental sites used for model calibration and validation. Herbs correspond to the PFTs small herbs, tall herbs and legumes.

Study site	**Attribute**	**Observation [%]**	**Simulation [%]**
GCEF intensive	Aboveground biomass	0.24	13.23
	Vegetation cover	1.15	2.89
GCEF extensive	Aboveground biomass	53.56	13.04
	Vegetation cover	72.91	2.80
GiFACE	Vegetation cover	37.23	23.88
AEG50	Vegetation cover	32.27	27.71
HEG26	Vegetation cover	11.68	28.94
SEG18	Vegetation cover	25.37	24.78

Table C.11: Values of the objective function at sites used for calibration and validation. Values of the total objective function C_{Total} and values of different terms of the objective function corresponding to community vegetation attributes $x_{i,t}$ (first term), proportional biomass of the PFTs $b_{PFT,t}$ (second term) and the proportional cover of the PFTs $c_{PFT,t}$ (third term).

Study site	**Total objective function C_{Total}**	**Community vegetation attributes $x_{i,t}$**	**Proportional biomass $b_{PFT,t}$**	**Proportional cover $c_{PFT,t}$**
GCEF intensive	1.87	1.12	0.62	0.13
GCEF extensive	2.42	0.50	0.54	1.38
GiFACE	0.56	0.11	NA	0.45
AEG50	2.11	1.27	0.40	0.44
HEG26	2.84	1.54	0.99	0.31
SEG18	1.56	1.02	0.40	0.14

D

APPENDIX OF CHAPTER 5: NETWORK SCIENCE APPLIED TO FOREST MEGAPLOTS: TROPICAL TREE SPECIES COEXIST IN SMALL-WORLD NETWORKS

D.1 SUPPLEMENTARY METHODS

D.1.1 *Geographic conditions of the study sites*

The investigated study sites are located in Panama (Barro Colorado Island), Sri Lanka (Sinharaja) and Taiwan (Fushan). All forests are old-growth forests (Tsai et al., 2015, Losos and Leigh, 2004). BCI has an annual rainfall of 2551 mm with a severe dry season from December to April or May (Losos and Leigh, 2004). The average diurnal temperature maximum is 31.1°C, the minimum 23.2°C. The plot is mostly located on a 140 m above sea level plateau including gentle slopes on the fringes. Unusually severe droughts associated with El Niño events (such as those in 1983 and 1998) are the most important natural disturbance that can provoke high tree mortalities and subsequent canopy openings3.

Sinharaja is with 5016 mm/year rainier than BCI, due to the missing distinct dry season. With 24.7°C as the average diurnal temperature maximum and 20.4°C as the minimum it is colder and has less temperature fluctuations. The 25 ha plot lies between 424 and 575 m above sea level and encompasses a central valley bounded by two slopes.

In Fushan, the annual rainfall is with 4271 mm/year between BCI and Sinharaja (Su et al., 2007). Due to monsoons and typhoons it is cool and rainy in winter and warm and humid in summer. This results in an average temperature of 18.2°C. The plot has a hill in the western part and a small creek traversing the eastern and southern parts. The woody plant community at the Fushan plot is subject to frequent natural disturbances primarily driven by typhoon induced flooding, landslides, soil-erosion, and wind-induced branch damage1.

D.1.2 *Sensitivity to allometric relationships of the networks*

For each tree individual, we chose equal allometric relationships for calculating tree crown diameter and tree height, regardless of species identities. To assess the influence of possible variations among different species, we conducted analyses in which we put noise on (i) tree crown diameters (interaction zones) and on (ii) tree heights (see 5.5 Methods, equation (5.11) and (5.12)). For each species, we therefore multiplied uniformly distributed factors ε_1, ε_2 within a certain range (e.g., between 0.8 and 1.2 for 20 % noise extent) to the parameters of the allometric relationships (for (i): i_1 and i_2, for (ii): h_1 and h_2, see Table D.6):

$$d^{\varepsilon}_{int}(dbh) = f \cdot (i_1 \cdot \varepsilon_1) \cdot dbh^{(i_2 \cdot \varepsilon_2)} \tag{D.33}$$

$$h^{\varepsilon}(dbh) = (h_1 \cdot \varepsilon_1) \cdot dbh^{(h_2 \cdot \varepsilon_2)} \tag{D.34}$$

As the mean interaction diameter ($\overline{d^{\varepsilon}_{\text{int}}}$) differed with increasing noise, we corrected the calculated values by a linear shift ($-(\overline{d^{\varepsilon}_{\text{int}}} - \overline{d_{\text{int}}})$) to obtain in total a mean interaction diameter equal to that of the network without noise ($\overline{d_{\text{int}}}$). Note that analysis (ii) affected only the directed networks, as tree heights are not relevant for the undirected networks of the main manuscript. Both analyses revealed that deviations of tree crown diameters and tree heights from the initial allometric relationships have only minor impact on the resulting tree networks and species networks (Tables D.8 and D.9, Fig. D.13).

D.1.3 *Sensitivity analysis of the interaction zone*

The interaction zone (diameter of the tree disk) is assumed to be proportional to the tree crown diameter which is related to the stem diameter of a tree (e.g., (Bohlman and O'Brien, 2006), see 5.5 Methods for details). The proportionality factor f is derived as 1.5, for which all trees (nodes) in the network are connected (e.g., at BCI). Due to the changing insolation angle of the sun during the day and the lateral root expansion an interaction zone larger than 1 (i.e. identical to the tree crown projection area) seems to be reasonable (Schenk and Jackson, 2002). A factor of 1 would result in a tree network with more than 700 components that means a forest network with many isolated tree clusters independent from each other. Figure D.12 shows that the shape of the node degree distribution $P_\mathrm{t}(k)$ of the tree network and the cumulative distribution $P_\mathrm{s,cum}(k)$ of the species network are not influenced by the selection of different proportionality factors. In addition, there are only minor changes in the relation between the clustering coefficient C and the average path length L (Table D.7). Consequently, the small-world behavior of the species interaction network does not depend on the size of the chosen interaction zone.

D.1.4 *Testing the scale-free property*

Scale-free networks are characterized by a node degree distribution which follows a power law. To test for this behavior, we fit a power law with exponential cut-off to the logarithmic binned frequencies of node degrees and compared it to a power-law distribution. For the truncated power-law fit we conduct the method proposed by Barabási (2016) to find the fitting parameters k_min, k_cut and γ:

$$p(k) = \frac{(1/k_\mathrm{cut})^{1-\lambda}}{\Gamma(1-\lambda, k_\mathrm{min}/k_{cut})} k^{-\gamma} e^{-k/k_\mathrm{cut}} \tag{D.35}$$

This includes the combination of a maximal log-likelihood function to estimate γ with fixed k_min and k_cut and the identification of k_min and k_cut for which the Kolmogorov-Smirnov statistic is minimal. We set a minimum of five binned data points as a condition for the fitting range and compute the root-mean-square error (RSME). To compare the fit with a power law we use the following fitting function with the same k_min value

$$p(k) = \frac{\gamma - 1}{k_\mathrm{min}} (k/k_\mathrm{min})^{-\gamma} \tag{D.36}$$

and analyze the likelihood ratio and Vuong test.

