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Functional trait dissimilarity drives both species complementarity and competitive disparity

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Summary

1. Niche complementarity and competitive disparity are driving mechanisms behind plant community assembly and productivity. Consequently, there is great interest in predicting species complementarity and their competitive differences from their functional traits as dissimilar species may compete less and result in more complete use of resources.

2. Here we assessed the role of trait dissimilarities on species complementarity and competitive disparities within an experimental gradient of plant species richness and functional trait dissimilarity. Communities were assembled using three pools of grass and forb species based on a priori knowledge of traits related to (1) above- and belowground spatial differences in resource acquisition, (2) phenological differences, or (3) both. Complementarity and competitive disparities were assessed by partitioning the overyielding in mixed species communities into species complementarity and dominance effects.

3. Community overyielding and the underlying complementarity and competitive dominance varied strongly among the three plant species pools. Overyielding and complementarity was greatest among species that were assembled based on their variation in both spatial and phenological traits. Competitive dominance was greatest when species were assembled based on spatial resource-acquisition traits alone.

4. In communities that were assembled based on species variation in only spatial or phenological traits greater competitive dominance was predicted by greater differences SLA and flowering initiation respectively, while greater complementarity was predicted by greater dissimilarity in leaf area and flowering senescence, respectively. Greater differences in leaf area could also be linked to greater species complementarity in communities assembled based on variation in both phenological and spatial traits, but trait dissimilarity was unrelated to competitive dominance in these communities.

5. Our results indicate that complementarity and competitive disparity among species are both driven by trait dissimilarities. However, the identity of the traits that drives the complementarity and competitive disparity depends on the trait variation among species that comprise the community. Moreover, we demonstrate that communities assembled with the greater variation in both spatial and phenological traits show the greatest complementarity among species.

Key-words biodiversity, competition, community ecology, Jena Experiment, Trait Based Experiment (TBE)

Introduction

It has long been observed that plant species mixtures are frequently more productive than the average of the respective species monocultures; often referred to as an overyielding effect (Darwin 1859; de Wit 1960; Hector et al. 1999; Tilman et al. 2001). However, the mechanisms by which diversity drives overyielding are still widely debated as species diversity-productivity relationships are highly variable (Adler et al. 2011). Furthermore, species number alone holds little information as to how species interact and function as a community to drive the overall functioning of a diverse community of species (Petchey & Gaston 2002). Thus, functional traits that reflect the species strategies for acquiring resources are considered to be a key to empirically assess, and predict, how species partition and compete for the local resource pool that drives the productivity in mixed species communities (Chesson 2000; Lavorel & Garnier 2002; Ackerly & Cornwell 2007).

Conceptual frameworks emphasizing the importance of functional traits to infer niche differences among species are based on the hypothesis that phenotypic and phylogenetically similar species have similar ecological requirements and will thus compete more strongly; coined the ‘limiting-similarity hypothesis’ (MacArthur & Levins 1967; Mayfield & Levine 2010). Under the trait-similarity hypothesis, it can be expected that greater differences among species in functional traits should reflect greater niche differentiation that allows species to avoid competition and partition the local resource pool (Westoby et al. 2002; Falster & Westoby 2003; Grime 2006; Cadotte et al. 2013; Kraft et al. 2014). For instance, resource partitioning may arise from differences in plant height, rooting patterns, and phenology that allow different species to utilize different spatial and temporal resources. Although taller or more shallow rooted plant species may have priority in acquiring particular resources, they are likely not able to completely capture all available resources due to trade-offs in optimizing certain resource capture traits over others (Westoby et al. 2002; Falster & Westoby 2003; Wright et al. 2004; Reich 2014; Dìaz et al. 2016). This provides opportunity for species with a different suite of traits optimized for capturing the resource margin, such as those species specialized in capturing understory light or resources deeper in the soil profile, to coexist and contribute to community-level resource capture and overyielding (Liira & Zobel 2000; Fargione & Tilman 2005; Aarssen et al. 2006). Greater resource use partitioning in mixed species communities is often considered as niche ‘complementarity’ that can be reflected in the greater performance of species in mixture relative to their monoculture performance (Loreau & Hector 2001; Hector et al. 2002).

However, greater differences among species in functional traits may also reflect differences in their competitive abilities to capture resources over competing neighbouring species. For instance, taller and larger plants can pre-empt light over smaller plants (Freckleton & Watkinson 2001; Falster & Westoby 2003; Weiner & Damgaard 2006; Roscher et al. 2015). Belowground, greater root-length density can provide a species with a competitive advantage in capturing more soil nutrients over neighbouring species (Casper et al. 1997; Fargione & Tilman 2006; Fort et al. 2014). Therefore, species with a particular suite of traits that are more favourable in pre-empting resource capture within a given environment, relative to neighbouring species, can result in a competitive hierarchy among species; referred to as the 'competition-trait hierarchy' hypothesis (Mayfield & Levine 2010; Kunstler et al. 2012; Kunstler et al. 2016). Plants with traits that allow them to effectively acquire the local resources that provides them with a better competitive advantage over neighbouring plant species can result in the species disproportionate contribution to the productivity in a mixed species community. The presence of a particularly productive species that drives the productivity in a community can be considered as a 'selection' effect, where the inclusion of a particularly productive species drives the community performance (Loreau 2000; Loreau & Hector 2001). Further, a 'dominance effect' can occur as part of the 'selection effect when such highly productive species drive the performance of the community at the expense of subordinate species (Fox 2005).

