Mechanisms underlying biodiversity effects on community productivity

Inaugural dissertation

of the Faculty of Science,

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presented by

Clemens Kleinspehn

from Germany

Supervisor of the doctoral thesis:

Prof. Dr. Markus Fischer

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"*Success is not final, failure is not fatal,*

it is the courage to continue that counts."

- Sir Winston Churchill

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Chapter 1

General introduction

Evolution of insights into biodiversity

Our insights into biodiversity is ever increasing. After centuries of observations of the distributions of organisms, and subsequent conclusions on the species richness and composition of communities in various types of environments, in the early 1990s first interest arose on how biodiversity, typically species richness, affects the productivity of communities and ecosystem functioning (Tilman *et al.* 1996). Research seeking to identify the mechanistic links between biodiversity and ecosystem functioning identified that species richness alone did not relate to the effects of biodiversity in a consistent manner. Besides species richness, species abundance appeared to be an important factor determining diversity effects (Hill 1973). Two commonly used diversity indices, Shannon Diversity and the Simpson Index, incorporate both richness and abundance (Shannon 1948; Simpson 1949).

The next insight was that dissimilarity between species is relevant in determining species diversity effects on ecosystem functioning (Chapin III *et al.* 1996; Tilman 2001). Recognizing that different types of plants may affect ecosystem function differently, plant species were assigned to plant strategies or functional groups of species with potentially similar contribution to ecosystem function. Sometimes, this assignment of functional groups was based on their taxonomic relationships. (Grime 1988; Tilman 2001; Roscher *et al.* 2004). Increasing species richness with species from different functional groups results in stronger biodiversity effects than increasing species richness with species from the same functional group (Tilman 2001). More recent approaches use specific attributes of plants linked to factors such as resource acquisition to assign gradual spectrums of plant strategies and function, instead of clearly separated categories (Wright *et al.* 2004; Díaz *et al.* 2016). The plant functional traits more precisely describe the dissimilarity of plant species and their respective contribution to biodiversity effects (Ebeling *et al.* 2014). However, uncertainty remains about the relevance and explanatory power of specific plant traits for different biodiversity mechanisms, and about which plant traits are most suited to inform about biodiversity effects on ecosystem functioning.

Potentially relevant traits

Aboveground plant traits are especially interesting for biodiversity research, as the aboveground production of biomass is one of the best investigated ecosystem functions affected by diversity (Hector *et al.* 2010; Cardinale *et al.* 2012; Duffy *et al.* 2017). Furthermore, plant-plant interactions aboveground are more asymmetric than belowground interactions (Silvertown & Charlesworth 2001). Aboveground plant traits respond strongly to light conditions as seen in shade-avoidance and shade-tolerance responses of plants to light limitation (Valladares & Niinemets 2008; Gommers *et al.* 2013). As light attenuation is one of the abiotic factors that changes with community diversity, optimized light interception via shifts in plant traits could present a mechanistic pathway for biodiversity effects (Bachmann *et al.* 2018). Optimization could happen evolutionarily through selection of phenotypes better adapted to their local light conditions via rapid evolution or via phenotypic plasticity (van Moorsel *et al.* 2019). Optimization could also happen by complementary use of space. Resource partitioning along the vertical axis of above and belowground resources (e.g. by water-uptake from different soil layers, or light-capture from different canopy layers) did not explain biodiversity effects (Chen *et al.* 2017; Jesch *et al.* 2018; Barry *et al.* 2020). Thus, horizontal aboveground small-scale plant cover patterns based on biotic interactions might provide an alternative approach (Saiz *et al.* 2016). The test of these hypotheses requires finding consistent contributions of plant traits and spatial patterns of plant cover to diversity-ecosystem functioning relations.

Semi-natural grassland experiments as testing grounds

Biodiversity effects have been systematically tested in large semi-natural experimental grasslands (Hector *et al.* 2010; Tilman *et al.* 2014; Weisser *et al.* 2017). Researchers have used this ecosystem as a testing ground for understanding biodiversity effects because of its direct applicability for commercial fodder production, convenient management, responsiveness due to relatively short generations of grassland species, and to some degree also by historic tradition. One of the first experimental grasslands in this context was the Cedar Creek experiment, which found that fertilization reduced the species richness of the experimental communities (Tilman & Downing 1994). Soon the observations on species richness in the Cedar Creek experiment led to the insight that species richness itself affects community productivity and its stability in the presence of inter-annual environmental fluctuations. Later

iterations of the Cedar Creek experiment (BioCON) specifically manipulated species richness to test its effect independent of fertilization treatments (Reich *et al.* 2001). The Cedar Creek experiment inspired other experimental set ups, like the European BIODEPTH experiment that tested the generality of species richness effects on communities in different ecosystems across Europe (Spehn *et al.* 2005). This thesis was done in the context of the Jena Biodiversity Experiment (Roscher *et al.* 2004) and the Jena Trait Based Experiment (TBE) (Ebeling *et al.* 2014), which are focusing on community compositions and how they modulate biodiversity effects.

Biodiversity experiments have been questioned for their relevance for real-life ecosystems (Lepš 2004; Wardle 2016), but their furthering of insights into biodiversity mechanisms is now widely accepted (Buchmann *et al.* 2018; Jochum *et al.* 2020). The systematically varied community compositions of the Jena Biodiversity Experiment presented a great opportunity to approach aboveground biodiversity mechanisms affecting community productivity from three angles:

First, our understanding of plant characteristics to diversity effects is still incomplete. Thus, Chapter 2 of this thesis attempted to narrow down the number of potentially relevant plant traits by differentiating between plant functional diversity along two trait gradients. One gradient focused on diversity in traits related to usage of space, i.e. leaf and root traits, and the other on diversity in traits related to usage of time, i.e. phenology. Additionally, I used the approach of partitioning biodiversity effects into complementarity and selection effects (Loreau & Hector 2001) for assessing community biomass responses to diversity. Further splitting these responses into individual complementary and selection effects on shoot biomass and shoot density provided additional information on the extent to which positive diversity effects on community biomass are due to an increase in individual plant biomass or due to increasing plant density.

Second, studying plant cover and its dynamics could provide additional insights into how community diversity affects the usage of aboveground space via biotic interactions (Saiz *et al.* 2016). Thus, in Chapter 3, I zoomed into the potential role of more effective resource use through complementary use of space by plants as a driver of higher productivity in more diverse communities. I linked fine-scale occurrence patterns of plants and their dynamics to community diversity and productivity.

Finally, if the use of aboveground space is a strong mechanism for biodiversity effects, these effects are possibly mediated by light interception (Hautier *et al.* 2009). Community responses by changing leaf traits to reduced light availability have been observed in diverse grassland communities (Bachmann *et al.* 2018). If community diversity affects light interception of species and their use of space as response to the environmental conditions, these changes likely affects the evolution of plant traits as well. Local environment can drive rapid selection of ecotypes (van Moorsel et al. 2019; Puy et al. 2020). As light availability changes substantially with changing diversity of plant communities, I expect adaption of aboveground traits to local plant community diversity and composition. Thus, in the Chapter 4 I used a quantitative genetics approach to test the adaptation of plants to diversity backgrounds and light availability.

Jena Experiment

The Jena Biodiversity Experiment, established in 2002, continued the tradition of semi-natural experimental grassland communities (Roscher *et al.* 2004). In its first approach, it established the insight that species richness alone does not predict strength of biodiversity effects reliably. Instead, classifying species according to their attributes or traits in functional groups and systematically combining these groups results in more diversity and stronger diversity effects than adding species of only one functional group. The next approach of the Jena Biodiversity Experiment, the Jena Trait Based Experiment (TBE), established in 2005, expanded on this concept by including gradients of functional classification instead of distinct functional groups (Ebeling *et al.* 2014). Specifically, the Jena TBE allowed me to test diversity in spatial resource acquisition with constant phenology, and diversity in phenology with constant spatial resource acquisition. This orthogonal design allows detecting which aspect of functional diversity drives the reported effects of species richness.

The Jena TBE is comprised of 138 communities ranging from one to eight species mixtures. Its communities combined altogether 20 species of the Arrhenaterion plant association in three species pools each of eight species. The first species pool, the “spatial” species pool, consists of species with different space occupation like i.e. rooting depth, flowering height or leaf areas, but similar phenology. The second species pool, the “phenology” species pool, consists of species with similar space occupation, but different phenology. The third species pool, the “combination” species pool, consists of species with

very different space occupation and phenology. This experimental set up of full factorial combination of species richness and diversity along the spatial and phenological diversity provided a unique opportunity to test which type of diversity drives the species richness effects specifically and the biodiversity effects more generally. The period of eleven years between establishment of the communities and the measurements in this thesis ensured that the communities were mature enough for potential biodiversity effects to have been established.

Approaches by chapter

In Chapter 2 of this thesis, I assessed the context dependency of species richness effects on biomass production analysing community and species level biomass, shoot density, and shoot biomass in the JENA TBE. I measured the communities twice, once at the peak of spring biomass, in May 2015, and once at the peak of summer biomass, in August 2015, just before mowing. I analysed whether strengths of biodiversity effects on biomass, shoot density or individual shoot biomass depended on diversity in spatial traits, diversity in phenology or a combinations of both. I used the additive partitioning of biodiversity effects (Loreau & Hector 2001) to assess whether biodiversity effects on biomass, shoot density and individual shoot biomass in the three sub experiments were driven by complementarity or selection effects.

In Chapter 3 of this thesis, I observed and analysed spatial patterns in the JENA TBE. The observed cover patterns could provide additional information into how the diversity of communities interacts with aboveground use of space. I used 1 cm resolution within 80 x 80 cm grid cells within the communities to analyse plant species cover data and changes in cover between October 2014 and October 2015. Additionally, I analysed spatial associations of species pairs, and whether these associations related to community species richness. Finally, I tested whether the spatial cover turnover between years and the association patterns were linked to the biomass production of species and communities as recorded in Chapter 1.

In Chapter 4 of this thesis, I tested whether differences in environmental conditions of species-poor communities and more diverse communities affected the evolution of aboveground plant traits. We collected seeds of 18 plant species from the main Jena Biodiversity Experiment. The seeds were raised and grown for two years, 2015 and 2016, in a common garden experiment. I differentiated environmental and genetic influences on the plant phenotypes, and assessed whether divergent selection of progeny happened in 13 years

of community history in the Jena Biodiversity experiment. Furthermore, I applied a shading treatment, to test whether light limitation was a key selection pressure on phenotypes in species rich communities.

The final chapter of this thesis summarizes and discusses the most important findings of the experimental chapters and their interlinkages. Additionally, I outline future experiments that might allow answering questions motivated by this thesis.

Chapter 2

Biodiversity effects on plant biomass production are stronger for communities with species differing in spatial than in temporal traits

Clemens Kleinspehn, Lena Neuenkamp, Anna Roeder, Christiane Roscher and Markus Fischer

Abstract

Positive effects of biodiversity on biomass production have frequently been reported. However, the strength of the biodiversity effect can vary depending on the functional composition of the plant communities and on the season in which effects are observed. Here we analyze the biodiversity-productivity relationship of 138 plant communities from the Jena Trait Based Experiment. The species in these communities vary in functional diversity either with respect to spatial resource use, phenology, or both. We recorded biomass production and shoot density in these communities in spring and summer 2015. Average community biomass increased by about 50% from monocultures to four-species mixtures in the spring season, but remained constant in the summer season, possibly due to lower biotic activity in summer. We found biodiversity effects on community productivity to be strongly driven by shoot density. Communities composed of species with traits indicative of complementary use of space supported a higher density of shoots without proportionate loss of individual biomass, and thus strongly increased biomass production per area. Communities composed of species differing in phenology showed much weaker biodiversity effects. We conclude that small-scale spatial mechanisms are essential for strong biodiversity effects.

Introduction

Grassland biodiversity can affect ecosystem functions above and below ground (Weisser *et al.* 2017). The most frequently discussed ecosystem function is net primary productivity. Often measured as aboveground plant biomass production, productivity has been shown to be disproportionally higher in plant communities with higher numbers of species, species richness hereafter, than it would be expected from the productivity of the respective monocultures (Loreau & Hector 2001; Cardinale *et al.* 2007). Despite the broad consensus that species richness has positive effects on biomass production, the strength of these effects varies considerably across studies (Fanin *et al.* 2018) suggesting their context-dependency in response to abiotic and biotic factors. We address the influence of two environmental contexts on species-richness effects, community composition and seasonal variation.

Depending on community composition, competition between species can vary with potential consequences for species richness effects. Plant species with similar growth forms, e.g. similar flowering height or rooting depth, compete for similar space. Alternatively, based on their phenology, plant species could strongly compete with each other if they make use of the same space at the same time of the year. Thus, communities composed of plant species with more similar growth form or phenology could have weaker species richness effects than communities composed of more different growth forms and phenologies. Large-scale biodiversity experiments (Roscher *et al.* 2004; Ebeling *et al.* 2014) can experimentally test the influence of community composition by systematically combining species with different growth strategies (Díaz *et al.* 2016). Seasonal context can also be tested in biodiversity experiments, by sampling at different times of the year.

In temperate ecosystems, abiotic conditions largely vary throughout the growing season. In Europe, managed grasslands often show a lower biomass production during the summer regrowth, after the first mowing in June (Hossain & Beierkuhnlein 2018). Observations in wet managed grasslands suggest that in addition to lower summer productivity, the species richness effect on biomass production also decreases during summer (Doležal *et al.* 2019). Whether such seasonal differences do apply generally or are related to specific compositions remains an open question.

For a more detailed understanding of species-richness effects on biomass production, the net biodiversity effect can be partitioned into complementarity and selection effects (Loreau & Hector 2001). Complementarity effects assess how well all species forming the community perform on average in a species mixture compared with growing in monocultures. Selection effects assess how well individual species perform in mixtures compared with their monoculture. Hence, positive selection effects mean that highly productive species benefit more from growing in mixtures than less productive ones do. Complementary effects and selection effects can be positive or negative, and can add to a positive, neutral, or negative net biodiversity effect on community biomass production (Loreau & Hector 2001). Additive partitioning can be applied to any variable for which both a community measure and measures of the contributions of all individual species are available (Grossiord *et al.* 2013). Biomass production of a community is the function of two components of productivity of the species composing the community: abundance or density, and individual size, often quantified as biomass per individual (Barry *et al.* 2018). Applying the additive partitioning method to these two components allows insights into variation underlying biodiversity effects on community biomass production in differing environmental contexts.

Variation in community biomass production and biodiversity effects is based on the variation of individual species performance. In confined habitats, numbers of individuals (shoot density) and individual sizes (shoot biomass) of a given species are usually negatively correlated. This trade-off between density and size has been thoroughly investigated in population biology (Lonsdale & Watkinson 1983; Ramírez & Bellot 2009). An earlier community study indicates that mixtures can achieve higher shoot densities than monocultures without a proportionate decrease in shoot biomass (Marquard *et al.* 2009). Another community study found simultaneous increases in shoot density and shoot biomass in mixtures for large species, at the cost of the densities of smaller species (Roscher & Schumacher 2016). Studying individual species in systematically arranged species compositions providing different contexts, i.e. species composition and season, could provide further insight into mechanisms underlying biodiversity effects on community biomass production.

In this study, we assessed the context-dependency of species richness effects on biomass production analyzing community and species level biomass, shoot density, and shoot biomass in 138 grassland communities of varying species richness and functional

compositions from a total pool of 20 plant species. Importantly, the species in these communities vary in functional diversity either with respect to spatial resource use or in phenology or in both. We measured the communities twice, once at the peak of spring biomass, in May 2015, and once at the peak of summer biomass, in August 2015, just before mowing.

We investigated:

1. How do community composition and season affect community biomass production, shoot density, and species richness effects on biomass?
2. How do complementary effects and selection effects on community biomass production depend on context?
3. How do community composition and season affect the density and biomass of shoots per species?

Methods

Study area

We worked in the Trait-Based Biodiversity Experiment (TBE), which forms part of the group of long-term grassland biodiversity experiments called the "Jena Experiment" (Roscher *et al.* 2004). The experimental site is located in the valley of the Saale river close to the city of Jena, Germany, 130 m a.s.l, 50°57 N, 11°37 E, where the mean annual temperature is 9.9° C, and mean annual precipitation is 610 mm (1980-2010 Jena/Sternwarte; Hoffmann *et al.* 2014).

Experimental design

The TBE plant communities were systematically designed to create a gradient of species trait asymmetry along a spatial and a phenological dimension. During the establishment of the TBE in 2010, 20 non-legume plant species of the *Arrhenatherion* vegetation alliance (Leuschner & Ellenberg 2017) were sown in 138 plots of 3.5 m x 3.5 m size in three blocks (Ebeling *et al.* 2014). The 20 plant species were chosen from a pool of 48 non-legume plant species present in the Jena Main Experiment (Roscher *et al.* 2004). Of these 20 plant species, three slightly overlapping species pools were created, each consisting of eight plant species. The different species pools aimed to maximize diversity in different sets of plant traits. Species pool one, the "spatial" pool, combined plant species with different strategies in spatial resource acquisition, ranging from "small" to "large" species. Species pool two, the "phenology" pool, combined plant species that access resources at different times of the growing season, from "early" to "late". Species pool three, the "combination" pool, combined plant species differing most in both spatial resource acquisition and phenological strategies. In each species pool, communities were sown with species richness levels of one, two, three, four, or all eight species. At sowing, total seed density was constant across all communities, i.e. 1000 seeds per m^2, adjusted for germination rates from standard laboratory tests (Ebeling *et al.* 2014). Sown seeds were equally distributed among species, resulting in a lower initial seed number of species-specific seeds in more species rich communities than in their respective monocultures. The communities of the experiment were mowed twice a year and mown biomass was removed, mimicking the management of extensive hay meadows in the

region. No fertilizer was added. Furthermore, all communities were weeded three times per year to maintain the originally sown species compositions.

Community measurements

For assessing community and species biomass production, shoot density and shoot biomass, we established two transects in each of the 138 communities. Each transect covered an area of 10 cm x 80 cm. In the transect area we cut all aboveground biomass close to the ground, sorted it by species and counted the number of shoots. We counted the number of the shoots (ramets) instead of the number of individuals (genets), since individuals of clonal plants cannot be distinguished reliably in the field. If the number of shoots exceeded 100, we estimated total shoot number based on total biomass and the biomass of 100 shoots. We dried the samples at 70° C for two days before weighing. We collected all data in two seasons: in spring (25 May to 2 June 2015) and in summer (21 to 27 August 2015) at the peak of biomass, shortly before mowing.

The data set contained four response variables: the biomass of the community (community biomass), the biomass of individual species in the community (species biomass), the number of shoots of each species (shoot density), and the average mass of the shoots for each species (shoot biomass). We pooled data of both transects per plot and scaled them up to units per square meter. Shoot biomass was calculated by dividing species biomass of both transects by the number of shoots of both transects. We multiplied species biomass and shoot density by the species richness of the community to correct for lower initial seed density resulting from the substitutive design of the sown communities. We calculated shoot biomass by dividing species biomass by shoot density.

Statistical analysis

Effects of community composition, season and species richness were analyzed with linear mixed modelling. For community biomass, we sequentially fitted a linear mixed effect model with restricted maximum likelihood (REML). Based on the experimental design we defined plot ID nested in block and block as random effects. We sequentially added the fixed effects of log-linear transformed species richness, species pool, and season, as well as all their interactions. We estimated the significance of terms with ANOVA Type I F-Tests with estimated denominator degrees of freedom based on Welch-Satterthwaite's approximation,

to adjust for repeated measurements of communities in two seasons (Satterthwaite 1946). We chose the sequential ANOVA Type I approach with the above order of fixed effects, based on the experimental design of the communities, and to maintain consistency with earlier studies of the Jena Biodiversity Experiments.

We applied additive partitioning (Loreau & Hector 2001) to the data on community biomass, shoot density and shoot biomass. The calculation for shoot density was analogous to the calculation for community biomass, as community shoot density is the sum of shoot density of individual species within the community. However, community shoot biomass cannot be calculated as sum of individual species. Therefore, we followed Grossiord et al.'s approach to calculate a community weighted mean of shoot biomass under the assumption that all species contributed equally, setting the weighting factor W_{Oi} as the inverse of species richness (Grossiord *et al.* 2013). We fitted sequentially linear mixed effects models with REML to net, complementarity and selection effects of community biomass, shoot density and shoot biomass. We defined plot ID nested in block and block as random effects. We sequentially added the fixed effects log-linear transformed species richness, species pool, and season, as well as all their interactions. We estimated significance of terms with ANOVA Type I F-Tests with estimated denominator degrees of freedom based on Welch-Satterthwaite's approximation.

Finally, for species biomass and shoot biomass, we fitted sequentially a linear mixed effects model with REML. We defined plot ID nested in block and block as random effects. We added sequentially the fixed effects log-linear transformed species richness, species pool, species identity and season. We fitted all interactions of fixed effects, except for interactions "species pool : species identity" and "species pool : species identity : season", since the interaction "species pool : species identity" is not fully factorial by nature. We estimated significance of terms with ANOVA Type I F-Tests with estimated denominator degrees of freedom based on Welch-Satterthwaite's approximation. For shoot density, we fitted a negative binomial model. Parameters and their interactions were fitted sequentially and identical to the other species-level models. We estimated the significance of terms of the negative binomial model sequentially with log-likelihood ratio tests against a Chi^2 distribution.

