Limited evidence for spatial resource partitioning across temperate grassland biodiversity experiments

Kathryn E. Barry,[1,2,25] Jasper van Ruijven,[3] Liesje Mommer,[3] Yongfei Bai,[4] Carl Beierkuhnlein,[5,6] Nina Buchmann,[7] Hans de Kroon,[8] Anne Ebeling,[9] Nico Eisenhauer,[2,10] Claudia Guimarães-Steinicke,[1,2] Anke Hildebrandt,[2,9] Forest Isbell,[11] Alexandru Milcu,[12,13] Carsten Neßhöver,[14] Peter B. Reich,[15,16] Christiane Roscher,[2,17] Leopold Sauheitl,[18,19] Michael Scherer-Lorenzen,[20] Bernhard Schmid,[21] David Tilman,[11,22] Stefanie von Felten,[7,23,24] and Alexandra Weigelt[1,2]

[1]*Systematic Botany and Functional Biodiversity, Institute of Biology, Leipzig University, Johannisallee 21, Leipzig 04103 Germany*
[2]*German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, Leipzig 04103 Germany*
[3]*Plant Ecology and Nature Conservation Group, Wageningen University, P.O. Box 47, Wageningen NL-6700 AA The Netherlands*
[4]*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing 100093 China*
[5]*Department of Biogeography, University of Bayreuth, Universitätstraße 30, Bayreuth 95447 Germany*
[6]*Bayreuth Center for Ecology and Environmental Research, Universitätstraße 30, Bayreuth 95447 Germany*
[7]*Institute of Agricultural Sciences, ETH Zurich, Universitätstrasse 2, Zürich 8092 Switzerland*
[8]*Department of Experimental Plant Ecology, Institute for Water and Wetland Research, Radboud University, Heyendaalseweg 135, Nijmegen NL-6525 AJ The Netherlands*
[9]*Institute of Geosciences, Friedrich Schiller University, Jena, Burgweg 11, Jena 07745 Germany*
[10]*Institute of Biology, Leipzig University, Deutscher Platz 5e, Leipzig 04103 Germany*
[11]*Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, Minnesota 55108 USA*
[12]*The European Ecotron of Montpellier (UPS-3248), Centre National de la Recherche Scientifique (CNRS), Campus Bailarguet, Montferrier-sur-Lez, France*
[13]*Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175), Centre National de la Recherche Scientifique (CNRS), EPHE, IRD, Université de Montpellier, Université Paul Valéry, Montpellier Cedex 5, France*
[14]*Department of Conservation Biology, UFZ-Helmholtz Centre for Environmental Research, Permoserstrasse 15, Leipzig 04318 Germany*
[15]*Department of Forest Resources, University of Minnesota, Saint Paul, Minnesota 55108 USA*
[16]*Hawkesbury Institute for the Environment, Western Sydney University, Richmond, New South Wales 2753 Australia*
[17]*Department of Physiological Diversity, UFZ – Helmholtz Centre for Environmental Research, Permoserstrasse 15, Leipzig 04318 Germany*
[18]*Institute of Soil Science, University of Hannover, Herrenhäuser Strasse 2, Hannover 30419 Germany*
[19]*Department of Soil Physics, University of Bayreuth, Bayreuth, Germany*
[20]*Geobotany, Faculty of Biology, University of Freiburg, Schänzlestrasse 1, Freiburg 79104 Germany*
[21]*Department of Geography, University of Zürich, Winterthurerstrasse 190, Zürich 8057 Switzerland*
[22]*Bren School of Environmental Science and Management, University of California Santa Barbara, Santa Barbara, California 93106-5131 USA*
[23]*Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland*
[24]*Oikostat GmbH, Ettiswil, Switzerland*

Abstract. Locally, plant species richness supports many ecosystem functions. Yet, the mechanisms driving these often-positive biodiversity–ecosystem functioning relationships are not well understood. Spatial resource partitioning across vertical resource gradients is one of the main hypothesized causes for enhanced ecosystem functioning in more biodiverse grasslands. Spatial resource partitioning occurs if species differ in where they acquire resources and can happen both above- and belowground. However, studies investigating spatial resource partitioning in grasslands provide inconsistent evidence. We present the results of a meta-analysis of 21 data sets from experimental species-richness gradients in grasslands. We test the hypothesis that *increasing spatial resource partitioning along vertical resource gradients enhances ecosystem functioning in diverse grassland plant communities above- and belowground.* To test this hypothesis, we asked three questions. (1) Does species richness enhance biomass production or community resource uptake across sites? (2) Is there evidence of spatial resource partitioning as indicated by resource tracer uptake and biomass allocation above- and belowground? (3) Is

evidence of spatial resource partitioning correlated with increased biomass production or community resource uptake? Although plant species richness enhanced community nitrogen and potassium uptake and biomass production above- and belowground, we found that plant communities did not meet our criteria for spatial resource partitioning, though they did invest in significantly more aboveground biomass in higher canopy layers in mixture relative to monoculture. Furthermore, the extent of spatial resource partitioning across studies was not positively correlated with either biomass production or community resource uptake. Our results suggest that spatial resource partitioning across vertical resource gradients alone does not offer a general explanation for enhanced ecosystem functioning in more diverse temperate grasslands.

   Key words: grassland; niche complementarity; niche partitioning; productivity; resource uptake; resources; standing root biomass.

INTRODUCTION

Worldwide, humans are propelling drastic environmental changes leading to biodiversity loss at regional and global scales (Tittensor et al. 2014, Newbold et al. 2015). Many studies predict that the rate of species loss will accelerate in the coming decades (Pereira et al. 2010, Pimm et al. 2014). Yet, biodiversity improves the ability of ecosystems to produce biomass, sequester carbon, and retain nitrogen, among many other crucial functions (Hooper et al. 2005, Cardinale et al. 2012, Isbell et al. 2017, Weisser et al. 2017, Chen et al. 2018). Thus, continuing biodiversity loss will likely have serious consequences for ecosystem functioning (Cardinale et al. 2012). However, the mechanisms driving enhanced ecosystem functioning in diverse mixtures are still poorly understood (Tilman et al. 2014, Barry et al. 2019). Further, understanding these mechanisms may allow us to better predict the response of ecosystems to biodiversity change (Isbell et al. 2017, Barry et al. 2019).

Here, we focus on how plants take up resources across vertical space. If plant species alter their resource uptake or have different innate uptake strategies to divide resources in vertical space, then the available resource pool will be more completely used in more diverse communities (Dimitrakopoulos and Schmid 2004, Fargione and Tilman 2005, Mueller et al. 2013, Williams et al. 2017). For example, different plant species may take up nutrients or water from different soil layers (Parrish and Bazzaz 1976, Berendse 1982, 1983, Mommer et al. 2010). If some species have shallow roots and others have deep roots, then plant communities including both shallow- and deep-rooted species will better fill the available soil volume (Dornbush and Wilsey 2010). If more diverse plant communities more completely use the available soil volume in this way, the community may have higher community resource uptake, standing root biomass, and aboveground productivity compared with less diverse communities (as examined by von Felten et al. 2012, Mueller et al. 2013, Prechsl et al. 2015, Husse et al. 2016, Jesch et al. 2018, Oram et al. 2018). We refer to this phenomenon as spatial resource partitioning across vertical resource gradients, one commonly invoked potential driver of positive biodiversity–ecosystem functioning relationships in grasslands (Berendse 1983, Tilman 1999, Lehman and Tilman 2000, von Felten et al. 2009, Mueller et al. 2013).