Although functional trait differences among species can result in potential opposing outcomes of competition under the 'limiting-similarity' and 'competition-trait hierarchy' hypotheses (Mayfield & Levine 2010), both mechanisms may influence community overyielding in diverse communities. Conveniently, overyielding in plant communities can be partitioned into the 'complementarity' effect and the 'selection' effect (Hector & Loreau 2001). Both complementarity and selection effects can operate simultaneously within a community (see Hector et al. 2002 for all potential scenarios) and sum to the overyielding of a community. Importantly, the selection effect can be further partitioned into a 'dominance' effect where particularly productive species result in reduced productivity of subordinate species, as well as a 'trait-complementarity' effect where highly productive species drive the community performance, but at no cost to subordinate species (Fox 2005). However, there is little evidence as to how functional trait dissimilarities among species relate to the complementarity, selection, and dominance effects that together determine the overyielding effect of mixed species assemblages.

Here we test the hypotheses that the assembly of species with greater functional trait dissimilarity will influence the overyielding of a community by favouring either (*i*) niche partitioning and promote a complementarity effect, or (*ii*) provide a competitive advantage over neighbouring species to promote a selection and dominance effect. However, it is conceivable that the role of plant functional trait dissimilarity among species within a community may depend upon the variation in particular functional traits of species that comprise a community. Therefore, we assess the conditionality of our hypotheses that increased trait dissimilarity among species predicts complementarity and competitive interactions by using three different pools of plant species that were known to vary in 1) spatial above- and belowground traits (pool 'S'), 2) phenological traits (pool 'P'), or 3) both spatial and phenological traits (pool 'SP'). We tested our hypotheses in experimental grassland plant communities that were designed to represent a gradient of plant species richness crossed with varying levels of pre-determined functional trait diversity levels within each of the three species pools (Ebeling et al. 2014). Such an experimental design allows us to explore the influence of spatial and temporal functional trait compositions on the underlying competitive and complementarity mechanisms that determine the overall functioning of a community.

Materials and methods

Experimental design

In order to test our hypotheses that greater trait differences among species can predict niche complementarity or competitive disparity we used 20 plant species (see Table S1 in Supporting Information) selected from the pool of 60 species that occur within the Jena Experiment (Roscher et al. 2004). These 20 plant species were selected for their variation in their phenology as well as aboveground and belowground resource-acquisition traits (Ebeling et al. 2014). Specifically, plant height, leaf area, rooting depth, and root length density were considered as traits associated with spatial resource acquisition, while the date of growth and flowering initiation were considered as phenological traits. Based on these traits, plant species were grouped into three partially overlapping pools of species that vary in trait dissimilarities from being highly similar to highly dissimilar (see Ebeling et al. 2014 for details). In brief, species trait variation was assessed by PCA, where the PCA axis 1 separated species based upon their above-belowground spatial resource use traits, while PCA axis 2 separated species based on phenological traits (see Fig. S1). Species in pool ‘S’ species were selected based on variation in above- and belowground spatial traits (i.e. selected across a range of small to large differences along the PCA axis 1). Species in pool ‘P’ were selected based on variation in phenology (i.e. selected across a range of small to large differences along the PCA axis 2). Pool ‘SP’ consisted of species that were selected for their variation in both spatial and phenological traits. Each pool consisted of eight species with different combinations of grasses, tall forbs, and small forbs according to the functional group classification of the Jena Experiment (Roscher et al. 2004). Four of the 20 species occur in two species pools (see Table S1). Further details on the selection of species are described in detail in Ebeling et al. (2014)

The experimental plant communities were sown into 138 plots within the Jena Experiment field site located near Jena, Germany (50° 57’ 3” N, 11° 37’ 35” E, 130 m a.s.l.). Initial sowing took place in autumn 2010 and re-sown in summer 2011 ensure a successful establishment of the plant communities and all sown plant species were observed to be present in the plots during data collection in 2012. Plots were 3.5 × 3.5 m in size and arranged in three spatial blocks to account for edaphic factors along the Saale River. Plant communities were sown in plots with a species richness of 1, 2, 3, 4, or 8 plant species from a given species pool, and the species combinations in each plot covered a range of functional trait dissimilarities (Ebeling et al. 2014). Species were sown in equal proportions with a total density of 1000 germinable seeds per m^{-2} based on laboratory germination rates, such that the expected initial number of individuals per species would be relatively equivalent. In 2011 and 2012, plots were weeded in summer (July) and autumn (October), as well as in early spring (March) 2012, in order to maintain the sown plant community composition. Biomass harvest occurred in 2012 in spring (late May) and was harvested again in summer (late August). The biomass of each plot was harvested by cutting all plants approximately 3 cm above the soil surface within two randomly allocated 0.1 m^2 subplots within each plot, which is typical in long-term plant biodiversity experiments with large plot size (Tilman et al. 1997; Hector et al. 1999; Tilman et al. 2001; Roscher et al. 2004; Marquard et al. 2009; Roscher et al. 2011). Following each harvest, the plots were mown to a height of 5 cm as is typical for managed hay meadows in the region. Harvested plant material was then sorted to species. Biomass of species that were not initially sown into the plots was pooled together as weed biomass. All plant material was dried at 70°C for 48 h and subsequently weighed to quantify the biomass of individual sown plant species and weed biomass. The spring and summer biomass measurements of each species were summed to obtain the annual productivity.