Statistical analyses were performed with R 4.0.5 software (R Core Team 2021) including packages *lme4* (Bates *et al.* 2015) for linear mixed effect modelling, *MASS* (Venables & Ripley 2002) for negative binomial models*, lmerTest* (Kuznetsova *et al.* 2017)*, broom.mixed*

(Bolker & Robinson 2021) for model testing and interpretation; *ggplot2* (Wickham 2016), and *cowplot* (Wilke 2018) for graphical display; *data.table* (Dowle & Srinivasan 2018) and *tidyverse* (Wickham 2017) for consistent and efficient data management.

Results

Community performance

Communities with higher species richness produced more biomass than species poor communities (Figure 1, Table 1). However, the effect of additional species was stronger in species pools combining species with varying spatial functional traits, namely spatial species pool and the combination species pool, than in the species pool containing species with only varying phenology (Figure 1, Table 1). This indicates that diversity in spatial functional traits is essential for species richness effects, while diversity in phenology is rather secondary. Communities of the combination species pool were less productive than communities of the other species pools, which could be related to the identity of the species used to compose communities in this pool.

Additive partitioning of biodiversity effects

Season affected the biomass production and the species richness effect on biomass production. Community biomass production was higher in May than in August in all species pools (Figure 1, Table 1). On average, community biomass was 306.9 ± 10.6 g m^{-2} in May and 135.9 ± 11.6 g m^{-2} in August. Season altered the relationships between species richness and community biomass production. In May, community biomass increased with species richness. In August, communities produced similar amounts of biomass, independent of species richness. The “combination” species pool produced significant less biomass than the other species pools in May, but lost less absolute biomass from May to August. Thus, community biomass production was similar for all species pools in August (Figure 2, Table 1). These results highlight the context dependency of biomass production and species richness effect. Biomass production and its variability between seasons depended strongly on species composition. Depending on diversity in spatial traits and on season species richness effects could vary in strength or even presence.

Additive partitioning underlined the context dependency of species composition and season. In May, positive complementarity effects outweighed negative selection effects on community biomass, resulting in a positive net effect in mixtures (Figure 3, Table 2). In August, both positive complementarity effects and negative selection effects had similar effect sizes, resulting in a neutral net biodiversity effect on community biomass (Figure 3, Table 2). In May,

the complementarity effects on community biomass increased with species richness, while in August effect sizes did not change significantly with species richness (Figure 3, Table 2). The increase in complementarity effects with species richness in May can be attributed to the more pronounced complementarity effects with species richness in the spatial species pool than in the other species pools (Supplementary Table S1), which had stronger species richness effects than the other species pools (Figure 3, Table 2). In August the combination species pool had larger effects sizes than the other species pools, without a species richness effect on complementarity effects (Figure 3, Table 2).

Complementarity in spatial traits appeared crucial for higher biomass production. When analyzing biodiversity effects for the spatial species pool, additive partitioning of shoot density showed positive complementarity effects outweighing negative selection effects, resulting in a positive net effect (Figure 3, Table 2). Positive complementarity effects increased with species richness, while negative selection effects did not change significantly with species richness (Figure 3, Table 2). Thus, the net effect on shoot density increased with species richness. Biodiversity effects on shoot density were present across all species pools, although the phenology species pool had smaller effect sizes than the other species pools (Figure 3, Table 2, Supplementary Table S1).

As for community biomass, especially complementarity in spatial usage increased shoot density (Figure 3, Table 2). This provides further support for the hypothesis, that community biomass production increases are related to denser stands of individuals in mixed communities with varying growth forms.

Additive partitioning of shoot biomass showed small effect sizes for complementarity effects and selection effects (Fig. 3, Table 2), which did not change with species richness. Biodiversity effects on shoot biomass were consistent between species pools, except for the combination species pool in May. However, the strong negative complementarity and selection effects on shoot biomass in this species pool were heavily driven by the monoculture of *Anthriscus sylvestris (L. Hoffm.)*. Analyses excluding communities with *A. sylvestris* did consistently not show biodiversity effects on shoot biomass (Supplementary Figure S2).

Species biomass, shoot density, and shoot biomass

Corrected species biomass, i.e. the biomass per species multiplied by the diversity level (see methods), depended on species pool, species identity, and sampling season (Figure

4, Table 3). Plant species in the combined species pool had consistently lower corrected biomass production than species of the other two species pools. Plant species had consistently less corrected biomass in August than in May. Species richness had a more negative effect on corrected species biomass in August than in May. However, individual effects on corrected species biomass varied from species to species.

Corrected shoot density depended on species pool, species identity, and sampling season. Plant species in the spatial species pool had higher corrected shoot densities than plant species of other two species pools. Plant species had higher corrected shoot density in May than in August. The effect of species richness on corrected shoot density depended on the plant species within the species pools.

Shoot biomass depended on species pool, species identity, and sampling season. Plant species in the combination species pool had higher shoot biomass than species of the phenology species pool, but not significantly higher than species of the spatial species pool. Shoot biomass varied between species and was consistently higher in May than in August. Species richness had no effect on shoot biomass in either season.

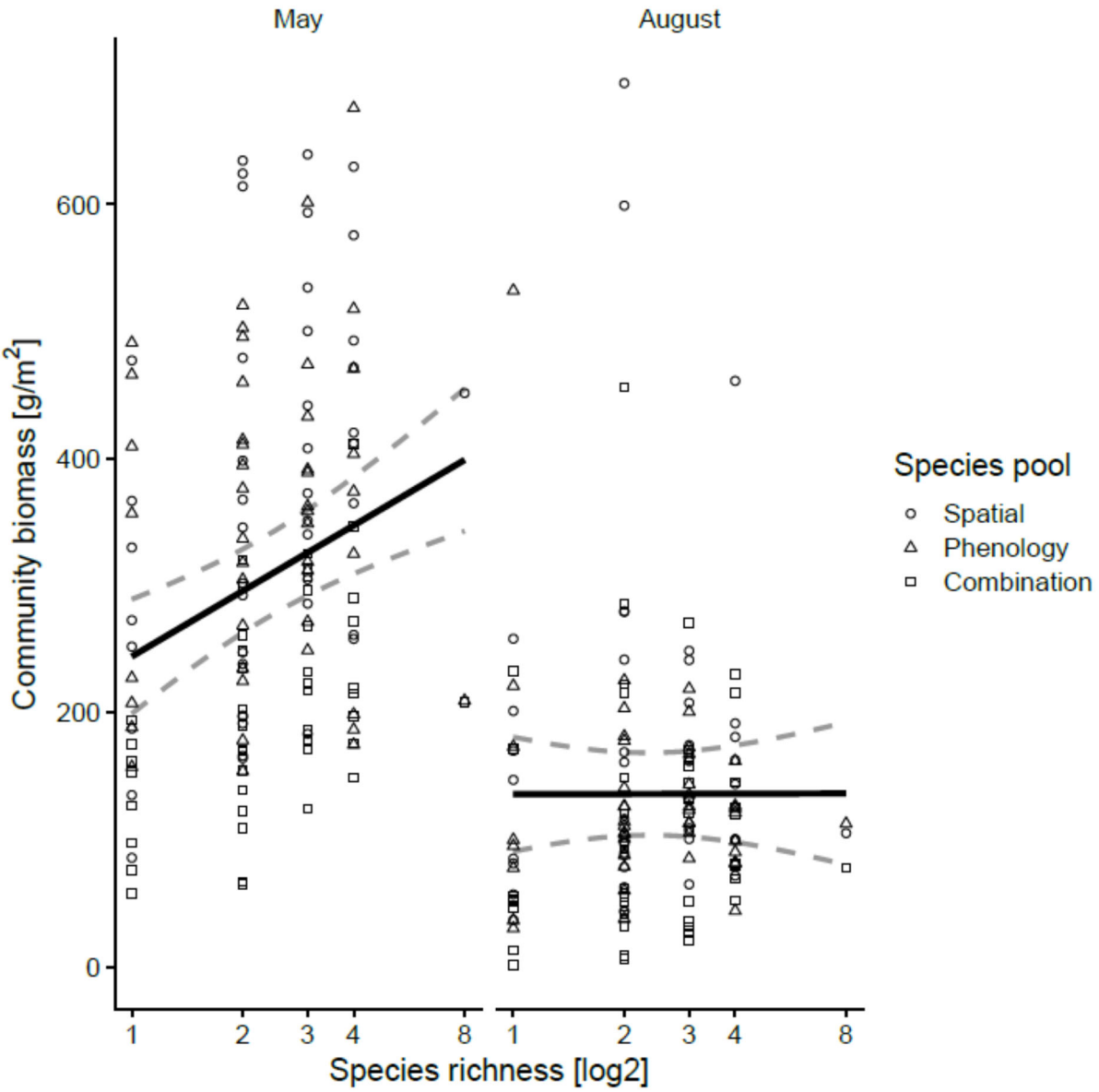

Figure 1: Community biomass plotted against species richness, separated for season (May and August). Symbols represent the three species pools: “spatial” as circles, “phenology” as triangles, and “combination” as squares.

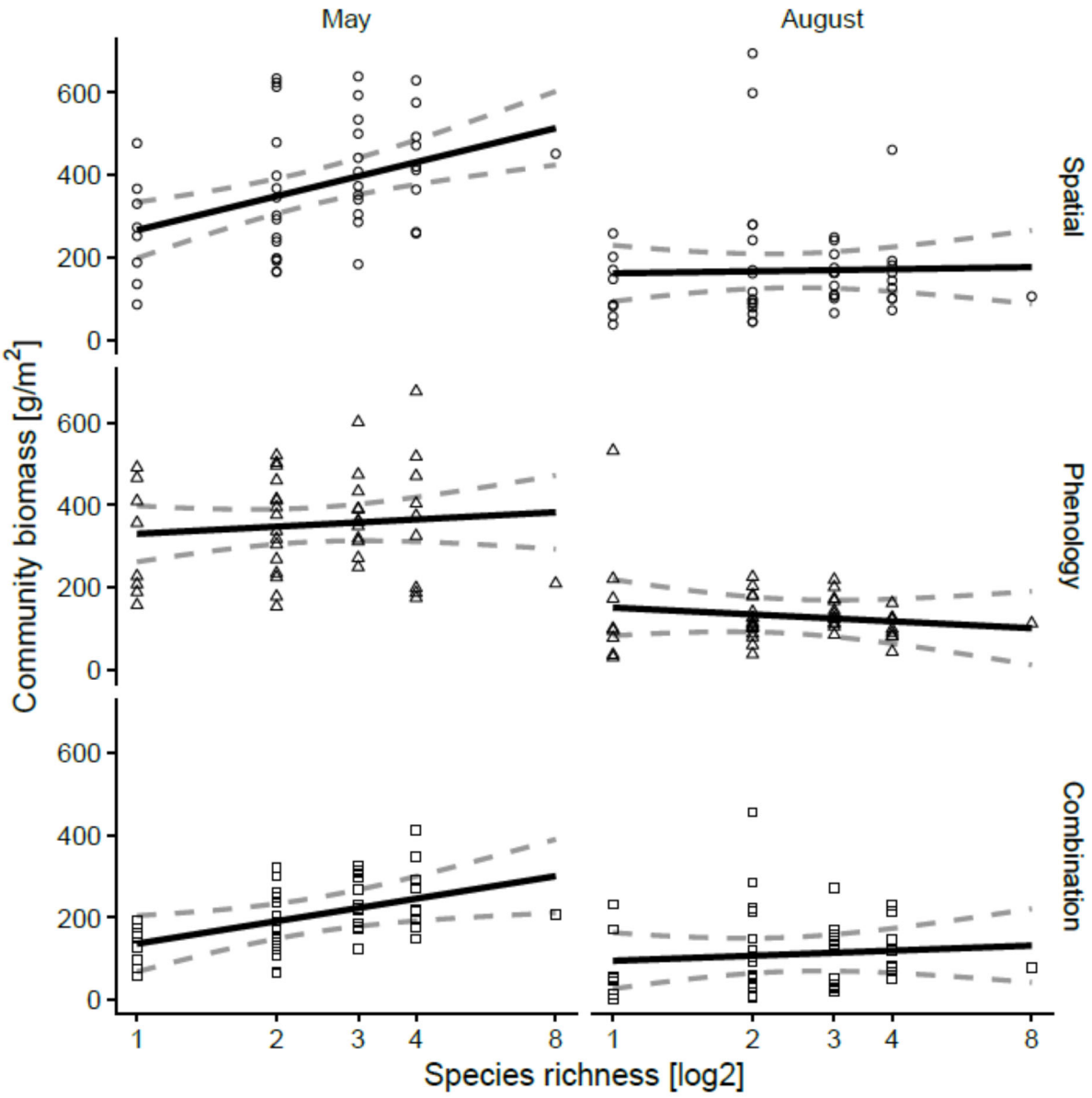

Figure 2: Community biomass plotted against species richness, separated for season (May and August) and species pools. Symbols represent the three species pools: “spatial” as circles, “phenology” as triangles, and “combination” as squares.

Table 1: ANOVA type I table of REML fitted community biomass model. Fixed effects tested with F-test, denominator degrees of freedom estimated with Welch-Satterthwaite's approximation. Significance levels indicated by number of *. * p <0.05, ** p <0.01, *** p <0.001. Significance of random intercept expressed as explained variance ratio compared to residual variance.

	Community biomass		
Fixed effects	NumDF	DenDF	F value
Species richness (log)	1	130	5.73 *
Species pool	2	130	19.1 ***
Season	1	132	278.53 ***
Species richness (log) : species pool	2	130	1.46
Species richness (log) : season	1	132	12.52 ***
Species pool : season	2	132	14.81 ***
Species richness (log) : species pool : season	2	132	0.84
Variance ratio random effects			
Plot ID : block	0.36		
Block	0.05		
Residual	0.59		

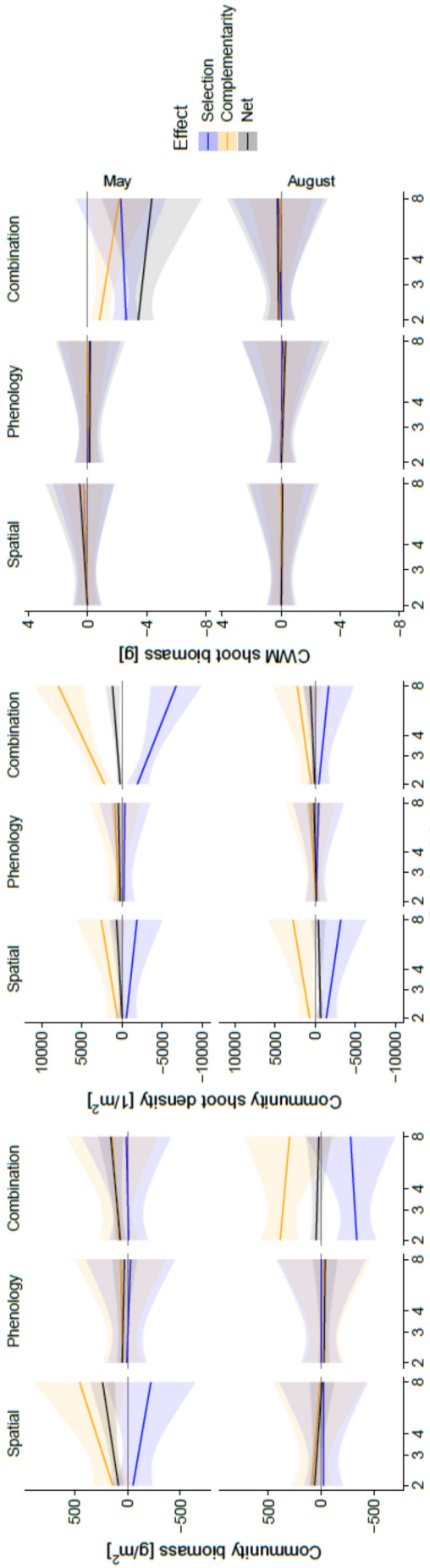

Figure 3: Additive partitioning according to Loreau & Hector 2001 for community biomass, shoot density and shoot biomass. Selection effects in blue, complementarity effects in orange and net effect in black. Ribbons indicate 95% confidence intervals. Relationships are split by seasons (May and August) and species pools ("spatial", "phenology", "combination").

Table 2: ANOVA type I table of REML fitted biodiversity effect partitioning models for 1) community biomass, 2) shoot density and 3) shoot biomass. Fixed effects tested with F-test, denominator degrees of freedom estimated with Welch-Satterthwaite's approximation. Significance levels indicated by number of *. * p <0.05, ** p <0.01, *** p <0.001. Significance of random intercept expressed as explained variance ratio compared to residual variance.

1) Community biomasss	Net effect biomass			Complementarity effect biomass			Selection effect biomass		
Fixed effects	NumDF	DenDF	F value	NumDF	DenDF	F value	NumDF	DenDF	F value
Species richness (log)	1	106	0.28	1	106	0.11	1	214	0.04
Species pool	2	106	7.31 **	2	106	5.44 **	2	214	3.47 *
Season	1	108	41.17 ***	1	108	0.09	1	214	2.61
Species richness (log) : species pool	2	107	0.25	2	107	0.076	2	2.15	0.11
Species richness (log) : season	1	108	6.16 *	1	108	6.24 **	1	214	0.14
Species pool : season	2	108	0.8	2	108	0.12	2	214	5.42 **
Species richness (log) : species pool : season	2	108	2.35	2	108	0.25	2	214	0.04
Variance ratio random effects									
Community ID : block	0.43			0.07			<0.01		
Block	0.03			0.01			0.02		
Residual	0.54			0.93			0.98		

2) Shoot density	Net effect shoot density			Complementarity effect shoot density			Selection effect shoot density		
Fixed effects	NumDF	DenDF	F value	NumDF	DenDF	F value	NumDF	DenDF	F value
Species richness (log)	1	108	3.94 *	1	106	5.54 *	1	106	2.97
Species pool	2	108	6.92 **	2	106	6.73 **	2	106	5.00 **
Season	1	108	20.48 ***	1	108	8.84 **	1	108	2.7
Species richness (log) : species pool	2	108	0.26	2	107	1.03	2	107	0.75
Species richness (log) : season	1	108	0.39	1	108	0.82	1	108	0.52
Species pool : season	2	108	2.66	2	107	6.99 **	2	108	9.00 ***
Species richness (log) : species pool : season	2	108	0.22	2	108	1.1	2	108	0.94
Variance ratio random effects									
Community ID : block	0.27			0.29			0.31		
Block	<0.01			<0.01			<0.01		
Residual	0.73			0.71			0.69		

3) Shoot biomass	Net effect shoot biomass			Complementarity effect shoot biomass			Selection effect shoot biomass		
Fixed effects	NumDF	DenDF	F value	NumDF	DenDF	F value	NumDF	DenDF	F value
Species richness (log)	1	103	0.27	1	106	<0.01	1	193	0.36
Species pool	2	97	13.22 ***	2	99	2.27	2	193	9.19 ***
Season	1	98	12.28 ***	1	101	3.05	1	193	7.3 **
Species richness (log) : species pool	2	104	0.06	2	107	0.37	2	193	0.02
Species richness (log) : season	1	104	0.44	1	107	0.05	1	193	0.32
Species pool : season	2	98	16.71 ***	2	101	4.69 *	2	193	9.32 ***
Species richness (log) : species pool : season	2	105	0.1	2	108	0.26	2	193	0.01
Variance ratio random effects									
Community ID : block	<0.01			<0.01			<0.01		
Block	<0.01			0.03			<0.01		
Residual	>0.99			0.96			>0.99		

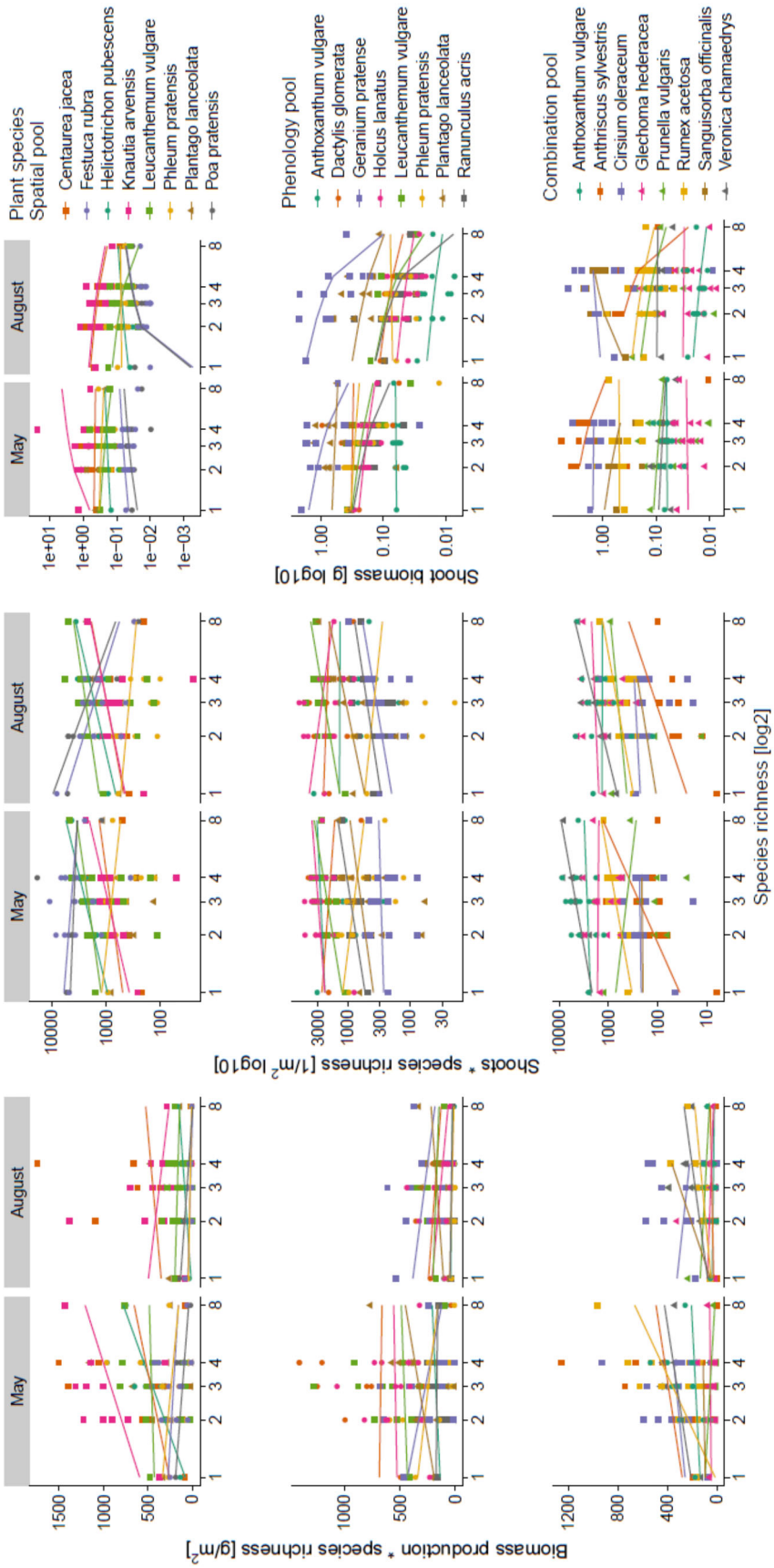

Figure 4: Species biomass, number of shoots and average biomass per shoot plotted against species richness. Species biomass was corrected for sown proportions, number of shoots was corrected for sown proportions and log transformed (log10 scale), average biomass per shoot was log transformed (log10 scale), and species richness was log transformed (log2 scale). Data are shown separately for plant species, species pool, and sampling season. Different colors indicate different species, and different symbols indicate different functional groups: Grasses in circles, small herbs in triangles, and tall herbs in squares.

