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Focusing on individual plants to understand community scale biodiversity effects: the case of root distribution in grasslands

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Spatial resource partitioning between species via differences in rooting depth is one of the main explanations for the positive biodiversity–productivity relationship. However, evidence for the importance of this mechanism is limited. This may be due to the community scale at which these interactions are often investigated. Community measures represent net outcomes of species interactions and may obscure the mechanisms underlying belowground interactions. Here, we assess the performance of ~1700 individual plants and their heterospecific neighbours over three growing seasons in experimental grassland plots containing one, four or sixteen different plant species and tested whether their performance in mixtures compared to monocultures was related to their own rooting depth versus the rooting depth of their heterospecific neighbours. Overall, individuals of deep-rooting species performed better in mixtures and this effect significantly increased when surrounded by more shallow-rooting species. This effect was not apparent for the shallow rooting species. Together, including both deep and shallow rooting species increased mixture performance. Our results show that taking the perspective of the individual rather than the community can elucidate the interactions between species that contribute to positive biodiversity effects, emphasizing the need for studies at different scales to disentangle the myriad interactions that take place in diverse communities.

Keywords: biodiversity, grasslands, rooting depth, root–root interactions, trait indices

Introduction

Numerous biodiversity experiments have shown an increase in plant community productivity with plant diversity (Hooper et al. 2005, Marquard et al. 2009, Van Ruijven and Berendse 2009, Cardinale et al. 2012). Yet, the underlying mechanisms driving this positive relationship remain debated (Hooper et al. 2005, de Kroon et al. 2012, Tilman et al. 2014, Wright et al. 2017, Barry et al. 2019). One of the most commonly proposed mechanisms for positive biodiversity productivity relationships is resource partitioning between plant species (Tilman et al. 1997, Fridley 2001, Hooper et al. 2005, Barry et al. 2019). This hypothesis predicts that differences in resource uptake strategies among plant species can drive enhanced community-level resource uptake

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and thus biomass production when species grow in mixtures as compared to monocultures. One classic example of resource partitioning is differentiation in rooting depth between species (Parrish and Bazzaz 1976, Yeaton et al. 1977, Berendse 1982). In grasslands, several studies have shown clear differences in rooting depth among species (Fitter 1986, Van Duuren et al. 2003, Wardle and Peltzer 2003, Dimitrakopoulos and Schmid 2004). If species with different rooting depths grow together in mixtures, resources can be acquired from both shallow and deep soil layers. This may result in more complete soil exploration, increased total community nutrient uptake and enhanced biomass production (Tilman et al. 1997, Hooper et al. 2005, Cardinale et al. 2011).

If species partition belowground resources in space, then we expect communities that contain a high diversity of deep and shallow rooting species to perform better than communities that lack deep or shallow rooting species. Yet, experimental evidence that differences in rooting depth between species contribute to the positive effect of biodiversity on plant productivity is limited (reviewed by Barry et al. 2020). For example, Mueller et al. (2013) found that increasing aboveground community biomass with species richness coincided with an increase in community root biomass in deep soil layers. Similarly, another study showed that increased root biomass in mixtures was positively related to the average rooting depth of the community but not to spatial root partitioning (Oram et al. 2018).

These two studies suggest that deep rooting plays a role in the positive relationship between plant species richness and biomass production. However, they do not necessarily demonstrate that differences in rooting depth between species drive positive biodiversity–productivity relationships, as would be predicted if species partition resources. For example, the positive link between rooting depth and increased productivity in mixtures as found by Mueller et al. (2013) could also be explained by deep-rooting species performing better in diverse plant communities than shallow-rooting species. This may be due to deep-rooting species reaching additional sources of nutrients and water in deeper soil layers and therefore being better competitors (Comas et al. 2013, Barkaoui et al. 2016, Zeiter et al. 2016). A more direct test for a relationship between interspecific variation in rooting depth and enhanced biomass production in mixtures was performed by Oram et al. (2018), by linking functional diversity in rooting depth among species (calculated as functional dispersion, FDis; Laliberté and Legendre 2010) to belowground biodiversity effects. However, Oram et al. (2018) found a weak negative, rather than a positive relationship between diversity in rooting depth and increased biomass production in mixture relative to monoculture. Other studies also found no evidence for positive effects of diversity in rooting depth on aboveground productivity (Roscher et al. 2012, Barkaoui et al. 2016, Wagg et al. 2017, Bakker et al. 2018, 2019). Further, a recent meta-analysis found no positive correlation between having an even root distribution across soil depth and having higher overall root biomass (Barry et al. 2020).

One reason for these mixed results may be the scale at which biodiversity effects are assessed. Most studies in grasslands focus on the community level, rather than on individual species. These community-level metrics focus on the net outcome of multiple interactions among species within a community and may mask individual species that partition resources. Moreover, averaging over the area of a plot may obscure a potentially wide range of outcomes of specific interactions between plant individuals, depending on variation in local neighbourhood species composition (Levine et al. 2017, Mommer and van Ruijven 2018). Consequently, we may find no evidence for resource partitioning at the community level, in spite of local resource partitioning between individual plants. In this study, we focus on individual plants and relate their performance in plant species mixtures to their rooting depth and those of their heterospecific neighbours to elucidate if variation in rooting depth contributes to enhanced biomass production in diverse communities. Specifically, we ask:

1) Do individuals of deep-rooting species perform better in mixtures compared to individuals of shallow-rooting species or vice versa?
2) Is the performance of an individual species in a mixture determined by the rooting depth of its heterospecific neighbours? Specifically, we expect shallow-rooting species perform better with deeper rooting neighbour species, while deep-rooting species will perform better when they have shallow-rooting neighbour species.
3) Does higher functional diversity in rooting depth at the individual level lead mixtures to produce more biomass than monocultures at the community level?

Here, we determined the aboveground biomass of over 1700 individual plants from 16 different species in monocultures and mixtures, as well as the total plot biomass per species over three growing seasons. We also assessed the rooting depth of these species in monocultures.

Material and methods

Experimental setup

A biodiversity experiment consisting of monocultures, 4-species mixtures and 16-species mixtures was established in April 2014 at an experimental field of Wageningen University, the Netherlands (51°99′N, 5°66′E). The design of this biodiversity experiment is described in more detail in Bakker et al. (2018). In short, we established 198 plots of 70 × 70 cm on sandy soil (organic matter content = 1.45 ± 0.04%, pH = 7.08 ± 0.07, N = 1.23 ± 0.08 (g kg^{-1}), P = 0.18 ± 0.01 g kg^{-1} and C = 15.11 ± 0.48 g kg^{-1} in the upper 50 cm, ± throughout refers to the standard error). Ninety-six plots were assigned to species monocultures (six per species), 90 to 4-species mixtures (45 different species compositions) and 12- to 16-species mixtures. The monocultures and mixtures were equally divided over three blocks.

We used eight grasses and eight forbs that are common in Dutch hay meadows (Schaminée et al. 1996). The grass species were *Agrostis stolonifera*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Briza media*, *Festuca rubra*, *Festuca pratensis*, *Phleum pratense*, *Trisetum flavescens* and the forb species *Achillea millefolium*, *Centaurea jacea*, *Galium mollugo*, *Leucanthemum vulgare*, *Leontodon hispidus*, *Prunella vulgaris*, *Sanguisorba officinalis* and *Ranunculus repens*. Seeds were bought from a native seed supplier. In each plot, seedlings (five weeks old) were planted in a grid of 8 × 8. In the 4-species mixtures, species were planted in such a way that each individual plant was planted next to all three heterospecific neighbours (Supporting information). In 4-species mixtures, individual plants were directly surrounded by five to eight heterospecific neighbours, and in the 16-species mixtures by six to eight heterospecific neighbours (Supporting information).