Species traits

In 2012, we collected trait data on the 20 plant species. Traits were measured in the species monocultures of the same year in which the biomass data was collected so that the measured trait values for each species coincides with the observed biomass production of each species. We measured flowering initiation and cessation as phenological traits that reflect the seasonal timing in resource capture as well as above- and belowground traits that reflect differences in how resources are captured spatially (Table 1). Flowering initiation was quantified as the week of the year in which the first flowers of a species appeared. Flowering cessation is the week of the year in which all flowers of the species have senesced. The maximum canopy height was measured just prior to harvesting biomass by averaging five canopy height measurements along a transect across the plot. Leaf characteristics were measured by sampling a total of 5-12 fully developed leaves from different individuals. Leaves were stored in moist paper in sealed plastic bags at 4°C overnight for rehydration and then blotted dry to remove any surface water. Leaf fresh weight was then measured, and the leaf surface area was measured with a portable Leaf Area Meter (LI-3100, LICOR, Lincoln, USA). Afterwards, leaf samples were dried at 70°C (48 h), and dry weights were recorded. Specific leaf area (SLA) was calculated as the ratio of leaf area to dry weight (mm^2 mg^{-1}), and leaf dry matter content (LDMC) is the ratio of dry weight to fresh weight (mg g^{-1}). Leaf area (cm^2) was calculated as the average of the sampled leaves.

Root traits were determined by taking eight soil cores (4 cm in diameter and 40 cm in depth) that were sectioned into depths of 0-5, 5-10, 10-20 cm, 20-30, and 30-40 cm (Ravenek et al. 2014). Sections were pooled by depths per plot and washed clean of soil and roots less than 2 mm diameter were stored in 70% EtOH. A subsample of roots was stained with neutral red mixed in 70% EtOH overnight and the root length was determined by scanning stained roots (600 dpi, Epson Expression 10000 XL scanner, Regent Instruments, Quebec, Canada) using WinRhizo software (Regent Instruments; manual pixel classification: 225). All root samples were then dried at 65°C for at least 48 h and weighed. Specific root length (SRL) was calculated as the ratio of root length to dry mass of the subsample (mm^2 mg^{-1}). Mean rooting depth (MRD) was calculated for each plot as the weighted mean of root mass per layer. Root mass density (RMD) was calculated from root mass per cm^3 of soil and averaged for each layer. Root length density (RLD) was calculated as the root mass per root length (mg cm^{-1}) and averaged for each layer. Due to the time and resource constraints on sampling and processing required to quantify root traits, root traits were only measured in the monocultures of species pools ‘S’ and ‘P’.

Community level indices

In order to test for community wide complementarity and competitive disparity among species we calculated the complementarity and selection effects were calculated following Loreau & Hector (2001) using the annual biomass production of the species. Specifically, we first calculated species relative yields (RY); which is the observed biomass of species in a mixture (O) divided by the species monoculture (M) such that $RY = O/M$ (de Wit 1960). The complementarity effect is calculated as $N\overline{\Delta RY}\,\overline{M}$, where N is the number of species in the mixture, ΔRY is the difference in the RY of a species from its expected relative yield ($1/N$) and M is the monoculture biomass. The complementarity effect is positive when species perform better than expected in the mixture on average and negative when performing poorly in mixture. The selection effect is calculated as $N\mathrm{cov}(\Delta RY, M)$ and is positive when highly productive species in monoculture are also highly productive in mixtures and negative when highly productive species contribute less than expected in the mixture. To better assess competitive disparity within the communities we further partitioned the selection effect into the dominance effect, calculated as $N\mathrm{cov}(M, RY/\Sigma RY - 1/N)$ and the trait-complementarity effect, calculated as $N\mathrm{cov}(RY - RY/\Sigma RY, M)$, following Fox (2005). The dominance effect is positive when highly productive species dominate the mixture at the expense of less productive species and negative when less productive species dominate the mixture at the expense of more productive species. The trait-complementarity effect is positive when highly productive species drive the productivity of the mixture, but not at the expense of less productive species and negative when less productive species drive the productivity of the mixture, but with no negative effect on the more productive species.

The ten plant traits were standardized ($\mu = 0$, $\sigma = 1$) and used to calculate Rao's quadratic entropy (*RaoQ*, un-weighted by species abundance) as an index of functional trait dissimilarity. We used *RaoQ* since it was also used in the initial experimental design (Ebeling et al. 2014), and it is highly similar to functional trait dispersion '*FDis*' (Laliberté & Legendre 2010; Clark et al. 2012). *RaoQ* was calculated separately for each species pool using all 10 traits, or only phenology, aboveground or belowground traits separately in order to identify the effect of the different suite of traits (aboveground, belowground or phenology). The *RaoQ* using all 10 traits was standardized (mean = 0, SD = 1) by species pool since not all traits were measured in pool 'SP' (i.e. no belowground traits measured). The mean pairwise difference (MPD) in individual traits was also calculated in order to assess the importance of the difference among species in individual traits.

Data analyses

All data processing and analyses were carried out using R version 3.02 (R Core Team, 2014). We first tested for overall effects of species pool, sown plant species richness, and the overall trait dissimilarity on the productivity of the communities, by ANOVA with species pool, richness, trait dissimilarity (*RaoQ* using all traits), and the interactions between pool with richness and trait dissimilarity as main terms. Block was included as a covariate. A contrast term testing for differences between the productivity of mixtures and monocultures (overyielding effect) and its interaction with species pool was also included. To test the hypothesis that greater trait dissimilarity can predict complementarity and competitive disparities we assessed the overyielding, complementarity, selection, dominance, and trait-complementarity effects as above, but omitting the contrast between monocultures and mixtures (since effects are only calculated in mixtures). Secondly, we independently assessed the effect of dissimilarity in phenological, aboveground, and belowground traits among species by substituting the trait dissimilarity (all traits) term in the above ANOVAs with the trait dissimilarity in only phenological, aboveground, or belowground traits. Finally, individual functional trait differences (calculated as MPD) were then assessed for their ability to predict complementarity, selection, dominance, and trait-complementarity effects by first standardizing ($\mu = 0$, $\sigma = 1$) all dependent variables (complementarity, selection, dominance, and trait-complementarity) and independent variables (all MPD indices) so that parameter estimates were comparable on a common scale. The standardized data were then used in lasso regression (Least Absolute Shrinkage and Selection Operator) for generalized linear model selection with penalized maximum likelihood (Tibshirani 1996, Friedman et al. 2010). The shrinkage parameter (λ) was determined using 10-fold cross-validation to obtain a λ that provided the minimum mean squared error using the function ‘cv.glmnet’ in the R package ‘glmnet’. Terms with non-zero coefficients were then included in a single linear multiple regression model.