Table 3: ANOVA type I table of REML fitted species biomass, and shoot biomass models. Fixed effects tested with F-test, denominator degrees of freedom (DenDF) estimated with Welch-Satterthwaite's approximation. Shoot density model fitted a negative binomial model. Significance of predictors tested with likelihood ratio against a Chi^2 distribution test. Significance levels indicated by number of *. * p <0.05, ** p <0.01, *** p <0.001. Significance of random intercept expressed as explained variance ratio compared to residual variance.

	Biomass production			Shoot density		Shoot biomass		
Fixed effects	NumDF	DenDF	F value	df	LRT	NumDF	DenDF	F value
Species richness (log)	1	604	3.4	1	5.18	1	127	0.2
Species pool	2	606	12.51 ***	2	11.03 **	2	141	3.22 *
Plant species	19	605	14.19 ***	19	569.37 ***	19	591	7.55 ***
Season	1	604	142.40 ***	1	8.16 **	1	536	13.68 ***
Species richness (log) : species pool	2	595	2.19	2	4.42	2	130	0.51
Species richness (log) : plant species	19	605	1	19	61.78 ***	19	594	0.49
Species richness (log) : season	1	604	4.38 *	1	0.03	1	536	0.27
Species pool : season	2	604	5.07 **	2	0.22	2	536	0.86
Plant species : season	19	604	4.83 ***	19	77.12 ***	19	537	2.79 ***
Species richness (log) : species pool : season	2	604	1.07	2	2.05	2	535	0.72
Species richness (log) : plant species : season	19	604	0.52	19	9.09	19	536	0.43
Variance ratio random effects								
Plot ID : block	<0.01					0.2		
Block	<0.01					<0.01		
Residual	>0.99					0.98		

Discussion

Biodiversity effects and species composition

The net biodiversity effects on community biomass, on shoot density and on shoot biomass depended on species composition, i.e. species pools, and season, highlighting the context-dependency of species richness effects on biomass production (Fanin *et al.* 2018). In line with previous studies, positive net biodiversity effects on community biomass were based on positive complementarity effects and negative selection effects (Spehn *et al.* 2005). Both, complementarity effects and selection effects varied with the composition of the plant community and were strongest in the "spatial" species pool and weakest in the "phenology" species pool. This supports that biodiversity effects depend on the involved species (Hodapp *et al.* 2016). Moreover, it extends these findings by suggesting that the complementary use of available space by different species is more crucial for community biomass production than is the complementary phenology of species. The combination of positive complementarity effects and negative selection effects suggests that mixtures benefit plant species, which are less productive in monocultures (Loreau & Hector 2001). This is in line with studies also reporting a disproportional contribution of some species to the enhanced productivity of species-rich communities (Marquard *et al.* 2009, 2013; Roscher & Schumacher 2016).

Our results on the additive partitioning of biodiversity effects on shoot density supported the higher relevance of space over phenology for biodiversity effects, as complementarity effects and selection effects on shoot density were pronounced in the spatial and combination species pool, but only weakly present in the phenology species pool. A weakness of the additive partitioning approach is its high dependence on monoculture performance, which all mixture performances are compared with according to the method by Loreau and Hector (Loreau & Hector 2001).

In our study biodiversity effects on shoot biomass only appeared strong in the combination species pool. However, *Anthriscus sylvestris* (L. Hoffm.), part of the combination species pool, had a very low monoculture shoot biomass. Thus, it influenced the additive partitioning of the combination species pool strongly. In analyses excluding communities with *A. sylvestris*, the effect sizes of complementarity effects and selection effects in the combination species pool were strongly reduced (Supplementary Figure S2). With this limitation taken into account, additive partitioning did not show complementarity and

selection effects on shoot biomass in neither species pool. This supports earlier findings that biodiversity effects on community biomass are more strongly mediated by increased shoot density than by increased shoot biomass in experimental grasslands (Roscher *et al.* 2007; Marquard *et al.* 2009). Our data extend these findings by indicating that complementary use of space by species in mixtures strengthens biodiversity effects on shoot density and consequently on community biomass production. Research on the positioning and dynamics of plant individuals in mixed communities could provide more insight on how spatial patterns contribute to biodiversity effects.

Seasonal variation in biodiversity effects

Our results expand on the widely accepted general pattern of higher biodiversity increasing biomass production by also showing seasonal variation in biodiversity effects between May and August, where the former were much stronger than the latter. This may well reflect that seasonal changes in resource competition and in other biotic interactions could cause shifts in species richness – biomass production relationships (Doležal *et al.* 2019). Species-rich plant communities were reported to be associated with higher microbial activity, mobilising mineral soil nutrients and making them available to the plants (Allan *et al.* 2013; Lange *et al.* 2015; Strecker *et al.* 2016). In Mediterranean and temperate grasslands, the activity of soil microbes decreases during summer (Waldrop & Firestone 2006; Siebert *et al.* 2018). If this was also the case for our experimental system, it may well explain the quite similar biomass production at all species-richness levels in August.

Conclusion

In our study we found the strengths of biodiversity effects varied depending on the species composition of communities and on season. Increasing shoot density turned out to be a crucial component of increased community biomass production. In line with the spatial relevance of increased density, biodiversity effects were especially strong in communities composed of plant species differing in their use of space.

Acknowledgments

We thank Ngo Viet Ha Pham, Trung Son Ta, Thi Thu Thuy Tran, Duc Toan Chu and Xuan Truong Lee for their assistance with field measurements, Daniela Naglatzki for assistance with

biomass weighing, Daniel Prati and Sebastian Keller for statistical advice, and Seraina Cappelli for discussions about biodiversity effect partitioning.

Supplementary material

Table S1: Summary of pairwise Tukey's HSD contrasts between pairs of species pools, i.e. between the "spatial", "phenology" and "combination" pools, and seasons. Statistical significance of differences between combination of species pools and season are indicated by *: *p <0.05, ** p <0.1, *** p <0.001.

	estimated species biomass difference
Phenology May - spatial May	-0.95
Combination May - spatial May	-10 ***
Spatial August - spatial May	-12.22 ***
Phenology August - spatial May	-14.48 ***
Combination August - spatial May	-15.71 ***
Combination May - phenology May	-9.05 ***
Spatial August - phenology May	-11.27 ***
Phenology August - phenology May	-13.53 ***
Combination August - phenology May	-14.53 ***
Spatial August - combination May	-2.22
Phenology August - combination May	-4.48
Combination August - combination May	-5.71 *
Phenology August - spatial August	-2.26
Combination August - spatial August	-3.49
Combination August - phenology August	-1.23

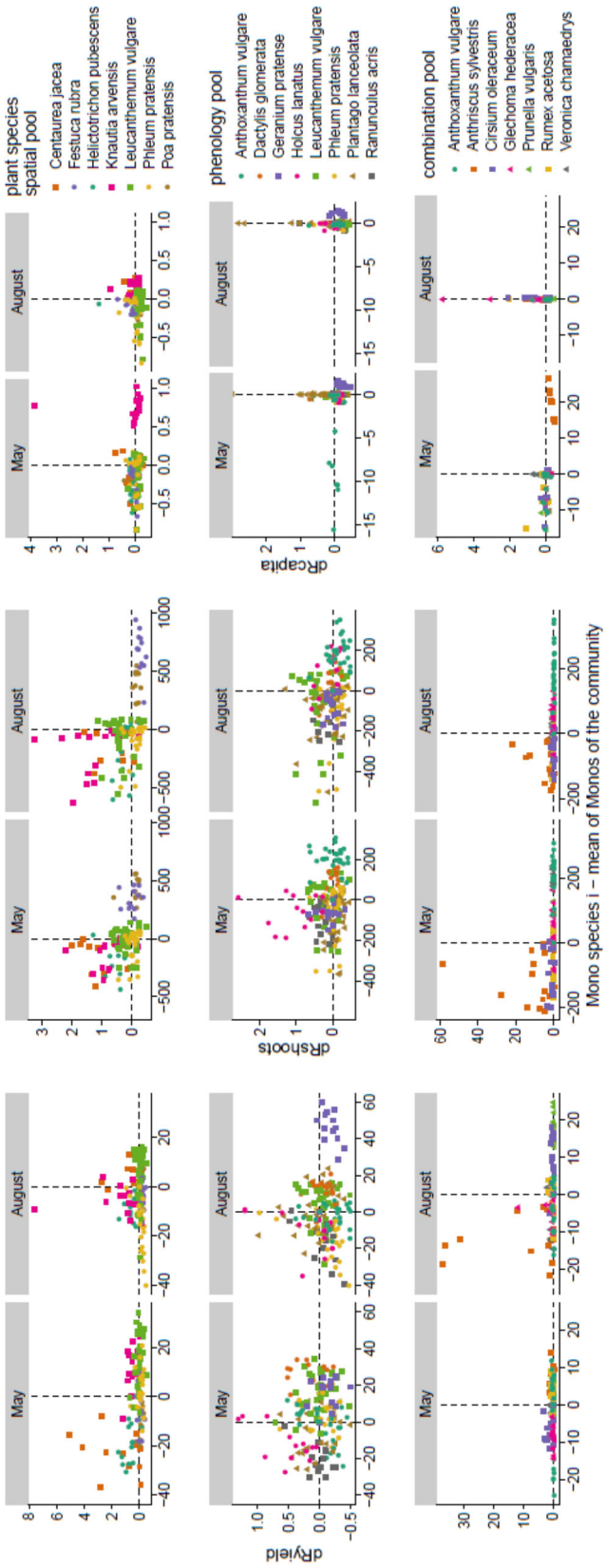

Figure S1: Contribution of individual species to additive partitioning. Difference of relative responses of biomass, shoot number and shoot biomass, plotted against the monoculture value of individual species minus the average monoculture value of species contributing to the mixture. Method following advice from Seraina Cappelli. Data are shown separately for plant species, species pool, and sampling season. Different colors indicate different species, and different symbols indicate different functional groups: Grasses in circles, small herbs in triangles, and tall herbs in squares.

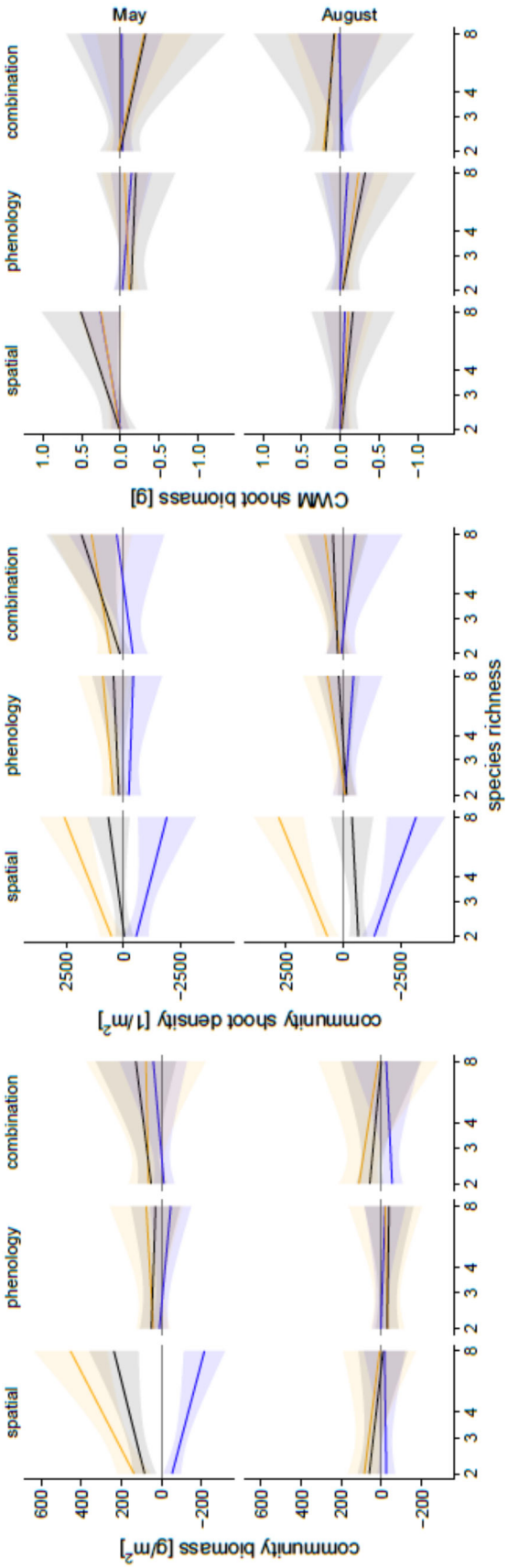

Figure S2: Additive partitioning omitting communities containing *Anthriscus sylvaticus*. Selection effects in blue, complementarity effects in orange and net effect in black. Ribbons indicate 95% confidence intervals. Relationships are split by seasons (May and August) and species pools ("spatial", "phenology", "combination").

Chapter 3

Small-scale plant cover dynamics and their relation to biodiversity and productivity in experimental grasslands

Clemens Kleinspehn, Lena Neuenkamp, Anna Roeder, Christiane Roscher and Markus Fischer

Abstract

Spatial dynamics have been largely neglected in studies of the relationship between biodiversity and community stability. We studied the small-scale spatial dynamics across a two-year period of plant cover by different species and the spatial association between plant species in 138 experimental grassland communities varying in plant species richness from 1 to 8 species and composed of species from three different species pools. One of these pools was comprised of species differing in their use of space, another was comprised of species differing in phenology, and the third was comprised of species differing in both respects. We asked how plant cover and spatial species associations changed between years, and how they were related to biodiversity and biomass. In October 2014 and 2015, we recorded species cover for all plant species for 1 x 1 cm grid cells within plots of 80 x 80 cm in each of the 138 experimental grassland communities. We found 60 % mean plant-cover turnover of species in monocultures, which increased to 71 % in 2-species mixtures and to even 90 % in 8-species mixtures, without a net gain or loss of species cover between years. Lower plant-cover turnover per species in species-poor communities coincided with spatial segregation between plant species. High plant-cover turnover per species in more species-rich communities coincided with lower segregation and neutral species associations. Thus, plant-cover dynamics of individual species appear to be inverse to cover stability of the whole community, just as productivity instability of species ensures stability in productivity of communities.

High plant-cover turnover per species was also associated with high biomass production per species, which may suggest that spatial species dynamics within communities enable more efficient resource use, e.g. by exploiting different microhabitats. This could be a mechanism underlying positive biodiversity – biomass relations. We conclude that

biodiversity may affect stability in terms of small-scale spatial dynamics, and we suggest that spatial patterns and dynamics might contribute to biodiversity – ecosystem function relations at the community level.

Introduction

The relationship of biodiversity and stability of communities has been a long-standing discussion among ecologists with two lines of argument (reviewed in Tilman *et al.* 2014). Observational studies suggested that diverse communities were more stable and resistant to invasion of new species compared to species poor communities (Elton 1958). In contrast, population modelling approaches suggested that adding more species to a community should decrease stability by introducing more complex interaction networks between the species (May 1974). The discussion has been resolved by unifying both lines of thought and by agreeing that diverse communities overall are more stable because of the flexibility of their variable elements (Yachi & Loreau 1999). Stability in this discussion has typically been defined as the stability of population numbers of community members over time or stability ecosystem functions like biomass production over time. Recent research has suggested the importance of spatial features for biodiversity effects on plant species in grasslands (Marquard *et al.* 2009). Consequently, we ask whether the biodiversity – stability relationship applies also to the stability of spatial patterns (e.g. cover distributions) of plant species in diverse communities. If the biodiversity-stability relationship observed on functions like populations numbers or biomass production (Tilman & Downing 1994; Yachi & Loreau 1999) applies to other population features like spatial patterns as well, we would expect greater stability in total community cover in species rich communities.

Local biotic interactions depend on local neighbors (Gallien 2017), raising the question of how the identity and diversity of the local neighbors alters the local biotic interactions and the spatial patterns they create. If local neighbors are similar in their growth form, phenology and use of space, local interspecific competition for space could be strong and lead to non-random spatial patterns. In contrast, diverse local neighbors with different growth forms, phenology and use of space might experience lower interspecific competition and thus exhibiting less structured, random spatial patterns (Chesson 1991).

How stability of spatial patterns affects the productivity of the community or species remains unclear. Analogous to mechanism behind stability of population numbers or biomass (Yachi & Loreau 1999, May 1974), dynamic, thus adaptable, individual species cover could safeguard stable total community cover, and thereby community productivity. Persistent patterns could provide opportunities for individuals to grow larger and thus more productive.

In contrast, dynamic patterns could provide opportunities to select the most productive species best suited for each micro site and thus to maximize the resource usage within the community. Aside from individual species cover and its dynamics, spatial associations of species (i.e. whether they grow more aggregated or segregated with other species) are another piece of information brought about by spatial patterns with potential consequences for productivity. For instance, plant species segregate from each other in grasslands, indicating avoidance of competition (Saiz & Alados 2012). Avoidance of competition by spatial segregation could increase the biomass production of communities and lead to higher growth or reproduction (Silvertown 2004).

High resolution mapping at small scales offers the opportunity to examine spatial patterns of plant species and their cover stability on almost individual level. Cover changes can be mapped by dividing the plot into fine grid cells and mapping the spatial extension and position of plant species via the number and position of the grid cells their cover (Saiz & Alados 2012). Since individuals of vegetatively reproducing plant species are difficult to distinguish in the field, high resolution cover data can serve as a helpful proxy to map changes in community cover and the cover extension of individual species. Whether segregation of grassland plant species prevails in grasslands other than those studied by Saiz & Alandos (2012), varying in species richness and species composition remains unexplored until now.

In this study we observed and analyzed spatial patterns in the Jena Trait Based Biodiversity experiment. In 138 communities of varying species composition and species richness, we recorded high resolution cover data of plant species and their dynamic between two years, 2014 and 2015. We analyzed spatial patterns of community members, and whether they were related to community richness and composition. Finally, we compared the spatial patterns with recorded biomass production data of these communities and their members.

We investigated:

1. How does plant species cover change between years in communities of varying species richness and composition?
2. How do species associations change with species richness of communities?