D.1.5 *Software used for the analyses*

Different software was used for this study. The construction of all networks and calculation of network measures was done in C++ (Embarcadero RAD Studio XE5). With Matlab we created the network visualizations and adjacency matrices (Fig. 5.1 and Figs. D.4, **??**). The truncated power-law fit and analysis was done with the Matlab packages of Virkar and Clauset (2014). For plotting the results we used Matlab, R and Microsoft Excel.

D.2 SUPPLEMENTARY RESULTS

D.2.1 *Results of the directed networks*

By construction, the average node degree $\langle k \rangle$ and network density D of the directed tree networks correspond to half of the values in the undirected case. Concerning the in-degrees ('overshadow indices') we obtain a clustering coefficient of $C \approx 0.35$ and for the out-degrees ('shadow indices') a coefficient of $C \approx 0.16$, which was similar for all forest sites. The outgoing node degree distributions decrease monotonically because there are many small trees that overshadow only few other trees while a few large trees overshadow many small trees (Fig. D.9a). Consequently, the proportion of shade-tolerant species tend to decline at the BCI forest with increasing out-degree (Fig. D.9c). In contrast, the incoming node degree distributions rather follow Poisson distributions (Fig. D.9b).

Note that a maximum value of 0.5 for the clustering coefficient C results from the fact that the directed tree network is acyclic. The difference between the values for the out-degrees and in-degrees can be explained by the typically decaying tree size distribution of undisturbed forests (Muller-Landau et al., 2006, Enquist and Niklas, 2001). The 'deeper' we look into the forest from above, the more smaller trees and thus, with smaller interaction zones occur. By this, more nodes with an out-degree of $k_{out} = 1$ or 0 and with a local clustering coefficient $C_i = 0$ are detected (concerning the 'shadow index') which results in a lower global clustering coefficient C.

Considering the species networks, there is no functional relation between the average node degrees of the undirected and the directed networks. The directed species network shows an average node degree of $\langle k \rangle = 57.55$ at BCI (50 ha), at Sinharaja $\langle k \rangle = 49.21$ and at Fushan $\langle k \rangle = 31.27$. For the directed species networks, we obtain a clustering coefficient lying between $C = 0.66$ and $C = 0.74$ for the out-degrees ('shadow index') and between $C = 0.72$ and $C = 0.86$ with regard to the in-degrees ('overshadow index').

D.2.2 *Node degree distribution of the tree networks*

As expected for node degree distributions that resemble Gamma (or log-normal) distributions, the analyzed tree networks can be considered as thin tailed but not scale-free (Barabási, 2016). An additional analysis showed that a power law with exponential cut-off approximates the degree distribution better than a power-law distribution (Fig. D.3), similar to observations in other geometric networks (e.g., Provero, 2002, Herrmann et al., 2003).

Over 30 years, the tree data inventory of BCI shows on average a tree mortality of 11.6 % and around 11.4 % tree recruits in every five years (standard deviations $s = 0.009$ and $s = 0.015$, respectively). Nevertheless, there is no significant change in the node degree distributions (Fig. D.7).

D.2.3 *Influence of plot size on network characteristics*

When plot size was changed (from 50 ha to 25 ha), most network characteristics remained unchanged in the example of BCI.

Some global network properties of the tree network scale in a predictable way with plot size: the number N of nodes (i.e., trees) is proportional to plot size and also the number E of edges since connections between nodes are local. As a consequence, network density D scales proportionally to 1/plot size (see equation (3) in Methods). However, local neighborhood properties such as the mean node degree $\langle k \rangle$, maximal node degree kmax, node degree distribution and clustering coefficient C are independent from plot size (Tables D.1 and D.2, Fig. D.14a), although the probability is higher to find a node with a higher degree in plots of larger size. The average path length L and the diameter d of a network scales approximately with the increase of the maximal possible distance among points, as shown in Table D.1.

The scaling with plot size of characteristics of the species network that is constructed on top of the tree network is difficult to predict, except for the number of nodes N that scales with the species-area relationship. A doubling of plot size caused only a slight increase in network size (the number of nodes N and edges E, Tables D.1 and D.2) and in node degrees ($\langle k \rangle$, k_{max} and node degree distribution). However, the shape of the node degree distribution remained constant (Fig. D.14b). More connections between the species resulted in a slightly lower average path length L and a slightly higher clustering coefficient C (Table D.1). The characteristics that change with plot size do not affect our general conclusions about the small-world and scale-free property in the networks of tree individuals and of tree species.

D.3 SUPPLEMENTARY FIGURES

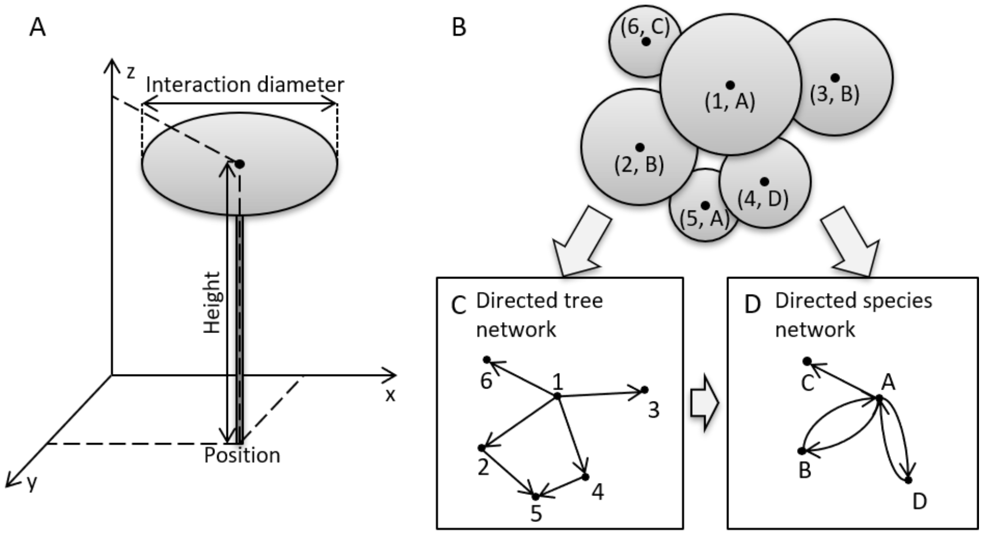


Figure D.1: Construction of proximity networks for forests. (A) Visualization of the approach used for the network analysis. Relevant parameters like the tree position, height and interaction diameter of the tree are recorded in forest inventories or derived from measured stem diameters and allometries (see Methods for details). (B) Construction of the directed tree and species networks. Disks show interaction zones of trees from a top view perspective. Numbers in the disks identify single trees and letters their tree species. (C) In the directed tree network, two trees (numbered nodes) are linked from the higher to the lower tree if their interaction zones (disks) overlap. (D) The species network arises by aggregating tree nodes in the directed tree network (C) which belong to the same species (letters A, B, C, D). The edges of undirected networks have no directions.