Unfortunately, seeds of one forb species, *L. hispidus*, turned out to be contaminated (70%) with seeds from another closely related species, *Leontodon autumnalis* (recently also referred to as *Scorzoneroides autumnalis*). As it was not possible to replace the *L. autumnalis* plants in time, both species share one position in the design. Therefore, the experiment contained 17 species instead of 16 species. For reasons of clarity, we still refer to 4-species mixtures and 16-species mixtures. In addition, well after planting, the perennial species *R. repens* turned out to be an annual species of the same genus: *R. sardous*. As these plants died after the first growing season, their positions in each plot were replanted with *R. repens* seedlings in March 2015. In this study, biomass data of *R. sardous* and *R. repens* were excluded, however, when *R. repens* was a neighbour species its deep rooting fraction contributed to the neighbour deep rooting fraction.

Data collection

In total, 1690 individual plants were selected for this experiment. Only individuals planted in the inner 6 × 6 grid were included to avoid potential edge effects. Of these 36 individuals, we randomly selected six individuals in each monoculture and two individuals of each species in 4-species mixtures. In the 16-species mixtures, all individuals (two or three per species; 0–3 for *L. hispidis* and *L. autumnalis*) were included.

We clipped aboveground biomass in September 2014, July 2015 and October 2016, two cm above the soil surface. The selected individuals were collected separately by clipping the aboveground biomass of a species that was found at the original planting position (a square measuring 8.75 × 8.75 cm). The remaining aboveground biomass in the rest of the plot was pooled per species. Aboveground biomass was oven dried at 70°C for at least 48 h before weighing. For individuals of three species (*A. millefolium*, *A. stolonifera*, *F. rubra*), biomass may have been underestimated. These species are capable of clonal spread by several cm per year (Klimešová et al. 2017) and may have had biomass outside the original planting position. Unfortunately, this was impossible to determine without disturbing the experiment.

To determine species-specific rooting depth, three soil cores were taken (50 cm deep × 2.5 cm diameter) in each monoculture in 2015. Soil cores were divided into four soil layers: 0–5, 5–15, 15–30 and 30–50 cm. The three samples of each layer were pooled per plot and carefully washed over 0.5 mm sieves to collect the roots. Root biomass was oven dried at 70°C for 72 h and weighed.

Calculations

Individual level

Species-specific rooting depth values were calculated as the deep root fraction (DRF), which is the fraction of root biomass in the deep (30–50 cm) layer compared to total root biomass in the entire 0–50 cm soil layer (Mueller et al. 2013, Bakker et al. 2019). These monoculture DRF values are used as a species' own rooting depth, hereafter referred to as $\mathrm{DRF}_{\mathrm{own}}$. For each individual, we also calculated the average heterospecific neighbour deep root fraction ($\mathrm{DRF}_{\mathrm{neighb}}$), using the average deep-rooting fraction (based on monoculture values) of the other species that had been planted around the measured individuals (Supporting information). Here, we focus on the interaction between individuals and their heterospecific neighbours thus conspecific neighbours were excluded. The traits were measured in monoculture, which means that conspecific neighbours have the exact same trait values as the target individuals (100% correlation) Including the trait values of conspecifics would lead to an inherent bias towards a positive relationship between $\mathrm{DRF}_{\mathrm{own}}$ and $\mathrm{DRF}_{\mathrm{neighb}}$. As this positive relationship is an artefact of how the data are derived rather than biologically meaningful, we opted to focus our questions on heterospecific neighbours.

To assess the change in performance of individual plants in mixture relative to that in monoculture, we calculated the change in yield (dY) as the difference in the natural logarithm (ln) of the biomass (g) of an individual of a species in a mixture and that of the average biomass of the individuals of the same species *i* in monocultures.

$$\mathrm{dY} = \ln\left(\mathrm{biomass}_{\mathrm{mixture}}\right) - \ln\left(\mathrm{mean}\left(\mathrm{biomass}_{\mathrm{monoculture}}\right)\right)$$

dY > 0 indicates that plants perform better in mixture than in monoculture, whereas dY < 0 indicates that plants perform worse in mixture.

Community level

In order to assess the performance of plant mixtures relative to monocultures at the community, we calculated the relative yield total (RYT) which is the sum of the species' relative yields. A RYT greater than one indicates that a community performs better than expected from the monoculture yields of its component species.

Several functional diversity indices can be used to assess trait variation in species mixtures. Generally, for rooting depth, earlier studies (Roscher et al. 2012, Wagg et al. 2017, Oram et al. 2018, Bakker et al. 2019) used functional dispersion (FDis) or Rao's quadratic diversity (Rao's Q). The values of these indices increase with increasing differences in trait values between species, thus separating mixtures with deep and shallow rooting species from mixtures consisting of species with small differences in rooting depth. However, these indices are also sensitive to the evenness of the distribution of trait values across species. For example, both indices will assign a higher value to a community consisting of two deep and two shallow species than to communities consisting of one deep and three shallow species (or vice versa). The question is whether the evenness of the trait distribution is as important as the differences in trait values for enhanced resource partitioning. To test this, we compared the performance of FDis and Rao's Q as predictors of complementarity effects to that of functional richness. This index also captures the difference in rooting depth between species but is less sensitive to the distribution of trait values across species. The three indices of functional diversity were calculated for each plot in each year using the FD package (Laliberté and Shipley 2011).

Statistical analyses

All statistics were done in R ver. 3.1.3 (<www.r-project.org>) with R studio ver. 1.0.143 (<www.r-project.org>). Throughout, we construct mixed-effect models using the 'nlme' (Pinheiro et al. 2016) package. We then used mixed-effect ANOVAs with type III sums of squares to examine how our predictor variables affected our response variables using the ANOVA function that is built into the 'nlme' package. Denominator degrees of freedom were estimated by the default function in nlme which estimates denominator degrees of freedom as in Pinheiro and Bates (2000).

Differences in DRF among species and plant functional groups (grass or forb) in monoculture were tested with a linear mixed-effect model with block and plot as random factors after a square root transformation. Because the variance in these models was heterogeneous across species, we weighted the model variance by species identity (using VarIdent = Species, in nlme, Zuur et al. 2009). Effects of species identity, species richness and year on aboveground biomass of individuals were tested using a linear mixed-effect model (restricted maximum likelihood, REML) with species, species richness, year and their interaction as fixed factors, and plant ID, plot number, block and species composition as random factors.

The effects of a species own rooting depth (DRF_{own}), species richness (4 or 16), year and the rooting depth of the heterospecific neighbours (DRF_{neighb}) on the relative performance of individuals in mixture (LRR) were tested using a similar linear mixed model with own rooting depth as fixed factor, neighbour rooting depth, species richness, year and their interactions as fixed factors, and plant ID, plot number and block as random factors (Burnham and Anderson 2002, Fijen et al. 2015). To find the most parsimonious model, the function 'dredge' of R package 'MuMIn (ver. 1.15.6)' (Bartoń 2016) was used, which returns a list of models with all possible combinations (subsets) of the fixed effect terms and the model outputs including the information criterion value (AIC). The best model was chosen based on the lowest AIC, with a minimum difference of two ΔAIC compared to other competing models (Burnham and Anderson 2002). The relative importance of the variables in the final model were calculated according to Burnham and Anderson (2002). Supporting information for model selection procedures.