3. How do changes in species cover and species associations correspond with biomass production?

Methods

Study area

We worked in the Trait-Based Biodiversity Experiment (TBE) belonging to the Jena Biodiversity Experiment, a large grassland biodiversity experiment (Roscher *et al.* 2004). The experimental site is located in the valley of the Saale river close to the city of Jena, Germany, 130 m a.s.l, 50°57 N, 11°37 E. At the weather station Jena/Sternwarte, mean annual temperature, measured between 1980 and 2010 (without 1997), was 9.9° Celsius, and mean annual precipitation was 610mm (Hoffmann *et al.* 2014).

Experimental design

The Jena TBE plant communities were designed to experimentally test diversity in two gradients of traits. One gradient covered diversity along spatial traits and another gradient covered diversity along phenological diversity. During the establishment of the TBE in 2010, 20 non-legume plant species of the *Arrhenatherion* vegetation alliance (Leuschner & Ellenberg 2017) were sown in 138 plots of 3.5 meter x 3.5 meter size in three blocks (Ebeling *et al.* 2014). The 20 plant species were chosen from a pool of 48 non-legume plant species present in the Jena Main Experiment (Roscher *et al.* 2004). Of these 20 plant species, three slightly overlapping species pools were created, each consisting of eight plant. The different species pools aimed to maximize diversity in different sets of plant traits. Species pool one, the “spatial” pool, aimed to combine plant species with different strategies in spatial resource acquisition, from “small” to “large” species. Species pool two, the “phenology” pool, aimed to combine plant species, which access resources at different times through the growing season, from “early” to “late”. Species pool three, the “combination” pool, aimed to combine plant species, which differ most in both spatial and phenological strategies. In each species pool, communities were sown with species richness levels of one, two, three, four, or all eight species. At sowing, total seed density was constant across all communities, i.e. 1000 seeds per m^2, adjusted for germination rates from standard laboratory tests (Ebeling *et al.* 2014). Sown seeds were equally distributed among species, resulting in a lower initial seed number of species-specific seeds in more species rich communities than in their respective monocultures. The communities of the experiment were mowed twice a year and mown biomass was removed, mimicking the management of extensive hay meadows in the region.

No fertilizer was added. Furthermore, all communities were weeded three times per year to maintain original sown species compositions.

Sampling gridline intersection method

In the 138 plant communities, we established quadratic plots of 80 x 80 centimeter. The Y-axis had an East - West orientation. Starting from the zero line of the Y-axis we established 21 transects at four centimeter interval per plot (Figure 1). Along each transect we recorded the presence of plant species crossing the transect line at one cm intervals, once in October 2014 and once in October 2015.

To measure community biomass, we sampled biomass down to one centimeter above the ground in two 10 x 80 centimeter transects within each of the quadratic plots. These 10 x 80 cm transects paralleled the East and West borders of the quadrats, respectively, in 10 cm distance. We weighed the samples after drying them at 70 degrees Celsius for two days and scaled biomass up to grams per square meter.

Data analysis

We transformed the transect data into grid data with a grid cell size of 1 x 1 cm, and 21 x 81 = 1701 cells in total per grid (Figure 2). Species-specific cover was measured as number of occupied grid cells. We calculated inter-annual cover change per plant species by subtracting the 2014 grid data from 2015 grid data. Cover shift was analyzed as ratio of cover change and maximum cover across both years.

The association between plant species was assessed by comparing the observed co-occupied grid cell number with the neutral expectation based on independent random distribution of species (Saiz & Alados 2012; Saiz *et al.* 2016). The number of expected co-occupied grid cells is the product of the probability of each grid cell being occupied by each focal plant species multiplied by the total number available of grid cells.

For a two-fold interaction:

$$N_{exp} = \frac{N_{obs\,i}}{N_{total}} * \frac{N_{obs\,j}}{N_{total}} * N_{total} = \frac{N_{obs\,i} * N_{obs\,j}}{N_{total}}$$

For a n-fold interaction:

$$N_{exp} = \frac{N_{obs\,i} * \ldots * N_{obs\,n}}{N_{total}^{(n-1)}}$$

where N_{exp} is the number of expected co-occupied grid cells, N_{obs} the number of observed grid cells with plant species i, j, or n, respectively, and N_{total} is the number of total cells available in the grid. We measured association strength in our study as the difference of observed co-occupied grid cells and expected co-occupied grid cells standardized by expected co-occupied grid cells.

$$Association\ strength = \frac{N_{obs} - N_{\exp}}{N_{\exp}}$$

We tested the statistical significance of association or dissociation by checking, whether N_{obs} fell outside of the 95% confidence interval of a Poisson distribution with N_{exp} as λ (Saiz & Alados 2012). We fitted generalized linear mixed models with restricted maximum likelihood (REML) with species-specific cover, annual shift, and the association strength of plant species pairs as response variables. Species richness, species composition (species pools) and sampling year (except for the annual shift response) were treated as fixed factors. Community identity was treated as random factor. Count data, i.e. absolute cover data, were modeled with a Poisson error distribution, association strength was modeled with a Gaussian error distribution, and percentage cover data were modeled with a binomial error distribution. Overdispersion was accounted for, if necessary, with quasi-Poisson or beta-binomial error distribution models, respectively (Zuur *et al.* 2009). Significance of parameters was estimated by type II Wald Chi^2 testing for consistent testing between models.

We performed all statistical analyses with the R 4.0.5 software (R Core Team 2021), including the packages *lme4* (Bates *et al.* 2015) for linear mixed effect modelling, *glmmTMB* (Brooks *et al.* 2017) for betabinomial models*, lmerTest* (Kuznetsova *et al.* 2017)*, broom.mixed* (Bolker & Robinson 2021)*,* and *effects* (Fox & Weisberg 2018) for model testing and interpretation; *ggplot2* (Wickham 2016)*,* and *cowplot* (Wilke 2018) for graphical display; *data.table* (Dowle & Srinivasan 2018) and *tidyverse* (Wickham 2017) for consistent and efficient data management.

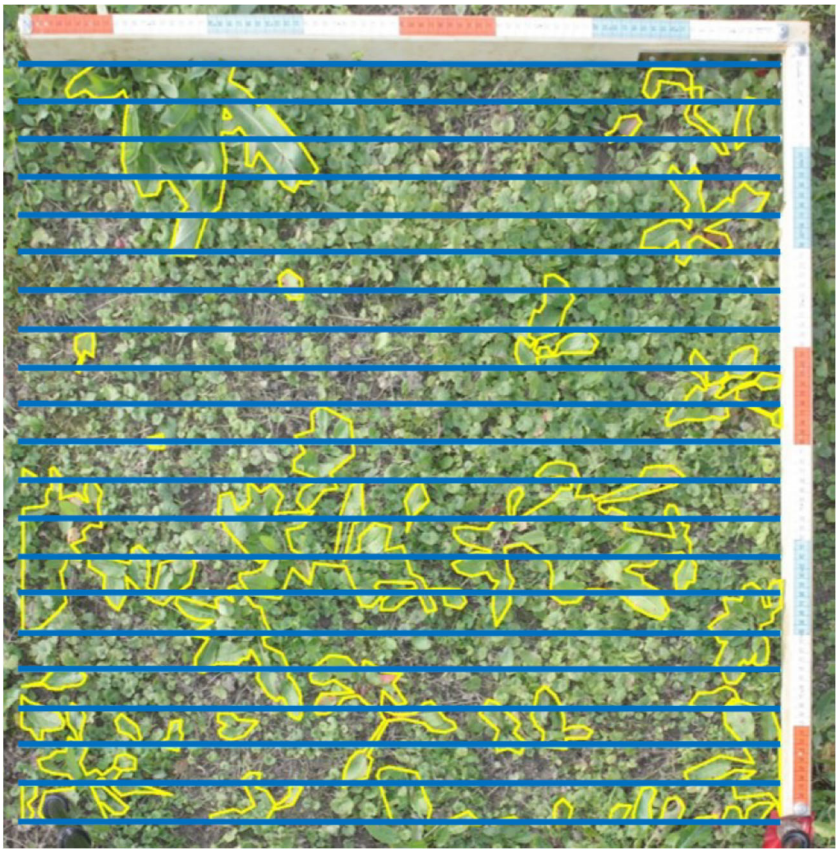

Figure 1: Example of mapping species cover in a plot. Plot 132; *Rumex acetosella* outlined in yellow, transects indicated as blue lines.

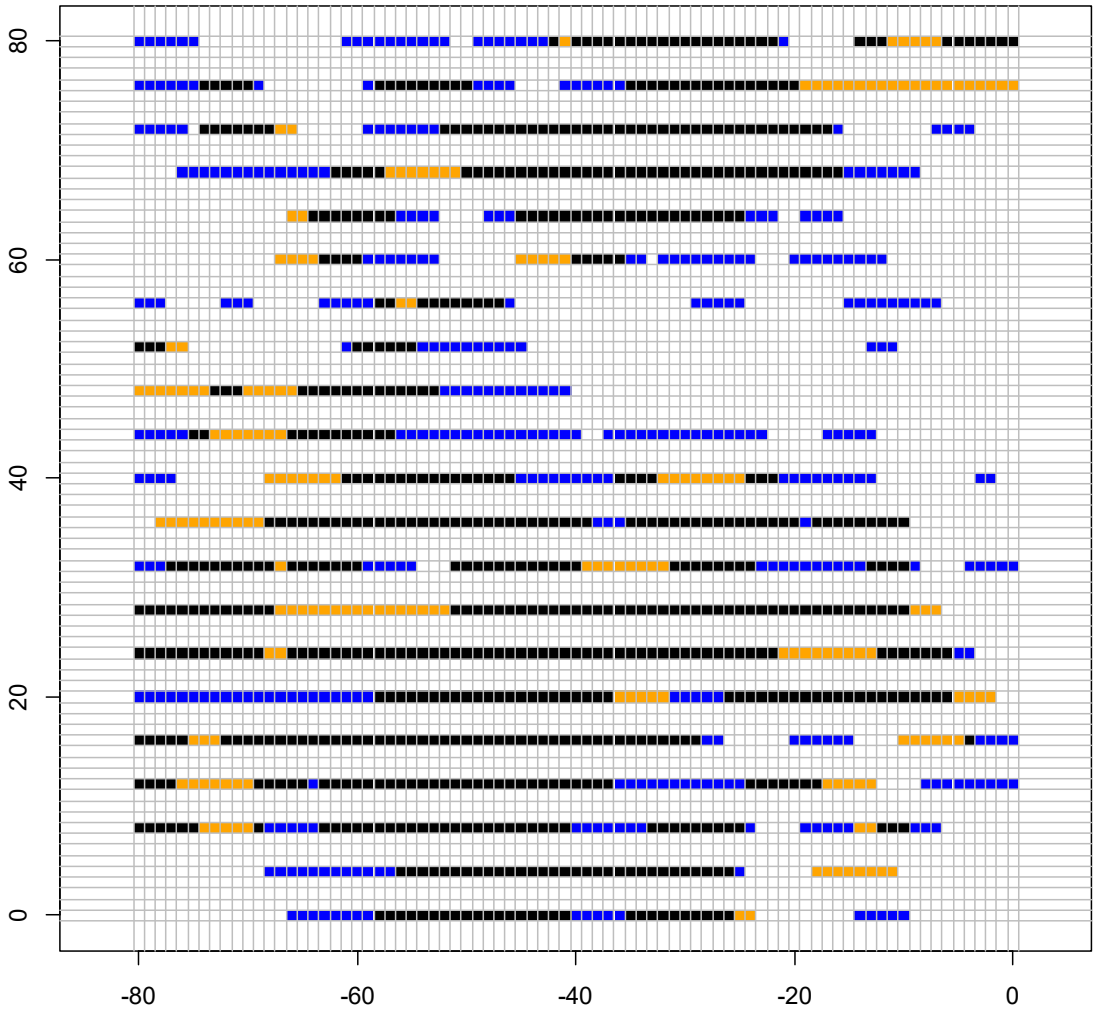

Figure 2: Exemplary grid map of *Leucanthemum vulgare* in Plot 3. Black represents cells occupied in both 2014 and 2015. Orange represents grid cells occupied only in 2014, and blue represents grid cells occupied only in 2015.

Results

Plant cover change

Community attributes, species richness and composition affected plant cover and cover dynamics in our experiment. In the 138 experimental grassland communities, total community plant cover decreased from 2014 to 2015 (Supplementary Table S1). In 2014, communities had a mean plant cover of 71.8 ± 1.6 % (mean ± SE), and in 2015, 60.7 ± 1.6 %. In both years, plant cover increased with species richness of the communities. In 2014, mean plant cover increased from 60.1 ± 3.5 % in monocultures to 82.4 ± 3.0 % in mixtures with eight species. In 2015, mean plant cover increased from 44.3 ± 3.4 % in monocultures to 76.9 ± 3.5 % in mixtures with eight species.

Species-specific cover within communities was independent of species richness and community composition. With increasing species richness of the communities, most plant species increased the proportion of their cover that changed locations between 2014 and 2015, hereafter referred to as “cover turnover”, independent of the composition of the communities (Figure 3,

Table *4*). On average, plant species changed the location of 58.4 (± 8.0) % of their maximum cover in monocultures, while in eight-species mixtures plant species changed the location of 91.8 (± 3.3) % of their maximum cover.

Species-association change

Species pairs showed distinct spatial patterns of cover that were different from random spatial associations (Supplementary Figure S3). Segregation of the cover of species pairs (i.e. species growing less associated from each other than expected under random spatial associations) was more prevalent than aggregation (i.e. species growing more associated to each other than expected under random spatial associations). However, segregation was more frequent in species-poor than in species-rich communities (Figure 4, Table 5). In both years, the proportion of segregated species pairs decreased with increasing species richness from an average of 84.6 ± 2.6 % in communities with two species to 38.6 ± 6.2 % in communities with eight species. The proportion of neutrally associated pairs increased with increasing species richness from 15.2 ± 2.6 % in communities with two species to 51.2 ± 6.2 % in communities with eight species. In 2014, the proportion of aggregated associations increased with increasing species richness from 0.9 ± 0.6 % in communities with two species to 20.3 ± 6.5 % in communities with eight species, while such increase was absent in 2015. Spatial species associations were detectable at resolutions below a grid scale of 8 x 8 centimeter, while all associations appeared neutral at scales of 8 x 8 centimeter or larger (Supplementary Figure S5).

Relationship between changes in species cover and species associations with biomass production

High cover turnover of plant species in more species-rich communities correlated with high species biomass (Figure 5, Table 6). While this effect was significant in the "spatial" and "phenology" species pools, in the "combined" species pool there was no such trend (Supplementary Table S3). For an illustration of this trend, in the "spatial" species pool mean adjusted biomass per species increased from 1111 ± 150 g/m^2 at 40 % cover turnover to 2412 (± 114) g/m^2 at 100 % cover turnover. In the "phenology" species pool mean adjusted biomass per species increased from 1061 ± 142 g/m^2 at 40 % cover turnover to 1864 ± 108 g/m^2 at 100 % cover turnover. The proportion of segregation showed no consistent correlation with

community productivity across species pools (Figure 6, Table 7). Only for the “spatial” species pool in 2014, the proportion of negative interactions negatively decreased significantly with community productivity (Supplementary Table S4).

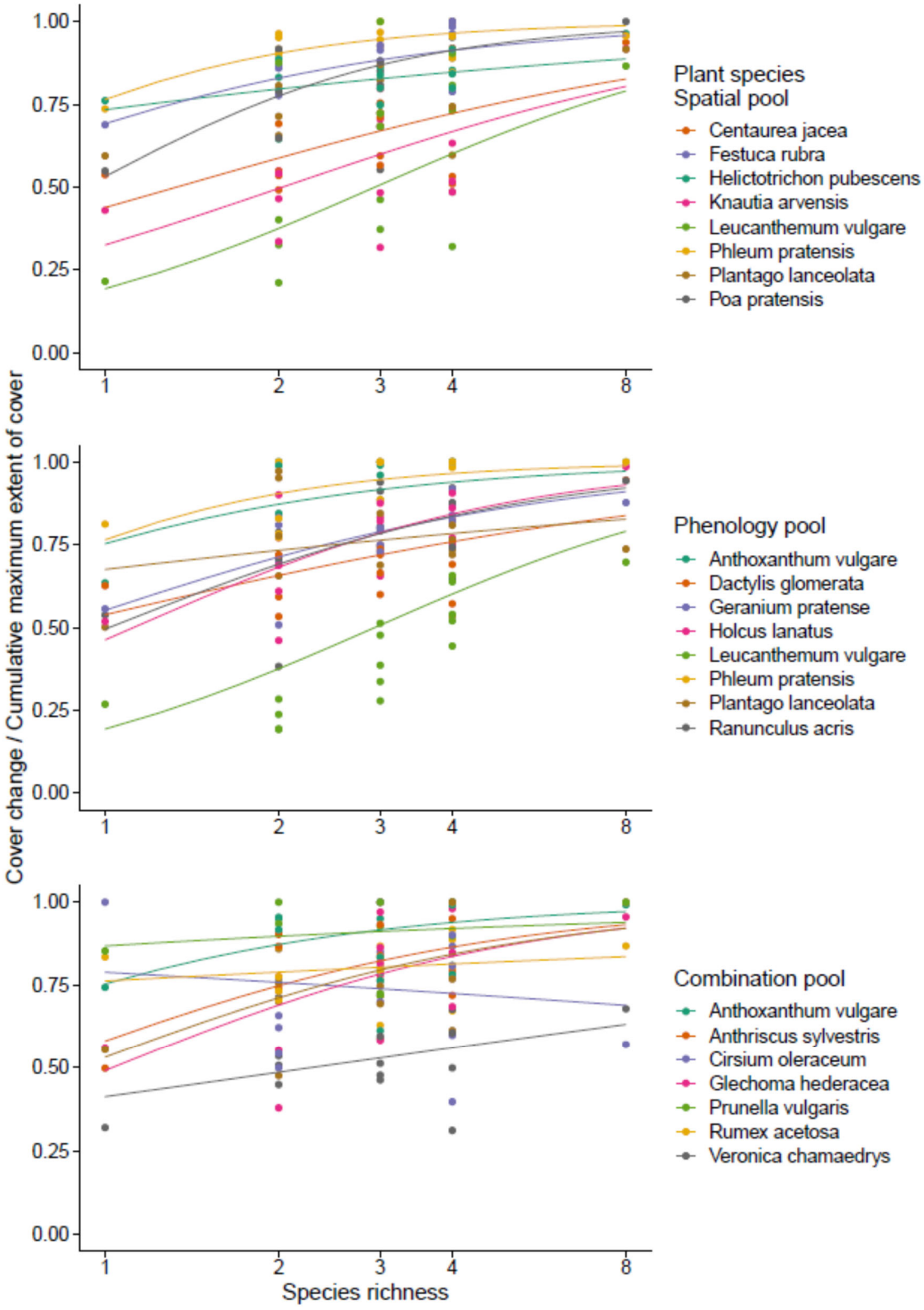

Figure 3: Ratio of changed plant cover between 2014 and 2015 relative to maximum extend of cover (i.e. number of covered grid cells in either 2014 or 2015). Split according species pools and plant species.

Table 4: Beta-binomial mixed-effects model of plant cover changes between 2014 and 2015 relative to the maximum cover in response to species richness, species composition (species pool) and plant species as well as their interactions. We tested the significance of terms with a type II Wald chi square test. * p <0.05, ** p <0.01, *** p <0.001.