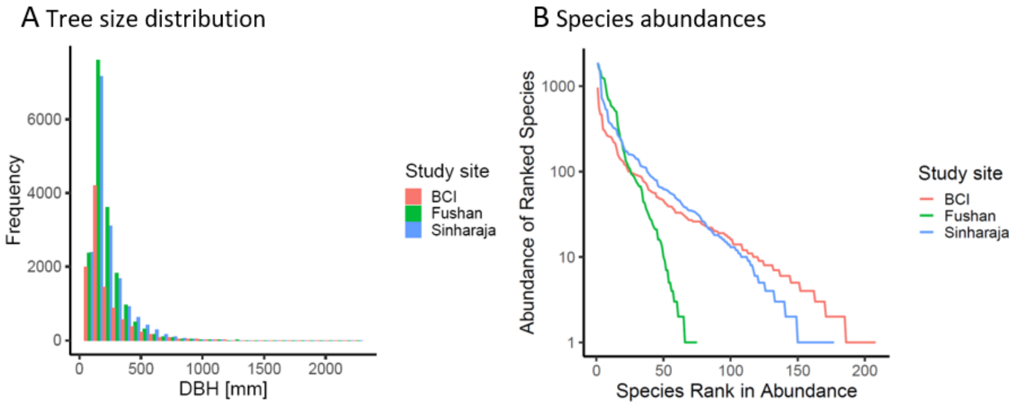


Figure D.2: Tree size distribution (diameter at breast height, DBH) and species abundances at all three study sites (BCI 25 ha, left side). Mean tree sizes are DBH = 223 mm (BCI, left side), DBH = 226 mm (Sinharaja) and DBH = 215 mm (Fushan). Mean species abundances are 49 (BCI, left side), 96 (Sinharaja) and 235 (Fushan).

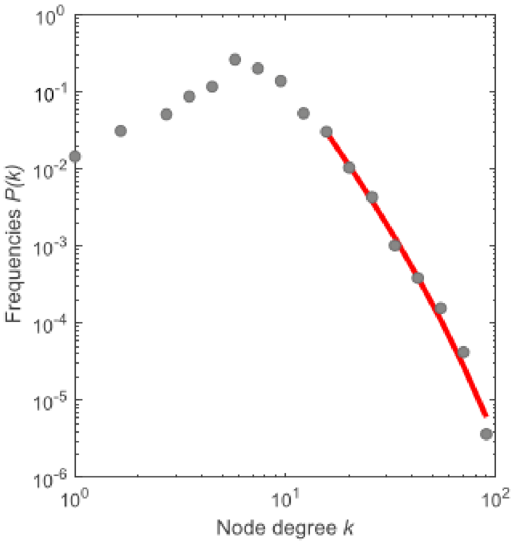


Figure D.3: Power-law fit with exponential cut-off ($k_{\text{min}} = 16$, $k_{\text{cut}} = 48$ and $\gamma = 3.408$, $RMSE = 3.08e - 04$) to the logarithmically binned frequencies of node degrees $P_t(k)$ in the tree network at BCI (50 ha). The truncated power law with exponential cut-off fits the node degrees significantly better than a power-law with same starting value kmin (likelihood ratio = -4.52, Vuong test, $p = 0.0335$, see D.1 Supplementary Methods for details). For graphical purposes only, frequencies are normalized (with regard to network size and bin width of node degrees).

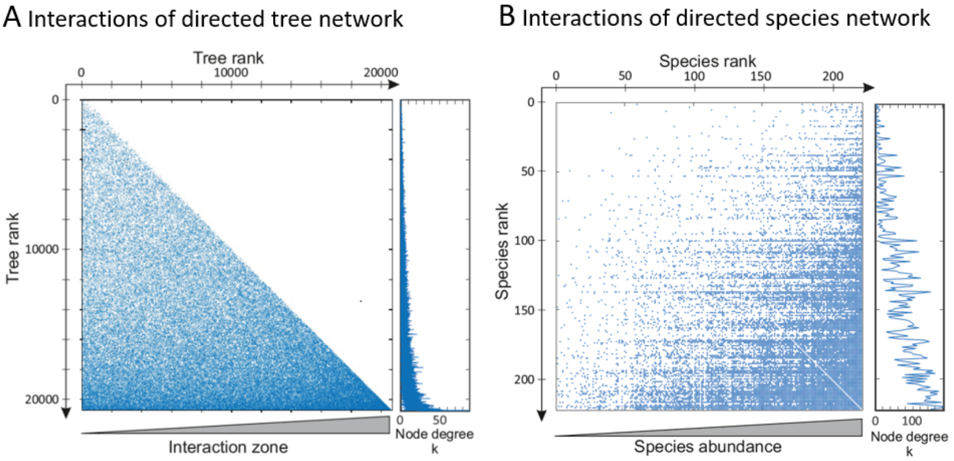


Figure D.4: Adjacency matrices of the directed tree and species network for BCI (50 ha). The rows and columns stand for the existing trees or species (nodes). Each blue dot represents a directed connection between a pair of trees or species. Consequently, the number of dots in one row represents the out-degree ('shadow index') of the concerning node. Nodes in the tree network in (A) are ordered by tree sizes starting from the smallest tree (low tree rank). Nodes in the species network in (B) are ordered by their species abundance starting from the species with lowest number of trees (low species rank). The small panels along the y-axis show the node degrees of (A) individual trees and (B) species.

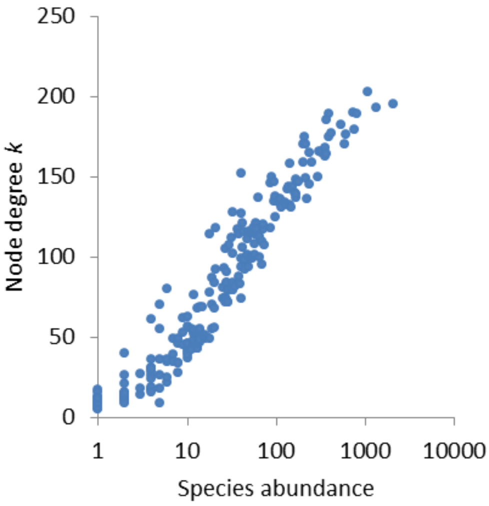


Figure D.5: Relation of species abundance to existing node degrees in the species network at BCI (50 ha, year 2010).