The effects of species richness and year on community aboveground biomass, relative yield total were tested using a linear mixed-effect model with species richness, year and their interaction as fixed effects and plot number nested in block as random factor. The relationships between relative yield total and functional diversity in rooting depth (measured as FDis, RaoQ or FR) were tested using a linear mixed-effect model (REML) with one of the functional diversity indices as fixed factor and species composition as random factor. In the analyses of biomass per individual, zeros were excluded: individuals that were not present in a given year were no longer taken into account that year and any following years (see the Supporting information for survival). Individual and community biomass was natural log transformed to meet model assumptions for normally distributed residuals.

Because these models included many fixed effects, we used the function 'dredge' from the package 'MuMIn (ver. 1.15.6)' (Bartoń 2016) to find the most parsimonious final model and report the results of these models. Dredge returns a list of models with all possible combinations (subsets) of the fixed effect terms and the model outputs including the

Table 1. The species used in the experiment, the functional group (FG) they belong to and their rooting depth, measured as deep root fraction (DRF): the proportion of root biomass in the 30–50 cm soil layer relative to total root biomass in the 0–50 cm soil layer. These values were obtained in species monocultures in 2015 (n = 6 per species).

Species	FG	DRF
Agrostis stolonifera	Grass	0.17 ± 0.03
Anthoxanthum odoratum	Grass	0.12 ± 0.02
Arrhenatherum elatius	Grass	0.20 ± 0.04
Briza media	Grass	0.07 ± 0.02
Festuca pratensis	Grass	0.21 ± 0.03
Festuca rubra	Grass	0.22 ± 0.04
Phleum pratense	Grass	0.15 ± 0.03
Trisetum flavescens	Grass	0.08 ± 0.02
Achillea millefolium	Forb	0.42 ± 0.07
Centaurea jacea	Forb	0.38 ± 0.03
Galium mollugo	Forb	0.30 ± 0.05
Leontodon autumnalis/hispidus	Forb	0.32 ± 0.03
Leucanthemum vulgare	Forb	0.21 ± 0.03
Prunella vulgaris	Forb	0.17 ± 0.04
Sanguisorba officinalis	Forb	0.35 ± 0.05

information criterion value (AIC). The best model was chosen based on the lowest AIC, with a minimum difference of two ΔAIC compared to other competing models (Burnham and Anderson 2002). The relative importance of the variables in the full model was calculated according to Burnham and Anderson (2002). See the Supporting information for model selection procedures. Additionally, we used the function 'check_collinearity' in the package 'performance' to check that the remaining variables in the final models were not significantly collinear. All individual variables included in the final models had variance inflation factors <10 indicating an acceptable level of multicollinearity.

Finally, we used the package 'visreg' (Breheny and Burchett 2017) to visualise the model fits in figures from the interactive effect of own rooting depth and neighbour rooting depth on relative performance of individuals in mixture.

Results

Species rooting depths

Across all 16 plant species, the deep root fraction (DRF) was 0.22 ± 0.03, meaning that 22% of the root biomass (0–50 cm) was found in the deeper (i.e. 30–50 cm) soil layer and 78% in the top (0–30 cm) soil layer. However, the fraction of roots in the deeper layer differed significantly between species (Table 1; $F_{14,72} = 8.1$, $p < 0.001$), ranging from 7% (*B. media*) to 42% (*A. millefolium*). On average, forbs had a greater proportion of roots in the deeper soil layer than the grasses (Table 1; 31% ± 2 compared to 15% ± 1; $F_{1,85} = 43.9$, $p < 0.001$), but species also differed significantly in DRF within these functional groups (Table 1; $F_{7,38} = 3.4$, $p < 0.01$ and $F_{7,37} = 6.1$, $p < 0.001$ for grasses and forbs respectively).

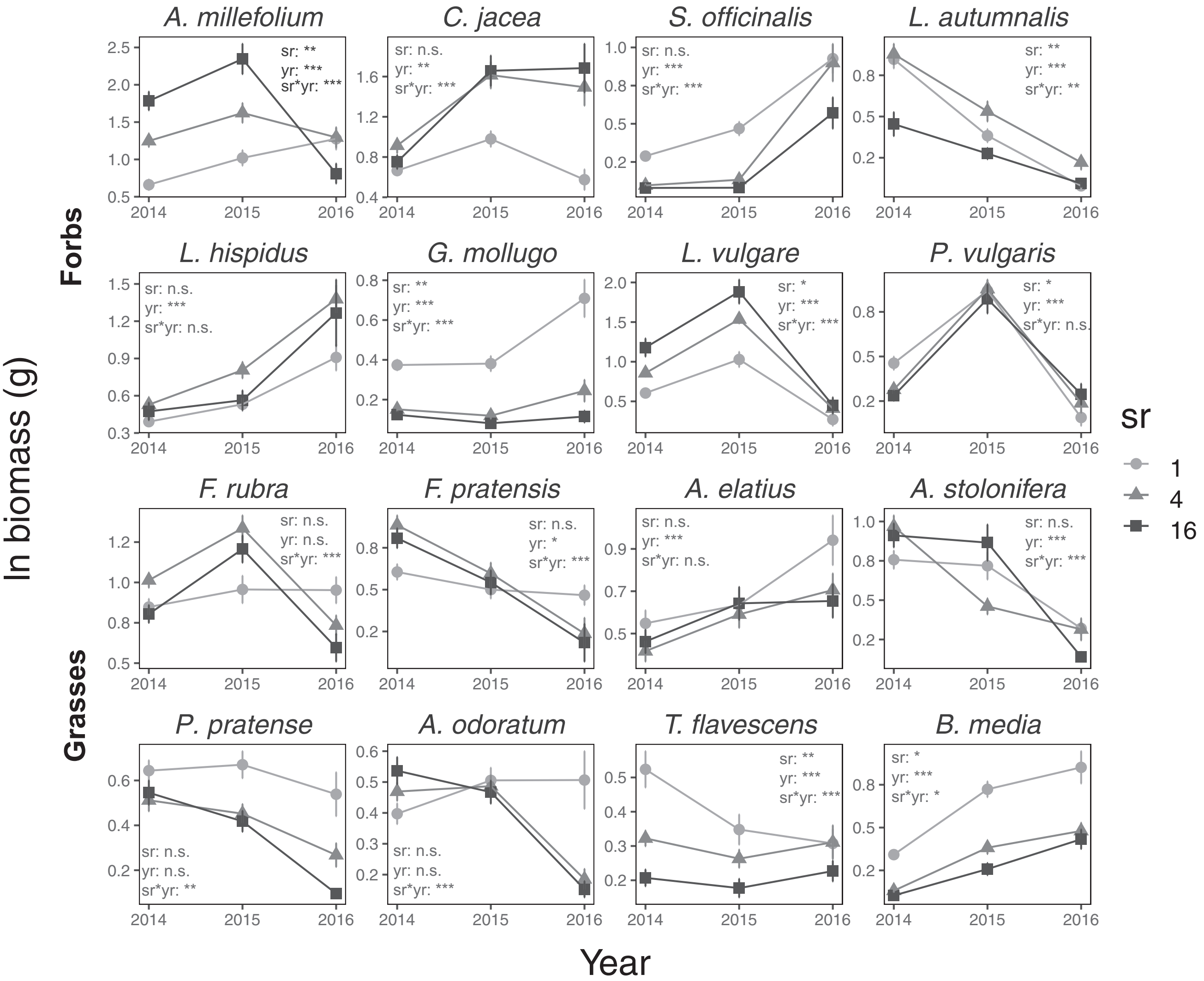

Figure 1. Average biomass of individual plants of each species in monocultures, 4-species mixtures and 16-species mixtures in three growing seasons (2014–2016). Species are ordered from deep (*A. millefolium*) to shallow (*B. media*) rooting depth, as measured in monocultures (Table 1). sr = species richness, yr = year, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant. Symbols show means ± SE.