Fixed effect	df	Chi^2
Species richness (log transformed)	1	8.31 **
Species pool	2	0.73
Plant species	19	25.51
Species richness (log) : species pool	2	0.72
Species richness (log) : plant species	19	2.63

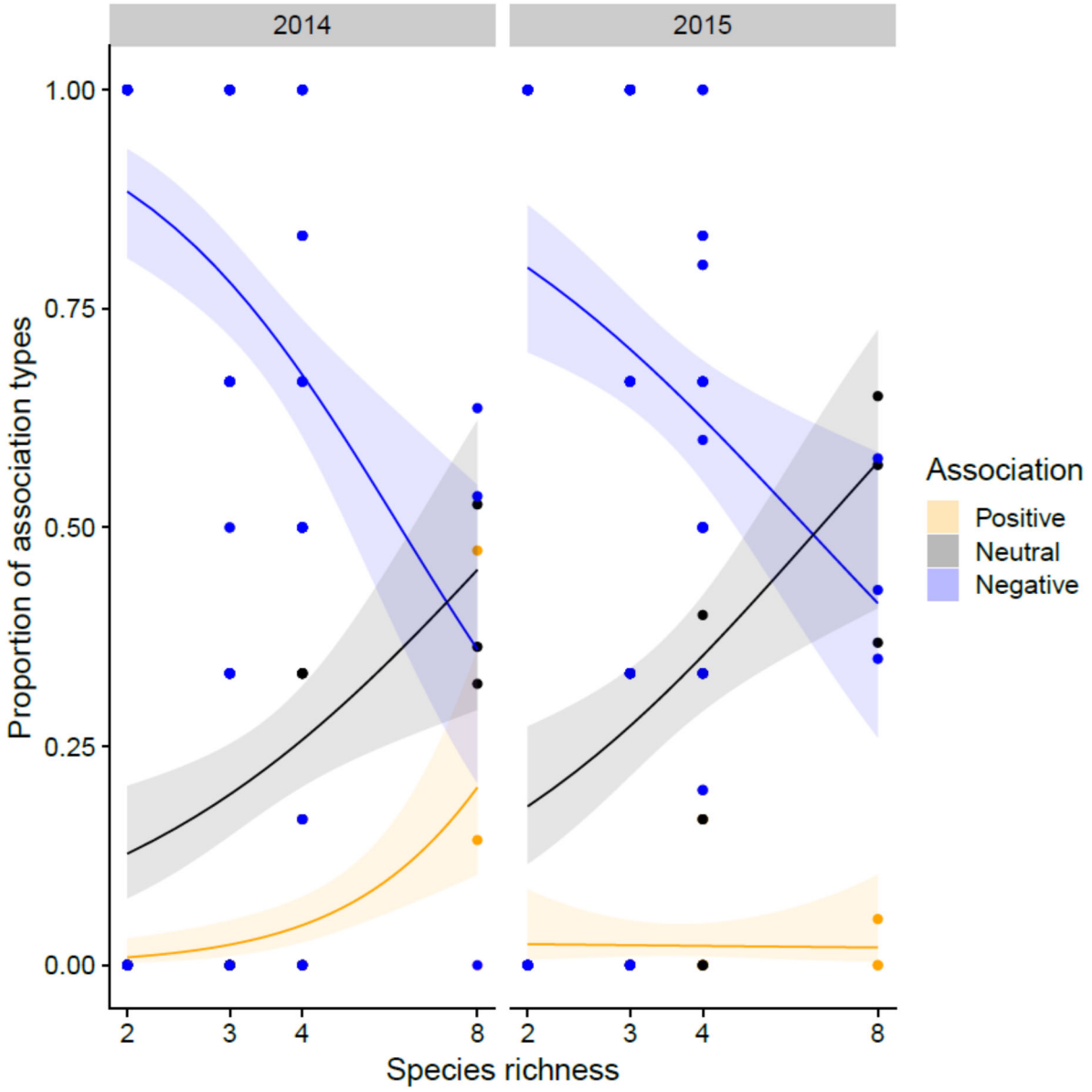

Figure 4: Proportion of significantly positive (aggregation), significantly negative (segregation) and neutral association in communities. Split according species richness level and year. Significance of association metrics based on the results of one-sided Poisson tests of observed association metrics vs the random expectation based on probability statistics

Table 5: Binomial mixed-effects models of the response of association proportions to species richness, year and their interaction. We estimated the significance of terms with a type II Wald chi square test. * p <0.05, ** p <0.01, *** p <0.001.

		Type of association		
		Positive	Neutral	Negative
Fixed effects	df	Chi^2	Chi^2	Chi^2
Species richness (log transformed)	1	9.56 **	20.43 ***	26.23 ***
Year	1	2.04	4.82 *	2.07
Species richness (log) : year	1	4.56 *	0.01	1.14

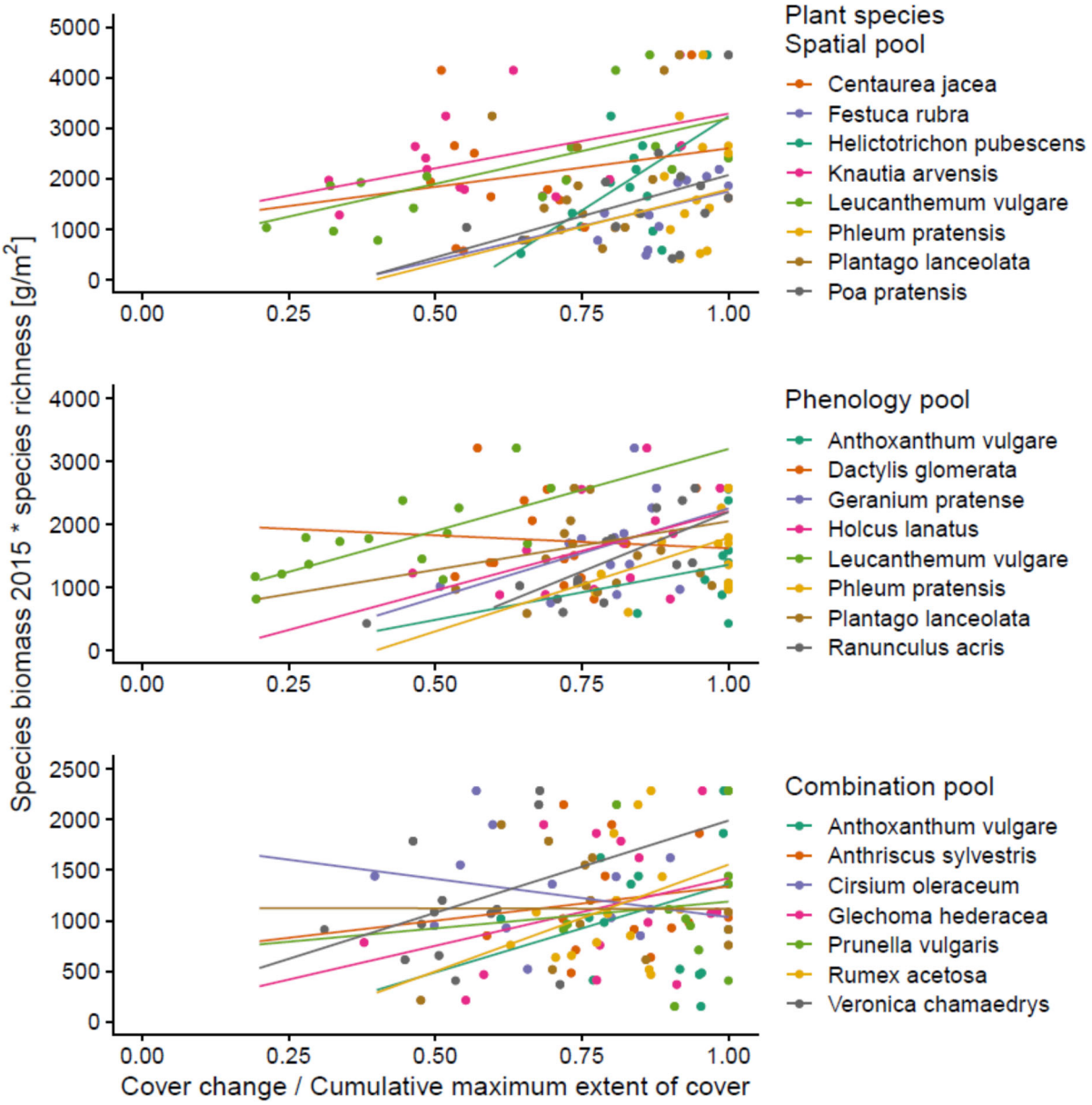

Figure 5: Biomass per plant species in 2015 (adjusted for sowing density) in relation to cover change relative to maximum extent of cover for the three species pools.

Table 6: Summary table of a REML model fitting species biomass in response to cover change, species pool and plant species nested within pools. Fixed effects in the mixed-effects model were tested with F-tests, and the denominator degrees of freedom (DenDF) were estimated with Welch-Satterthwaite's approximation. * p <0.05, ** p <0.01, *** p <0.001. Significance of random intercept expressed as explained variance ratio compared with residual variance.

Fixed effect	NumDF	DenDF	F value
Changed cover	1	592	67.61 ***
Species pool	2	593	2.57
Plant species	19	593	2.05 **
Changed cover : species pool	2	592	4.27 *
Changed cover : plant species	19	593	1.31
Variance ratio random effects			
Block	0.01		
Residual	0.99		

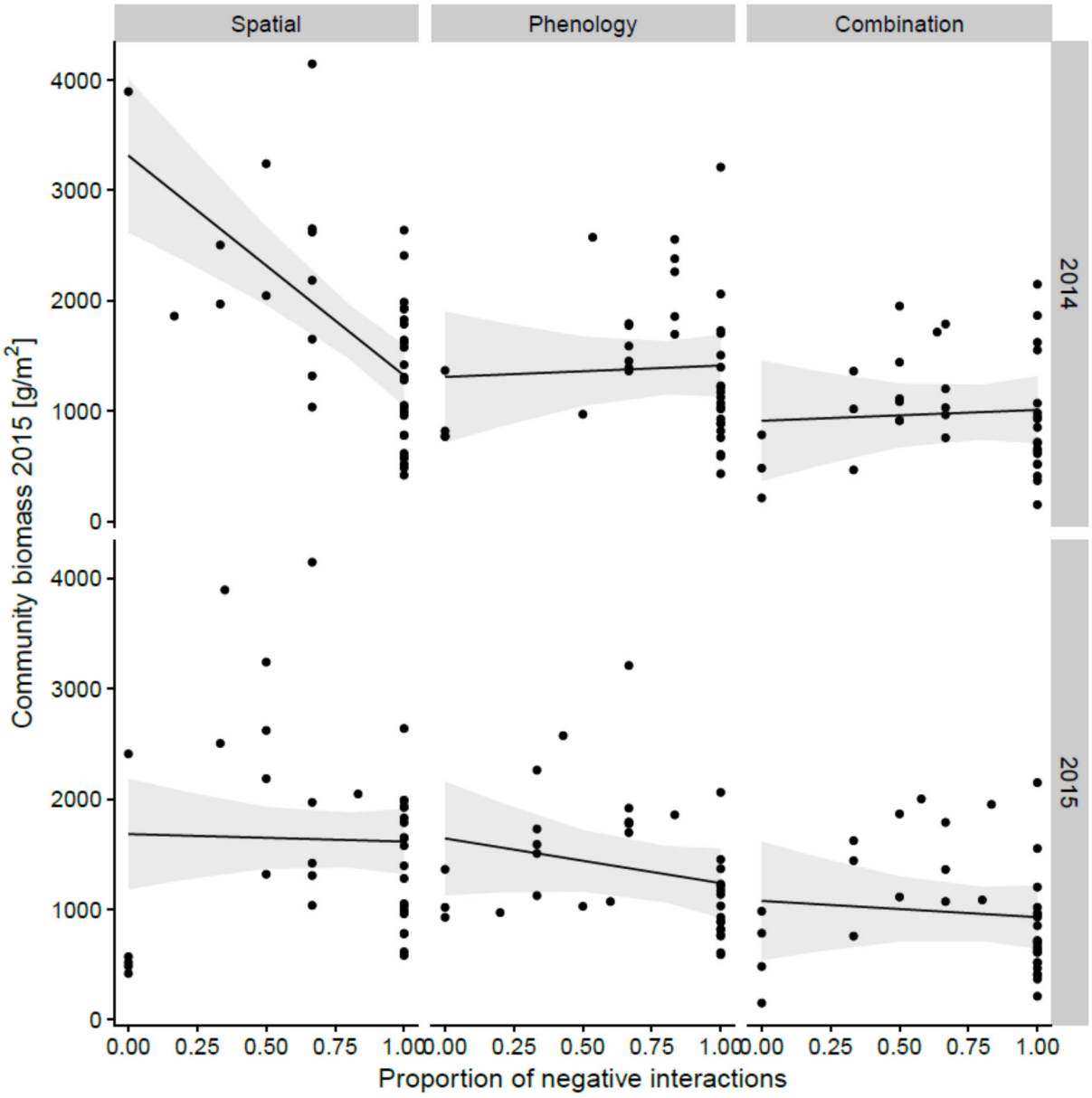

Figure 6: Biomass per community in 2015 in relation to the proportion of negative interactions for the three species pools (spatial, phenology and combination) and the two years.

Table 7: ANOVA type II table of REML fitted species biomass over proportion of negative interactions mixed effect model. Fixed effects tested with F-test, denominator degrees of freedom (DenDF) estimated with Welch-Satterthwaite's approximation. . * p <0.05, ** p <0.01, *** p <0.001. Significance of random intercept expressed as explained variance ratio compared with residual variance.

Fixed effect	NumDF	DenDF	F value
Proportion negative interaction	1	209	5.28 *
Species pool	2	210	10.63 ***
Year	1	209	1.66
Neg interaction : species pool	2	210	3.03
Neg interaction : year	1	210	1.34
Species pool : year	2	210	6.92 **
Neg interaction : species pool : year	2	210	7.3 ***
Variance ratio random effects			
Block	0.02		
Residual	0.98		

Discussion

In this study, we recorded the spatial cover patterns of 138 plant communities of varying species richness and species composition. Below we first discuss the increasingly dynamic species cover and decreasing segregation of cover of species pairs with increasing species richness of the communities. Then we discuss the relations of spatial patterns, spatial turnover and species associations with biomass production.

Increase of cover dynamics with species richness

With increasing species richness of the communities, for almost all plant species in this study, a higher proportion of individuals (i.e. proportion of total cover) changed their location leading to a higher spatial dynamic between the sampling years in species rich communities. This instability reached almost complete turnover of species cover in the eight species mixtures, and could be analogous to the instability of population size with increasing community diversity and thus complexity. This is, because the more interacting individual actors are part of a population, the less stable is their performance (May 1974). As has been shown in Chapter 1 of this thesis and reported by earlier studies (e.g. Marquard et al. 2009), species-rich mixed communities tend to have a greater relative density of plant individuals than respective monocultures. The smaller distances between individuals of different species could result in more complex and more intense biotic interaction networks between multiple species, like i.e. intransitivity (Gallien 2017; Soliveres & Allan 2018). The higher instability of complex, intense biotic interactions, in turn, could reflect in the larger cover instability of species in mixed communities as seen in Figure 3.

Decreasing segregation in diverse communities

Plant species tend to segregate their cover in grasslands (Saiz *et al.* 2016). Our data shows, that segregation changes with the species richness of communities. As cover turnover increased with species richness of the communities, segregation of species cover decreased. As spatial association on small scale can inform about biotic interaction, and segregation is assumed to indicate negative biotic interactions (Saiz & Alados 2012). Negative biotic interactions between two given species, appear to be less impactful in mixed communities, similar to the dilution effect observed on herbivores and pathogens (Otway *et al.* 2005) and

could thus be one mechanism behind the decrease in segregation with species richness of communities as observed in our study. If segregation dynamics were indeed related to presence of soil pathogens (negative plant-soil feedback), which increases over time (Hawkes *et al.* 2013), the effect of negative biotic plant-plant interactions can be expected also to increase in time. A frequent relocation between as growing season could hinder the establishment of clear spatial patterns driven by negative biotic interactions. Furthermore, biotic interactions between two species depend on other local species (Soliveres & Allan 2018). The complexity of biotic interactions of multiple species might watering down the distinct spatial patterns created by two-species interactions.

Another interesting hypothesis could be, that the stronger segregation of species cover in species poor communities and less segregated, more intermixed cover in species rich communities lead to an enhanced species richness effect, beyond a simple additive effect of additional species. In communities with segregated cover, species form islands of monocultures with only individuals on the edge interacting with other species, whereas in species rich communities every focal individual is interacting with individuals of other species. Edge effects are usually investigated on the landscape scale (Erdős *et al.* 2019), but depending on the sensation range of plants edge effects could have an impact on a scale smaller than ten centimeters (Supplementary Figure S5).

Spatial patterns and biomass production

Spatial turnover and corrected species-specific biomass increased with species richness of the communities. This correlation could be, as mentioned above, related to mitigation of negative soil feedback by increasing species richness (Petermann *et al.* 2008, Hawkes *et al.* 2013). Simultaneously, a reduction of clear spatial segregation in species cover that occurred in species-rich communities would also hinder negative soil feedback accumulation. Indeed, lower proportions of spatial segregation of species coincided with higher community productivity of species poor communities of spatial species pool in 2014. If weak segregation increases interaction of plant individuals of diverse species, many of the biodiversity mechanisms explaining mixture productivity could apply to the small scale as well (Yachi & Loreau 1999).

Although cover turnover and spatial segregation were correlated with biomass production of species and communities, respectively, all three components were correlated

with the species richness of communities as well. The latter makes disentangling the causality difficult. However, regressions of biomass production over species richness, analogous to models in Chapter 1 of this thesis provided a better fit of data than models with the spatial features as predictors. This could be an indication that our recorded spatial features are only one component of the species richness effect, while species richness effects also include other mechanism like negative soil feedback (Petermann *et al.* 2008) and reduced herbivore or pathogen pressure (Otway *et al.* 2005). Our experimental set up did not allow separation of the spatial feature effects from the species richness effect, as the experimental design of the communities had a different scientific focus than the explicit spatial features we tested. Nevertheless, our analyses provide arguments that a full factorial experiment addressing spatial features and species richness independently should be considered in the future.

Conclusion

As hypothesized, we found biodiversity-stability relationships to apply to spatial plant cover pattern as well. With higher species richness of the communities, we found increased cover turnover of the community members, which might have contributed to their higher relative biomass production compared to monocultures. Species cover segregation as described for grasslands earlier (Saiz *et al.* 2016) appeared mainly in species poor communities, without consistent links to lower community productivity. Overall, these findings suggest stability of spatial patterns works on a similar principle as stability of ecosystem functions in diverse communities. High spatial variability of multiple species safeguards overall spatial stability of the community. Moreover, this study encourages the investigation of biodiversity–stability relationships beyond classic ecosystem functions and the recognition of spatial limitations of biotic interactions depending on the species richness of the communities.

Acknowledgments

We thank Ngo Viet Ha Pham, Trung Son Ta, Thi Thu Thuy Tran, Duc Toan Chu and Xuan Truong Lee for assistance in sampling data. We thank Daniela Naglatzki for assistance in biomass weighing, and Hugo Saiz for statistical advice.

Supplementary Material

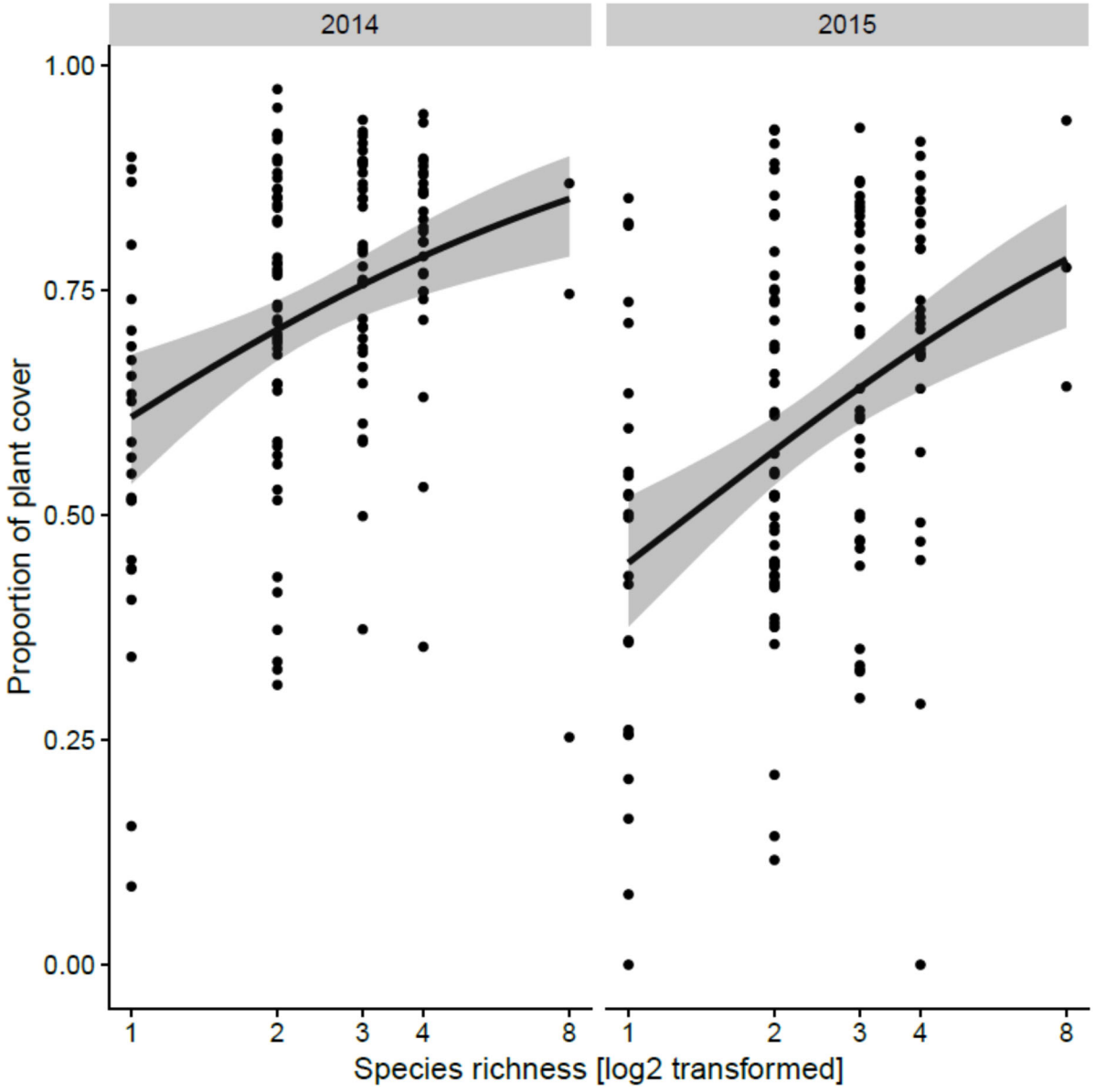

Figure S1: Proportion of total plant cover per community in relation to species richness for the two study years.

