

Complementarity in both plant and mycorrhizal fungal communities are not necessarily increased by diversity in the other

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Summary

1. Higher species diversity can improve community performance within a species guild when different species complement each other in their use of the available niche, such as through resource partitioning. However, species in one guild of organisms may act as resources for another such that the diversity in one guild alters the realized niche for species in another. Yet, it remains largely untested as to whether diversity in one guild of organisms influences species complementarity in another.

2. The productivity and diversity in plant and arbuscular mycorrhizal (AM) fungal communities can be positively associated with each other through their typically mutualistic exchange of resources. Here, we utilized these two interacting species guilds to determine whether greater diversity in one influences species complementarity in the other. This was performed by creating monocultures and a mixture of a grass, forb and legume in a full factorial design with monocultures and a mixture of four AM fungi.

3. The presence of AM fungi reduced differences in the performance among plant species and greater diversity of fungi generally improved plant productivity over the average of the fungal monocultures. However, plant species complementarity was not greatest with a higher diversity of fungi and was only positive with a particular fungal monoculture.

4. AM fungal abundance was not affected by plant diversity, but was greatly reduced in the grass monoculture compared to the other plant communities. Variation in fungal complementarity among plant communities was low overall and was little influenced by plant diversity.

5. *Synthesis.* Using a model plant-mycorrhizal system, our results suggest that the composition rather than the diversity of species within one guild may be more influential in determining how species function within an associated species guild. However, our model system does not represent a broad gradient of diversity in either plant or fungal communities and only assesses the initial growth phase. Nonetheless, our results highlight that changes in species compositions in one species guild can affect the functioning of species diversity in another.

Key-words: community ecology, horizontal biodiversity effects, mutualisms, plant–soil (below-ground) interactions, vertical biodiversity effects

Introduction

The role of biodiversity has been a focal point in ecology over the past few decades as the loss of species within an

ecosystem can adversely affect the ability of the ecosystem to maintain its functioning (Zavaleta *et al.* 2010; Cardinale *et al.* 2012; Hooper *et al.* 2012; Wagg *et al.* 2014). A positive biodiversity–ecosystem functioning relationship has been shown in numerous studies demonstrating that greater species diversity can enhance the overall community performance,

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particularly in plant communities (Balvanera *et al.* 2006; Cardinale *et al.* 2006). Such effects have also been demonstrated in various groups of organisms including bacteria (Bell *et al.* 2005; Gravel *et al.* 2011), plant symbiotic fungi (van der Heijden *et al.* 1998; Wagg *et al.* 2011a) and soil decomposers (Eisenhauer, Reich & Isbell 2012).

The relationship between species diversity, or greater species richness, and ecosystem functioning, such as net primary productivity, can be attributed to dissimilarities among species in their exploitation of the biotope (Tilman *et al.* 1997; Dimitrakopoulos & Schmid 2004; Hooper *et al.* 2005; Turnbull *et al.* 2013). Greater species diversity may increase productivity when species in more diverse communities enhance the overall resource capture of the community through niche differentiation and facilitation. For instance, including species that differ in resource acquisition strategies in more species rich communities may reduce niche overlap thereby relaxing competition and improving performance of the plant community (Tilman *et al.* 1997; Turnbull *et al.* 2013). This is commonly termed as species complementarity (Loreau & Hector 2001; Hector, Loreau & Schmid 2002). On the other hand, increasing species diversity may also increase the probability of including species that are particularly productive and competitive for resources in plant mixtures. This can result in the so-called selection effect when the higher productivity in species mixtures results from the inclusion of particularly productive species that drives the productivity of the plant mixture (Loreau & Hector 2001; Hector, Loreau & Schmid 2002). Both complementarity and selection effects can lead to a greater productivity in a plant species mixtures and when summed together represent the net biodiversity effect, which is the difference of the performance of species mixtures from the average performance of the respective species in monocultures.

As biodiversity effects can be dependent upon resource acquisition abilities of individual species, factors that alter the ability of species to acquire resources may determine whether a more diverse community functions via a complementarity or selection effect. For instance, increased biotope space below-ground (e.g. increasing available rooting space) or increasing resource heterogeneity can result in a more positive effect of biodiversity on ecosystem functioning that is driven by a complementarity effect (Dimitrakopoulos & Schmid 2004; Wacker *et al.* 2008; Jousset *et al.* 2011; Wagg *et al.* 2011a). Conversely, in situations where the ability of species to differentially acquire resources is low, such as in a limiting and homogenous resource environment, increasing the number of species may consequently lead to a lower complementarity effect and/or a greater selection effect (Wagg *et al.* 2011a; Becker *et al.* 2012).