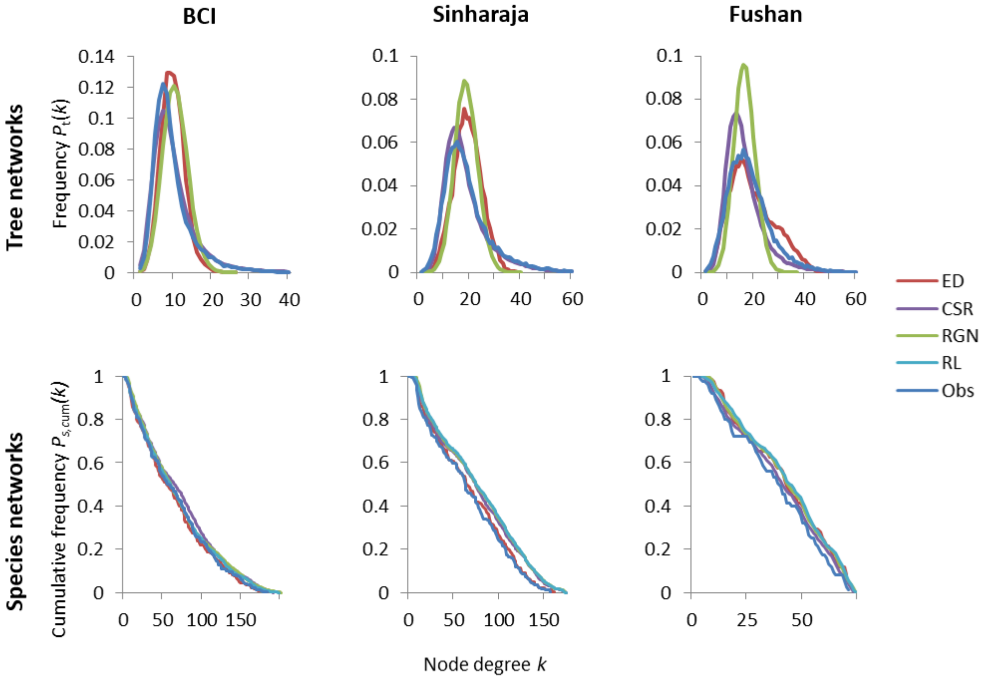


Figure D.6: Node degree distributions of the tree networks $P_t(k)$ and the species networks $P_{s,cum}(k)$ (cumulative distributions) for BCI (25 ha, left side), Sinharaja and Fushan (Obs) and their related null communities (ED – Equal Diameter, CSR – Complete Special Randomness, RGN – Random Geometric Network, RL – Random Labeling), respectively. The curves of the null communities are averages of 19 simulations. In the tree networks node degrees are cut at $k = 40$ or $k = 60$.

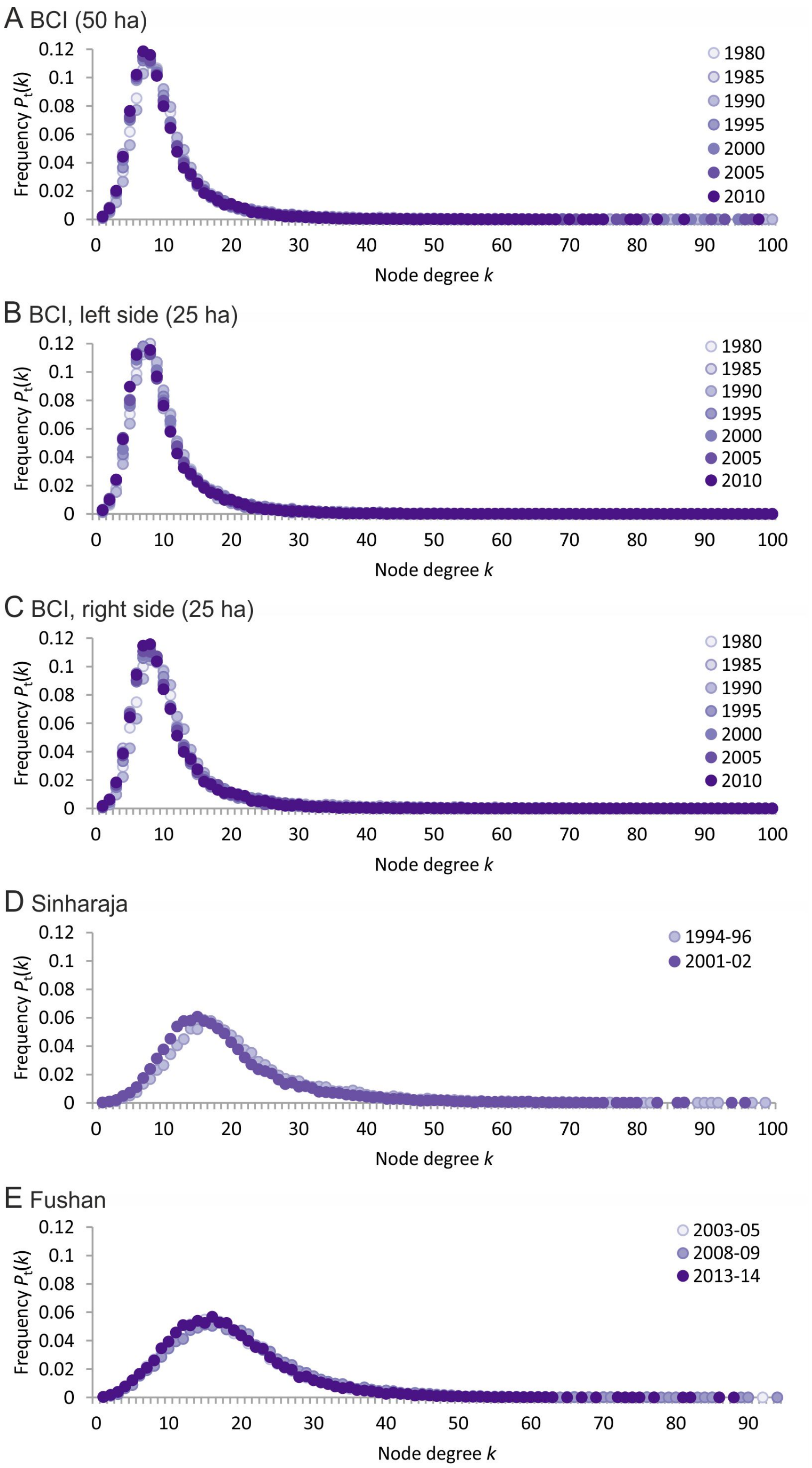


Figure D.7: Temporal variations in node degree distributions $P_t(k)$ of the tree networks at (A) BCI (50 ha), (B) BCI, left side (25 ha), (C) BCI, right side (25 ha) censused in years 1981 to 1983, and every five years from 1985 to 2010, at (D) Sinharaja censused in years 1994 to 1996 and 2001 to 2002 and at (E) Fushan censused in years 2003 to 2005, 2008 to 2009 and 2013 to 2014. For graphical purposes node degrees have been cut at $k = 100$.

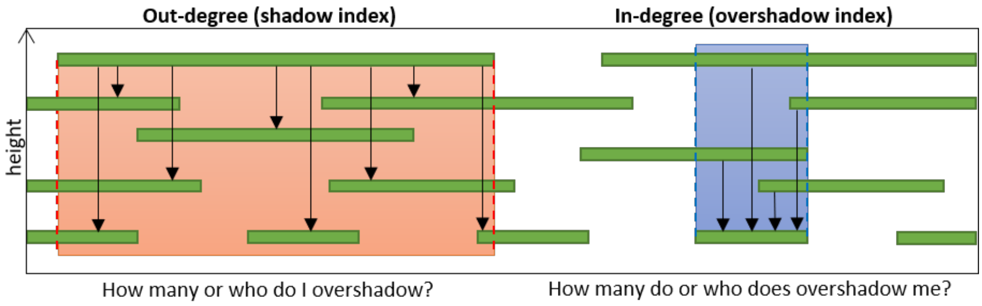


Figure D.8: Out-degree ('shadow index') and in-degree ('overshadow index') derived for the directed tree network. Green horizontal bars represent single trees in the forest (side view). Orange and blue areas visualize the interaction zones of the tallest tree and one of the smallest trees. Arrows show the directed connections for both focal trees (always going from the top to the bottom). The out-degree of the focal tree on the left side is eight (and its in-degree is zero), while the in-degree of the tree on the right side is four (and its out-degree is zero).