Across a gradient of plant species richness, we expect that species will differ in their spatial resource uptake to decrease interspecific competition in vertical space (Schoener 1970). That is, species will change the portion of the soil or canopy (species' resource partition, Jesch et al. 2018) from which they acquire resources to overlap less with competing species as the number of species with which they must compete for resources increases (von Felten et al. 2009, Williams et al. 2017). In terms of vertical resource partitioning, we expect that grassland communities as a whole will occupy more of the available vertical space in soil and in the canopy with increasing species richness (Naeem et al. 1994, Fargione and Tilman 2005, Lorentzen et al. 2008, Skinner and Comas 2010, Ravenek et al. 2014). As a consequence, we expect that plant species will invest more biomass in deeper soil and higher canopy layers, respectively, as plant species richness increases (Spehn et al. 2000, Fargione and Tilman 2005, Mueller et al. 2013). We refer to the way in which plants invest biomass across vertical space as the plant's biomass distribution. This different biomass distribution with increasing diversity may be due to the addition of tall or deep-rooting species to mixtures or to individual species allocating biomass differently to avoid strong interspecific competition in the topsoil/lower canopy in more diverse communities.

Recent empirical studies were unable to provide compelling evidence that spatial resource partitioning along vertical resource gradients occurs across diversity gradients. Several studies found that plants have deeper roots in more diverse mixtures (Mueller et al. 2013, Oram et al. 2018, but see Ravenek et al. 2014), although these communities do not necessarily have more even biomass distributions (Oram et al. 2018). Similarly, resource tracer uptake studies also provided contrasting results. For example, von Felten et al. (2009) found that plants used less overlapping nitrogen sources and had smaller resource partitions in mixture but that this was not associated with increased total community resource uptake. Alternatively, Jesch et al. (2018) found that plants did not have smaller and less overlapping resource partitions in mixture in spite of higher community resource uptake (Bachmann et al. 2015). Similarly, Husse et al. (2016) found that plant communities did not use different foliar

architecture to intercept more light in mixture in spite of overall higher biomass production.

Here, we present a meta-analysis of spatial resource partitioning across vertical resource gradients in grassland biodiversity–ecosystem functioning experiments (reviewed in Appendix S1: Table S1). We use this meta-analysis to test the hypothesis that *increasing spatial resource partitioning across vertical resource gradients drives enhanced ecosystem functioning in more diverse grasslands.* To test this hypothesis, we assess (1) as a prerequisite, if plant species richness enhances community biomass production or resource uptake at these sites. Then, we test (2) if there is evidence of spatial resource partitioning along vertical resource gradients (Fig. 1), and (3) if this evidence of spatial resource partitioning is positively correlated with community biomass production or resource uptake. We require that all of these three conditions (increase in community biomass production or resource uptake with increasing species richness, evidence of spatial resource partitioning [Fig. 1], and positive correlation between evidence for spatial resource partitioning and community biomass production or resource uptake) be met in order to support this long-standing ecological hypothesis.

Methods

We define resource partitioning as differences between species in how they acquire resources (Schoener 1970, 1974, Roughgarden 1976). We conducted a review of the biodiversity–ecosystem functioning literature through March 2018 (Appendix S1). From this review, we collected data sets from an experimental species richness gradient greater than four species in a field or large controlled environment facility (Ecotron) context with typical grassland species (including both grasses and forbs). To measure vertical resource partitioning, we required that biomass be collected in layers by either soil depth or canopy height (see Appendix S1: Table S2 for experiment details and supplementary methods for data requirements). In addition to biomass data sets, we also collected data sets where resource tracers were injected at different soil depths. We were able to collect 21 total data sets: 12 aboveground biomass by canopy height, 6 belowground biomass by soil depth, 1 nitrogen uptake by soil depth, 1 nitrogen and potassium uptake by soil depth, and 1 water uptake by soil depth. Throughout, we refer to the last three studies as a group as "resource tracer uptake" studies. Of these 21 data sets, 19 reported either total community resource uptake or total community biomass. For the one data set where water uptake was measured, we could not calculate summed water uptake per plot (total community resource uptake, the measure of ecosystem functioning for resource tracer uptake studies) because water is not immobilized, stored, or accumulated in plants (Guderle et al. 2018). For another data set, we could not determine total aboveground biomass

(Guimarães-Steinicke et al., 2019). Thus, we did not include these two data sets in analyses that included total community uptake or total community biomass. Most of our data sets are from Western Europe with one site, with multiple experiments from the United States (Tilman et al. 1996, Reich et al. 2001, Tilman 2001). Seven of the data sets are unpublished while the other 14 are published (Appendix S1: Table S2).

Individual data set analysis

Prior to conducting our meta-analysis, we fitted linear mixed-effects models using the package *lme4* (Bates et al. 2015) with the package *lmerTest* to calculate Satterthwaite approximations of denominator degrees of freedom (Kuznetsova et al. 2017) for each individual data set. For each site, we fit the model with the dependent and independent variables and random effects and transformations that were relevant at the individual site. That is, if an experiment used a blocked experimental design, block was a random effect in the model. If a data set was collected over multiple years or seasons, then year or season was a random effect in the model. We log-transformed variables when the residuals of an individual model were significantly nonnormally distributed according to a Shapiro-Wilk test (see Appendix S1: Table S3 for full individual model details).

Question 1: Does species richness enhance total community biomass or total community resource uptake?

We measured ecosystem function as either total biomass (above- or belowground) in a plot for biomass studies or total community resource uptake for resource tracer uptake studies. Each of these is the sum of either biomass or the measured resource tracer uptake in a given plot. We then analyzed the relationship between species richness and either total biomass or total community resource uptake using a linear mixed-effects model at each site with the total function as the dependent variable and species richness as the independent variable.

Question 2: Is there evidence of spatial resource partitioning along vertical resource gradients?

To answer this question, we used a two-pronged approach (Fig. 1). First, we asked, does the community vertical biomass evenness increase with increasing species richness (Fig. 1a)? For community data sets, we measured this in terms of the inverse of the coefficient of variation (community inverse CV) by either rooting depth or canopy height:

community inverse CV

$$= \frac{\text{Mean biomass across depth/height}}{\text{Biomass standard deviation across depth/height}}.$$

(1)