Although it is well documented that manipulating the number of species within a community will alter the functioning of that community (horizontal diversity effects), it is less understood how changes in species diversity in one guild of organisms affect the functioning of diversity in another (vertical diversity effects) (Duffy *et al.* 2007). Understanding the effect of greater diversity between guilds of organisms

(vertical diversity) on the functioning of an ecosystem has been recognized as a key issue for identifying underlying mechanisms that affect ecosystem performance. This is because the presence and diversity of species within one guild of organisms can act as resources and construct niches for other guilds of organisms. Therefore, changes in species diversity in one guild of organisms can have cascading effects across multiple guilds of organisms (McCann 2000; Silvertown 2004; Duffy *et al.* 2007; Estes *et al.* 2011; Eisenhauer 2012).

The functioning of diverse plant communities can be influenced by the presence and diversity of below-ground organisms, such as pathogens, decomposers and mutualists, that affect resource acquisition abilities in plants and alter plant–plant competition (Klironomos *et al.* 2000; Silvertown 2004; Maron *et al.* 2011; Schnitzer *et al.* 2011; Wagg *et al.* 2011a, 2014; Eisenhauer, Reich & Isbell 2012). Specifically, several studies have shown that a widespread group of plant symbionts, the arbuscular mycorrhizal (AM) fungi, contribute to greater productivity and diversity in grassland communities by providing plants greater access to soil resources (Smith & Read 2008; van der Heijden *et al.* 2015). AM fungi vary in attributes by which they provide a benefit to plant hosts, from their influence on plant host pathogen defence to the acquisition of various soil resources (Newsham, Fitter & Watkinson 1995; Jansa, Mozafar & Frossard 2005; Powell *et al.* 2009; Thonar *et al.* 2011). Therefore, a more diverse AM fungal community may improve plant productivity by providing a variety of benefits to the host plants, such as by providing plants access to different soil resource pools (Koide 2000; Jansa, Mozafar & Frossard 2005; Thonar *et al.* 2011; Fig. 1a, b). In addition, a greater diversity in plant–AM fungal interactions may allow for differential resource capture among plant species (e.g. Wagg *et al.* 2011b; Fig. 1c,d). Therefore, AM fungal diversity holds the potential to influence whether plant communities exhibit a complementarity or selection effect by expanding the plant available resource pool and mediating resource partitioning among plants below-ground (Silvertown 2004; Eisenhauer 2012; and see Fig. 1). However, plant species also vary in the degree to which they benefit from associating with various AM fungi (Klironomos 2003). Resultantly, certain AM fungi may allow particular plant species greater access to soil resources than others and alter competitive interactions among plant species (Fitter 1977; Urcelay & Díaz 2003; Scheublin, van Logtestijn & van der Heijden 2007; Collins & Foster 2009).

At the same time, plant species can construct niches for soil organisms and thereby alter the composition of soil biota (Bever *et al.* 1996; De Deyn *et al.* 2004; Bezemer *et al.* 2010; De Deyn, Quirk & Bardgett 2011; van der Putten 2012). For instance, individual plant species influence the community structure of AM fungi in their rhizosphere such that different AM fungi show preference for different plant hosts (Eom, Hartnett & Wilson 2000; Bever 2002; Burrows & Pfleger 2002; Johnson *et al.* 2003; Vandenkoornhuyse *et al.* 2003; Croll *et al.* 2008). Thus, greater diversity in plant hosts could potentially allow for