Table S1: Type II Wald table of beta-binomial total plant cover in plot model. The response plant cover was the ratio of plant cover vs total space available in plot. * p <0.05, ** p <0.01, *** p <0.001.

	Total plot cover	
Fixed effects	df	Chi^2
Species richness (log transformed)	1	33.33 ***
Species pool	2	7.1 *
Year	1	27.17 ***
Species richness (log) : species pool	2	6.34 *
Species pool : year	1	0.4
Species richness (log) :year	2	2.27
Species richness (log) : species pool :year	2	1.74

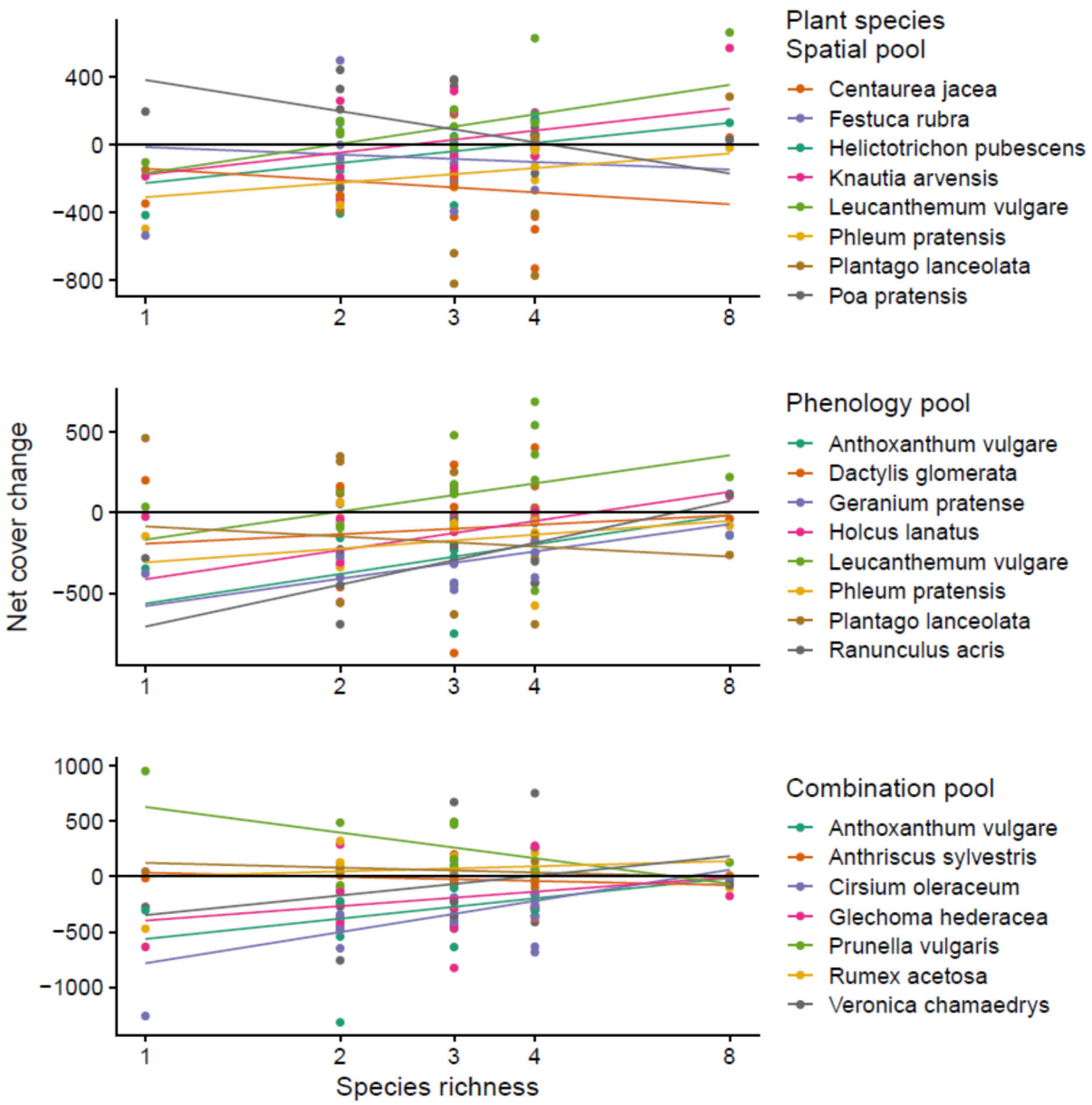

Figure S2: Net plant cover change over species richness of communities. Split according species pools and plant species.

Table S2: ANOVA type II table of REML fitted net cover change mixed effect model. Fixed effects tested with F-test, denominator degrees of freedom (DenDF) estimated with Welch-Satterthwaite's approximation. . * p <0.05, ** p <0.01, *** p <0.001. Significance of random intercept expressed as explained variance ratio compared with residual variance.

	Net cover change		
Fixed effect	NumDF	DenDF	F value
Species richness (log transformed)	1	309	13.57 ***
Species pool	2	309	4.83 **
plant species	19	310	4.17 ***
Species richness (log) : species pool	2	306	3.59 *
Species richness (log) : plant species	19	310	2.08 **
Variance ratio random effects			
Plot : block	0		
Block	<0.01		
Residual	>0.99		

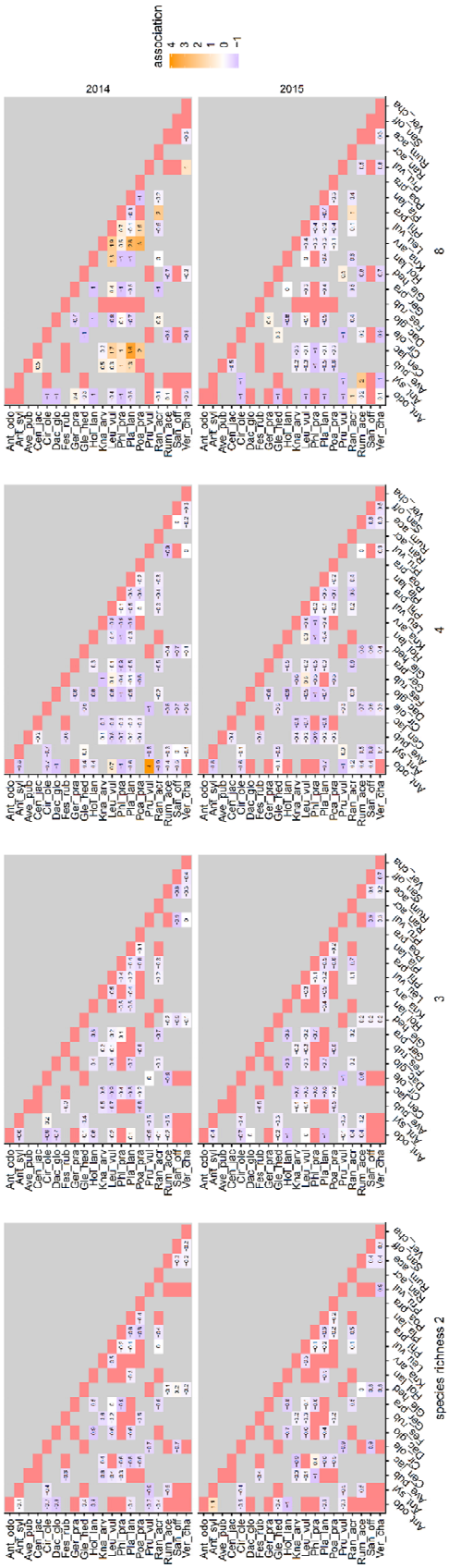

Figure S3: Association strength of pairwise species interactions in relation to species richness for the two study years. Red cells mark not realized plant associations, which were theoretically possible with the composition of Jena TBE communities. Grey cells mark species pairs, which were not possible with the composition of Jena TBE communities

Table S3: Least square trends of the relation between biomass 2015 and cover turn over in the different species pools

Pool	Trend estimate	Standard error
Spatial	5171	1567
Phenology	3932	1538
Combination	-1975	2328

Table S4: Least square trends of the relation between biomass 2015 and the proportion of negative interactions in the different species pools and years

Year	Species pool	Trend estimate	Standard error
2014	Spatial	-318.9	63.9
	Phenology	16.5	55.4
	Combination	15.8	54.7
2015	Spatial	-10.8	49
	Phenology	-64.8	52.4
	Combination	-23.6	51

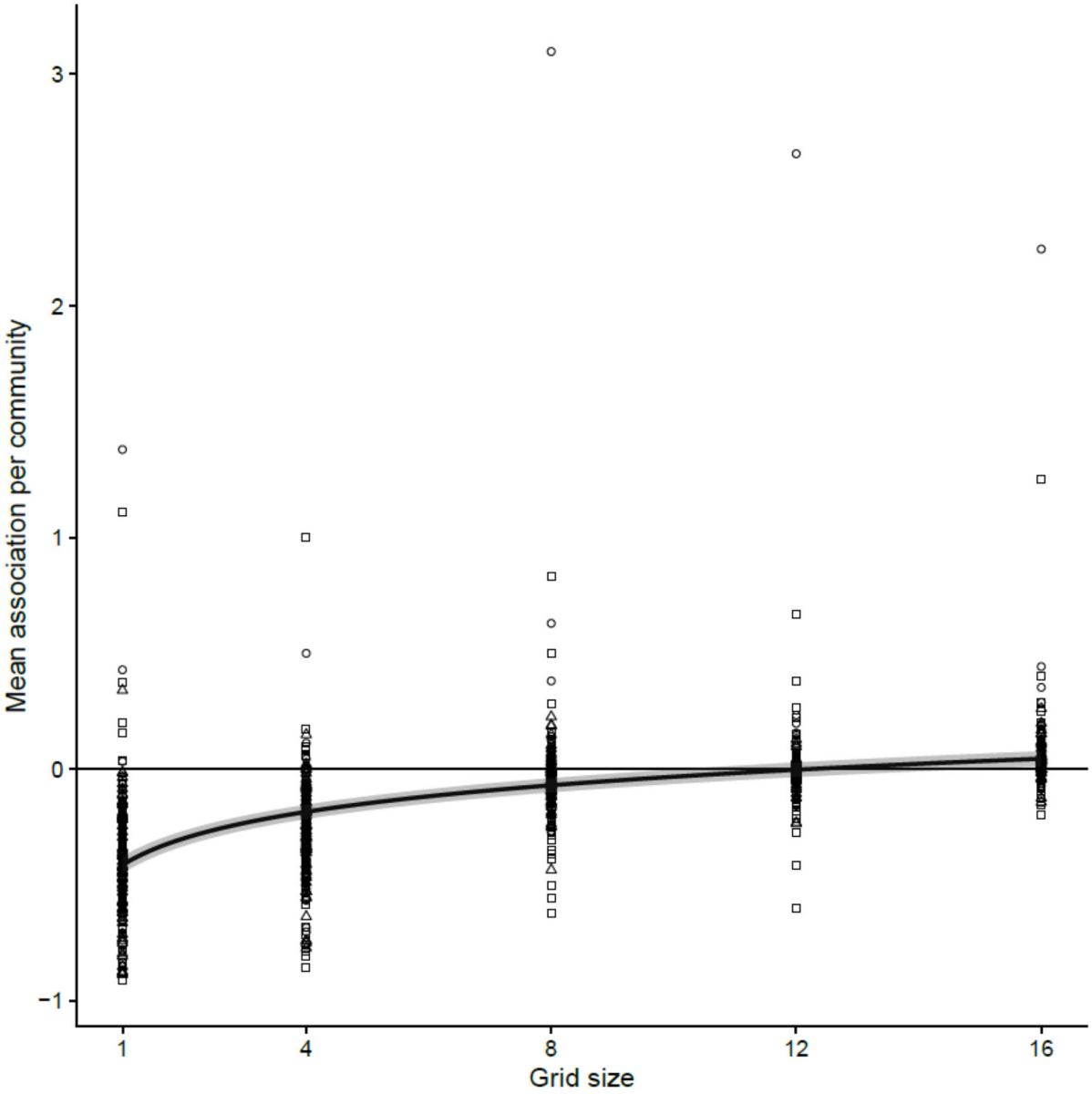

Figure S5: Mean association strength per community over size of the grid cell size.

Chapter 4

Legacy effects on light-related traits among the progeny of plants from 11-year-old experimental grassland communities differing in diversity and composition

Clemens Kleinspehn, Lena Neuenkamp, Christiane Roscher and Markus Fischer

Abstract

Plant community diversity and composition alter community biomass and light availability for the resident species. However, it is not known whether plant progeny differ in light-related plant traits according to the diversity and composition of their communities of origin.

We studied the progeny of 18 temperate grassland plant species in a 2-year common garden experiment, from 2014 to 2016. We grew the progeny from seeds collected in 79 experimental plant communities of the Jena Experiment in Germany, where these species had been grown at different species diversities and compositions for 11 years. In a common garden close to Bern, Switzerland, we grew the progeny in shade and full-light treatments to study how light availability affected their aboveground plant traits depending on the diversity and species composition of their communities of origin. After two growing seasons, we measured ten plant traits related to vegetative and generative growth on 6852 progeny individuals. We analysed trait differences with generalised linear mixed effect models.

Species diversity and legume presence of the communities of seed origin affected height and biomass of plant progeny. In full-light conditions, legume species from a species-poor community background grew more individual biomass than species from a species-rich community background, whereas tall herb species showed the opposite trend. In shaded conditions progeny biomass did not depend on the community background.

Communities of higher diversity and with legumes had progeny with higher common-garden floral investment and smaller leaf area, possibly enhancing the chance for progeny to

thrive after dispersal to sites with more light. Communities of higher diversity, but without legumes, had progeny with lower floral investment and larger leaf growth, possibly enhancing light capture at low-light conditions.

We show aboveground legacy effects of community diversity and composition via adaptation to light availability. Our findings add importantly to earlier findings of soil-mediated legacy effects of community diversity and composition. Moreover, we suggest that adaptation of plants to characteristics of their plant communities may be a generally prevalent element of community assembly.

Introduction

Plants may respond to their local environment via transgenerational genetic or epi selection or via phenotypic plasticity (Richards *et al.* 2017; Benito Garzón *et al.* 2019). Transgenerational effects have most frequently been investigated in response to environmental gradients of abiotic stress such as cold winters (He & Li 2018). The effects of biotic factors, such as species interactions, however, have been less well investigated (Alonso *et al.* 2019; Hargreaves *et al.* 2020). Offspring of the same plant species grown in experimental monocultures and mixtures of grassland species showed adaptive phenotype expression to their local environment (Zuppinger-Dingley *et al.* 2014), which was associated to genetic differences between monoculture and mixture offspring (van Moorsel *et al.* 2019). This local adaptation to community diversity and composition turned out to be related to soil-mediated legacy effects (Zuppinger-Dingley *et al.* 2016). In contrast, it is not known whether aboveground conditions, such as differences in light availability between plant communities with different diversity or species composition can cause transgenerational effects, too.

Plant community diversity often increases community productivity, via increased density of individuals (Marquard *et al.* 2009). This can reduce light availability and could cause selection of leaf traits (Bachmann *et al.* 2018). Expected trait shifts in response to reduced light availability include increases in specific leaf area (SLA) and plant height, as well as decreases in the number of branches or tillers, in reproductive effort, in dry biomass of vegetative structures and decreases in the numbers of seeds or fruits (Poorter *et al.* 2019). The direction of such trait shifts may depend on the competitive light strategy of the plant species. The two major strategies are shade tolerance and avoidance, which translate to maintaining maximum growth despite shading (shade tolerance) or outcompeting neighbours for light (shade avoidance), respectively (Gommers *et al.* 2013). Under shade tolerance one would expect selection of traits such as increased SLA, reduced chlorophyll A:B ratio, increased photosystem II:I ratio, while shade avoidance likely promotes selection of traits such as stem elongation, petiole elongation, hyponasty and reduced branching (Valladares & Niinemets 2008; Gommers *et al.* 2013). Similar trait shifts can be expected under compositional shifts that increase community productivity by enabling access to resources of nutrition not available in species poor communities (Barry *et al.* 2018), i.e. the presence of legumes through additional access to atmospheric nitrogen (Temperton *et al.* 2007). In the

case of transgenerational effects of community diversity and composition through differences in light availability, one would expect differentiation between plant progeny originating from monocultures and mixtures in traits related to shade-avoidance or shade-tolerance.

A classic approach to distinguish transgenerational genetic selection from reversible phenotypic plasticity in response to environmental factors is to place progeny from different environmental conditions into the shared environmental conditions of a common garden (Puy *et al.* 2020). Consistent phenotypic differences between progeny from different communities of origin despite shared local environmental conditions in a common garden, suggest transgenerational change in response to selection in their original community environments.

We collected seeds of 18 plant species from four functional groups in the experimental grassland communities of the Jena Biodiversity Experiment. These communities differed in their species diversity and species composition, and by the time of seed collection plants within these communities had shared their local community history for 11 years. We tested whether reported trait differences of plants from differently diverse communities (Schmidtke *et al.* 2010) were maintained in seed-derived progeny after two years of growth in a common garden.

We investigated:

1. Does different community diversity lead to transgenerational effects in a common garden?
2. Are such legacy effects of community diversity expressed as differences in light-related traits, and are they differently expressed in common light and shade treatments?
3. Does different community composition in the form of presence or absence of legumes modulate transgenerational effects of community diversity?

Methods

Seed material

In 2013, we collected seeds from 18 plant species in 79 grassland communities of the Jena Biodiversity Experiment. The Jena Biodiversity Experiment was established in Jena, Germany, in 2002 (Roscher *et al.* 2004) to explore the effect of species richness and functional group composition on ecosystem functioning. In the Jena Biodiversity Experiment, 60 plant species of the *Arrhenatherion* association (Leuschner & Ellenberg 2017) were sown in 82 communities ranging from monocultures to 60 species mixtures, with varying combinations of functional groups.

For the present study, seeds of five grass species (*Alopecurus pratensis, Arrhenatherium elatius, Bromus erectus, Festuca pratensis* and *Trisetum flavenscens)*, two legumes (*Lotus corniculatus* and *Trifolium pratense),* five small herbs (*Leontodon autumnalis, Leontodon hispidus, Plantago lanceolata, Plantago media* and *Prunella vulgaris),* as well as six tall herbs (*Crepis biennis, Geranium pratense, Knautia arvensis, Leucanthemum vulgare, Ranunculus acris* and *Pimpinella major)* were collected 11 years after establishment of the communities from the experimental plots in Jena. Seeds of *Alopecurus pratensis, Arrhenatherium elatius, Bromus erectus, Festuca pratensis, Crepis biennis, Knautia arvensis, Leucanthemum vulgare, Ranunculus acris* and *Trisetum flavescens* were collected in June 2013. Seeds of *Lotus corniculatus, Trifolium pratense, Leontodon autumnalis, Leontodon hispidus, Plantago lanceolata, Plantago media, Prunella vulgaris, Geranium pretense* and *Pimpinella major* were collected in September 2013. Depending on availability, seeds were collected from up to 22 maternal plants per plant species per given community. Seeds of the same maternal plant were referred to as seed family and were all siblings. Categorization of plant species into four functional groups was based on 17 morphological, phenological or physiological traits (Roscher *et al.* 2004).

Seedling preparation

Seeds were transported to Bern, Switzerland. Seeds of *Ranunculus acris* and *Pimpinella major* were soaked in 500 ppm Gibberellic acid overnight, and *Lotus corniculatus* were scrubbed with sand paper to increase germination probability. Seeds were sown in seedling boxes from 3rd November 2014 until 15th November 2014. Based on availability up

to eight seed families were sown for each realized combination of plant species and community of origin (N = 220), resulting in 1390 sown seed families in total. Seedling boxes were placed in a greenhouse of the city gardeners of Bern, Stadtgrün Bern, with daily watering, temperature limited between 14° Celsius and 22° Celsius during daytime and between 10° Celsius and 22° Celsius during nighttime, and artificial daylight from 8am until 8pm. Seedlings were pricked into single pots sized 11 cm x 11 cm x 13 cm from 3rd December until 22nd January 2015. If available, six individuals per seed family were pricked, totaling 7646 individuals. On 26th January, plants were sprayed with the insecticide Perfekthion®, BASF, to counter aphid infestation. From 20th April until 30th April plants were transferred from the greenhouse to an open-air common garden of the University of Bern in Muri bei Bern, close to Bern.

Common garden experiment

The main experiment was conducted in the common garden in Muri bei Bern. The pots were placed on the ground, which was covered by a weed-blocking fabric. The pots were arranged in 3 x 10 blocks with an equal distribution of plant species and seed families across all blocks. Blocks measured 230 cm x 175 cm, contained a maximum of 280 pots, and were located at a 50 cm distance from each other. Within blocks pots very placed next to each other. Plant species and seed families were distributed equally across blocks, the individual position within the block was assigned randomly.