a) Vertical evenness
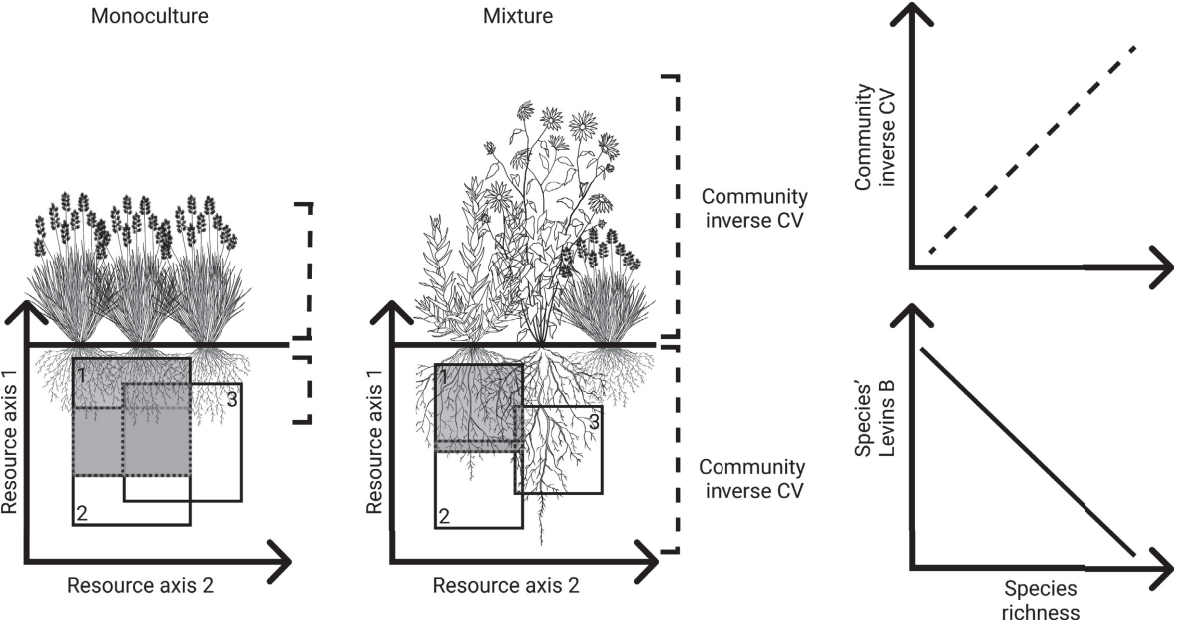
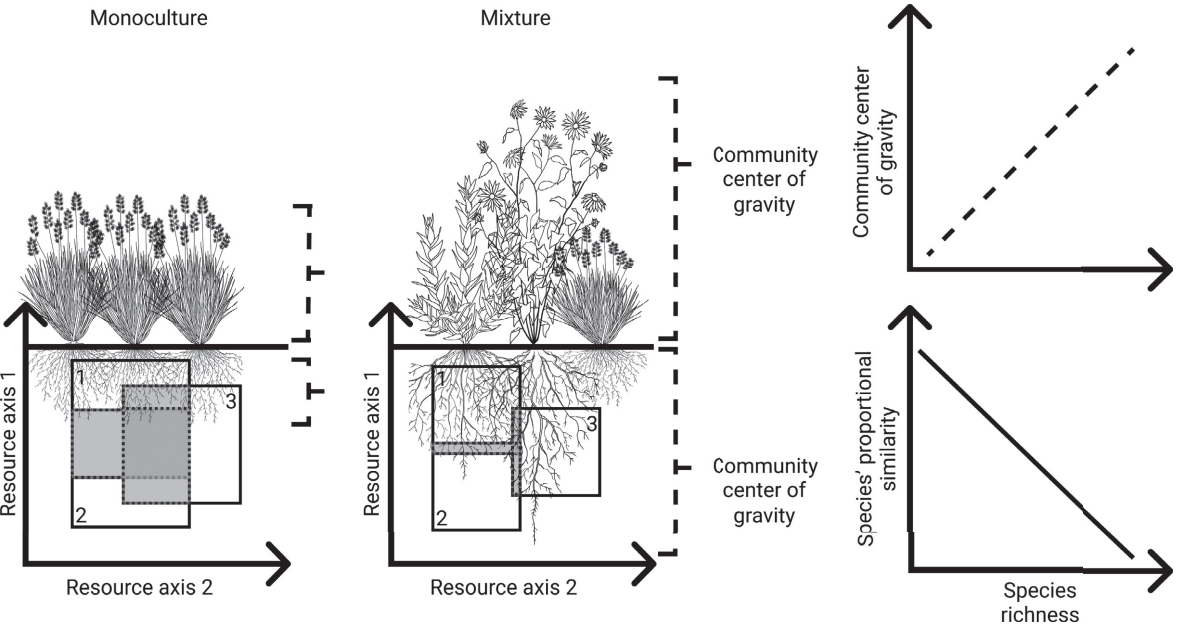b) Change of spatial resource partition location

Fig. 1. Theoretical depictions of predictions and analyses for question 2 of this meta-analysis. In order to test the hypothesis "increasing spatial resource partitioning across vertical resource gradients enhances ecosystem functioning in more diverse grassland systems," we used a two-part identifier for spatial resource partitioning across vertical resource gradients. The boxes represent a species' spatial resource partition in monoculture (left) and mixture (right). Gray coloring represents the highlighted measure. First, (a) in order for spatial resource partitioning to enhance ecosystem functioning in diverse mixtures, we expect that the vertical evenness of the community will increase (community inverse coefficient of variation) while the vertical evenness of the individual species' distribution will decrease as species specialize to avoid interspecific competition (species' Levins B). Second, (b) in order for spatial resource partitioning to enhance ecosystem functioning in diverse mixtures, we expect that the mean location of resource uptake must change in diverse mixtures relative to monocultures. We predict that, if species differ in their resource uptake strategies in mixture, the species' proportional similarity between species resource partitions will decrease while the community center of gravity of biomass will increase. Finally, if spatial resource partitioning drives enhanced ecosystem functioning in more diverse mixtures, we expect that our measures of spatial resource partitioning will be correlated with our measures of enhanced ecosystem functioning, total community resource uptake, and total biomass (not depicted).

When the community inverse CV is high, biomass is more evenly spread across all height or depth levels relative to the mean biomass. When the community inverse CV is low, biomass is concentrated in a single or few height or depth levels relative to the mean biomass across height or depth levels. We use the community inverse CV rather than the CV because its interpretation is more intuitive with regard to our results (Tilman 1999).

At the species level, we expect that the portion of the total resource uptake that a single species is responsible for will decrease if plants partition resources across vertical resource gradients, thus the species' resource uptake evenness will decrease as species richness increases. To measure the evenness of species resource uptake, we calculated species' Levins B as

$$B = \frac{1}{n \sum_{i=1}^{n} p_i^2} \qquad (2)$$

where p_i is the proportion of uptake of a species from a given resource i and n is the number of resources. Levins B is highest when all sources are used equally and lowest when one source is used exclusively by a species (Levins 1968, Parrish and Bazzaz 1976). Levins B, which we selected because it performs well at low sample size, is equivalent to the inverse Simpson index (Smith and Wilson 1996).

Second, we asked, does the location of the resource partition change with increasing diversity (Fig. 1b)? For community biomass data sets, we measured this location change in terms of the weighted mean biomass allocation of the community, which we calculated as the community center of gravity:

$$\text{community center of gravity} = \frac{\sum_j \text{Biomass}_j \times \text{Mean location}_i}{\text{Total community biomass}} \qquad (3)$$

where j is the soil depth or aboveground height layer from which the sample was collected, and the mean location is the mean height or depth of the layer. For example, in a plot with two soil layers, the mean depth would be the biomass in the first soil layer from 0 to 10 cm multiplied by 5 (the mean depth of the first layer), plus the biomass in the second soil layer from 10 to 20 cm multiplied by 15 (the mean depth of the second layer), divided by the total community biomass. This value increases as plants invest more biomass in higher levels aboveground and deeper levels belowground (adapted from Spehn et al. 2000, Mommer et al. 2010).

At the species level for resource tracer uptake studies, we measured the change in the location of the species resource partition as the change in the overlap between resource partitions (Fig. 1b). To measure the overlap between species' resource partitions, we calculated

proportional similarity (Schoener 1970, Colwell and Futuyma 1971):

$$\text{PS} = 1 - \left(0.5 \times \sum_{i=1}^{n} |p_{1i} - p_{2i}|\right) \qquad (4)$$

where p_i is the proportion of total resource uptake that is from a single resource taken up by a given species such that all p_i's together sum up to one for one species. Species' proportional similarity measures the intersecting area of the frequency distributions of resources used by two different species and ranges from 0 to 1, with 0 meaning no overlap and 1 meaning complete overlap. We calculated species' proportional similarity for all species pairs co-occurring in the same mixture plots and used the mean of these measures to characterize species' proportional similarity of mixtures with more than two species.

Once we calculated these metrics, we used linear mixed-effects models with the metric of choice as the dependent variable and species richness as the independent variable and site-specific random effects as needed (Appendix S1: Table S3).

Question 3: Is evidence of spatial resource partitioning positively correlated with total community biomass or total community resource uptake?