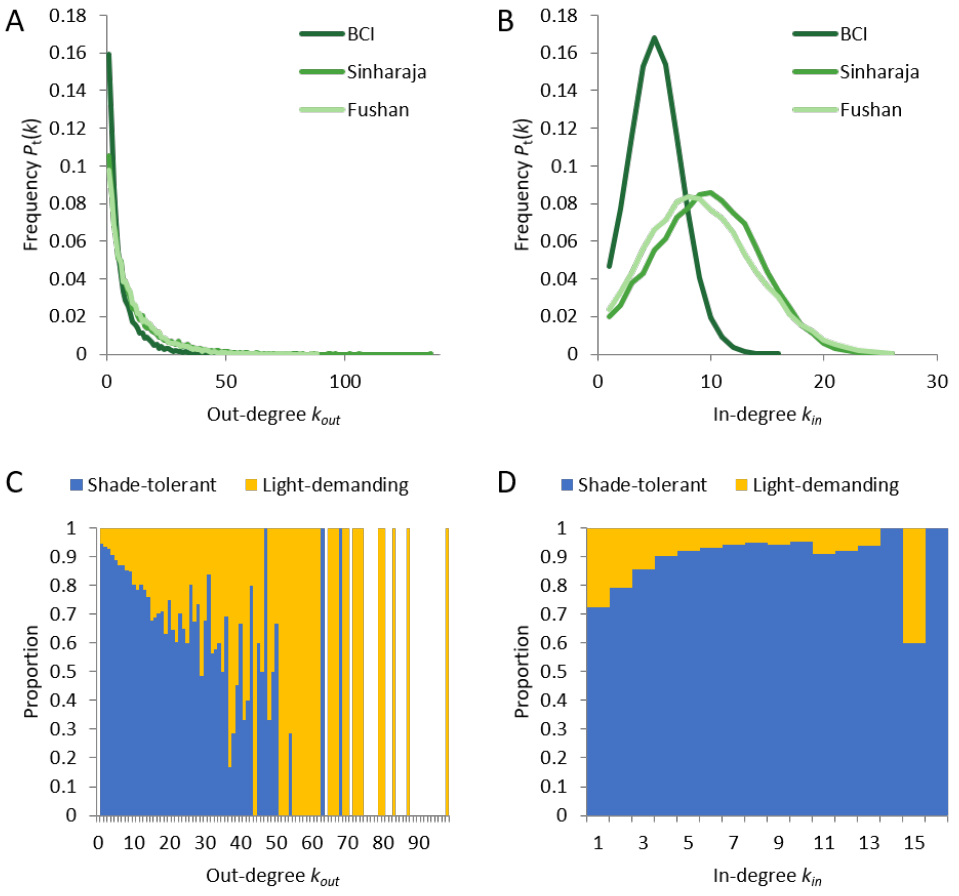


Figure D.9: Node degree distributions $P_t(k)$ of the directed tree networks (A) reflecting the out-degrees kout ('shadow index') and (B) the in-degrees k_{in} ('overshadow index') at different tropical forest sites (BCI of 50 ha, Sinharaja and Fushan of 25 ha, respectively). In (C) and (D) node degrees at BCI are divided into proportions of shade-tolerant (blue) and light-demanding species (yellow).

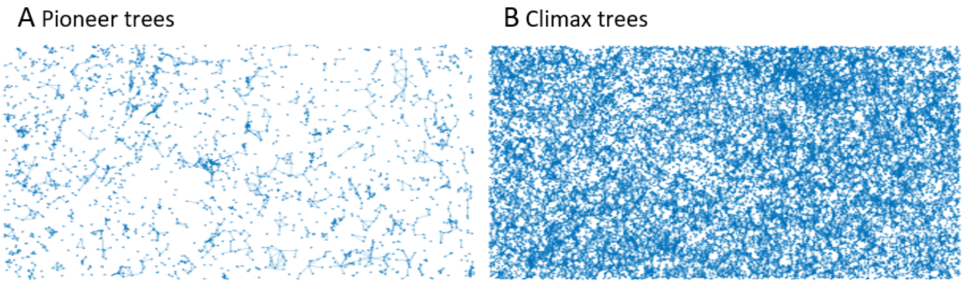


Figure D.10: Visualization of (A) network of pioneer trees (light-demanding trees) and (B) network of climax trees (shade-tolerant trees) at BCI (50 ha) censused in year 2010. The tree network in (A) includes 2269 trees (nodes) and 511 components (connections of trees isolated from others), while the tree network in (B) consists of 18466 climax trees and 40 components (the largest component contains 18383 trees). The positions of the visualized nodes correspond to the spatial positions of the trees at the forest site.

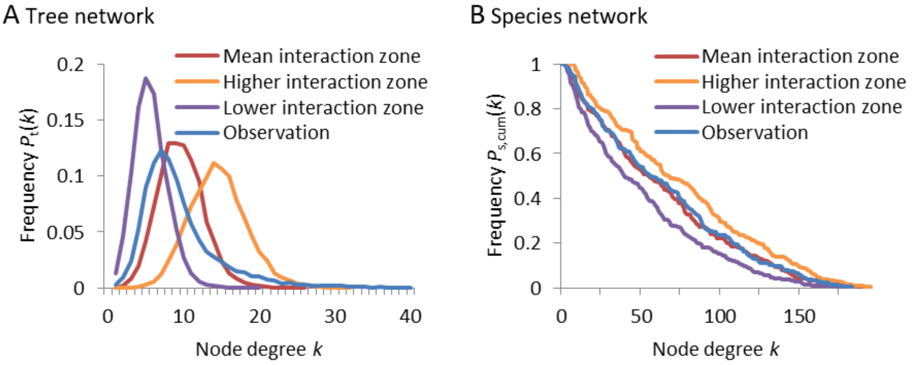


Figure D.11: Node degree distributions of (A) the tree networks $P_t(k)$ and (B) the species networks $P_{s,cum}(k)$ (cumulative distribution) for BCI (25 ha, left side) in comparison to networks of ED null communities (Equal interaction Diameter) with tree interaction zones that are equal to the mean interaction zone (red line, interaction diameter $\overline{d}_{int} = 20.7$ m), lower than the mean interaction zone (purple line, $\overline{d}_{int} = 15.9$ m) and higher than the mean interaction zone (orange line, $\overline{d}_{int} = 25.3$ m). In (A) node degrees are cut at $k = 40$ for graphical aspects.