Table 2. Summary statistics for the selected linear mixed effect model testing the effects of species' own rooting depth, neighbour rooting depth, species richness and year on relative performance of the individual in mixture compared to monoculture (dY). Significant effects are marked in bold. $\mathrm{DRF}_{\mathrm{own}}$ = species' own rooting depth; $\mathrm{DRF}_{\mathrm{neighb}}$ = neighbour rooting depth; df, = degrees of freedom. Supporting information for model comparisons.

	Individual plant performance (dY)		
	df	F-value	p-value
Intercept	1,2012	4.9	**0.027**
$\mathrm{DRF}_{\mathrm{own}}$	1,2012	21.4	**<0.001**
$\mathrm{DRF}_{\mathrm{neighb}}$	1,1011	0.5	0.468
Species richness (SR)	1,98	0.5	0.487
Year	2,2012	7.2	**<0.001**
$\mathrm{DRF}_{\mathrm{own}} \times \mathrm{DRF}_{\mathrm{neighb}}$	1,2012	7.9	**0.005**
$\mathrm{DRF}_{\mathrm{own}} \times \mathrm{SR}$	1,2012	0.5	0.497
$\mathrm{DRF}_{\mathrm{own}} \times \mathrm{Year}$	2,2012	5.2	**0.006**
SR × Year	2,2012	1.0	0.358
$\mathrm{DRF}_{\mathrm{own}} \times \mathrm{SR} \times \mathrm{Year}$	2,1873	6.6	**0.001**

Performance of individual plants

Individual aboveground biomass differed significantly between species (Fig. 1). These effects depended on species richness (species × SR: $F_{30,98} = 3.5$, $p < 0.001$) and year (species × SR × Year: $F_{60,3057} = 8.5$, $p < 0.001$). When analysed separately, the effects of species richness on individual biomass of most species (13 out of 16) differed between years (significant year × SR interactions), with positive effects in one year and neutral or negative effects in another, or vice versa (Fig. 1). Only two species (the forbs *G. mollugo* and *P. vulgaris*) showed a consistent (negative) effect of species richness over three years. Two other species (the forb *L. hispidus* and the grass *A. elatius*) showed a consistent (positive) effect of time, but no effect of species richness.

Here, we focus on the relative performance of individual plants in mixtures (dY). The final model revealed a strong effect of a species' *own* deep root fraction (Table 2): the relative performance of species in mixture increased significantly with their own deep root fraction (Fig. 2). On average, shallow-rooting species performed worse in mixtures than in monoculture ($dY < 0$), while deep-rooting species performed better ($dY > 0$). Although the slope of the relationship depended on the year and on the interaction between year and species richness (Table 2), it was significant and positive in all three years and at both levels of species richness (Fig. 2).

Importantly, the effect of the rooting depth of the heterospecific neighbours depended on the rooting depth of the species (significant $\mathrm{DRF}_{\mathrm{neighb}} \times \mathrm{DRF}_{\mathrm{own}}$ interaction; Table 2). Shallow-rooting species showed no response to the rooting strategy of their heterospecific neighbours, but deep-rooting species performed increasingly better in mixtures with more shallow-rooting heterospecific neighbours in the community (Fig. 3). When analysed separately, six species (three forbs and three grasses) showed the same positive response to shallow-rooting heterospecific neighbours (Fig. 4). However, the deepest-rooting species (*A. millefolium*), which clearly performed better in mixtures, did not show this response.

Mixture performance and rooting depth

At the community level, aboveground biomass increased with species richness each year (Supporting information). This increase was reflected in relative yield totals that are generally greater than one in all mixtures (Supporting information). Relative yield totals did not differ between 4-species and 16-species mixtures ($F_{1,98} = 1.5$; $p = 0.22$), year ($F_{2,194} = 1.6$; $p = 0.21$) or their interaction ($F_{2,194} = 0.4$, $p = 0.67$).

In 2014, the relative yield total increased significantly with functional richness, FDis and RaoQ of rooting depth (Table 4, Fig. 5). In 2015, the relative yield total increased significantly with increasing functional richness and Rao's Q. For these two years, functional richness was a better predictor of the relative yield total than FDis and Rao's Q. In 2016, however, the relative yield total did not increase with functional diversity but tended to increase ($p < 0.1$) with increasing Rao's Q and FDis which also represented a better model fit than functional richness in this year.

Discussion

Deep-rooting plant species performed significantly better in mixtures than shallow-rooting species. These benefits for deep-rooting species depended on the rooting strategy of their heterospecific neighbours: deep-rooting species performed better in mixtures when growing with shallow-rooting heterospecific neighbours than with deep-rooting heterospecific neighbours. The reverse did not occur: the performance of shallow-rooting species in mixtures was not affected by the rooting depth of their heterospecific neighbours. These effects at the level of individual plants were strong enough to affect community productivity: complementarity effects occurred in species mixtures and increased with diversity in rooting depth, at least when expressed as functional richness (FR).

Do individuals of deep-rooting species perform better in mixtures compared to individuals of shallow-rooting species or vice versa?

As hypothesized, species' rooting depth was an important predictor for the performance of species in mixture: deep-rooting individuals performed, on average, better, in mixtures compared to monocultures, than shallow-rooting species. Other studies indeed indicate that species-specific rooting depth is important for plant performance in grasslands. For example, rooting depth was positively related to water uptake (Fort et al. 2017) and species biomass production under drought (Hoekstra et al. 2015, Zeiter et al. 2016) in grasslands. The advantage for deep-rooting species may be the result of access to additional resources in the deeper layers compared to shallow species (Maeght et al. 2013), but also to the ability to switch to nutrient and water uptake from deeper layers during dry conditions (Kulmatiski and Beard 2013, Hoekstra et al. 2014).

Is the performance of an individual species in the mixture determined by the rooting depth of its heterospecific neighbours?

Deep-rooting individuals showed the highest individual performance when growing next to shallow heterospecific neighbours. In contrast to the deep-rooting species, shallow-rooting species showed no response to the rooting depth of their heterospecific neighbours. This raises the question of why the shallow-rooting species did not profit from growing next to species with a different – deeper – rooting strategy, while the deep-rooting species did. We suggest that this is related to the general distribution of roots over depth. In grasslands, the majority of the roots are found in shallow soil layers (Jackson et al. 1996, Bessler et al. 2009, Mueller et al. 2013). Even deep-rooting species often have the largest proportion of their roots in the upper soil layers. For example, in this study, the four deepest rooting species (DRF > 0.30) of the 16 species in the experiment allocated an average 63% of their roots to the upper 30 cm soil. Thus, shallow species, even when surrounded by deep-rooting species, probably face intense competition with many other roots in the upper soil layers (Wardle and Peltzer 2003, Nippert and Knapp 2007, Frank et al. 2010, Jesch et al. 2018). In contrast, competition may be less intense in the deeper layers, particularly in a community in which most species are shallow rooting thus providing a competitive advantage to deep rooting species.