To determine the relationship between each of our measures of resource partitioning and enhanced ecosystem functioning, we also used a linear mixed-effects model with each measure of resource partitioning (see methods, question 2) as the independent variable and overall community ecosystem functioning (see Question 1 above for calculations) as the dependent variable (Appendix S1: Table S3).

Meta-analysis

After conducting the individual linear mixed-effects models, we extracted Pearson's correlation coefficient r for each question for each data set (using the package *MuMIN*; Bartoń 2018), standard error, and sample size. We then used the package *metafor* (Viechtbauer 2010) to calculate Fisher's z-transformed correlation coefficients (r_z). The Fisher's z-transformed correlation coefficient normalizes the distribution of Pearson's r. We used r_z as the model input in mixed-effects meta-models with a nested random effect of site within experiment to control for the uneven distribution of our data sets among our sites and our sites within broader experimental units (e.g., at the BIODEPTH experiment, there are eight experimental sites but similar experimental designs, while, in the Jena Experiment, there are several experiments with different designs all located at the same site).

For each dependent variable (total community biomass, total community resource uptake, community inverse CV, Levins B, community center of gravity, or

proportional similarity), we ran up to five analysis sets of our total meta-data set: (1) all functions analysis set (above- and belowground biomass and resource uptake) used only for ecosystem functioning; (2) all biomass analysis set (above- and belowground); (3) aboveground-biomass only analysis set; (4) belowground biomass only analysis set; and (5) resource uptake only analysis set. By subsetting the data and running joint and separate analysis sets, we were able to determine whether patterns were stronger (i.e., had a larger r_z) for different subsets of the meta-data set. We performed all data analysis with R statistical computing software version 3.5.1 (R Core Team 2018) and made all graphics using the package *ggplot2* (Wickham 2009) with multiplot support from the package *cowplot* (Wilke 2016).

Results

Question 1: Does species richness enhance total community biomass or total community resource uptake?

We found that species richness enhanced ecosystem functioning across all data sets and data types (all functions set, $r_z = 0.462$, $P < 0.0001$; Fig. 2; Appendix S1: Table S4). Species richness enhanced aboveground biomass production overall (aboveground biomass only set, $r_z = 0.462$, $P < 0.0001$) and in 10 out of 11 individual data sets. Species richness also enhanced standing root biomass overall (belowground biomass only set, $r_z = 0.426$, $P = 0.001$) and in five out of six individual data sets. Finally, higher species richness never resulted in significantly lower biomass for either above- or belowground values. In contrast to above and belowground biomass, community resource uptake was not associated with higher species richness (resource uptake only set, $r_z = 0.082$, $P = 0.766$).

Question 2: Is there evidence for spatial resource partitioning along vertical resource gradients?

In contrast to our prediction (Fig. 1b), increased species richness did not increase the community inverse CV of the vertical biomass distribution (all biomass set, $r_z = -0.052$, $P = 0.616$, see Appendix S1: Fig. S1 for standard deviation and mean; Fig. 3). Alternatively, and as we predicted, we found that plants grew taller and had marginally deeper roots with increasing diversity as predicted (center of gravity, all biomass set, $r_z = 0.277$, $P < 0.001$). This pattern was nearly three times stronger above- than belowground (aboveground biomass only set, $r_z = 0.332$, $P = 0.001$ vs. belowground biomass only set, $r_z = 0.125$, $P = 0.058$). In terms of resource uptake, increasing species richness did not decrease the species' vertical evenness of resource uptake (Levins B, resource uptake only set, $r_z = -0.056$, $P = 0.828$). Similarly, increasing species richness did not decrease overlap between resource partitions (proportional similarity, resource uptake only set, $r_z = -0.145$, $P = 0.565$; Fig. 3).

Question 3: Is evidence of spatial resource partitioning positively correlated with total community biomass or total community resource uptake?

Overall, plants did not produce more biomass when the biomass of community was more evenly distributed (Fig. 4; Appendix S1: Table S6, inverse CV, all biomass model, $r_z = 0.069$, $P = 0.342$). However, aboveground, communities that had more evenly distributed biomass had marginally higher total aboveground biomass (inverse CV, aboveground biomass only set, $r_z = 0.130$, $P = 0.074$). Belowground, communities that had more evenly distributed biomass across the soil volume did not have higher root standing biomass (belowground biomass only set, $r_z = -0.024$, $P = 0.877$).

Biomass increased as predicted when communities had more biomass in higher/deeper layers (center of gravity, all biomass set, $r_z = 0331$, $P = 0.011$). However, this relationship was largely driven by aboveground data sets. Aboveground biomass production increased significantly with increasing aboveground community center of gravity (aboveground biomass only model, $r_z = 0.598$, $P < 0.001$). In comparison, we found no relationship between standing root biomass and the belowground center of gravity (belowground biomass only set, $r_z = -0.193$, $P = 0.202$). In terms of resource tracer uptake, we found that neither decreased species' Levins B (resource uptake only set, $r_z = 0.258$, $P = 0.357$) nor decreased species' proportional similarity (resource uptake only set, $r_z = 0.058$, $P = 0.463$) predicted enhanced ecosystem functioning.

Discussion

We found that plant species richness enhances ecosystem functioning especially in terms of total community biomass aboveground and belowground at the majority of the sites included in this meta-analysis, in line with earlier reviews and meta-analyses (Balvanera et al. 2006, Hector et al. 2009, Allan et al. 2013, Tilman et al. 2014, Barry et al. 2019). However, contrary to our predictions, we found little evidence for spatial resource partitioning along vertical resource gradients in more diverse grassland communities. Only 3 out of 21 data sets included in our analysis met our predictions for spatial resource partitioning along vertical resource gradients (Fig. 1; Appendix S1: Fig. S1). Further, we found that evidence of spatial resource partitioning was not correlated with the higher productivity or resource uptake that we found in more diverse communities. These results suggest that spatial resource partitioning across vertical resource gradients may not drive enhanced ecosystem functioning at these sites.