Results

Relationships between species richness, trait dissimilarity and productivity

We found that the species pool had the strongest effect on the overall productivity, where species pool ‘SP’ (species varying in both spatial and phenological traits) was significantly less productive than pools ‘S’ (species varying more in spatial traits) and ‘P’ (species varying more in phenological traits) (Fig. 1a, $F_{2,\,124} = 12.93$, $P < 0.001$, Table S2). Species richness had little overall effect on the net productivity of the communities (Fig. 1a, $F_{1,\,124} = 0.37$, $P = 0.542$) and showed no interaction with species pool ($F_{2,\,124} = 0.22$, $P = 0.806$, Table S2). There was an overall overyielding effect (mixed species communities performing better than the monoculture average, $F_{2,\,124} = 4.70$, $P = 0.032$, Table S2), which did not differ significantly among species pools ($F_{2,\,124} = 1.57$, $P = 0.212$). Moreover, we found productivity to be positively related to greater trait dissimilarity depending on the species pool (Fig. 1b, $F_{2,\,124} = 3.86$, $P = 0.024$, Table S2), where the trait dissimilarity-productivity relationship was only significant in species pool ‘SP’.

Effects of trait dissimilarity on overyielding, complementarity and selection effects

Overyielding, complementarity and the selection effects were not significantly related to plant species richness (overyielding: $F_{1,\,103} = 0.69$, $P = 0.408$, complementarity: $F_{1,\,103} = 0.50$, $P = 0.482$, selection: $F_{1,\,103} = 0.13$, $P = 0.718$, see Table S3). However, both overyielding and complementarity were influenced by greater overall trait dissimilarity depending on the species pool (overyielding: $F_{2,\,103} = 4.83$, $P = 0.010$, complementarity: $F_{1,\,103} = 5.11$, $P = 0.008$). More specifically, we found the complementarity effect in species pool ‘P’, declined with greater dissimilarity in phenological traits (Fig. 2a). However, complementarity was not related to phenological dissimilarity in species pools ‘S’ and ‘SP’, resulting in a marginal interaction between species pool and phenological trait dissimilarity ($F_{1,\,103} = 2.80$, $P = 0.066$, Table S3). Greater dissimilarity in phenological traits had little effect on overyielding in all three species pools (Fig. 2a, Table S3). The selection effect was also unrelated to phenological dissimilarity among species in each of the three species pools (Fig. 2a).

Greater dissimilarity in aboveground traits had the strongest effect on increasing overyielding and the selection effect in species pool ‘S’ (Fig. 2b). However, these relationships did not differ significantly from the same relationships in the other two species pools (overyielding: $F_{1, 103} = 1.88$, $P = 0.158$, selection: $F_{1, 103} = 1.57$, $P = 0.212$, Table S3). Increasing aboveground trait dissimilarity in pool ‘S’ was not to complementarity, indicating that the positive effect of aboveground trait dissimilarity on overyielding was due to an increased selection effect (Fig. 1b). Aboveground trait dissimilarity had no effect on the overyielding, complementarity and selection effects in species pool ‘P’. However, in species pool ‘SP’, both complementarity and overyielding increased with greater dissimilarity among species in aboveground traits, but not the selection effect (Fig. 1b), illustrating that the overyielding in species pool ‘SP’ was driven by a complementarity effect. The strong effect of aboveground trait dissimilarity on the complementarity effect in these communities (pool ‘SP’) resulted in a significant interaction effect between species pool and aboveground trait dissimilarity ($F_{1, 103} = 3.87$, $P = 0.024$, Table S3). The dissimilarity in belowground traits had little overall effect on the overyielding, complementarity and selection effects (Fig. 2c, Table S3). Overall, the species pool had the strongest effect on the overyielding, complementarity and selection effects (Fig. 2d, Table S3). Overyielding and the complementarity effect were lowest in species pool ‘S’ followed by species pool ‘P’ and were greatest in species pool ‘SP’. Conversely, the selection effect was greatest in species pool ‘S’ and lowest in species pool ‘SP’ (Fig. 2d).

Effects of trait dissimilarity on the dominance effect

By partitioning the selection effect into the “trait-complementarity” and “dominance” effect (Fox 2005), we found that both the dominance and trait-complementarity effects were greater in species pool ‘S’ and ‘P’ than in species pool ‘SP’, as observed in the selection effect (Fig. 3, Table S4, and see Fig. S2). However, the trait-complementarity effect was unrelated to phenological, aboveground or belowground trait dissimilarity (Table S4). The dominance effect was only significantly and positively related to the aboveground trait dissimilarity in species pool ‘S’ resulting in a significant species pool by aboveground trait dissimilarity interaction effect (Fig. 3, $F_{1,\,103} = 7.91$, $P = 0.001$, Table S3).