Light - shade treatment

In the greenhouse, prior to being moved to the common garden, individuals of the seed families were split in two equal groups. One group received a full light treatment for the duration of the experiment; the other group received a shade treatment. In case of uneven number of individuals in a seed family, the extra individual was attributed to the full light treatment group. During seedling germination in the greenhouse, the shade treatment was applied with a light filter foil (LEE Filters Fern Green N° 122) attached to wooden frames sized 165 cm x 230 cm x 70 cm (Figure 1). The frames were placed over the pots after pricking of plant individuals and removed before the transfer of the experiment to the open-air common garden.

At the open-air common garden, the shade treatment was realized by covering 15 blocks with a cloth with a 63% light absorption rate (Neeser AG shadow cloth 63%) attached to wooden frames sized 165 cm x 230 cm x 175 cm (Figure 2). The shading frames were stacked over the blocks in a checkerboard pattern to minimize orientation bias. The shade treatment in the open-air common garden was applied from July 2015 until 15th December 2015 and from 18th March 2016 until the end of the experiment on the 31st August 2016.

Measurements

We cut the biomass of all plants in the experiment about 1 cm above ground from 19th October 2015 until 3rd November 2015, mimicking common grassland management regime. The biomass of each individual was collected in an individual paper bag, dried for two days at 70° Celsius and weighed. This data set is referred to as Biomass 2015, hereafter. Biomass harvest was repeated from 2nd May 2016 until 31st August, after a full growing season, referred to as Biomass 2016, hereafter. Data was collected for one plant species after the other to minimize seasonal variability within species (Supplementary Table S1).

In 2016 we measured multiple plant traits, which are related to plant performance: in addition to biomass, these were plant height, leaf area, number of leaves, vegetative stems, total stems, floral stems, flowers per stem and total flowers. Some traits were not measured for all species due their different growth forms (Supplementary Table S1).

Statistical analyses

We used linear mixed models with a Gaussian error distribution to analyze biomass 2015, biomass 2016, plant height and leaf area. We used generalized linear mixed models with a negative binomial error distribution for countable responses, i.e. numbers of leaves, vegetative stems, floral stems, all stems, flowers per stem and flowers per plant. Effects of seed origin diversity, functional group, shade treatment and their interactions were estimated with sequential ANOVA Type I F-Tests with estimated denominator degrees of freedom based on Welch-Satterthwaite's approximation, to adjust for the nested data structure of plant species, seed families, and Jena Experiment block and community ID (Satterthwaite 1946). We estimated the significance of nested random effects with explained variance ratios. We chose the sequential ANOVA Type I approach based on the experimental design of the

communities of seed origin in Jena, and to maintain consistency with earlier studies of the Jena Biodiversity Experiment.

Statistical analyses were performed with the R 4.0.5 software (R Core Team 2021) including the packages *lme4* (Bates et al. 2015) for linear mixed effect modelling, *glmmTMB* (Brooks *et al.* 2017) for generalized mixed negative binomial models, *lmerTest* (Kuznetsova et al. 2017), *broom.mixed* (Bolker & Robinson 2021), *effects* (Fox & Weisberg 2018) for model testing and interpretation; *ggplot2* (Wickham 2016) *ggsignif* (Ahlmann-Eltze 2019), and *cowplot* (Wilke 2018) for graphical display; and *data.table* (Dowle & Srinivasan 2018) and *tidyverse* (Wickham 2017) for efficient data management.

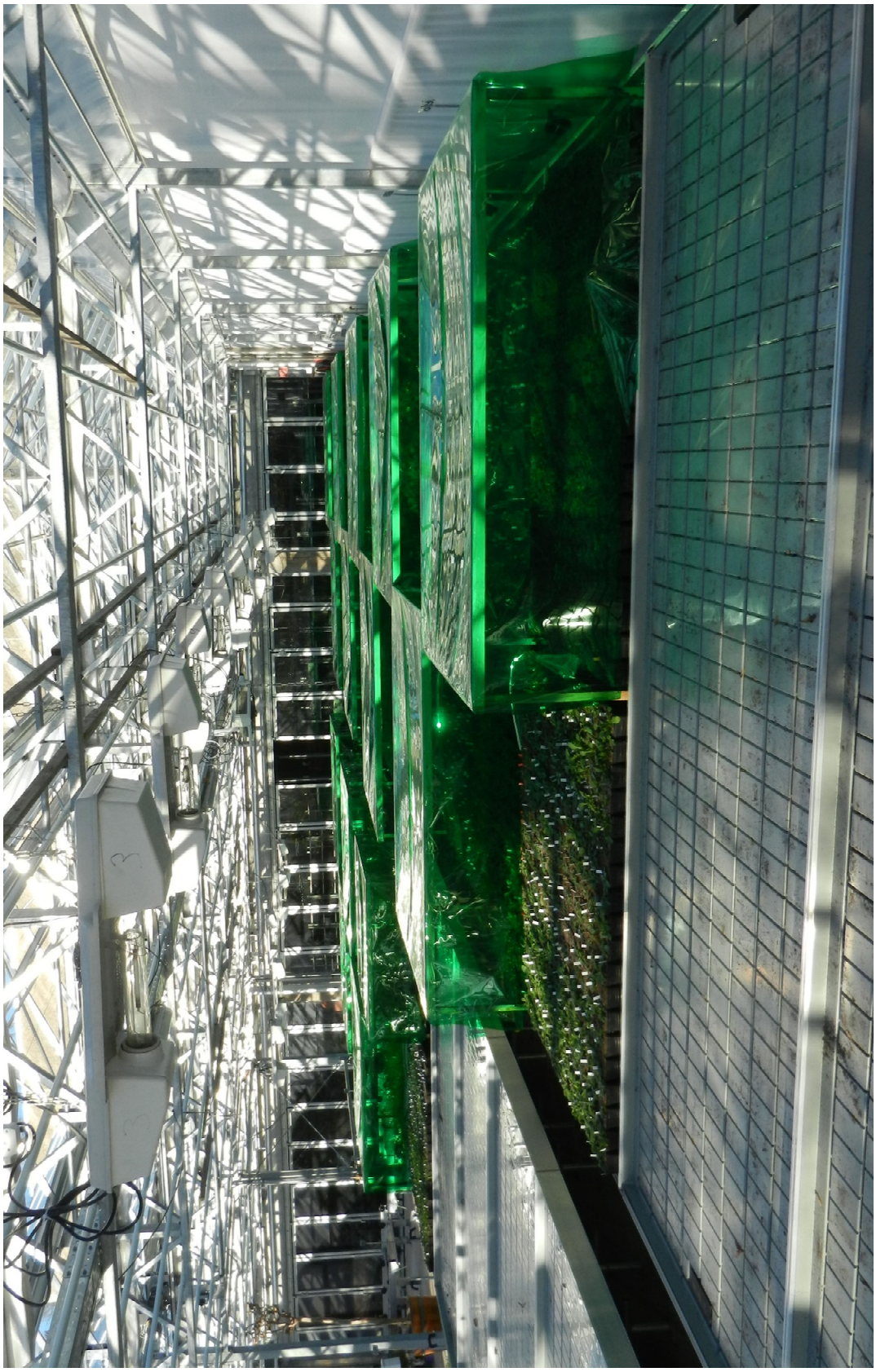

Figure 1: The greenhouse phase of the experiment on 6 March 2015, with light-filter shades providing the shade treatment.

Figure 2: The open-air common-garden phase of the experiment on 24 July 2015, with shadow cloth shades providing the shade treatment.

Results

Seedling survival

Out of 8168 pricked individuals in January 2015, 7675 individuals (≈ 94 %) survived until the biomass harvest in October 2015, and 6852 individuals (≈ 84 %) survived until the final trait measurement in August 2016. Major causes of loss were herbivory by snails and mice, who gnawed through some plastic pots and built a few nests. Snail attacks focussed on *Leontodon autumnalis* and *Geranium pratense* resulting in poor survival in these two species (*Leontodon autumnalis* N = 47, *Geranium pratense* N = 39).

Effect of the diversity of the communities of origin on plant traits

Plant height and biomass 2016 decreased with increasing diversity of the communities of seed origin (Table 1, Figure 3). The overall effect of seed origin on plant biomass was rather weak, since the strength and direction of seed origin effects on biomass depended on the shade treatment and its interaction with the focal species' functional group (Table 1). Plant biomass tended to decrease with higher diversity of the communities of seed origin in the in shade treatment, while it increased in the full light treatment (Figure 3, Supplementary Table S2). Biomass responses of all functional groups showed a similar negative trend in the shade treatment. However, strength and direction of biomass responses differed between functional groups in the full light: the biomass of legumes decreased with increasing diversity of the communities of seed origin, the biomass of tall herbs increased, and the biomass of grasses and small herbs did not change (Figure 3). In summary, these results show that several plant traits of the progeny grown in the common-garden differed between communities of seed origin of different diversity and composition, indicating adaptation within the relatively short experimental period of 11 years.

Effect of the presence of legumes in the communities of origin

The presence of legumes in the communities of seed origin altered the effect of community diversity on two plant traits of several non-legume species in the common garden experiment: total number of stems and leaf area (Figure 4, Table 2). Further, it also did so for the number of flowers and of floral stems of the only non-legume species, for which these two traits were recorded, *Prunella vulgaris*.

Legume presence in the community of seed origin altered the direction of effects of the diversity of seed origin on two traits of non-legume species - number of stems and number of flowers – from negative (without legumes) to positive (with legumes) (Figure 4a, b). These effects were similar for both shade treatments (Table 2).

Legume presence in the community of seed origin also inverted the effects of community diversity on two further traits – leaf area and number of floral stems - and these effects depended on the shade treatment (Figure 4e, f). First, shading decreased leaf area only for individuals stemming from communities without legumes, and negative shading effects on the number of floral stems were slightly more pronounced for individuals stemming from communities were legumes were present (Figure 4c, d; Supplementary Table S2).

Second, legume presence in the communities of origin inverted also the effects of community diversity on leaf area and number of floral stems in the common garden (Figure 4e, f). Under full light, leaf area increased with increasing diversity of communities of seed origin with legumes and decreased for communities of origin without legumes (Figure 4e). The opposite was the case for the number of floral stems, which increased with increasing diversity of the communities of seed origin in the full light treatment for communities without legumes, but decreased for communities with legumes (Figure 4f). Under shade, these trends were inversed (Figure 4e, f).

In summary, the composition of the communities of seed origin community mattered along with their diversity for progeny traits related to light competition (leaf area, number of stems) and reproduction (number of flowers, number of floral stems).

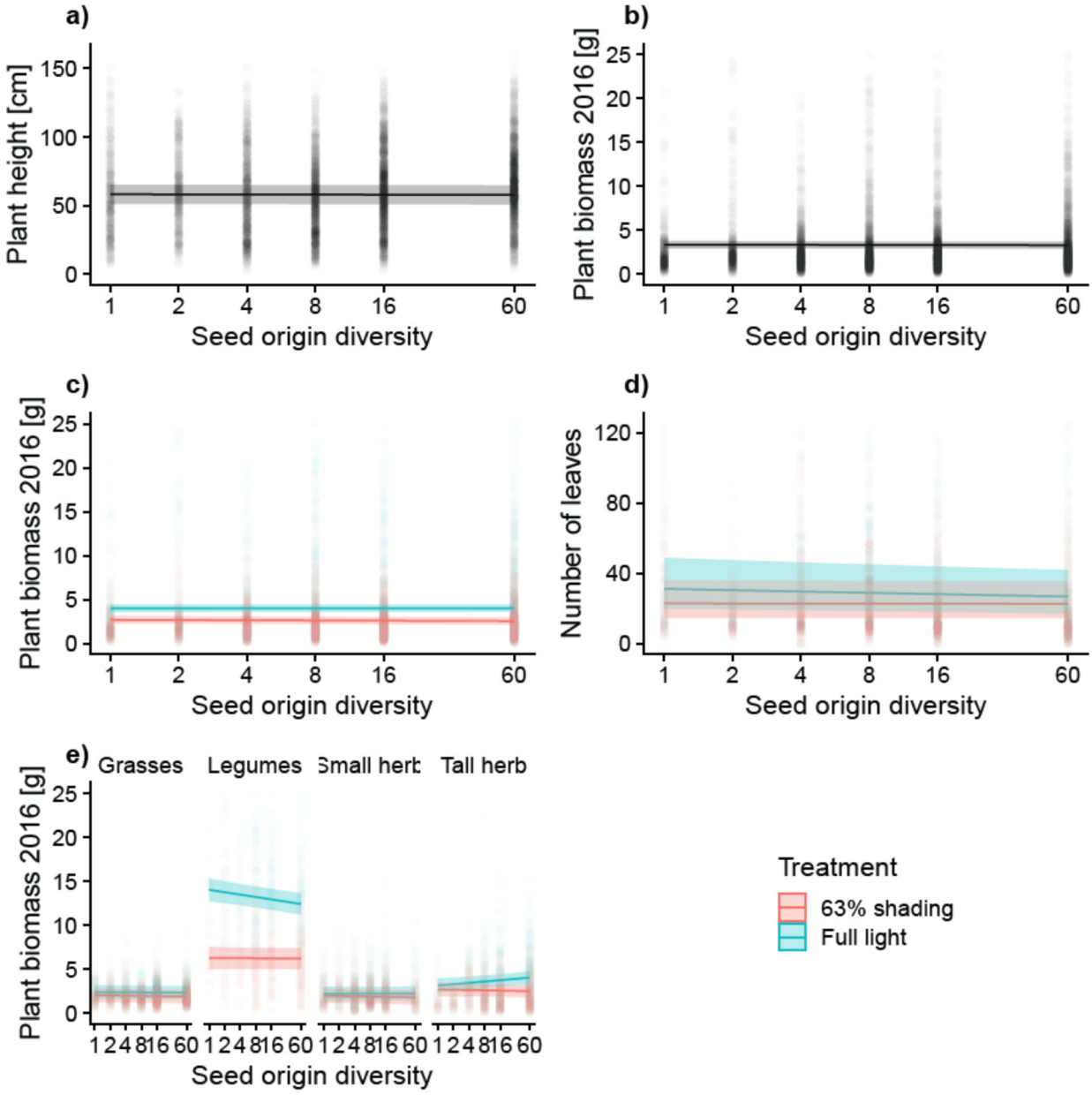

Figure 3: Significant effects of the diversity of the communities of seed origin on plant height, plant biomass in 2016 and number of leaves. (a, b) overall effects of diversity, (c, d) effect of the shade treatment in the common garden on the diversity effects, and (e) effects of the shade treatment on the diversity effect for the four functional groups.

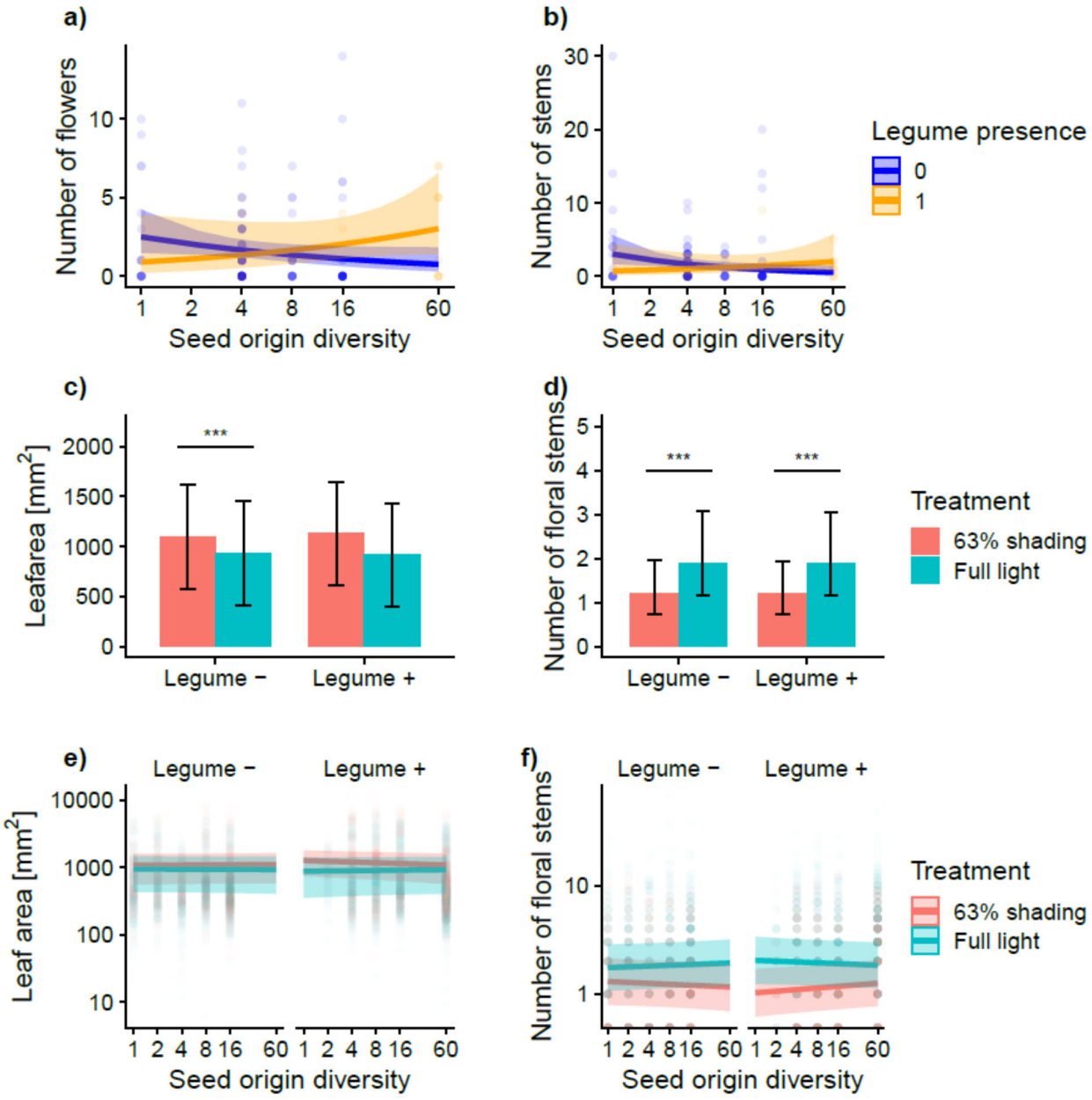

Figure 4: Significant effects of legume presence in the communities of seed origin on the number of inflorescences, total number of stems, leaf area and number of floral stems of non-legume species. (a, b) general effect of legume presence on the effects of the diversity of the communities of seed origin on numbers of inflorescences and stems (only one species, *Prunella vulgaris).* Blue lines show the diversity effect in communities without legumes, and orange lines the diversity effect in communities with legumes. (c, d) the effect of legume presence on the shade treatment effect, and (e, f) effects of legume presence on the effect of the diversity of the communities of seed origin for the full light and shade treatment. Significant group mean differences (c, d) are indicated with asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Trends of regression lines can be found in Supplementary Table S2.

Table 1: Summary table for models including the diversity of communities of origin and functional group. The continuous traits plant height, biomass and leaf area were fitted with REML generalized linear mixed models and tested with type I ML models. Denominator degrees of freedom were estimated with the Satterthwaite-Welch approximation. The countable traits leaf number, numbers of inflorescences per stem, floral stems, vegetative stems, total inflorescences and total stems were fitted with REML binomial models and tested with type II ML models. Significance of fixed effects: * p < 0.05, **p < 0.01, *** p < 0.001. Importance of random effects expressed as ratio of variance not explained by fixed effects. Note that negative binomial models do not provide a residual variance.