Mechanisms may change across contexts

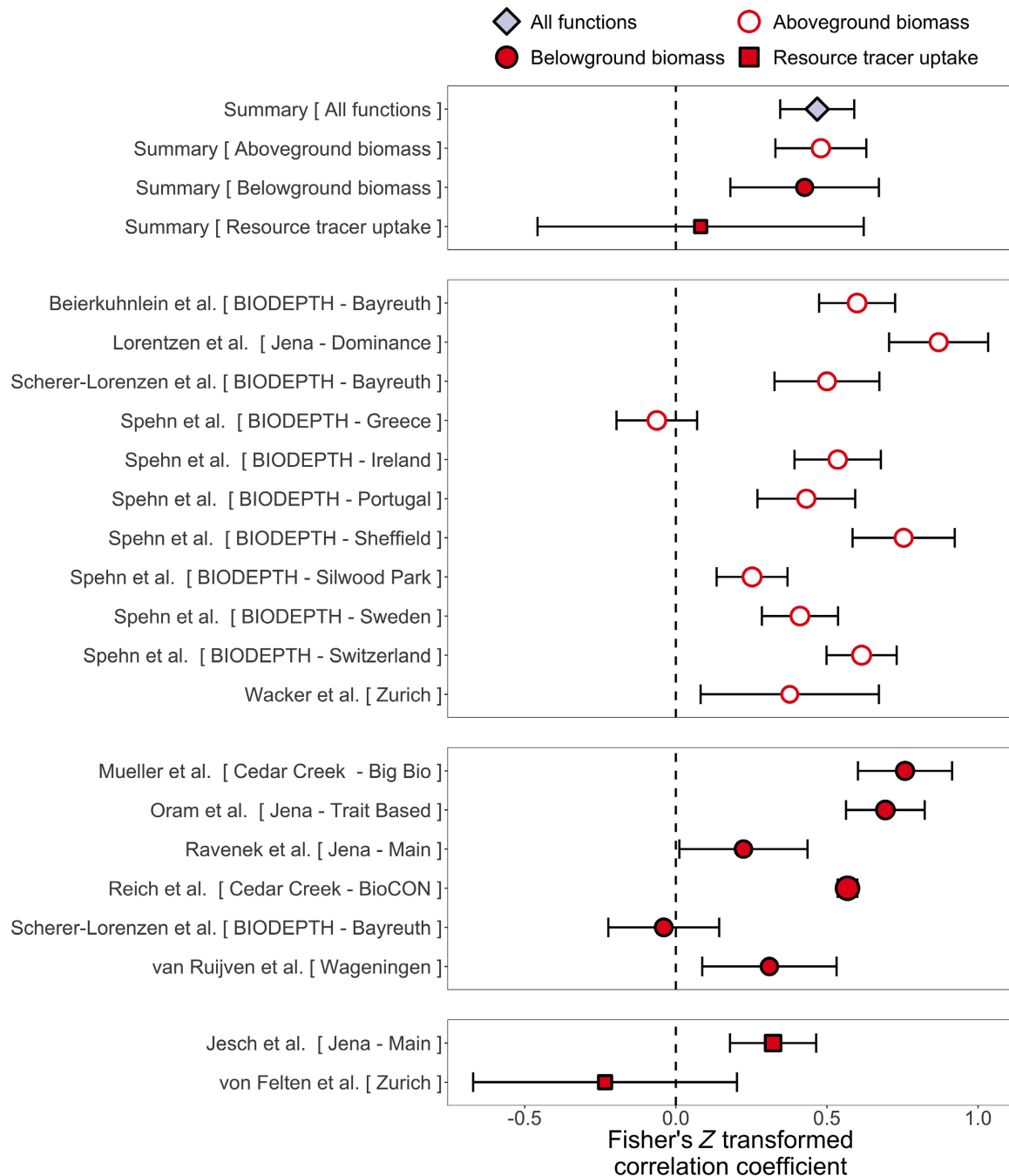To our knowledge, our study is the first meta-analysis of biodiversity–ecosystem-functioning experiments in

FIG. 2. Meta-analysis results for question 1: *Does species richness enhance total community biomass or total community resource uptake?* Error bars represent 95% confidence intervals. Error bars that do not overlap with the dotted line are considered statistically significantly different from zero ($P < 0.05$). Point size is proportional to the confidence relative to the study sample size surrounding a given data set. Smaller points have lower relative confidence while larger points have larger relative confidence. Model summaries for each analysis set are presented in the top panel. For biomass studies, the function measured is total community biomass. For resource tracer uptake studies, the function measured is total community resource uptake. The summary for the all-functions-analysis set is presented in gray. See Appendix S1 for complete references.

grasslands that attempts to directly quantify the evidence for a given mechanism across sites. However, several studies demonstrate that the extent to which positive biodiversity–ecosystem -functioning relationships are derived from reduced performance in monoculture vs. enhanced performance of mixtures is context dependent in grasslands (Meyer et al. 2016, Guerrero-Ramirez et al. 2017). For example, Guerrero-Ramirez et al.
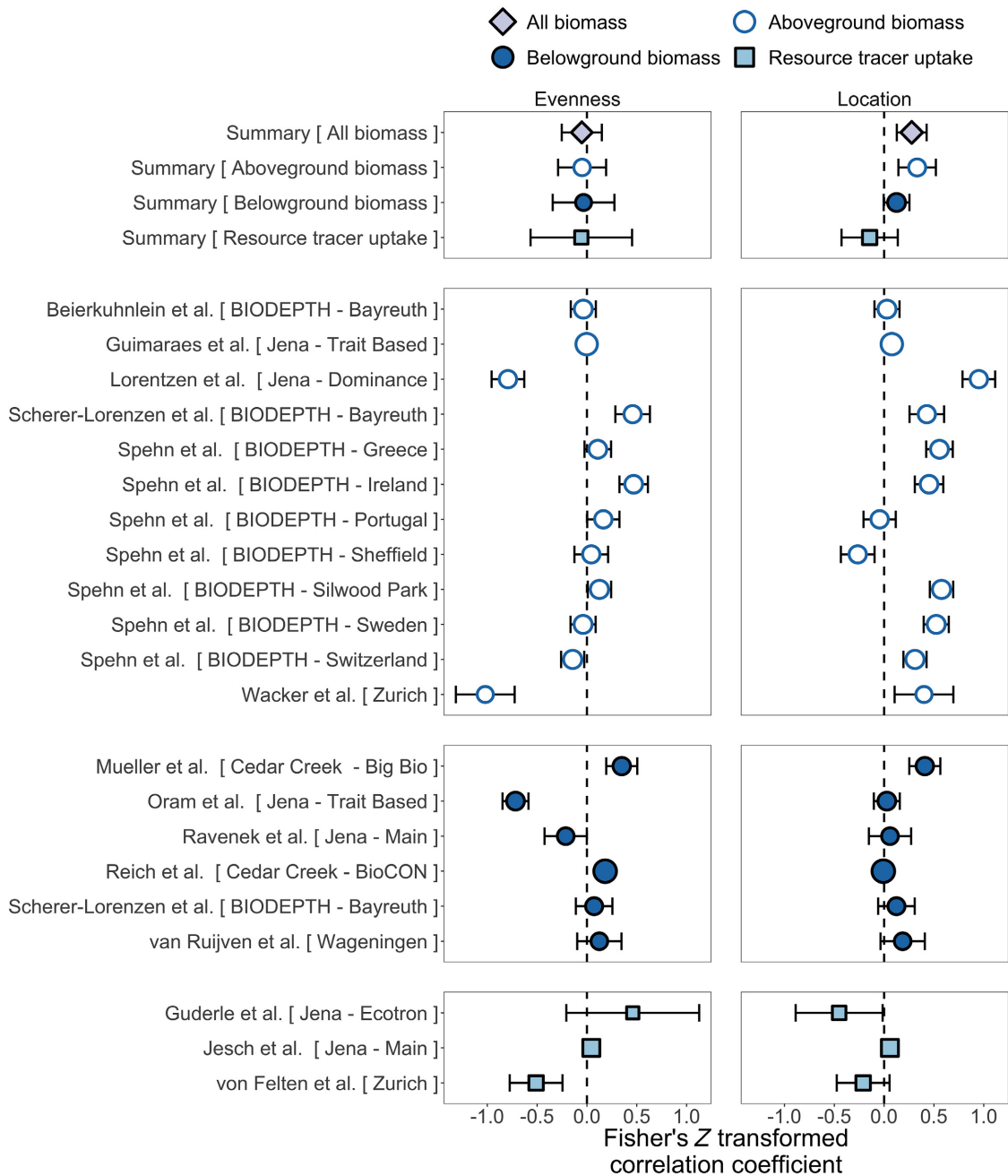
FIG. 3. Meta-analysis results for question 2: *Is there evidence for spatial resource partitioning along vertical resource gradients?* Error bars that do not overlap with the dotted line are considered statistically significantly (*P* < 0.05) different from zero. Point size is proportional to the relative confidence surrounding a given model. Smaller points have lower relative confidence while larger points have larger relative confidence. All model summaries are presented in the top panel. The model summary for the biomass analysis set is presented in gray. The biomass measure for evenness of the biomass distribution is the community inverse coefficient of variation while the resource uptake measure is species' Levins B. The biomass measure for resource partition location is the community center of gravity while the resource uptake measure for resource partition location is species' proportional similarity (Fig. 1). See Appendix S1 for complete references.