Identifying effects of specific trait differences

Of the specific trait dissimilarities among species, we found greater dissimilarities in SLA could best predict both the selection and dominance effects in species pool ‘S’ (Fig. 4a). Additionally, we found that greater differences in leaf area best predicted greater complementarity in pool ‘S’ (Fig. 4a). In pool ‘P’ the selection and dominance effects were predicted by greater flowering initiation, while a lower species complementarity was predicted by greater dissimilarity in flowering senescence (Fig. 4b). The selection and dominance effects in communities from pool ‘SP’ were poorly predicted by the dissimilarity in all traits, but greater differences in leaf area best predicted greater species complementarity (Fig. 4c).

Discussion

Here we experimentally manipulated species functional trait dissimilarities to assess the role of species diversity and functional trait dissimilarities in predicting species complementarity and competitive disparities. Overall, we found that the pool from which species were assembled had the strongest influence on productivity, overyielding, and its underlying complementarity and competitive dominance effects. Specifically, the assembly of species chosen for the greatest variation in both spatial and temporal resource acquisition traits (species pool ‘SP’) resulted in the greatest complementarity, which the drove overyielding in these communities. This shows that the assembly of communities composed of species that vary in both temporal and spatial resource acquisition traits can predict greater overyielding through greater complementarity, providing support for the competition-trait similarity hypothesis (*i*). However, our results also reveal that the assembly of species based on variation in only spatial traits resulted in the community overyielding to be driven by greater competitive dominance. This provides support for the second hypotheses (*ii*) that greater functional differences among competitors lead to competitive disparity. These results parallel findings that a greater difference in functional traits between competitors can result in a 'competition-trait hierarchy' (Freckleton & Watkinson 2001; Kunstler et al. 2012; Fort et al. 2014; Kunstler et al. 2016). Overall, our study demonstrates that competitive disparity among species can occur through spatial or temporal resource pre-emption when species vary most in spatial or temporal resource capture traits respectively (e.g. species pools 'S' and 'P'), but also that species complementarity is best predicted when species vary more greatly in both temporal and spatial traits (e.g. species pool 'SP').

Effects of trait differences on species complementarity

The strong effect of the species pool in our study suggests that niche complementarity may be best predicted by greater differences in phenology in combination with greater differences in spatial resource acquisition, compared to only considering variation in spatial or phenological resource acquisition strategies alone. The finding that the combination of both spatial and temporal niche segregation, as reflected in species functional trait differences, together play a key role in species resource use complementarity is supported by previous findings that interactions among plant species are temporally dynamic (Connolly et al. 1990; McKane et al. 1990; Fargione & Tilman 2005).

The assessment of individual trait differences revealed that greater differences in leaf area could best predict greater complementarity within species pools ‘S’ and ‘SP’, where the species spatial resources acquisition traits were varied. The link between larger leaf area differences and a greater complementarity effect is likely reflective of differences among species in light absorption strategies, such as investing differently in fewer larger leaves versus more numerous smaller leaves (Milla & Reich 2007; Whitman & Aarssen 2010). For instance, in our species pool ‘SP’, where complementarity was greatest and best predicted by leaf area differences, was composed mostly of small and tall forbs. Thus, the positive complementarity effect that drove overyielding in these communities may reflect that these two growth forms are adapted in leaf production strategies to minimize competition in light absorption as reflected in their differences in leaf area (Falster & Westoby 2003; Aarssen et al. 2006; Whitman & Aarssen 2010; Reich 2014). Such differences in leaf production strategies are thought to be a key mechanism by which plant species coexist and avoid competition (Aarssen et al. 2006; Wacker et al. 2009, Whitman & Aarssen 2010). Although not measured, root traits in our species pool ‘SP’ may have provided further information as to the increase in complementarity in these communities. However, since rooting traits had no apparent influence in species pools ‘S’ and ‘P’ it also likely had little effect in pool ‘SP’. Additionally, it has been observed that rooting traits may not always relate to aboveground productivity during initial community establishment, but may become important in time as the communities establish (Mommer et al. 2010; Ravenek et al. 2014).

It should be considered that since the complementarity effect in our study is the measure of average species performances in mixtures relative to their monocultures, intraspecific density dependence mechanisms might have also governed community productivity and complementarity aside from interspecific differences in resource acquisition traits (Schöb et al. 2015). Negative density-dependence in plants can result from the increase in plant species-specific pathogens, herbivores, and the depletion of key soil resources required by the species (Maron et al. 2011; Kulmatiski et al. 2012). These negative density-dependence mechanisms could potentially explain the positive species complementarity we observed that would not be captured by interspecific trait differences quantified in our study.

Effects of trait differences on competitive disparity

The similar increase in the selection and dominance effect with greater trait differences, such as in species pool 'S' with SLA and in species pool 'P' with flowering initiation, reveals that the selection effect in these communities was due to a dominance effect (where the presence of species that are particularly productive in monoculture drive the community productivity in mixtures at the expense of the less productive species). This result is supported by previous work that indicates the importance of size asymmetry in shaping competition and composition in plant communities (Weiner 1990; Freckleton & Watkinson 2001; DeMalach et al. 2016). Greater SLA values are known to be associated with increased photosynthesis, nutrient uptake, and rapid growth that consequently provides the species with a competitive advantage in productive systems (Poorter & Remkes 1990; van der Werf et al. 1993; Knops & Reinhart 2000; Fargione & Tilman 2002). In our study, this indicates that the greater differences in SLA among species that drove the competitive dominance effect in species pool 'S' favoured larger, faster growing species. We also observed a positive effect of greater dissimilarity in the timing of flowering initiation in our species pool 'P' (assembled for variation in phenological traits) on the dominance effect and a negative relationship between complementarity and dissimilarity in flowering senescence. These results may reflect that greater temporal resource pre-emption can favour the earlier developing plant species.