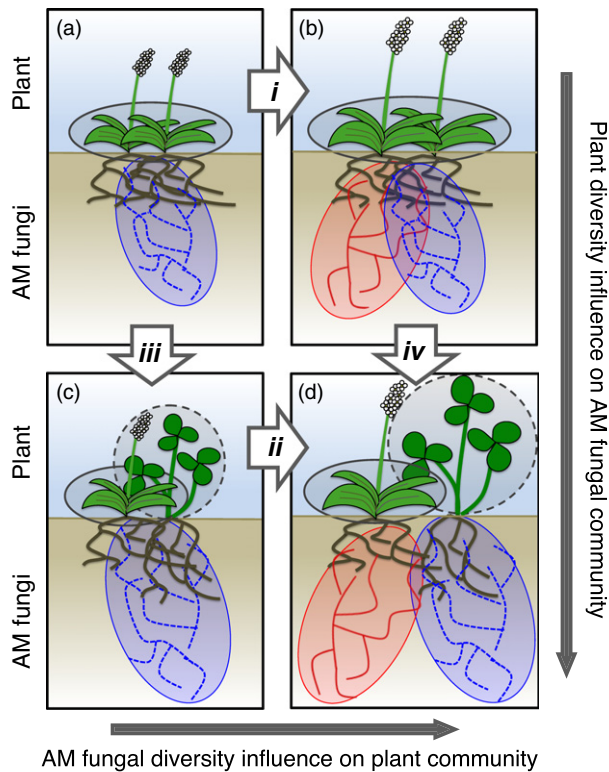


Fig. 1. Depiction of four hypothetical plant and arbuscular mycorrhizal (AM) fungal communities with differing levels of plant and AM fungal diversity. Panels (a) and (b) represent a low plant diversity, while (c) and (d) represent high plant diversity. Panels (a) and (c) represent low AM fungal diversity, while (b) and (d) represent high AM fungal diversity. The niche space occupied by each plant is indicated by the solid and dashed outlined grey ellipses, and the niche space occupied by each AM fungus is represented by the blue and red shaded ellipses to illustrate the hypotheses that (i) greater AM fungal diversity utilizes more of the below-ground niche and resultantly improves plant productivity, (ii) greater AM fungal diversity reduces niche overlap among inter-specific plants by expanding the available below-ground resource niche and allowing for greater resource partitioning, (iii) greater plant diversity expands the available niche for AM fungi below-ground allowing for greater AM fungal abundance, (iv) greater plant diversity reduces niche overlap among AM fungi by diversifying the below-ground biotope and expanding the available resource niche.

resource partitioning among AM fungi by colonizing different plant hosts such that competition among AM fungi is avoided or reduced (e.g. Fig. 1b,d). In addition, AM fungi are dependent on photosynthetically derived carbon from host plants to maintain hyphal development and the functioning of the plant–AM fungal mutualism (Smith & Read 2008). Considering this, greater plant diversity can be linked with a greater capture and allocation of carbon below-ground (Reich *et al.* 2001; Tilman, Hill & Lehman 2006; Steinbeiss *et al.* 2008; Ladygina & Hedlund 2010), greater plant diversity could expand the available resource pool for AM fungi allowing for greater AM fungal productivity and furthermore increased resource partitioning among AM fungi (e.g. Fig. 1). Therefore, it seems likely

that greater plant diversity may be a key mechanism for complementarity among AM fungi.

Greater AM fungal diversity is well known to enhance plant community productivity (e.g. van der Heijden *et al.* 1998) and plant and AM fungal diversity can be associated with one another in natural grassland communities (e.g. Hiiesalu *et al.* 2014). However, it remains unknown as to whether the positive effect of AM fungal diversity on ecosystem primary productivity results from improved resource partitioning and complementarity among plant species when AM fungal diversity is high. Likewise, it remains untested whether greater plant diversity is a mechanism for resource partitioning among AM fungi such that greater plant diversity allows for greater complementarity among AM fungi. Here, we address this issue by creating a model system in which we manipulated both plant and AM fungal communities to create different plant diversity levels (1 or 3 plant species) crossed with different AM fungal diversity levels (0, 1 or 4 AM fungi) to address the hypotheses that (i) greater AM fungal diversity would improve plant productivity (Fig. 1) and (ii) if greater AM fungal diversity improves plant productivity by reducing niche overlap among plant species, then greater AM fungal diversity should lead to greater plant complementarity (Fig. 1c,d). At the same time, AM fungi may benefit from greater plant diversity where we hypothesize that (iii) greater plant diversity improves AM fungal abundance (Fig. 1a,c) and (iv) if a greater plant diversity reduces niche overlap among AM fungi, then a greater plant diversity should improve complementarity among AM fungi (Fig. 1b,d).