(2017) found that, at some grassland sites, a positive biodiversity–productivity relationship was driven by reduced performance in monoculture over time. In others, a positive biodiversity–productivity relationship

was driven by enhanced performance in mixtures over time. This variation suggests that the mechanisms driving enhanced ecosystem functioning may similarly vary across sites. Furthermore, the variation between sites
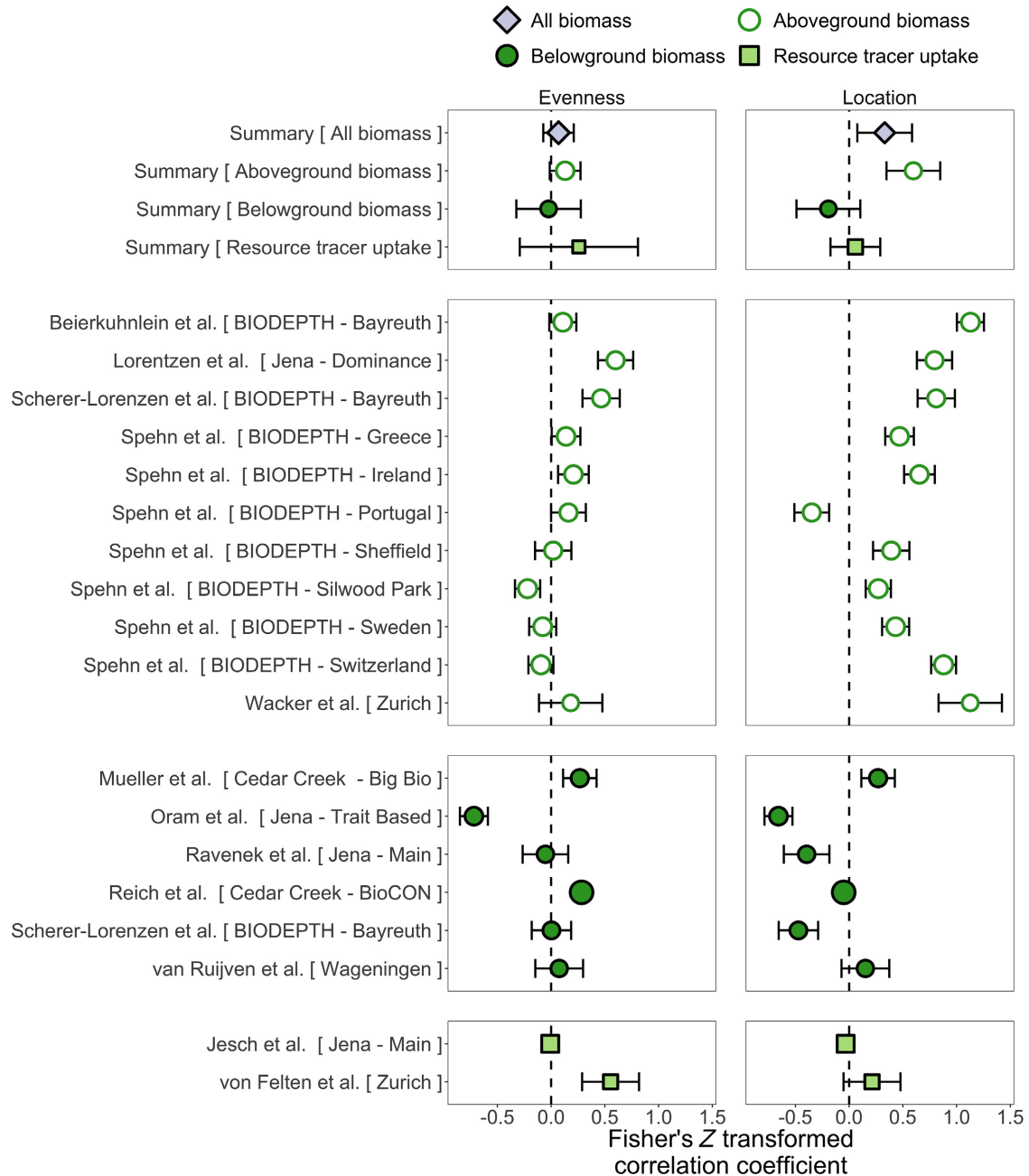
Fig. 4. Meta-analysis results for question 3: *Is evidence of spatial resource partitioning positively correlated with total community biomass or total community resource uptake?* Error bars that do not overlap with the dotted line are considered statistically significantly different from zero ($P < 0.05$). Point size is proportional to the relative confidence surrounding a given data set. Smaller points have lower relative confidence while larger points have larger relative confidence. The model summary for the biomass analysis set is presented in gray. The biomass measure for evenness of the biomass distribution is the community inverse coefficient of variation while the resource uptake measure is species' Levins B. The biomass measure for resource partition location is the community center of gravity while the resource uptake measure for resource partition location is species' proportional similarity (Fig. 1). For biomass studies, the function measured is total community biomass. For resource tracer uptake studies, the function measured is total community resource uptake. See Appendix S1 for complete references.

found by Guerrero-Ramirez et al. (2017) was strongly predicted by soil characteristics. The studies included in our meta-analysis also vary across soil characteristics. For example, we found evidence of spatial resource

partitioning belowground at Cedar Creek Ecosystem Science Reserve (Mueller et al. [Cedar Creek – Big Bio] from Mueller et al. 2013), a site where nutrients and perhaps water appear to be strongly limited due to the high

sand content of soils in this region. This strong limitation may increase the likelihood that spatial resource partitioning controls ecosystem functioning. Indeed, belowground spatial resource partitioning may be most likely in more arid, nutrient-limited regions such as savannas, where resource partitioning between trees and grasses has been documented (Kulmatiski et al. 2010). In more productive soils in temperate regions, vertical resource partitioning has not been observed (Ravenek et al. 2014, Bachmann et al. 2015, Jesch et al. 2018). Furthermore, the importance of these different mechanisms may differ in time (Meyer et al. 2016) or among species compositions. Yet, how mechanisms change across environmental contexts in space and time and across species compositions has very rarely been studied (Barry et al. 2019).

Resource partitioning in time, across horizontal space, or for different chemical forms may enhance ecosystem functioning

From other studies, there is limited evidence that resource partitioning in time (temporal resource partitioning), three-dimensional or horizontal space, or among different chemical forms of the same nutrients rather than resource partitioning in vertical space may enhance ecosystem functioning in temperate grasslands. Aboveground, Husse et al. (2016) found that communities where species produced biomass asynchronously had overall higher biomass production. However, Jesch et al. (2018) found no relationship between temporal resource partition breadth and overlap with diversity, indicating a lack of temporal belowground resource partitioning (see also Wagg et al. 2017). Alternatively, plants may partition resources in horizontal and three-dimensional space (see von Felten and Schmid 2008 for evidence for horizontal resource partitioning belowground). In addition, plants may partition different chemical forms of the same resources (McKane et al. 2002, Ashton et al. 2010).

Almost all data sets currently available for grassland biodiversity–ecosystem-functioning experiments provide data at spatial increments of 10 cm or greater (but see Bachmann et al. 2015 and Prechsl et al. 2015 for water uptake at smaller increments). Plants may partition resources at much finer spatial scales especially within the top 10 cm of the soil (Kulmatiski et al. 2010). However, Bachmann et al. (2015) measured the potential for resource partitioning at finer spatial scales in the first 10 cm of soil depth and found no evidence of spatial resource partitioning.

Finally, although this paper represents the most comprehensive effort to date to measure spatial resource partitioning across vertical resource gradients in grassland biodiversity experiments, community biomass distributions may not provide an accurate proxy for belowground resource uptake both in vertical and horizontal space. Resource uptake rates vary within plant root

systems and may therefore deviate from biomass distributions (Hodge 2004, Chen et al. 2004, Göransson et al. 2007, da Silva et al. 2011, Kiba and Krapp 2016, Kulmatiski et al. 2017, Guderle et al. 2018).