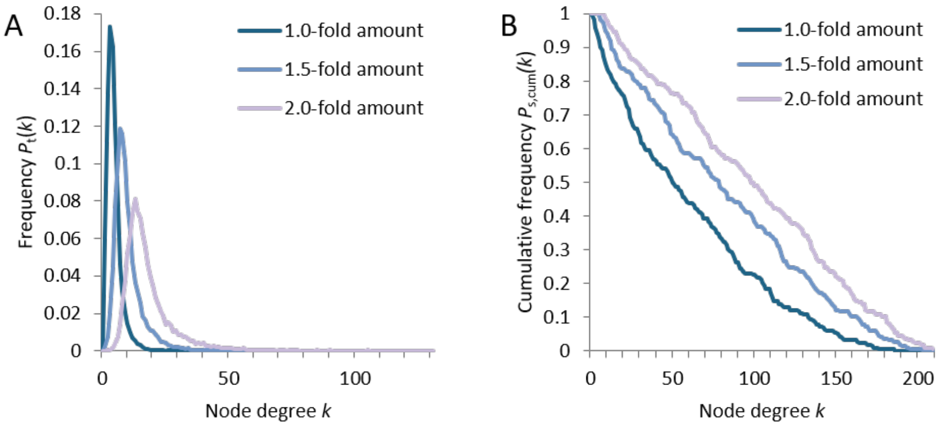


Figure D.12: (A) Node degree distributions $P_t(k)$ of the tree network and (B) cumulative node degree distributions $P_{s,cum}(k)$ of the species network at BCI (50 ha) with different proportionality factors f for deriving the size of interaction zones of trees.

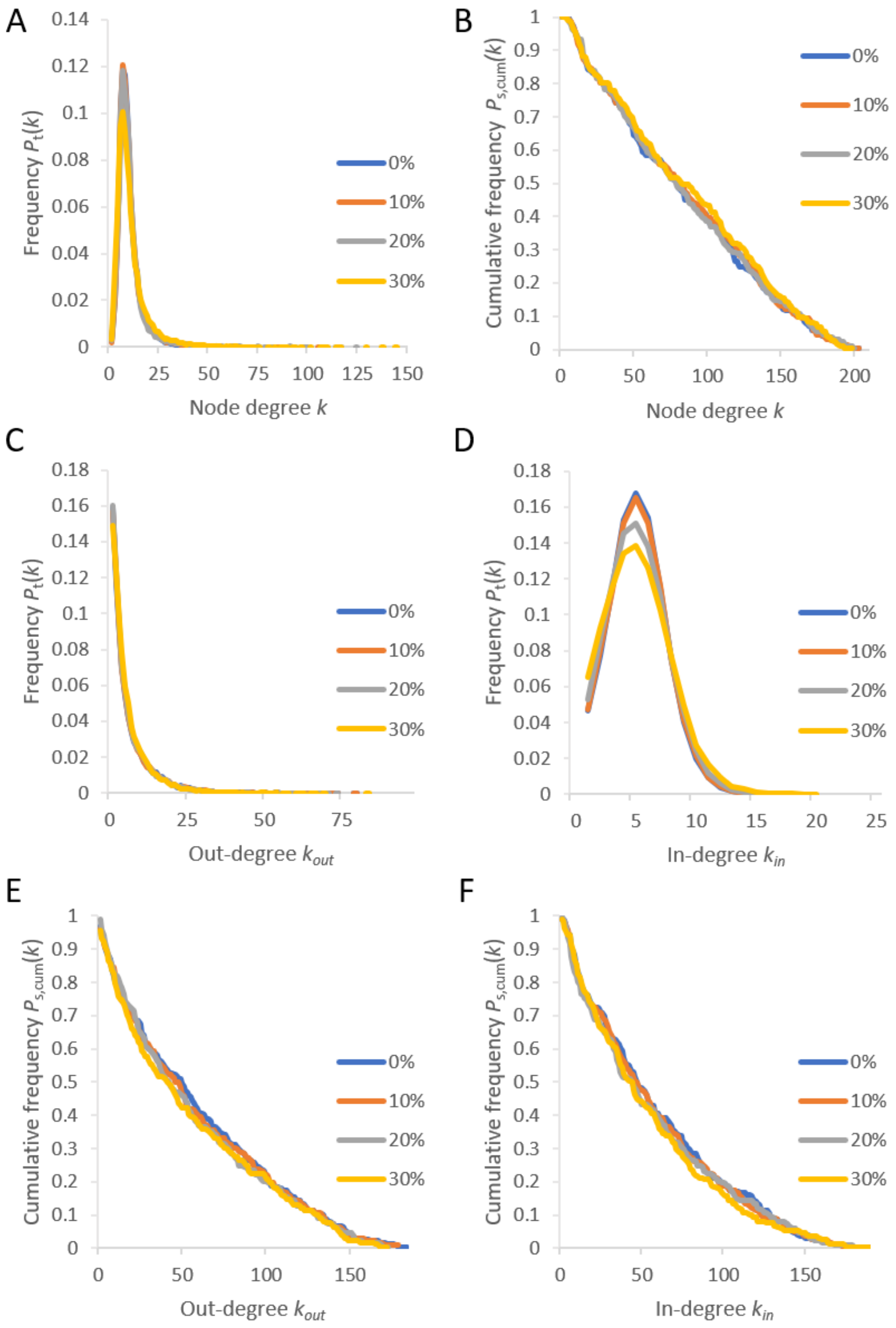


Figure D.13: Node degree distributions with noisy interaction zones and tree heights at BCI (50 ha). In (A) and (B) noise was added to parameters of the allometric relationship for the interaction zones per tree species of (A) undirected tree networks and (B) undirected species networks. In (C)-(F) noise was added to parameters of the allometric relationship for tree heights of (C)-(D) directed tree networks (out-degrees and in-degrees) and (E)-(F) directed species networks (out-degrees and in-degrees).

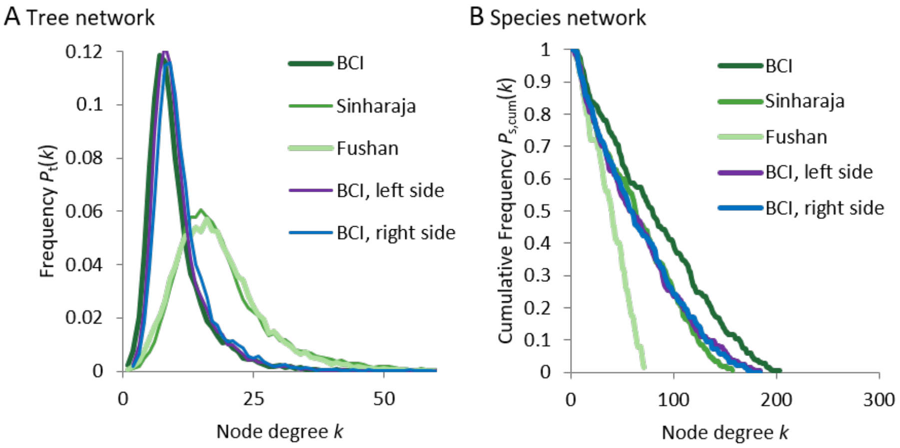


Figure D.14: Node degree distributions of (A) the tree networks $P_t(k)$ and (B) the species networks $P_{s,cum}(k)$ (cumulative distribution) for BCI (50 ha), left side of BCI (25 ha), right side of BCI (25 ha), Sinharaja (25 ha) and Fushan (25 ha), respectively. In a node degrees are cut at $k = 60$.