We used the rooting depth measured in monocultures to predict species performance in mixtures. As such, we assume that differences in rooting depths across species are

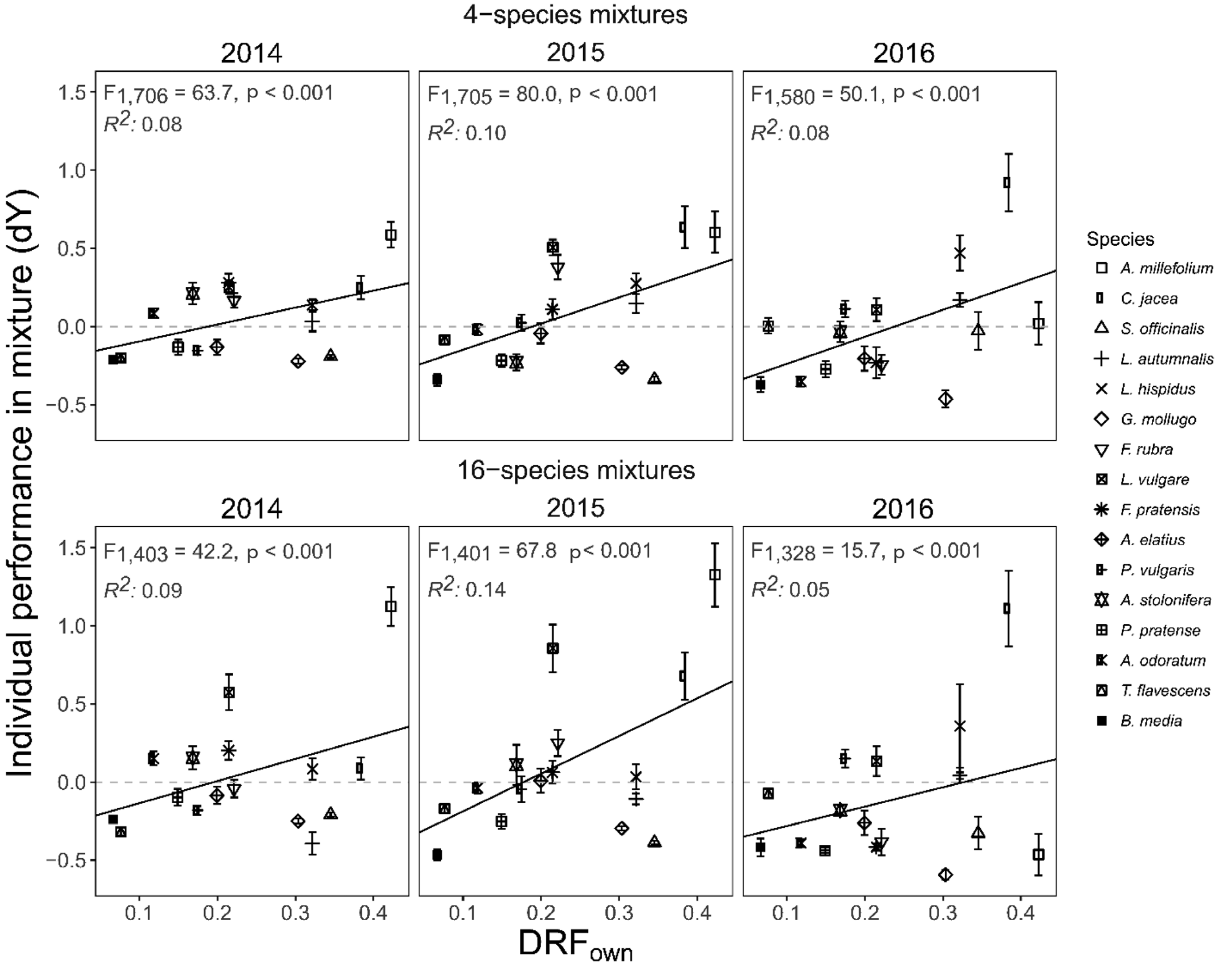

Figure 2. Species relative performance in mixture compared to monoculture (dY) as a function of their own rooting depth (DRF_{own}) in 4-species mixtures (above) and 16-species mixtures (below) in three subsequent years. In each year, dY increased with DRF_{own}: individuals with deeper roots (higher DRF_{own}) performed better in mixtures than species with shallow roots. Deep-rooting species had higher performance in mixtures than monocultures (dY > 0; above grey dotted line), while shallow-rooting species performed worse (dY < 0; below grey dotted line). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant. Symbols show means ± SE. Black solid lines represent regression results.

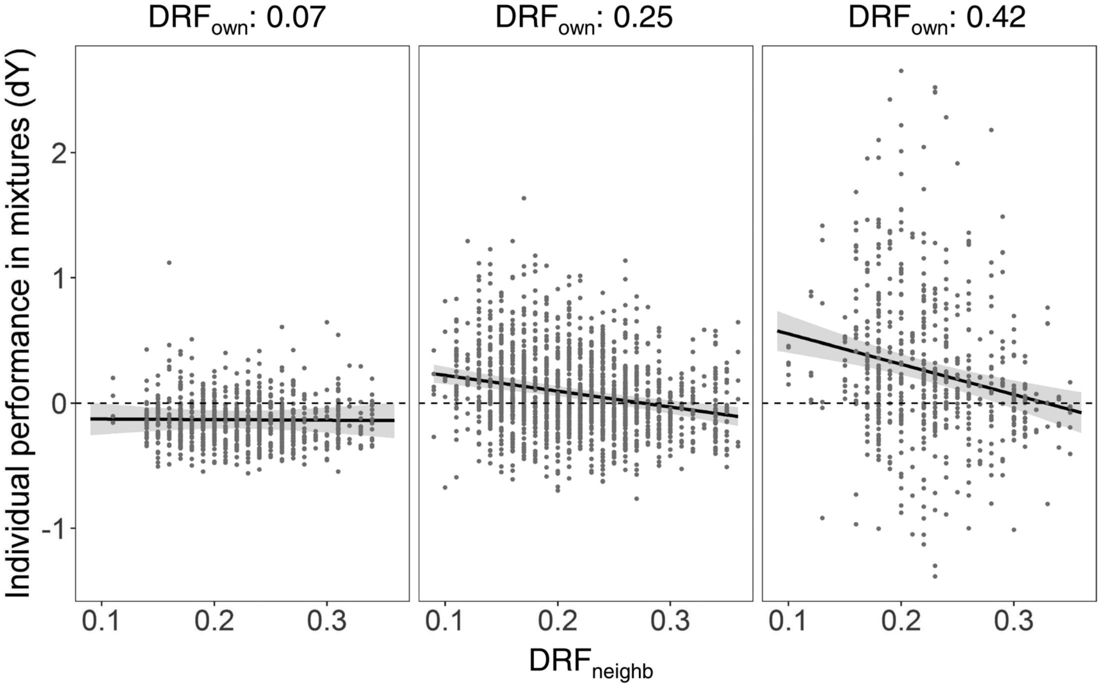

Figure 3. The interaction between species' rooting depth and the rooting depth of their heterospecific neighbours. The relationship between the individual performance in mixture (dY) and the average rooting depth of the neighbours (DRF_{neighb}) depends on how deep rooting a species is. The slope of the relationship between dY and DRF_{neigh} becomes more negative across a hypothetical shallow ($DRF_{own} = 0.07$), intermediate ($DRF_{own} = 0.25$) and deep-rooting ($DRF_{own} = 0.42$) species. The effect of the rooting depth of the neighbours depended on the rooting depth of the species: deep-rooting species ($DRF_{own} < 0.42$) performed better when surrounded by shallow neighbours (low DRF_{neigh}). In contrast, the performance of shallow-rooting species ($DRF_{own} < 0.07$) was not affected by the rooting depth of their neighbours. This figure was constructed using the package 'visreg' in R (Breheny and Burchett 2017). It illustrates the significant interaction between DRF_{own} and DRF_{neighb} (Table 2) based on model predictions (model in Table 2; see Methods and Table 3 for model selection) in 2014 in 4-species mixtures. The line here represents the expected value (based on our model predictions) with 95% confidence intervals. Points represent the partial residuals of the model for chosen values of DRF_{own}.