Asymmetric competition may drive investment in aboveground biomass higher

We found that evenness of the vertical biomass distribution aboveground was not positively correlated with total aboveground biomass, contrary to what we expected. Instead, plants appeared to invest biomass in only a few height layers rather than across the entire available space (see also Bachmann et al. 2018). One reason for the increase in biomass production with increased aboveground center of gravity found here may be asymmetric competition for light (Weiner 1990, DeMalach et al. 2016, Bachmann et al. 2018). This potentially strong asymmetric competition was associated with overall higher biomass production with increasing diversity in our study. However, this effect may not be driven by diversity per se but rather by density. At the Jena Experiment, Marquard et al. (2009) found that the positive biodiversity–productivity relationship was largely driven by an increase in density across the diversity gradient. Similarly, asymmetric competition is driven by changes in density with high-density communities experiencing much higher amounts of asymmetric competition (Weiner 1990, Schwinning and Weiner 1998, DeMalach et al. 2016).

Feedbacks between plants and between plants and their abiotic conditions

In several data sets included in this analysis, plants produce more root biomass when they invest roots in the same soil layers simultaneously, especially in the topsoil (see also Ravenek et al. 2014). This type of root aggregation may be beneficial because the upper soils of grasslands have higher limiting nutrient supply, more oxygen, and more water (Jobbágy and Jackson 2001, Griffiths et al. 2003). Further, microbial biomass and activity are higher in upper soils relative to lower soil layers (Bardgett et al. 1997, Fierer et al. 2003, 2009, Griffiths et al. 2003). Additionally, plant diversity likely provides a feedback on these factors with plants actively altering topsoil resource dynamics for themselves and other species (Oelmann et al. 2011, Reich et al. 2012 for nitrogen, Eisenhauer et al. 2010, for microbes, Milcu et al. 2016 and Fischer et al. 2019, for water). For example, Lange et al. (2015) found that the positive relationship between plant diversity and the soil microbial community was mainly related to the increased leaf area index at high plant diversity. This increased leaf area index caused higher shading and thus higher soil moisture in the top soil layer in more diverse communities (Chen et al. 2017, Fischer et al. 2019), which improved conditions for the microbial community.

Conclusions

The majority of predictions for species loss are predicated on the assumption of spatial resource partitioning, an assumption that is not supported empirical evidence for these grasslands. However, our results suggest that spatial resource partitioning along vertical resource gradients does not drive the positive biodiversity–ecosystem-functioning relationships in temperate grasslands. Instead, different mechanisms, including resource partitioning in time, biotic feedbacks between plants and their environment may be at work in different places, at different times and in different plant communities. If different mechanisms drive enhanced ecosystem functioning in more diverse mixtures in different contexts, as we suggest here, then we need to look at these specific contexts to look beyond the pervasive effect of species richness per se. Furthermore, these different mechanisms have different consequences for ecosystem functioning when species are lost due to long term persistent biodiversity decline. Therefore, understanding which mechanisms drive enhanced ecosystem functioning and when they do so is crucial to predicting the consequences of species loss (Barry et al. 2019).

Literature Cited

Allan, E., et al. 2013. A comparison of the strength of biodiversity effects across multiple functions. Oecologia 173:223–237.

Ashton, I. W., A. E. Miller, W. D. Bowman, and K. N. Suding. 2010. Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. Ecology 91:3252–3260.

Bachmann, D., A. Gockele, J. M. Ravenek, C. Roscher, T. Strecker, A. Weigelt, and N. Buchmann. 2015. No evidence of complementary water use along a plant species richness gradient in temperate experimental grasslands. PLoS ONE 10: e0116367.

Bachmann, D., C. Roscher, and N. Buchmann. 2018. How do leaf trait values change spatially and temporally with light availability in a grassland diversity experiment? Oikos 127:935–948.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9:1146–1156.

Bardgett, R. D., D. K. Leemans, R. Cook, and P. J. Hobbs. 1997. Seasonality of the soil biota of grazed and ungrazed hill grasslands. Soil Biology and Biochemistry 29:1285–1294.

Barry, K. E., et al. 2019. The future of complementarity: disentangling causes from consequences. Trends in Ecology & Evolution 34:167–180.

Bartoń, K. 2018. MuMIn: Multi-Model Inference. R package version 1.42.1. https://CRAN.R-project.org/package=MuMIn

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:60922.

Berendse, F. 1982. Competition between plant populations with different rooting depths. Oecologia 53:50–55.

Berendse, F. 1983. Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. Journal of Ecology 379–390.

Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Chen, H., L. Mommer, J. van Ruijven, H. de Kroon, C. Fischer, A. Gessler, A. Hildebrandt, M. Scherer-Lorenzen, C. Wirth, and A. Weigelt. 2017. Plant species richness negatively affects root decomposition in grasslands. Journal of Ecology 105: 209–218.

Chen, X., D. Eamus, and L. B. Hutley. 2004. Seasonal patterns of fine-root productivity and turnover in a tropical savanna of northern Australia. Journal of Tropical Ecology 20:221–224.

Chen, S., et al. 2018. Plant diversity enhances productivity and soil carbon storage. Proceedings of the National Academy of Sciences USA 115:4027–4032.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

da Silva, E. V., J.-P. Bouillet, J. L. de. M. Gonçalves, C. H. A. Junior, P. C. O. Trivelin, P. Hinsinger, C. Jourdan, Y. Nouvellon, J. L. Stape, and J.-P. Laclau. 2011. Functional specialization of Eucalyptus fine roots: contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths. Functional Ecology 25:996–1006.

DeMalach, N., E. Zaady, J. Weiner, and R. Kadmon. 2016. Size asymmetry of resource competition and the structure of plant communities. Journal of Ecology 104:899–910.

Dimitrakopoulos, P. G., and B. Schmid. 2004. Biodiversity effects increase linearly with biotope space. Ecology Letters 7:574–583.

Dornbush, M. E., and B. J. Wilsey. 2010. Experimental manipulation of soil depth alters species richness and co-occurrence in restored tallgrass prairie. Journal of Ecology 98:117–125.

Eisenhauer, N., et al. 2010. Plant diversity effects on soil microorganisms support the singular hypothesis. Ecology 91:485–496.

Fargione, J., and D. Tilman. 2005. Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. Oecologia 143:598–606.

Fierer, N., J. P. Schimel, and P. A. Holden. 2003. Variations in microbial community composition through two soil depth profiles. Soil Biology and Biochemistry 35:167–176.

Fierer, N., M. S. Strickland, D. Liptzin, M. A. Bradford, and C. C. Cleveland. 2009. Global patterns in belowground communities. Ecology Letters 12:1238–1249.

Fischer, C., et al. 2019. Plant species richness and functional groups have different effects on soil water content in a decade-long grassland experiment. Journal of Ecology 107:127–141.

Göransson, H., A.-M. Fransson, and U. Jönsson-Belyazid. 2007. Do oaks have different strategies for uptake of N, K and P depending on soil depth? Plant and Soil 297:119–125.

Griffiths, R. I., A. S. Whiteley, A. G. O'Donnell, and M. J. Bailey. 2003. Influence of depth and sampling time on bacterial community structure in an upland grassland soil. FEMS Microbiology Ecology 43:35–43.

Guderle, M., et al. 2018. Dynamic niche partitioning in root water uptake facilitates efficient water use in more diverse grassland plant communities. Functional Ecology 32:214–227.

Guerrero-Ramírez, N. R., et al. 2017. Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. Nature Ecology & Evolution 1:1639–1642.