D.4 SUPPLEMENTARY TABLES

Table D.1: Summary of undirected tree and species networks for three different forest sites (BCI, Sinharaja, Fushan). Different plot sizes and locations at BCI.

	Forest site	**Plot size (ha)**	N	E	D	$\langle k \rangle$	$k_{\max}$	C	L	d
Tree network	BCI (left + right side)	50	20730	104795	0.00049	10.1	98	0.633	31.6	86
	BCI, left side	25	10161	48961	0.00095	9.6	83	0.631	22.6	56
	BCI, right side	25	10567	55419	0.00099	10.5	98	0.637	20.6	58
	Sinharaja	25	17015	163266	0.00113	19.2	136	0.635	21.3	53
	Fushan	25	17647	161285	0.00104	18.3	88	0.630	22.6	58
Species network	BCI (left + right side)	50	222	9201	0.375	82.9	203	0.80	1.6	3
	BCI, left side	25	208	6799	0.316	65.4	184	0.77	1.7	3
	BCI, right side	25	198	6522	0.334	65.9	174	0.78	1.7	3
	Sinharaja	25	177	5727	0.368	64.7	157	0.81	1.6	3
	Fushan	25	75	1404	0.506	37.4	71	0.86	1.5	3

N: number of trees or species (nodes), E: number of connections (edges), D: network density, $\langle k \rangle$: average node degree, $k_{\max}$: maximal node degree, C: clustering coefficient, L: average path length, d: diameter of the network.

Table D.2: Results for the species network in BCI (50 ha) assuming different edge thresholds.

Minimum number of interacting trees for an edge	**Number of nodes (N)**	$\langle k \rangle$	D	**Local connectivity**		**Global connectivity**	
				C	$^*C_{\mathrm{ER}}$	L	$^*L_{\mathrm{ER}}$
1	222	83	0.374	0.799	0.3757	1.64	1.63
2	212	58	0.274	0.807	0.276	1.76	1.72
4	185	42	0.227	0.826	0.227	1.80	1.77
6	174	33	0.190	0.821	0.190	1.85	1.81
8	159	29	0.182	0.801	0.186	1.87	1.82
10	146	26	0.178	0.808	0.183	1.87	1.83
20	110	19	0.173	0.815	0.169	1.84	1.85
30	94	14	0.149	0.762	0.151	1.90	1.94
40	78	13	0.167	0.796	0.148	1.85	1.92
50	69	11	0.159	0.773	0.170	1.87	1.95

Trees of a species must interact with a minimum number of trees of another species for being considered as interacting. With increasing minimum number the network size N and average node degree $\langle k \rangle$ becomes smaller, while the clustering coefficient C, average path length L and especially small world property remains unchanged.
$^*C_{\mathrm{ER}}$ and L_{ER}: clustering coefficient and average path length of random graphs following the ER model of the same network size.

Table D.3: Properties of the analyzed null communities.

Null community	**Remains unchanged**	**Changes**
CSR – Complete Spatial Randomness	Species identities Tree size distribution Species abundances	Tree positions are spread evenly distributed on plot
RL – Random Labeling	Tree positions Tree size distribution Species abundances	Species identities are randomly relabeled
ED – Equal interaction Diameter	Tree positions Species identities Species abundances	Tree sizes are set equal to the mean tree size
RGN – Random Geometric Network	(Species identities) Species abundances	Tree positions are spread evenly distributed on plot Tree sizes are set equal to the mean tree size

Table D.4: Comparison between the characteristics of the species networks at three tropical forest sites (size 25 ha) and of analyzed null communities.

		N	E	D	$\langle k \rangle$	$k_{\max}$	C	L	d	C_{ER}	L_{ER}
BCI (left side)	Observation	208	6799	0.3158	65.4	184	0.772	1.69	3	0.314	1.7
	ED	208	6638	0.3083	63.8	189	0.775	1.70	3	0.307	1.7
	CSR	208	7365	0.3423	70.8	189	0.793	1.66	3	0.343	1.7
	RGN	208	7202	0.3323	69.0	198	0.789	1.67	3	0.334	1.7
	RL	208	7022	0.3262	67.5	194	0.791	1.68	3	0.325	1.7
Sinharaja	Observation	177	5727	0.3677	64.7	157	0.810	1.64	3	0.367	1.6
	ED	177	5939	0.3813	67.1	162	0.807	1.63	3	0.382	1.6
	CSR	177	6550	0.4205	74.0	173	0.843	1.58	3	0.421	1.6
	RGN	177	6717	0.4313	75.9	173	0.841	1.57	3	0.433	1.6
	RL	177	6751	0.4334	76.2	172	0.842	1.57	3	0.432	1.6
Fushan	Observation	75	1404	0.5059	37.4	71	0.856	1.50	3	0.513	1.5
	ED	75	1470	0.5297	39.2	70	0.854	1.47	3	0.533	1.5
	CSR	75	1480	0.5332	39.5	69	0.862	1.47	2	0.534	1.5
	RGN	75	1555	0.5602	41.5	73	0.862	1.44	2	0.560	1.4
	RL	75	1575	0.5677	42.0	73	0.863	1.43	2	0.565	1.4

CSR (complete spatial randomness) and RL (random labeling) are null communities affecting random tree positions (CSR) and random shuffling of existing species identities among trees (RL). ED (Equal Diameters) are null communities with equal interaction diameters (mean over observed interaction diameters) and RGN (Random geometric network) combines CSR and ED (averages of 19 simulations). All networks show the small-world property. N: number of nodes, E: number of edges, D: network density, $\langle k \rangle$: mean node degree, $k_{\max}$: maximal node degree, C: clustering coefficient, L: average path length, d: diameter of the network, C_{ER} and L_{ER}: clustering coefficient and average path length of random graphs following the ER model of the same size.

Table D.5: Comparison between characteristics of tree networks at three tropical forest sites (size 25 ha) and of related null communities.

		N	E	D	$\langle k \rangle$	$k_{\max}$	C	L	d
BCI (left side)	Observation	10161	48961	0.0010	9.6	83	0.631	22.6	56
	ED	10163	48962	0.0010	9.6	26	0.566	39.1	102
	CSR	10149	50727	0.0010	10.0	85	0.652	23.2	61
	RGN	10607	54722	0.0010	10.3	24	0.587	38.8	103
Sinharaja	Observation	17015	163266	0.0011	19.2	136	0.635	21.3	53
	ED	17016	163856	0.0011	19.3	39	0.588	33.4	88
	CSR	17034	158505	0.0011	18.6	132	0.642	20.5	54
	RGN	17034	158487	0.0011	18.6	37	0.593	33.3	89
Fushan	Observation	17647	161285	0.0010	18.3	88	0.630	22.6	58
	ED	17646	171714	0.0011	19.5	47	0.592	34.9	98
	CSR	17649	145337	0.0009	16.5	106	0.636	22.9	60
	RGN	17649	144860	0.0009	16.4	35	0.592	36.6	98

ED (Equal Diameters) are null communities with equal interaction diameters (mean over observed interaction diameters) and CSR (complete spatial randomness) are null communities affecting random tree positions. RGN (Random geometric network) combines ED and CSR (averages of 19 simulations). N: number of nodes, E: number of edges, D: network density, $\langle k \rangle$: mean node degree, $k_{\max}$: maximal node degree, C: clustering coefficient, L: average path length, d: diameter of the network.