the same in monoculture and mixture. Roots are plastic and known to respond to both the abiotic and biotic conditions of a community (Hodge 2004, Bartelheimer et al. 2006, Mommer et al. 2010, Belter and Cahill 2015). While studies have shown that roots respond plastically to being in mixture versus monoculture (Oram et al. 2018, Mommer et al. 2010) and the identity of their neighbours (Chen et al. 2020), these studies do not demonstrate that these shifts are sufficiently large to better predict biodiversity effects (Oram et al. 2018) in spite of variation in root depth distributions.

Our finding that rooting depth of both the target species and its heterospecific neighbours drive the relative performance of individual plants in mixtures may seem inconsistent with previous studies that found no or only a very small positive effect of root trait diversity on community performance (Roscher et al. 2012, Barkaoui et al. 2016, Wagg et al. 2017, Bakker et al. 2018, Oram et al. 2018). However, these studies related variation in rooting depth between species to performance assessed at the community level. Our study highlights that focusing on the performance of individual species within mixtures can provide a different perspective on the importance of mechanisms driving biodiversity effects. Our approach not only increased the sample size (in our study, the number of observations increased from 102 mixture plots to ~1700 individual plants in different neighbourhoods), but probably also reduced the chance that the effects of particular trait differences are obscured by effects of other interactions simultaneously taking place in communities.

This approach also highlights the importance of species-specific dynamics in biodiversity–ecosystem functioning relationships. We found that six species (three forbs and three grasses) showed the same positive response to shallow-rooting heterospecific neighbours (Fig. 4). Yet, the deepest-rooting species (*A. millefolium*) did not react to the rooting depth of its heterospecific neighbours. In spite of this lack of response to the rooting depth of its heterospecific neighbours, *A. millefolium* produced significantly more biomass in higher diversity communities. This anomalous species response may be important for driving biodiversity–ecosystem functioning relationships at the community level when *A. millefolium* is included in higher diversity communities. Species like *A. millefolium* may contribute to the overall biodiversity effect through time because they are drought tolerant (Belluau and Shipley 2017) which may stabilize plant productivity over time.

Does higher functional diversity in rooting depth at the individual level lead mixtures to produce more biomass than monocultures at the community level?

Aboveground relative yield total, calculated at the community level, increased with increasing functional diversity in rooting depth in our study in two out of three years and tended to increase with increasing Rao's Q and functional dispersion of rooting depth in the final year. This result differs from a wealth studies which have found that increasing functional diversity or other measures of root segregation do not result in increased community biomass production (Roscher et al. 2012, Barkaoui et al. 2016, Wagg et al. 2017, Bakker et al. 2018, 2019, Oram et al. 2018). We propose that our study differs from these other studies in two ways: 1) the functional diversity indices used and 2) the environmental and community context of the study.

First, in the past two decades, several indices have been developed to assess the functional trait diversity of a community by quantifying the distribution of trait values among species (Botta-Dukát 2005, Villéger et al. 2008, Mouchet et al. 2010, Mason et al. 2013). Previous studies focused on root traits used Rao's Q (Roscher et al. (2012), Wagg et al. (2017) or FDis (Oram et al. 2018). The value of these indices does not only increase with an increasing difference in rooting depth between species, but also includes the distribution of the species over the range in rooting depth. As a consequence, a community consisting of two shallow and two deep species is considered more diverse than a community that contains one deep species and three shallow rooting species. The question is whether the distribution of species over the trait range is as important as the trait range itself. Our results suggest this is not the case: functional richness, which captures the size of the trait space but is less sensitive to the distribution of species within the space, was a better predictor of relative yield total than FDis and RaoQ. We suggest that the presence of at least one deep and one shallow rooting species was most important for positive biodiversity effects in our study.

Future research may profit from critical evaluation of different functional diversity indices in relation to the ecological mechanism under consideration. That is, differences between functional diversity indices in predicting the relative yield total may offer mechanistic insight. For example, if resource partitioning drives increases in relative yield total then we would expect that a community that in addition to having a clear range in trait values (as captured by functional richness), also shows a more even distribution across the given trait spectrum (as incorporated by FDis or Rao's Q) would show the highest relative yield total. Alternatively, if the evenness of the distribution is not important or shows a negative relationship, this may suggest that mechanisms other than resource partitioning are responsible. For example, having one deep-rooted species may be sufficient to increase water availability for shallow-rooted species if the deep-rooted species performs