Although larger and faster growing species may hold a competitive advantage during early stages of community establishment, during later stages in more established communities, competition may favour slower-growing species (van der Werf et al. 1993). For instance, it is often observed that species complementarity increases, and selection or dominance effects decrease, as plant communities develop and undergo compositional re-assembly (Tilman et al. 2001; Marquard et al. 2009; Reich et al. 2012). Therefore, our trait dissimilarity-driven dominance parallels the concept that communities initially sown with high functional trait variation can result in competitive disparity among species during the early stages of community establishment that shifts the proportional abundances of species in favour of more productive species (Loreau 2000). The increasing dominance effect in our plant communities at higher trait dissimilarity may be best reflective of greater community-wide competition aboveground following the initial assembly of the communities; which is in line with the first years of many longer running biodiversity experiments (Tilman et al. 2001; Marquard et al. 2009; Roscher et al. 2011; Reich et al. 2012; Ravenek et al. 2014). However, it should also be noted that the same suits of traits did not predict the dominance effect and complementarity across the three species pools in our study, reflecting the importance of the differences in the trait variation among species within pools. Therefore, the way in which particular assemblages of species may compete can depend upon the trait variation among the larger pool of species from which it originates.

Conclusion

Our results provide evidence that species with greater differences in both spatial and temporal resource acquisition strategies can result in greater complementarity (i.e. tall versus small forbs in our pool ‘SP’). However, our study also demonstrates that the assembly of plant species in an experimental functional trait diversity gradient can result in greater competitive disparity during early establishment of the community, likely through greater spatial and temporal resource pre-emption as evidenced in our species pools ‘S’ and ‘P’. These results parallel a slowly growing literature base that demonstrates greater functional trait dissimilarities among species does not always relate to species complementarity and reduced resource competition (Cahill et al. 2008; Mommer et al. 2010; Kunstler et al. 2012; Fort et al. 2014). In our study, the increase in the competitive disparity among species with greater SLA in communities assembled with greater variation in spatial resource capture traits, and flowering initiation in communities assembled with greater variation in phenological traits, indicates the competitive advantage of larger and faster-growing species following initial assembly and early establishment in productive landscapes (Poorter & Remkes 1990; van der Werf et al. 1993; Knops & Reinhart 2000; Fargione & Tilman 2002). Overall our study provides empirical insights as to how functionally dissimilar species establish and compete to shape community composition in a novel environment in support of previous conceptual and empirical studies on how plant traits may predict community assembly processes and functioning (Loreau 2000; Grime 2006; Mayfield & Levine 2010; HilleRisLambers et al. 2012). If competitive disparity begets functional complementarity in the temporal assembly process of species compositions, tracking the temporal change in the link between functional dissimilarities and community level performance will be of key importance. Such empirical observations are required to gain a better mechanistic and predictive understanding of ecological linkages among functional traits, stable competition-coexistence mechanisms, and the multi-functionality of diversity.

Authors' Contributions

WW, BS, HH, NE, AE and CR designed the experiment. AE, CR, JR, DB, LM and NB collected and contributed the data. CW analyzed the data and wrote the manuscript with

contributions from all authors to produce the final manuscript.

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Data Accessibility

Data are available at: https://doi.pangaea.de/10.1594/PANGAEA.876731

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Tables

Table 1. List of traits that were measured on the species in their monocultures with abbreviations in parentheses and their measured units

Trait	Trait type	Units
1. Flowering initiation (F. init)	Phenological	week of year
2. Flowering senescence (F. sene)	Phenological	week of year
3. Specific leaf area (SLA)	Aboveground	mm^2/mg
4. Leaf dry matter content (LDMC)	Aboveground	mg/g
5. Leaf area (L. area)	Aboveground	cm^2
6. Maximum canopy height (Height)	Aboveground	cm
7. Mean Rooting Depth (MRD) †	Belowground	cm
8. Root Mass Density (RMD) †	Belowground	mg/cm^3
9. Specific Root Length (SRL) †	Belowground	mm/mg
10. Root Length Density (RLD) †	Belowground	mg/cm

† Traits only quantified in species pool ‘S’ and ‘P’ (see Methods)