Table D.6: Parameters of the allometric relationships to derive tree height and tree crown diameter (interaction zone) from stem diameter dbh (equation (5.11) and (5.12)) for each forest site (Su et al., 2007, Kohyama et al., 2003).

	Tree height allometry		**Tree crown diameter allometry**	
	h_1	h_2	i_1	i_2
BCI	2.74	0.60	0.37	0.67
Sinharaja	2.78	0.69	0.40	0.66
Fushan	2.74	0.60	0.37	0.67

Table D.7: Results of network analysis assuming different proportionality factors f.

	Proportionality factor f	N	E	D	C	L
Tree network	1.0-fold amount	18285	41648	0.00025	0.567	84.37
	1.5-fold amount	20730	104795	0.00049	0.633	31.61
	2.0-fold amount	20735	188905	0.00088	0.641	19.54
Species network	1.0-fold amount	222	6724	0.274	0.763	1.76
	1.5-fold amount	222	9201	0.375	0.799	1.63
	2.0-fold amount	222	11052	0.451	0.816	1.55

N: number of trees or species (nodes), E: number of connections (edges), D: network density, C: clustering coefficient, L: average path length.

Table D.8: Results of network analysis assuming different noise extents on the interaction zones of tree individuals in BCI (50 ha).

	Noise extent	N	E	D	$\langle k \rangle$	$k_{\max}$	C	L	d	$\overline{d_{\text{int}}}$	$\overline{d_{\text{shifted}}}$
Tree network	± 0 %	20730	104795	0.00049	10.1	98	0.633	31.6	86	8.56	8.56
	± 10 %	20724	106175	0.00049	10.2	142	0.642	28.5	76	8.38	8.56
	± 20 %	20720	111002	0.00052	10.7	179	0.666	22.4	62	8.74	8.56
	± 30 %	20719	118562	0.00055	11.4	179	0.696	19.8	54	8.56	8.56
Species network	± 0 %	222	9201	0.375	82.9	203	0.80	1.6	3	8.56	8.56
	± 10 %	222	9254	0.377	83.4	200	0.80	1.6	3	8.38	8.56
	± 20 %	222	9610	0.392	86.6	198	0.80	1.6	3	8.74	8.56
	± 30 %	222	8779	0.358	79.1	209	0.81	1.6	3	8.56	8.56

N: number of nodes, E: number of edges, D: network density, $\langle k \rangle$: mean node degree, $k_{\max}$: maximal node degree, C: clustering coefficient, L: average path length, d: diameter of the network, $\overline{d_{\text{int}}}$: mean interaction diameter of trees before linear shift [m], $\overline{d_{\text{shifted}}}$: mean interaction diameter of trees after linear shift [m].

Table D.9: Results of network analysis assuming different noise extents on the height of tree individuals in BCI (50 ha).

	Noise extent	N	E	D	$\langle k \rangle$	$k_{\max,\text{in}}$	$k_{\max,\text{out}}$	C_{in}	C_{out}
Tree network	± 0 %	20730	104795	0.00024	5.1	16	98	0.350	0.132
	± 10 %	20730	104795	0.00024	5.1	16	98	0.347	0.136
	± 20 %	20730	104795	0.00024	5.1	18	98	0.340	0.144
	± 30 %	20730	104795	0.00024	5.1	25	98	0.326	0.159
Species network	± 0 %	222	12536	0.256	56.5	189	179	0.704	0.660
	± 10 %	222	12200	0.249	55.0	181	173	0.684	0.656
	± 20 %	222	11824	0.241	53.3	189	172	0.671	0.596
	± 30 %	222	12536	0.256	56.5	189	179	0.704	0.660

N: number of trees or species (nodes), E: number of connections (edges), D: network density, $\langle k \rangle$: average node degree, $k_{\max,\text{in}}/k_{\max,\text{out}}$: maximal node degrees of the directed networks, $C_{\text{in}}/C_{\text{out}}$: clustering coefficients of the directed networks. Subscripted characters denote network attributes with regard to the in-degrees (‘overshadow indices’) and out-degrees (‘shadow indices’).

Table D.10: Summary of directed tree and species networks for three different forest sites (BCI, Sinharaja, Fushan). Different plot sizes and locations at BCI.

	Forest site	N	E	D	$\langle k \rangle$	$k_{\mathbf{max,in}}$	$k_{\mathbf{max,out}}$	$C_{\mathbf{in}}$	$C_{\mathbf{out}}$
Tree network	BCI (left+right side)	20730	104795	0.00024	5.1	16	98	0.350	0.132
	BCI, left side	10161	48961	0.00047	4.8	16	83	0.346	0.131
	BCI, right side	10567	55419	0.00050	5.2	16	98	0.354	0.133
	Sinharaja	17015	163266	0.00056	9.6	26	136	0.356	0.181
	Fushan	17647	161285	0.00052	9.1	29	88	0.347	0.188
Species network	BCI (left+right side)	222	12776	0.260	57.5	188	184	0.716	0.659
	BCI, left side	208	9153	0.213	44.0	169	155	0.662	0.635
	BCI, right side	198	8662	0.222	43.7	166	156	0.653	0.618
	Sinharaja	177	8710	0.280	49.2	142	147	0.780	0.712
	Fushan	75	2340	0.422	31.2	60	69	0.860	0.745

N: number of trees or species (nodes), E: number of connections (edges), D: network density, $\langle k \rangle$: average node degree, $k_{\text{max,in}}/k_{\text{max,out}}$: maximal node degrees of the directed networks, $C_{\text{in}}/C_{\text{out}}$: clustering coefficients of the directed networks. Subscripted characters denote network attributes with regard to the in-degrees (‘overshadow indices’) and out-degrees (‘shadow indices’).

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Acronym	Explanation
AGB	Aboveground biomass
ANPP	Aboveground net primary productivity
BCI	Barro Colorado Island
CSR	Complete spatial randomness
CTFS	Center for tropical science
CV	Coefficient of variation
DBH	Diameter at breast height (stem)
DDS	Dynamically dimensioned search
ED	Equal diameters
ForestGEO	The forest global earth observatory
FORMIND	Forest model individual-based
G	Grasses
GCEF	Global Change Experimental Facility
GiFACE	Giessen long-term Free Air Carbon dioxide Enrichment Experiment
GRASSMIND	Grassland model individual-based
GPP	Gross primary productivity
KS	Saturated conductivity
LAI	Leaf area index
L	Legumes
NPP	Net primary productivity
NRMSE	Normalized root mean square error
PET	Potential evapotranspiration
PFT	Plant functional type
PWP	Permanent wilting point
RL	Random labeling
RGN	Random geometric network
S	Small herbs
SN	Species network
SW	Small world
T	Tall herbs
TN	Tree network
UFZ	Helmholtz Centre for Environmental Research

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ERKLÄRUNG

Erklärung über die Eigenständigkeit der erbrachten wissenschaftlichen Leistung

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet.

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Die Arbeit wurde bisher weder im In- noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

Ort, Datum	Unterschrift