Materials and methods

PLANTS

Three plant species commonly found in natural temperate grasslands that represent major plant functional groups were used for the study; a forb (*Plantago lanceolata* L.), a grass (*Lolium multiflorum* Lam.) and a legume (*Trifolium pratense* L.). Seeds of each of these three plant species were surface sterilized in 2.5% sodium hypochlorite (50% household bleach), rinsed in distilled H₂O and germinated on 1.5% water agar medium for 3–5 days. Seedlings appearing free from contamination were transplanted into pots in either monoculture or mixture resulting in three plant monocultures and one plant mixture (four plant community treatments). All plant communities were planted with 27 individuals in predetermined evenly spaced positions. The plant species mixture consisted of nine individuals of each of the three plant species randomly distributed within the pot. Plants not surviving the transplantation were replaced within 2 weeks of the initial planting. Plant mortality overall was very low and was independent of plant and AM fungal treatments (see Figure S1 in the Supporting Information).

FUNGI

As with the plant species, the four AM fungal species were inoculated as a monoculture of one of the four taxa and all together as a mixture into all plant community combinations. The AM fungi were as

follows: *Funneliformis mosseae*, *Rhizoglyphus irregularis*, *Claroideoglomus claroideum* and *Diversispora celata*. These AM fungi were selected based on our past experience with the isolates and the availability of the molecular tools to quantify the abundance of these fungi within a mixed AM fungal community (Wagg *et al.* 2011a,b; Thonar, Erb & Jansa 2012). These fungi are also abundant in Swiss grassland (e.g. Oehl *et al.* 2010). Although these fungi may not represent the broad spectrum in the AM fungal phylogenies, these fungi can vary in functional characteristics such as foraging strategies and effects on host plant performance (Jansa, Mozafar & Frossard 2005; Thonar *et al.* 2011; Wagg *et al.* 2011a). It should be noted that these four fungi are the same isolates used by Wagg *et al.* (2011a,b), but *R. irregularis*, *F. mosseae* and *C. claroideum* are renamed due to the recent reclassification of their genera (Schüßler & Walker 2010; Krüger *et al.* 2012; Sieverding *et al.* 2014).

These isolates, as well as a non-mycorrhizal control inoculum, were cultivated on *P. lanceolata* for 6 months in a sterilized 1 : 9 field soil–quartz sand mixture. Each inoculum was prepared by allowing the culture pots to dry and roots were cut into small fragments and homogeneously mixed with the culture pot substrate. Each experimental pot received 90 g of inoculum, comprised of colonized roots and substrate containing spores and hyphae and non-AM control pots received 90 g of control inoculum. Pots inoculated with all four fungi received 22.5 g of each AM fungal inocula, such that the total inoculum amount was 90 g per pot. To correct for differences in microbial communities between inocula treatments, 50 g of each inoculum was sieved with 800 mL of dH₂O through a sieve series with the smallest being <10 µm. The inocula washes were pooled, and 20 mL was added to each pot. An additional microbial wash was created using a total of 1 kg of fresh field soil from a natural grass clover field with 4 L of dH₂O and sieved through a series of sieves down to <10 µm. Each pot received 20 mL of this additional microbial wash to further standardize the microbial communities within the pots and ensure the presence of rhizobia. The latter was confirmed by the presence of root nodules on *T. pratense* in all pots at the final harvest. Moreover, this did not introduce unintended AM fungi from the field as no AM fungal colonization was detected in the non-AM control plants.

EXPERIMENTAL CONDITIONS

The experiment was a complete factorial design with four plant communities (three species monocultures and one mixture) and six AM fungal communities (four monocultures, one mixture of all four species and one non-AM control), which resulted in a total of 24 plant–AM fungal community combinations. Each combination was replicated eight times giving a total of 192 microcosms. These were randomly distributed throughout the glasshouse. The communities were grown in a substrate consisting of 75% field soil and 25% sand, which was sterilized by autoclaving at 121 °C for 90 min and allowed to settle for 2 weeks prior to inoculation. The field soil was collected from a natural grassland that was managed only by mowing twice per year for fodder. The sterilized substrate had a pH of 7.5 and contained 50.5 mg kg⁻¹ of water-soluble inorganic N (NO₃⁻ and NH₄⁺). Plant-available P₂O₅ and K₂O (CO₂-saturated water extraction) were 0.32 and 7.5 mg kg⁻¹, respectively. Total Ca, P, K and Mg (ammonium acetate–EDTA extracted) were 4.26 × 10³, 17.7, 24.4 and 161 mg kg⁻¹ respectively. The substrate conditions in which plants were grown may be considered to be similar to some calcareous grassland soils.