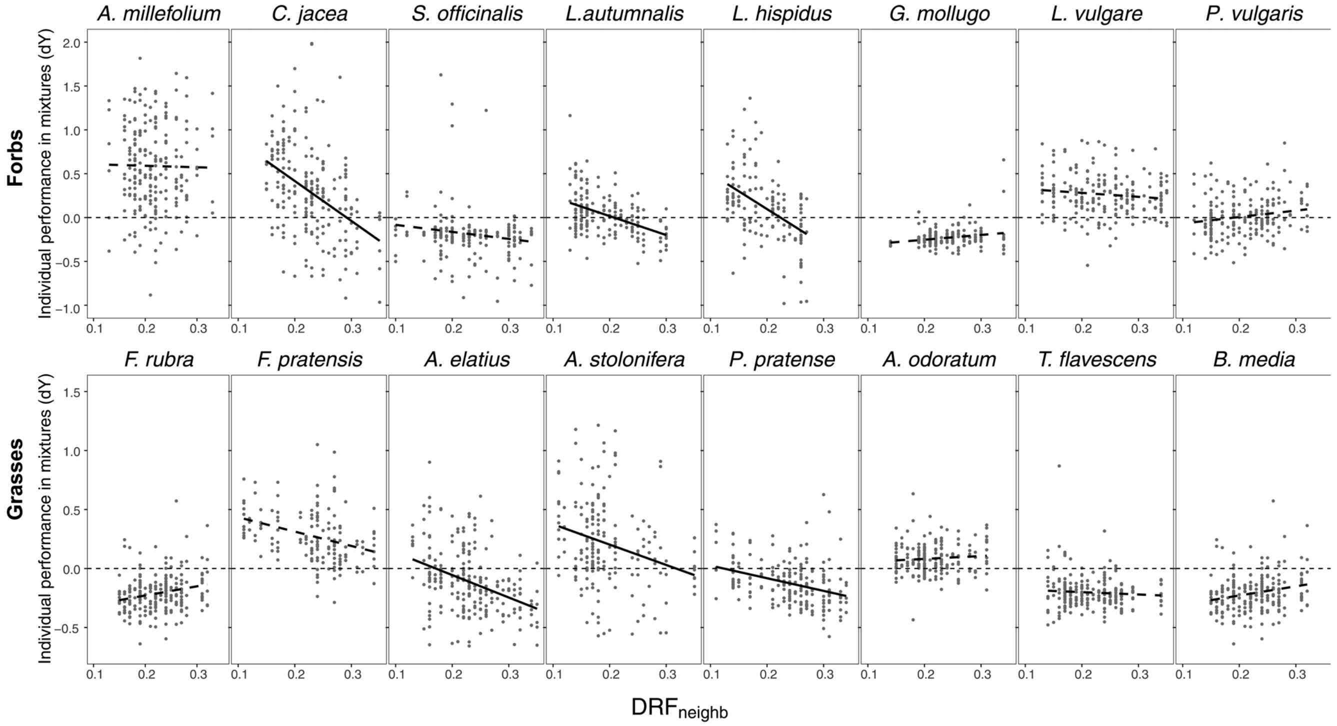

Figure 4. The relationship between individual performance in mixture (dY) and the average rooting depth of the heterospecific neighbours (DRF$_{neighb}$) for each of the species included in our experiment. Forbs (above) and grasses (below) are ordered from deep-rooting (left) to shallow-rooting (right). The graph illustrates species responses to neighbours' DRF$_{neighb}$ using 2014 and 4-species mixtures as an example, showing the expected value (black line), confidence interval (grey band) and partial residuals (dots). The main effect of DRF$_{neighb}$ using all years (2014–2016) is presented in the graph; the complete summary of the model results is shown in Table 3.

Table 3. Summary statistics for a linear mixed-effect model testing for each species the effects of neighbour rooting depth, species richness and year on plant performance in mixture compared to monoculture (dY). PFT, plant functional type, DRF$_{\text{neighb,}}$, average rooting depth of the neighbouring plants; sr, species richness. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$, n.s. = not significant.

Species	PFT	Intercept	Slope	sr	Year	DRF$_{\text{neighb}}$	sr × year
A. millefolium	forb	0.62	−0.17	$F_{1,35}=6.7^{*}$	$F_{2,35}=14.9^{***}$	$F_{1,35}=0^{\text{n.s.}}$	$F_{2,35}=19.8^{***}$
C. jacea	forb	1.32	−4.54	$F_{1,35}=1.5^{\text{n.s.}}$	$F_{2,35}=14.6^{***}$	$F_{1,35}=5.8^{*}$	$F_{2,35}=1.6$
S. officinalis	forb	−0.01	−0.76	$F_{1,33}=0.1^{\text{n.s.}}$	$F_{2,33}=7.5^{***}$	$F_{1,33}=1.9^{\text{n.s.}}$	$F_{2,33}=3.2^{*}$
L. autumnalis	forb	0.45	−2.16	$F_{1,27}=19.5^{***}$	$F_{2,27}=3.1^{(*)}$	$F_{1,27}=12.1^{**}$	$F_{2,27}=4.9^{**}$
L. hispidus	forb	0.91	−4.07	$F_{1,18}=0.0^{\text{n.s.}}$	$F_{2,18}=7.5^{***}$	$F_{1,18}=15.8^{***}$	$F_{2,18}=0.4^{\text{n.s.}}$
G. mollugo	forb	−0.39	0.64	$F_{1,35}=0.0^{\text{n.s.}}$	$F_{2,35}=40.4^{***}$	$F_{1,35}=3.1^{(*)}$	$F_{2,35}=2.4^{(*)}$
L. vulgare	forb	0.32	−0.27	$F_{1,37}=4.6^{*}$	$F_{2,37}=18.4^{***}$	$F_{1,37}=0.1^{\text{n.s.}}$	$F_{2,37}=9.2^{***}$
P. vulgaris	forb	−0.32	0.82	$F_{1,37}=0.3^{\text{n.s.}}$	$F_{2,37}=9.5^{***}$	$F_{1,37}=2.7^{\text{n.s.}}$	$F_{2,37}=0.8^{\text{n.s.}}$
F. rubra	grass	0.1	0.36	$F_{1,37}=4.3^{*}$	$F_{2,37}=41.8^{***}$	$F_{1,37}=0.2^{\text{n.s.}}$	$F_{2,37}=0.4^{\text{n.s.}}$
F. pratensis	grass	0.53	−1.12	$F_{1,34}=0.3^{\text{n.s.}}$	$F_{2,34}=24.1^{***}$	$F_{1,34}=2.6^{\text{n.s.}}$	$F_{2,34}=0.1^{\text{n.s.}}$
A. elatius	grass	0.33	−1.93	$F_{1,41}=0.0^{\text{n.s.}}$	$F_{2,41}=4.8^{*}$	$F_{1,41}=7.0^{*}$	$F_{2,41}=1.3^{\text{n.s.}}$
A. stolonifera	grass	0.55	−1.72	$F_{1,37}=0.2^{\text{n.s.}}$	$F_{2,37}=15.7^{*}$	$F_{1,37}=9.1^{**}$	$F_{2,37}=8.3^{\text{n.s.}}$
P. pratense	grass	0.14	−1.09	$F_{1,35}=0.1^{\text{n.s.}}$	$F_{2,35}=5.8^{**}$	$F_{1,35}=4.9^{*}$	$F_{2,35}=3.5^{*}$
A. odoratum	grass	0.05	0.17	$F_{1,37}=1.2^{\text{n.s.}}$	$F_{2,37}=86.6^{***}$	$F_{1,37}=0.1^{\text{n.s.}}$	$F_{2,37}=0.2^{\text{n.s.}}$
T. flavescens	grass	−0.17	−0.13	$F_{1,41}=4.5^{*}$	$F_{2,41}=17.0^{***}$	$F_{1,41}=0.1^{*}$	$F_{2,41}=0.2^{\text{n.s.}}$
B. media	grass	−0.41	0.88	$F_{1,37}=0.1^{\text{n.s.}}$	$F_{2,37}=10.1^{***}$	$F_{1,37}=3.7^{(*)}$	$F_{2,37}=1.4^{\text{n.s.}}$

hydraulic lift (Dawson 1993, Emerman and Dawson 1996, Ludwig et al. 2004, Sekiya and Yano 2004).

Second, the relative importance of the different mechanisms that can drive the positive effect of biodiversity on productivity is likely context-dependent (Guerrero-Ramírez et al. 2017, Barry et al. 2019). A recent meta-analysis found that the likelihood that communities exhibit a signature consistent with resource partitioning at the community level was likely higher in systems that were more strongly nutrient limited (Barry et al. 2020). This context dependence may influence our results in several ways. First, in contrast to our study, several of the studies mentioned above included legumes (Roscher et al. 2012, Wagg et al. 2017). The presence of legumes and their interactions with other plant species can strongly enhance mixture performance (Lambers et al. 2004, Marquard et al. 2009). Legumes increase the availability of nitrogen and thus decrease nutrient limitation. This decline in nutrient limitation likely causes a decline in the extent to which species partition resources (Harpole et al. 2016). Second, during the course of our experiment, a drought occurred in Europe (Ionita et al. 2017). Increased performance of deep rooting species may be exacerbated under drought conditions when water availability is decreased. Under drought conditions, species that are able to access deeper groundwater or perform hydraulic lift may be at a competitive advantage.