Guimarães-Steinicke, C., A. Weigelt, A. Ebeling, N. Eisenhauer, J. Duque-Lazo, B. Reu, C. Roscher, J. Schumacher, C. Wagg, and C. Wirth. 2019. Terrestrial laser scanning reveals temporal changes in biodiversity mechanisms driving grassland productivity. Pages 133–161 in N. Eisenhauer, D. A. Bohan and A. J. Dumbrell, editors. Advances in ecological research. Academic Press, Cambridge, Massachusetts, USA.

Hector, A., T. Bell, J. Connolly, J. Finn, J. W. Fox, L. Kirwan, M. Loreau, J. McLaren, B. Schmid, and A. Weigelt. 2009. The analysis of biodiversity experiments: from pattern toward mechanism. Pages 94–104 in S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective. Oxford University Press, New York, New York, USA.

Hodge, A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytologist 162:9–24.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Husse, S., O. Huguenin-Elie, N. Buchmann, and A. Lüscher. 2016. Larger yields of mixtures than monocultures of cultivated grassland species match with asynchrony in shoot growth among species but not with increased light interception. Field Crops Research 194:1–11.

Isbell, F., et al. 2017. Linking the influence and dependence of people on biodiversity across scales. Nature 546:65.

Jesch, A., et al. 2018. Below-ground resource partitioning alone cannot explain the biodiversity–ecosystem function relationship: a field test using multiple tracers. Journal of Ecology 106:2002–2018.

Jobbágy, E. G., and R. B. Jackson. 2001. The distribution of soil nutrients with depth: Global patterns and the imprint of plants. Biogeochemistry 53:51–77.

Kiba, T., and A. Krapp. 2016. Plant nitrogen acquisition under low availability: regulation of uptake and root architecture. Plant and Cell Physiology 57:707–714.

Kulmatiski, A., K. H. Beard, R. J. T. Verweij, and E. C. February. 2010. A depth-controlled tracer technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savanna. New Phytologist 188:199–209.

Kulmatiski, A., P. B. Adler, J. M. Stark, and A. T. Tredennick. 2017. Water and nitrogen uptake are better associated with resource availability than root biomass. Ecosphere 8:e01738.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:16770.

Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. American Naturalist 156:534–552.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, New Jersey, USA.

Lorentzen, S., C. Roscher, J. Schumacher, E.-D. Schulze, and B. Schmid. 2008. Species richness and identity affect the use of aboveground space in experimental grasslands. Perspectives in Plant Ecology, Evolution and Systematics 10:73–87.

Marquard, E., A. Weigelt, V. M. Temperton, C. Roscher, J. Schumacher, N. Buchmann, M. Fischer, W. W. Weisser, and B. Schmid. 2009. Plant species richness and functional composition drive overyielding in a six-year grassland experiment. Ecology 90:3290–3302.

McKane, R. B., et al. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415:68–71.

Meyer, S. T., et al. 2016. Effects of biodiversity strengthen over time as ecosystem functioning declines at low and increases at high biodiversity. Ecosphere 7:e01619.

Milcu, A., et al. 2016. Plant functional diversity increases grassland productivity-related water vapor fluxes: an Ecotron and modeling approach. Ecology 97:2044–2054.

Mommer, L., J. Van Ruijven, H. De Caluwe, A. E. Smit-Tiekstra, C. A. M. Wagemaker, N. Joop Ouborg, G. M. Bögemann, G. M. Van Der Weerden, F. Berendse, and H. De Kroon. 2010. Unveiling below-ground species abundance in a biodiversity experiment: a test of vertical niche differentiation among grassland species. Journal of Ecology 98:1117–1127.

Mueller, K. E., D. Tilman, D. A. Fornara, and S. E. Hobbie. 2013. Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. Ecology 94:787–793.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368:734–737.

Newbold, T., et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Oelmann, Y., et al. 2011. Plant diversity effects on aboveground and belowground N pools in temperate grassland ecosystems: Development in the first 5 years after establishment. Global Biogeochemical Cycles 25:GB2014.

Oram, N. J., et al. 2018. Below-ground complementarity effects in a grassland biodiversity experiment are related to deep-rooting species. Journal of Ecology 106:265–277.

Parrish, J. A. D., and F. A. Bazzaz. 1976. Underground niche separation in successional plants. Ecology 57:1281–1288.

Pereira, H. M., et al. 2010. Scenarios for global biodiversity in the 21st century. Science 330:1496–1501.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1246752.

Prechsl, U. E., S. Burri, A. K. Gilgen, A. Kahmen, and N. Buchmann. 2015. No shift to a deeper water uptake depth in response to summer drought of two lowland and sub-alpine C3-grasslands in Switzerland. Oecologia 177:97–111.

R Core Team. 2018. R: a language and environment for statistical computer. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Ravenek, J. M., et al. 2014. Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. Oikos 123:1528–1536.

Reich, P. B., D. Tilman, F. Isbell, K. Mueller, S. E. Hobbie, D. F. Flynn, and N. Eisenhauer. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. Science 336:589–592.

Reich, P. B., J. Knops, D. Tilman, J. Craine, D. Ellsworth, M. Tjoelker, T. Lee, D. Wedin, S. Naeem, and D. Bahauddin. 2001. Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. Nature 410:809–810.

Roughgarden, J. 1976. Resource partitioning among competing species—A coevolutionary approach. Theoretical Population Biology 9:388–424.

Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447–455.

Skinner, R. H., and L. H. Comas. 2010. Root distribution of temperate forage species subjected to water and nitrogen stress. Crop Science 50:2178–2185.

Smith, B., and J. B. Wilson. 1996. A consumer's guide to evenness indices. Oikos 76:70–82.

Spehn, E. M., J. Joshi, B. Schmid, M. Diemer, and C. Körner. 2000. Above-ground resource use increases with plant species richness in experimental grassland ecosystems. Functional Ecology 14:326–337.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474.

Tilman, D. 2001. Diversity and productivity in a long-term grassland experiment. Science 294:843.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and ecosystem functioning. Annual Review of Ecology, Evolution, and Systematics 45:471–493.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720.

Tittensor, D. P., et al. 2014. A mid-term analysis of progress toward international biodiversity targets. Science 346:241–244.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the "metafor" package. Journal of Statistical Software 36:1–48.

von Felten, S., A. Hector, N. Buchmann, P. A. Niklaus, B. Schmid, and M. Scherer-Lorenzen. 2009. Belowground nitrogen partitioning in experimental grassland plant communities of varying species richness. Ecology 90:1389–1399.

von Felten, S., P. A. Niklaus, M. Scherer-Lorenzen, A. Hector, and N. Buchmann. 2012. Do grassland plant communities profit from N partitioning by soil depth? Ecology 93:2386–2396.

von Felten, S., and B. Schmid. 2008. Complementarity among species in horizontal versus vertical rooting space. Journal of Plant Ecology 1:33–41.

Wagg, C., et al. 2017. Functional trait dissimilarity drives both species complementarity and competitive disparity. Functional Ecology 31:2320–2329.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends in Ecology & Evolution 5:360–364.

Weisser, W. W., et al. 2017. Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: patterns, mechanisms, and open questions. Basic and Applied Ecology 23:1–73.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York, New York, USA.

Wilke, C. 2016. cowplot: Streamlined plot theme and plot annotations for "ggplot2". https://ggplot2.tidyverse.org

Williams, L. J., A. Paquette, J. Cavender-Bares, C. Messier, and P. B. Reich. 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. Nature Ecology & Evolution 1:0063.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2905/suppinfo

DATA AVAILABILITY

Data are available from the Dryad Data Repository: https://doi.org/10.5061/dryad.7c01654