Figures

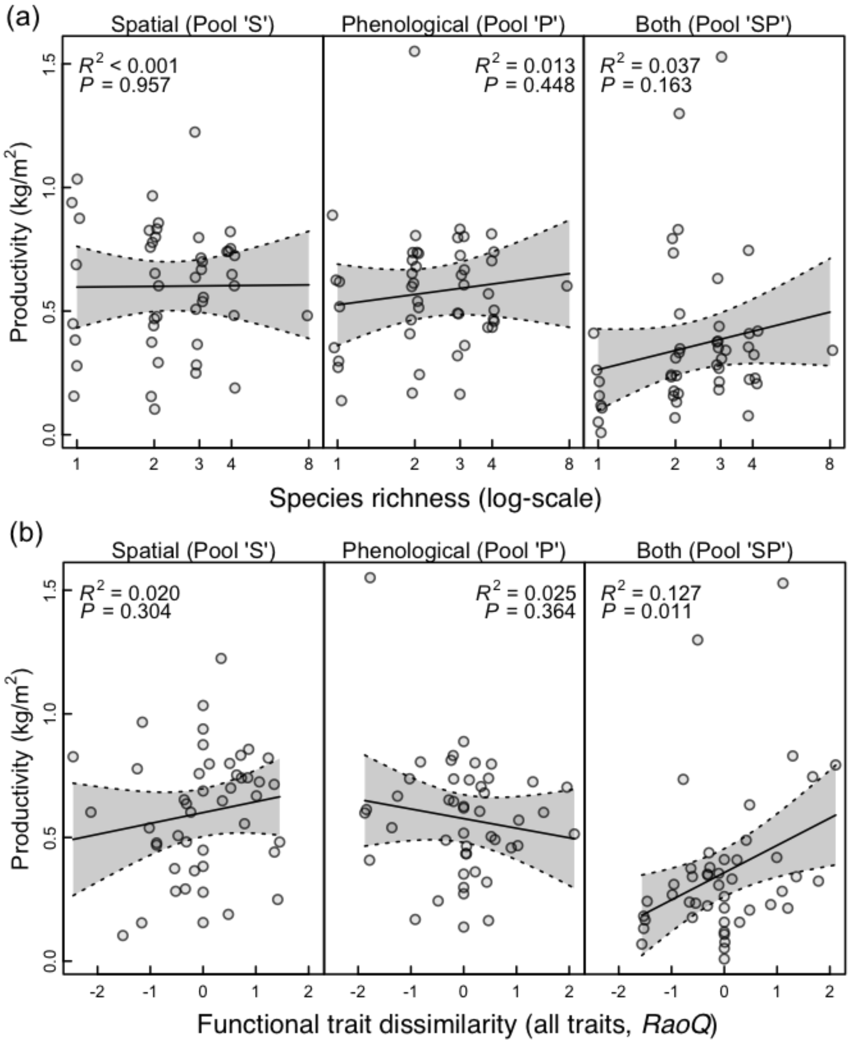

Figure 1. The relationship between the productivity in each plant species pool and (a) the sown species richness and (b) the overall functional trait dissimilarity (standardized by pool, see methods). Fit statistics (R^2 and P-values) are indicated for each. Solid lines indicate regression relationships, and the grey shaded region is the 95% confidence band for the relationship.

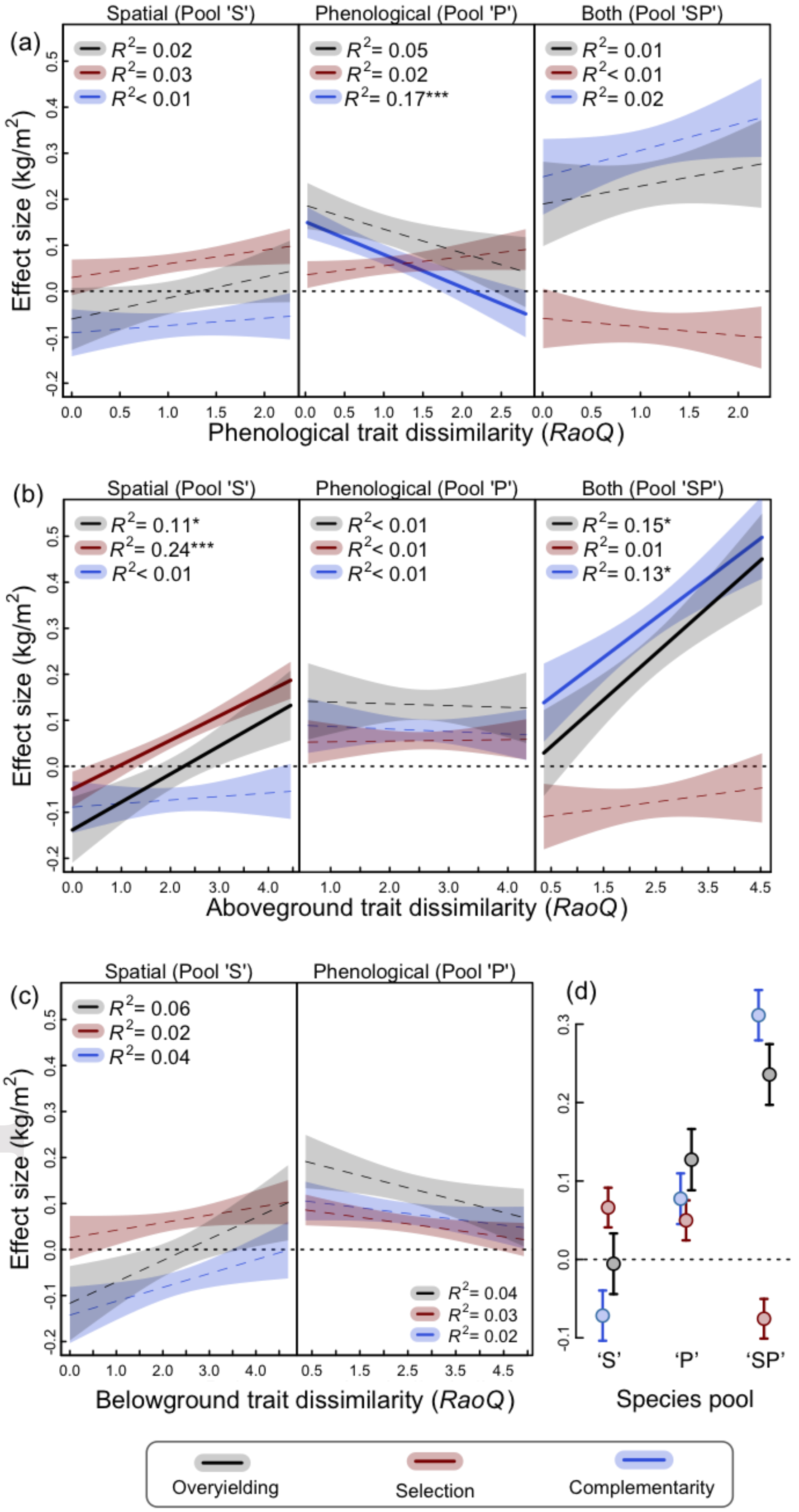

Figure 2. Relationships between the overyielding in species mixtures and the complementarity and selection effects with the variation in (a) phenological traits, (b) aboveground traits and (c) belowground traits (only measured in pool 'S' and 'P'). Solid lines