This context dependence may occur because different mechanisms are more or less important under different abiotic and biotic conditions. Our experiment likely dilutes the potential influence of these other mechanisms in four ways. First, we focus on heterospecific neighbours. Conspecific neighbours also have an important effect on root growth and resource uptake through intraspecific competition and facilitation. Second, the design of our experiment may dilute the influence of mechanisms such as positive or negative feedback from other plant species. These effects are often dependent on conspecific density which is deliberately controlled in our experiment (Barry et al. 2019). Further, we do not include conspecific root traits in our calculations for the neighbourhood due to their correlation with the target individual traits. This removal, and our experimental design, likely minimise the extent to which processes dependent on conspecific density dependence are relevant in this experiment. Third, we focus here on deep-rooting fraction. DRF$_{\text{own}}$ explained between 5 and 14% of the variation in individuals' performance in mixture which is comparable to the average amount of variation explained by traits in biodiversity ecosystem functioning research (van der Plas et al. 2020). We chose to focus on DRF because we felt that it was the most relevant trait for our questions. However, focusing on DRF makes it difficult for us to assess the likelihood that other mechanisms are at play in our system. Fourth, we only calculate DRF in monoculture. DRF has been shown to change in response to the community in which it is planted (Mommer et al. 2008, Mueller et al. 2013, Oram et al. 2018, Barry et al. 2020). These changes may occur if plants shift

Table 4. Summary statistics for linear mixed models predicting plant community total observed relative yield (RYT) using DRF diversity indices. RYT was ln transformed to meet model assumptions. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$, n.s. = not significant.

	2014		2015		2016	
Relationships between RYT and DRF diversity indices						
FR	$F_{1,50} = 22.3^{***}$	AIC: 36.1	$F_{1,50} = 18.1^{***}$	AIC: 9.0	$F_{1,45} = 0.7^{\text{n.s.}}$	AIC: 206.7
Rao's Q	$F_{1,50} = 7.0^{*}$	AIC: 50.5	$F_{1,50} = 4.3^{*.}$	AIC: 19.7	$F_{1,45} = 3.1^{(*)}$	AIC: 203.6
FDis	$F_{1,50} = 5.8^{*}$	AIC: 51.0	$F_{1,50} = 2.0^{\text{n.s.}}$	AIC: 21.3	$F_{1,45} = 3.9^{(*)}$	AIC: 202.1

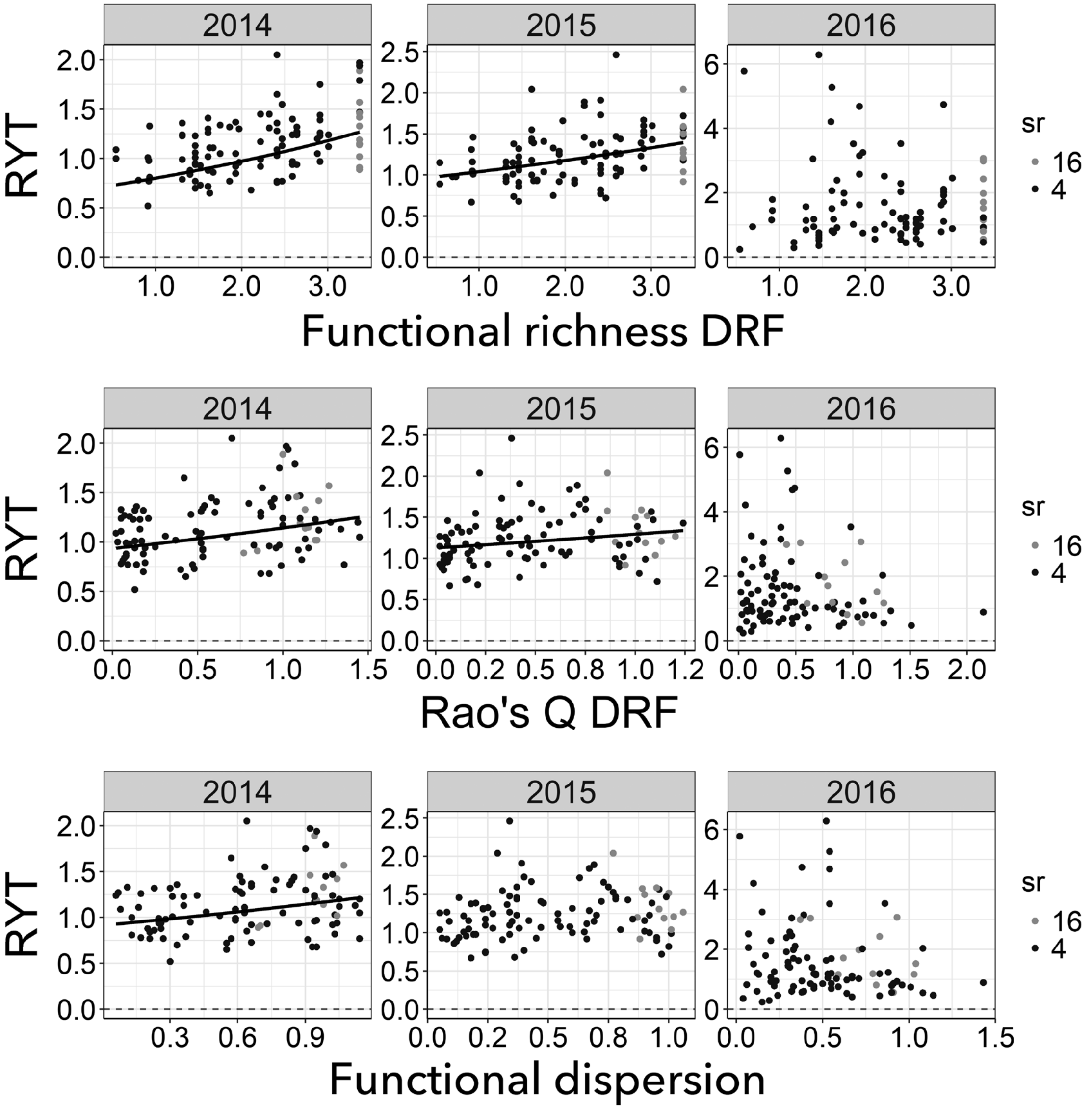

Figure 5. Relationships between aboveground relative yield total at the community level and rooting depth diversity, calculated as functional richness (top), Rao's Q (middle) and functional dispersion (bottom) of the deep rooting fraction (DRF). Statistics are shown in Table 4.

their biomass allocation to better partition resources with other species. We cannot account for these shifts in the DRF in response to biotic interactions because of our focus on DRF in monoculture.

Conclusions

Our results show that zooming in from the community to individual plants can reveal the importance of differences in rooting depth between species for the positive relationship between biodiversity and productivity. Deep rooting species performed better with shallow heterospecific neighbours while shallow rooting species did not respond to the rooting depths of their heterospecific neighbours. In our study, these biodiversity effects were strong enough to affect community performance. This shows that differences in rooting depth between species can contribute to the positive effects of plant species richness on plant productivity. Further, our work suggests that careful consideration of different trait indices in relation to the mechanism(s) under study may contribute to enhance our understanding of the mechanisms underlying positive biodiversity effects.

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Author contributions

Lisette M. Bakker: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Kathryn E. Barry**: Formal analysis (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Liesje Mommer**: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Supervision (lead); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jasper Van Ruijven**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (lead); Supervision (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.280gb5mqr> (Bakker et al. 2021).

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