	Plant height (cm)			Biomass 2015 (g)			Biomass 2016 (g)			Leaf area (mm^2)			Leaf number		Flowers per stem		Floral stems		Vegetative stems		Total flowers		Total stems	
Fixed effects	NumDF	DenDF	F value	NumDF	DenDF	F value	NumDF	DenDF	F value	NumDF	DenDF	F-value	df	Chisq	df	Chisq	df	Chisq	df	Chisq	df	Chisq	df	Chisq
Origin diversity (log transformed)	1	16	12.64 **	1	7	0.23	1	29	17.62 ***	1	7	0.02	1	3.51	1	1.92	1	0.1	1	0.13	1	<0.01	1	1.18
Functional group	3	10	15.77 ***	3	2	2.08	3	2	105.08 **	2	7	2.78	1	1.87	2	6.44 *	2	2.47	NA	NA	1	1.1	1	502.01 ***
Light-shadow treatment	1	6317	11.35 ***	1	6577	629.45 ***	1	6485	679.77 ***	1	5090	231.42 ***	1	151.01 ***	1	65.46 ***	1	257.12 ***	1	0.77	1	136 ***	1	187.26 ***
Origin diversity (log) : functional group	3	138	1.1	3	86	2.1	3	406	1.69	2	721	0.9	1	0.04	2	0.5	2	5.06	NA	NA	1	0.24	1	1.01
Origin diversity (log) : treatment	1	6323	0.17	1	6550	0.09	1	6484	24.78 ***	1	5097	0.09	1	4.61 *	1	1.06	1	0.94	1	0.48	1	0.18	1	2.23
Functional group : treatment	3	6261	53.98 ***	3	6551	0.28	3	6461	482.77 ***	2	5107	10.01 ***	1	55.12 ***	2	41.22 ***	2	31.64 ***	NA	NA	1	7.67 ***	1	0.15
Origin diversity : functional group : treatment	3	6258	0.45	3	6517	2.12	3	6451	4.97 **	2	5136	1.89	1	0.12	2	0.95	2	0.45	NA	NA	1	0.76	1	0.6
Variance ratio random effects																								
Random structure	0.85			0.73			0.62			0.94			0.61		0.7		0.8		0.06		0.33		0.04	
Residual	0.15			0.27			0.38			0.06			NA		NA		NA		NA		NA		NA	

Table 2: Summary table for models including the diversity of communities of origin and presence of legumes. The continuous traits plant height, biomass and leaf area were fitted with REML generalized linear mixed models and tested with type I ML models. Denominator degrees of freedom were estimated with the Satterthwaite-Welch approximation. The countable traits leaf number, numbers of inflorescences per stem, floral stems, vegetative stems, total inflorescences and total stems were fitted with REML binomial models and tested with type II ML models. Significance of fixed effects: * p < 0.05, **p < 0.01, *** p < 0.001. Importance of random effects expressed as ratio of variance not explained by fixed effects. Note that negative binomial models do not provide a residual variance.

	Plant height (cm)			Biomass 2015 (g)			Biomass 2016 (g)			Leaf area (mm^2)			Leaf number		Flowers per stem		Floral stems		Vegetative stems		Total flowers		Total stems	
Fixed effects	NumDF	DenDF	F value	NumDF	DenDF	F value	NumDF	DenDF	F value	NumDF	DenDF	F value	df	Chisq	df	Chisq	df	Chisq	df	Chisq	df	Chisq	df	Chisq
Origin diversity (log transformed)	1	19	<0.01	1	15	0.04	1	18	0.53	1	15	0.32	1	2.84	1	1.12	1	0.06	1	0.75	1	0.49	1	2.72
Legume presence	1	13	1.04	1	25	0.08	1	19	0.36	1	22	0.87	1	<0.01	1	0.03	1	<0.01	1	0.89	1	1.49	1	0.63
Light-shadow treatment	1	5241	30.04 ***	1	5671	724.79 ***	1	5086	222.64 ***	1	4388	204.44 ***	1	147.74 ***	1	35.57 ***	1	262.26 ***	1	0.73	1	3.08	1	9.89 **
Origin diversity (log) : legume presence	1	37	0.01	1	23	0.43	1	28	1.03	1	17	0.75	1	0.02	1	0.31	1	0.01	1	0.27	1	4.18 *	1	5.34 *
Origin diversity (log) : treatment	1	5211	0.25	1	5662	0.01	1	5029	19.26 ***	1	4422	0.13	1	0.44	1	1.56	1	1.69	1	1.42	1	0.34	1	0.6
Legume presence : treatment	1	5305	0.12	1	5675	0.38	1	5168	0.04	1	4431	12.52 ***	1	1.3	1	1.48	1	3.88 *	1	1.08	1	0.04	1	2.08
Origin diversity :legume presence : treatment	1	5284	0.01	1	5662	1.35	1	5121	0.13	1	4451	7.39 **	1	0.19	1	0.18	1	6.13 *	1	0.27	1	0.44	1	0.26
Variance ratio random effects																								
Random structure	0.56			0.5			0.36			0.82			0.7		1.03		0.94		0.06		0.08		0.37	
Residual	0.44			0.5			0.64			0.18			NA		NA		NA		NA		NA		NA	

Discussion

A large body of literature highlights the importance of biodiversity for important ecosystem functions (Tilman *et al.* 2014; Fraser *et al.* 2015; Weisser *et al.* 2017; van der Plas 2019). Biodiversity also drives changes in plant traits by presenting varying environmental filters for rapid selection or phenotypic plasticity (Hautier *et al.* 2009; Zuppinger-Dingley *et al.* 2014; Abakumova *et al.* 2016; van Moorsel *et al.* 2019). In this study, we showed that a relatively short period of 11 years of different community history in terms of plant diversity and composition induced transgenerational changes in several traits related to adaption to light availability and resource investment.

The diversity of communities of origin affects plant traits in progeny

The legacy effects observed in our study show that biodiversity not only has in situ effects i.e. productivity (Chapter 1, Marquard et al., 2009), but that it also imprints on the plant performance in the following plant generation. This may either reflect adaptation via natural selection or possibly epigenetic modification (van Moorsel *et al.* 2019). While earlier experiments emphasized the importance of soil legacy effects on plant progeny (Zuppinger-Dingley *et al.* 2016), we could demonstrate legacy effects of community diversity and composition on aboveground traits even under exclusion of soil interactions, and that these legacy effects were likely mediated by light-limitation in more diverse communities. Since diverse communities were also more productive (Chapter 1, Marquard et al., 2009) our results provide evidence for the important role of light limitation for mediating the biodiversity-productivity relationships in grassland communities (Hautier *et al.* 2009). Moreover, our results extend these findings by demonstrating that beyond in-situ effects of plant community diversity, adaptation of plant progeny to diversity-mediated aboveground environmental conditions such as light availability is an important mechanism in species-rich communities.

Biomass was the best-described and well-studied plant trait with observable selection based on diversity in our experiment. Decreasing individual seedling biomass with the diversity of the seed origin community observed agrees with earlier biodiversity research (Chapter 1, Marquard et al., 2009). Despite individual seedling biomass decreasing with community diversity, community productivity of more diverse communities is generally larger than the productivity of less diverse communities (Balvanera *et al.* 2006; Weisser *et al.* 2017;

van der Plas 2019). This is likely a result of higher density of individuals in more diverse communities, which outweighs their lower individual biomass (Marquard *et al.* 2009).

Effects of the diversity of communities of origin on plant traits relevant under competition for light

In support of the overall idea that diversity effects on plant performance might be mediated through higher light attenuation and thus competition for light in diverse plant communities (Bachmann *et al.* 2018), we found diversity-dependent responses of experimental seedling biomass, height and leaf number to the light treatment. Seedlings with a high-diversity background showed reduced loss in biomass and leaf number under shade than seedlings with a low-diversity background. This might reflect higher shade tolerance of seedlings with a high-diversity background (Valladares & Niinemets 2008; Gommers *et al.* 2013). The partially contrasting response of seedling biomass of tall herb progeny originating from high-diversity backgrounds, which increased in biomass under shade, might well reflect an increase in leaf area to increase light capture (Poorter *et al.* 2008), a well-known shade-tolerance strategy (Valladares & Niinemets 2008).

Reduced seedling height with increasing diversity of the community of origin supports the idea of increased investment in the growth of other plant organs rather than stem elongation. This does not mirror an increase in plant height with higher community diversity in field communities, interpreted as effect of stronger competition for light (Schmidtke *et al.* 2010; Roscher *et al.* 2017). This may suggest that plant height is largely phenotypically plastic, as stem elongation is not necessary in a common-garden environment without direct competition (Gommers *et al.* 2013).

Legume-presence in the communities of origin altering legacy effects of diversity

Legumes strongly influence community productivity by increasing the biomass of co-occurring species by making atmospheric nitrogen accessible (Temperton *et al.* 2007), and due to their own strong biomass accumulation in diverse communities. Via these cues of higher productivity, legume presence in communities likely causes stronger competition for light (Hautier *et al.* 2009), and thus could impose strong selection pressures for legacy effects on non-legume community members, which act simultaneously with legacy effects of community diversity. The results of our experiment support this idea by showing that legume-

presence in the communities of origin affected effects of the diversity of communities of origin on progeny and shade responses by the progeny (Figure 4). This suggests diversity-induced selection for shade tolerance (Valladares & Niinemets 2008; Gommers *et al.* 2013) that depends on the presence of legumes in the communities.

Conclusion

Our study on aboveground effects extends earlier findings, which demonstrated legacy effects of plant community diversity via altered soil characteristics. We could show that, even without any soil-legacy effects, the diversity of communities of seed origin affects aboveground plant traits related to shade avoidance and shade tolerance in their progeny. As the communities of seed origin of our study had only experienced 11 years of differences in diversity and composition, we suggest that adaptation of plants to characteristics of their plant communities may be a generally prevalent element of community assembly. Further, to some degree such rapid adaptation might also ameliorate effects of global change on plant communities.

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Supplementary material

Table S1: Overview of plant species, their functional groups, dates of trait sampling, and measured traits

Plant species	Functional group	Begin sampling	End sampling	Biomass 2015	Biomass 2016	Plant height	Leaf area	Number of leaves	Vegetative stems	Total stems	Floral stems	Flowers per stem	Total flowers
Alopecurus pratensis	grass	22.08.2016	25.08.2016	x	x	x	x		x		x		
Arrhenatherium elatius	grass	05.07.2016	12.07.2016	x	x	x	x		x		x		
Bromus erectus	grass	25.07.2016	28.07.2016	x	x	x	x		x		x		
Crepis biennis	tall herbs	06.06.2016	09.06.2016	x	x	x	x	x			x	x	
Festuca pratensis	grass	26.07.2016	28.07.2016	x	x	x	x		x		x		
Geranium pratense	tall herbs	09.08.2016	11.08.2016	x	x	x	x	x			x	x	
Knautia arvensis	tall herbs	07.06.2016	09.06.2016	x	x	x	x	x			x	x	
Leontodon autumnalis	small herb	09.08.2016	11.08.2016	x	x	x	x	x			x	x	
Leontodon hispidus	small herb	21.06.2016	28.06.2016	x	x	x	x	x			x	x	
Leucanthemum vulgare	tall herbs	31.05.2016	06.06.2016	x	x	x	x	x			x	x	
Lotus corniculatus	legume	29.06.2016	12.07.2016	x	x	x				x		x	x
Pimpinella major	tall herbs	03.08.2016	11.08.2016	x	x	x	x	x			x	x	
Plantago lanceolata	small herb	29.08.2016	31.08.2016	x	x	x	x	x			x		
Plantago media	small herb	12.07.2016	19.06.2016	x	x	x	x	x			x		
Prunella vulgaris	small herb	25.08.2016	29.08.2016	x	x	x	x	x		x			x
Ranunculus acris	tall herbs	02.05.2016	04.05.2016	x	x	x	x	x			x	x	
Trisetum flavescens	grass	19.07.2016	27.07.2016	x	x	x	x		x		x		
Trifolium pratense	legume	28.06.2016	29.06.2016	x	x	x				x		x	x

Table S2: Slope estimates of diversity effects. Slope estimates created by least square slopes.

Functional group models			
Response	Model	Diversity slope estimate	Std.error
Plant height	general	-0.1	0.3
Number of leaves	light all species	-0	0
	dark all species	-0	0
Biomass 2016	general	-0.1	0.3
	light all species	0	0.1
	dark all species	-0.1	0
	light grass	>-0.01	<0.01
	dark grass	-0.1	0
	light legume	-0.3	0.3
	dark legume	-0.1	0.2
	light small herb	0	0.1
	dark small herb	-0	0.1
	light tall herb	0.2	0.1
	dark tall herb	>-0.01	0
Legume models			
Response	Model	Diversity slope estimate	Std.error
Number of flowers	legume 0	-0.3	0.2
	legume 1	0.3	0.2
Number of stems	legume 0	-0.4	0.2
	legume 1	0.3	0.6
Leaf area	legume 0 dark	-18	105
	legume 0 light	-6.8	88
	legume 1 dark	-131	107
	legume 1 light	-87	91
Number of floral stems	legume 0 dark	0.1	0.1
	legume 0 light	0	0.1
	legume 1 dark	0	0.1
	legume 1 light	-0.1	0.1

Chapter 5

General discussion and conclusions

In this thesis, I investigated mechanisms of biodiversity effects from three angles. First, I tested whether trait gradients relating to use of space or phenology resulted in stronger diversity effects. Second, I investigated how community diversity influences cover patterns and spatial associations between species. Finally, I tested whether community diversity influences the evolution of aboveground traits with a specific focus on evolution in relation to light conditions. Together the results of this thesis suggest that biodiversity effects on plant community productivity have an explicit spatial component, which might be related to optimized light interception.

General discussion

In Chapter 2 of this thesis, I found that diversity effects in the Jena Trait Based Experiment (TBE) were strongest in plant communities composed of species differing in their respective use of space. My results support predictions of the spatial resource partitioning hypothesis, which had only limited support in earlier direct tests (Jesch *et al.* 2018; Barry *et al.* 2020). Previous evidence for the spatial resource hypothesis in the Jena Experiment (Wagg *et al.* 2017) focused only on species biomass while neglecting species density (i.e. shoot density). My study highlights that shoot density rather than individual biomass was an important mediator of increased productivity in diverse communities, in agreement with earlier studies (Marquard *et al.* 2009). These results suggest that effective use of space through complementary aboveground traits might be driving increased productivity in species rich community by enabling more dense communities and thus complete exploitation of one or multiple spatially explicit resources (Barry *et al.* 2018). As multiple spatial traits related to resource acquisition were included in the diversity gradients, I could not disentangle which specific resource use was most relevant. Diversity of spatial resource use in the Jena TBE was quantified by the aboveground traits plant height, leaf area as well as by the belowground traits rooting depth and root length density. The latter are indicators for access to deep soil nutrients and water, while the former are indicators for direct light

interception by plant species (Ebeling *et al.* 2014). Therefore, access to one of these resources is likely to be a strong driver of diversity effects in the experiment.

Expanding on the results of Chapter 2, highlighting the relevance of plant traits related to the complementary use of space for biodiversity effects, the Chapter 3 of this thesis focused directly and more specifically on the use of aboveground space by plant species in the Jena TBE communities. The analysis of small-scale spatial patterns and their turnover between years revealed decreasing segregation of species-specific plant cover and increasing cover turnover between years with increasing species richness of the experimental grassland communities. Segregation of cover in grassland species has previously been reported (Saiz *et al.* 2016), but my results show a context dependency with community diversity highlighting diversity-dependent spatial processes in the Jena TBE communities (Chapter 2, Wagg *et al.* 2017). While complementary use of space was theoretically expected along the vertical axes (rooting depth, plant height) despite limited empirical support (Jesch *et al.* 2018; Barry *et al.* 2020), my results suggest that complementarity use of horizontal space via plant-cover related mechanisms could present an important pathway by which biodiversity affects community productivity. The importance of shoot density for biodiversity effects observed in Chapter 2 supports the idea that plant distribution across horizontal space is likely to be an important driver of positive biodiversity effects on community productivity. Indeed, I could show that higher spatial turnover and less segregation in species-rich communities were correlated with higher species biomass, which would align with findings from other experiments at larger scales than my experimental plots, where random, not segregated, spatial patterns of communities were associated with higher ecosystem functioning (Rayburn & Schupp 2013). An important caveat is that the design of the Jena Experiment does not allow us to make strong conclusions about the absolute relevance of spatial patterns for community productivity, because spatial patterns and diversity were not fully independent of each other in the experimental plots.

Many aboveground traits and the spatial configuration of plants within communities, both revealed as factors mediating positive biodiversity effects on community productivity in Chapters 2 and 3 of this thesis, are related to maximising light interception and are responsive to community diversity (Ebeling *et al.* 2014; Bachmann *et al.* 2018). Thus, maximising of or adaptation to diversity-dependent light conditions in plant communities could be one underlying mechanism controlling variation in aboveground traits related to the use of space

and spatial dynamics of plant cover in grassland communities. Chapter 4 of this thesis supported these earlier findings and provided further evidence or light availability being a key component in diverse communities. The plant traits in the common garden experiment, which displayed inherited effects as affected by the diversity of the communities of seed origin, were traits related to light interception and those used for creating diversity in the "spatial" species pool of the Jena TBE: plant height, biomass and leaf area. These results again show that complementary use of space (Chapters 2, 3) is an important driver of biodiversity effects, but beyond that, they indicate that complementary use of space to maximise light interception might be the underlying mechanism controlling variation in use of space in the grassland communities. That light availability and plant traits related to light availability are important drivers of plant community composition and biomass production in grasslands is well known (Hautier *et al.* 2009; Neuenkamp *et al.* 2016), and has been shown by diversity-dependent trait adaptation to light conditions in the Jena Experiment (Bachmann *et al.* 2018). My study however, goes one step further in showing that diversity-dependent shifts in light conditions lead not only to plastic adaptation in plant traits as found by Bachmann et al. (2018) but also induce genetic selection observable in the offspring of plants. So far, this has been only shown for diversity-dependent soil conditions (van Moorsel *et al.* 2019), but not diversity-dependent aboveground conditions. Together these results highlight the profound and long-lasting effects that community composition and diversity can induce to its community members.

Future Directions

This thesis showed links community biodiversity and shoot density and cover patterns. However, whether they are direct pathways to community productivity could not be tested independently from species richness. Consequently, future experiments should aim to separate these potentially confounding factors. In Chapter 2, shoot density was a major factor, which increased with community species richness and was closely related to community productivity. However, shoot density and species richness were not modulated independently. Future research could control the density of individuals at different species richness at the community level to expand on the findings of chapter 2. Biotic interaction experiments that manipulate the density of conspecifics and allospecific plant species around a focal individual and record its individual performance to test intraspecific and interspecific competition are well established (Adler *et al.* 2018). In line with earlier studies (Marquard *et*

al. 2009), I identified in Chapter 2 that shoot density, rather than individual biomass, drives increases in community productivity. Thus, we need to go beyond individuals and use a whole-community approach to understand the mechanisms by which density mediates diversity effects on community productivity. An earlier study started with fixed densities, but allowed density to evolve over time and showed converging densities depending on the species richness (Schmitz *et al.* 2013). Future approaches could build upon this design by controlling density levels independently from other species richness effects.

The results of Chapter 3 showed links between species richness and spatial patterns (cover turnover, species associations). However, similar to shoot density in Chapter 2, the spatial patterns were observed as a function of species richness, and their relation to community productivity could not be investigated independently. Future projects could aim for experimentally testing these links by combining them in a full-factorial design. If the spatial features such as density and cover are a basis of biodiversity effects, it could confirm horizontal spatial features as mechanisms that enhance community production and at the same time disentangle their contributions. As discussed earlier with regards to density, research on cover segregation and turnover and their contribution to biodiversity effects should be tested independently of species richness. Experimental set-ups that allow and prohibit intermixing of cover at different species richness levels could test the effects of plant cover segregation on biodiversity effects.

Future research could also build upon findings from Chapters 3 and 4. As shown by the light related evolution of aboveground plant traits in Chapter 4, light is an influential factor influenced by community diversity. If the diversity related spatial patterns, observed in Chapter 3, are a form of horizontal resource complementarity for the light, we could test experimentally, whether cover segregation and cover turnover change with light conditions in different communities. Shading treatments of small-scale communities at different levels of diversity and recoding of resulting cover changes and of the consequences for community productivity could provide valuable insight.

Final Conclusions

This thesis underlines the importance of the spatial component of biodiversity effects. Plant communities exhibited the strongest biodiversity effects on productivity when their constituent species were diverse with regard to spatial resource acquisition traits. Further,

the strong biodiversity effects on productivity were closely related to increases in shoot density; an explicitly spatial and aboveground attribute of plant populations.

Analyses of cover patterns of plant species revealed that the biodiversity of plant communities affected interspecific segregation of cover and the cover turnover between years. These plant-cover related effects are additional indications of biodiversity effects mediated by explicitly spatial and aboveground attributes of plant populations. In contrast to predictions from niche theory, biodiversity effects could not be empirically linked to resource acquisition complementarity along the vertical axis of plants (Jesch *et al.* 2018; Barry *et al.* 2020). The findings suggest, however, that the effects of diversity on the horizontal arrangement of individuals, i.e. cover and density, could be a mechanism for the stronger biodiversity effects observed in diverse communities.

Finally, the rapid evolution of plant traits related to light interception caused by diversity between differences communities of seed origin underlines light conditions as an important abiotic factor in diverse communities, which can exhibit legacy effects across plant generations. Overall, my thesis contributes a new perspective on the field of biodiversity-light-productivity interactions (Parreño *et al.* 2021). Specifically, I suggest that horizontal space use in relation to diversity, a hitherto understudied dimension relating biodiversity to ecosystem function, deserves to become a stronger focus of future research community diversity and its consequences for ecosystem functioning.

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Declaration of consent

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I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 paragraph 1 litera r of the University Act of September 5th, 1996 and Article 69 of the University Statute of June 7th, 2011 is authorized to revoke the doctoral degree awarded on the basis of this thesis. For the purposes of evaluation and verification of compliance with the declaration of originality and the regulations governing plagiarism, I hereby grant the University of Bern the right to process my personal data and to perform the acts of use this requires, in particular, to reproduce the written thesis and to store it permanently in a database, and to use said database, or to make said database available, to enable comparison with theses submitted by others.

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