indicate the regression relationships and shaded regions indicate the standard error around the relationship. Fit statistics (R^2 and associated significance: *$P < 0.05$, ***$P < 0.001$) are indicated for each. Relationships are shown for each species pool (shown in the panels from left to right). The overall mean overyielding, selection and complementarity effects for each species pool are shown in (d) with standard errors. Note the complementarity and selection effects sum to the overyielding effect where greater overlap between overyielding with the selection or complementarity effect indicates the greater the contribution of the selection or complementarity effect to the overyielding of the community.

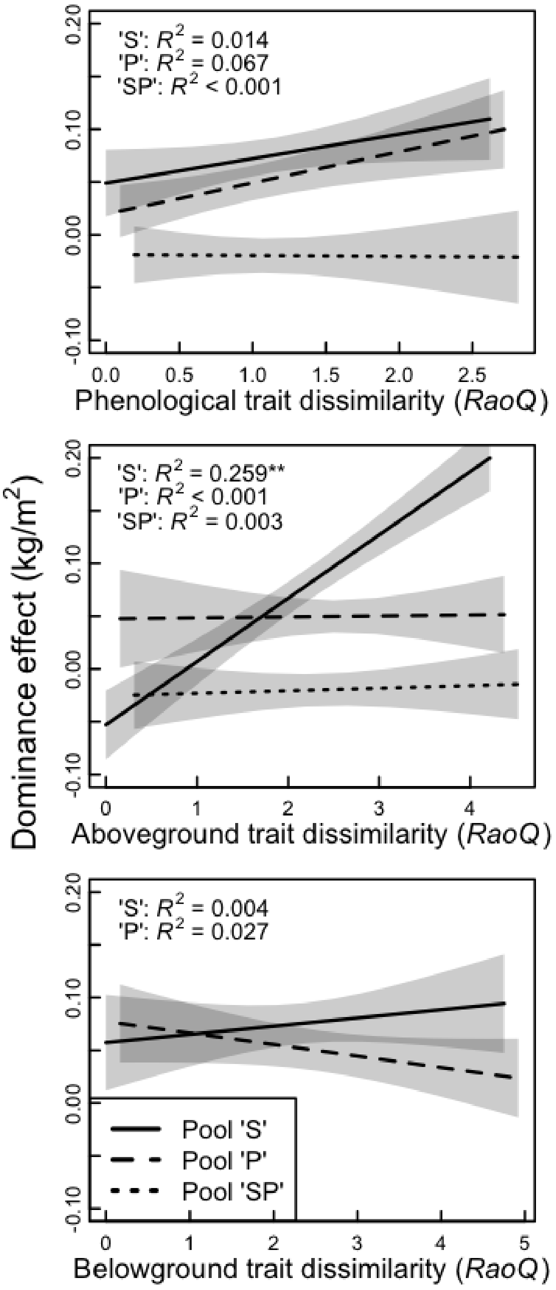

Figure 3. Relationships between the dominance effect and dissimilarity in phenological traits, aboveground traits and belowground traits are shown for each species pool (indicated by different regression lines). Lines indicate regression relationships and the grey shaded regions are the standard errors for the regression fit. The fit statistics (R^2) are provided for each (**$P > 0.01$).

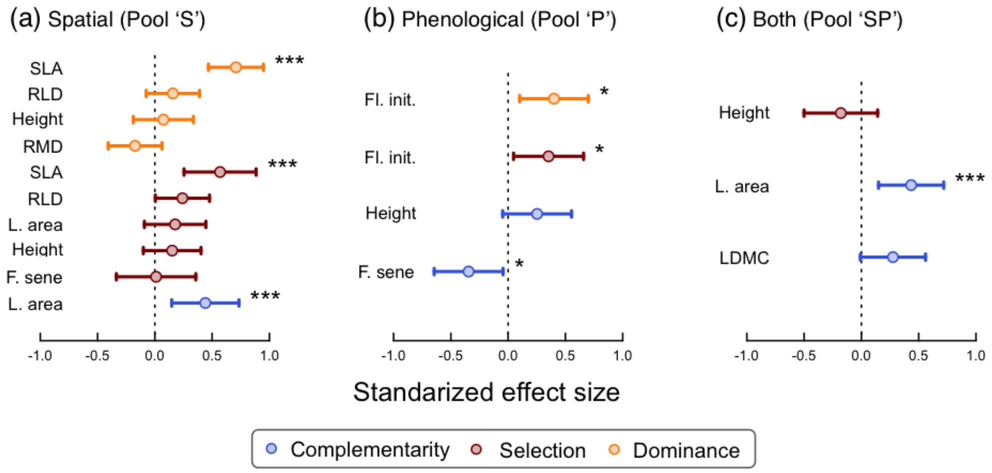

Figure 4. Standardized effects of the MPD in individual plant functional traits (see Table 1 for trait abbreviations) on the complementarity effect, selection effect, and the dominance effect. Error bars are 95% confidence intervals for a difference from 0 (no effect). Significance is indicated by: **P* < 0.05, ****P* < 0.001. See Figures S3 for all regression results.