Pots were 3 L in volume and were filled with 2500 g of sterilized substrate, and the 90 g of inocula was mixed throughout. Additional sterilized substrate was added on the surface to bring the total

substrate to 5000 g. The addition of the top layer was added to reduce any risk of cross contamination. The plant–fungal communities were grown in a glasshouse at the Agroscope Research Station in Zürich, Switzerland, for a total of 12 weeks. Plants received natural light subsidized by 400 W high pressure sodium lights to achieve a minimum of 300 W m⁻² of light for 16 h at 25–28 °C during the day. During the 8-h nights plants were exposed to an average temperature of 16 °C. Pots were watered with dH₂O to maintain soil moisture between 10% and 20% by weight.

PLANT AND FUNGAL DATA COLLECTION

Microcosms were harvested every 4 weeks post-initial seedling transplant to track the development of the microcosms. At 4 and 8 weeks post-initial planting plant shoots were collected 4–5 cm above the soil surface. At 12 weeks, plants were harvested at the soil surface. Shoots were sorted by species and dried at 60 °C to determine the biomass. As, in some pots, not all individual plants survived to the end of the experiment, the number of individuals of each plant species per pot was also recorded (see Figure S1). AM fungal communities colonizing roots were also sampled at each harvest. After 4 and 8 weeks of growth, plant roots were collected by extracting three soil cores (1.4 cm in diameter) to the depth of the pot that were then refilled with the same sterile substrate. At 12 weeks, entire plant community root systems were harvested. Roots were rinsed clean of soil, cut into small (1–2 cm) fragments, mixed for randomization, and a subsample was lyophilized and massed for molecular detection of AM fungi. However, at 4 and 8 weeks, the detection of AM fungi was frequently below the qPCR detection limit. Therefore, AM fungi could not be reliably detected in plant roots in a comparable manner among time points (see below for qPCR methods). For these reasons, we only use AM fungal abundance data collected during the final harvest when the entire root system was sampled.

DNA was extracted from lyophilized root samples using the Qiagen DNeasy 96 plant kit following manufacturer recommendations for the purification of total DNA from plant tissue (Qiagen Sciences, Germantown, MD, USA). The DNA extracted was quantified using PicoGreen[®] (Molecular Probes, Eugene, OR, USA) on a Cary Eclipse fluorescence spectrophotometer. The nuclear large ribosomal subunit of each of the four fungi was quantified in all root samples using primers and hydrolysis probes specific to each of them. The qPCRs were carried out using the Light Cycler 2.0 (Roche Applied Science, Rotkreuz, Switzerland), and the cycle threshold values were used to determine the number of DNA copies per mg of lyophilized roots (see Wagg *et al.* 2011a,b and Thonar, Erb & Jansa 2012 for details). Details on the primers and probes used, as well as the reagents and cycling conditions for the qPCR, are described in Wagg *et al.* (2011b) and Thonar, Erb & Jansa (2012). In addition, all non-AM control treatments were checked for AM colonization by microscopy and staining cleared roots with 5% pen ink – vinegar solution as outlined by Vierheilig *et al.* (1998). One non-AM pot of *P. lanceolata* was found to be colonized with AM fungi and thus removed from the data set.

INDICES OF PERFORMANCE AND THE PARTITIONING OF BIODIVERSITY EFFECTS

Total AM fungal abundance was determined as the total sum of target DNA copies detected per mg of root during the final harvest, which has been demonstrated to correlate with overall AM fungal abundance in roots (Jansa *et al.* 2014). Plant above-ground

biomass was pooled across harvests and plant species and used as the net productivity of communities in all analyses. Similarly, the biomass of each plant species was pooled separately across harvests to obtain the net productivity of each plant species. Complementarity, selection and net biodiversity effects in the plant and fungal communities were calculated using the additive partitioning approach described by Loreau & Hector (2001), which is described in detail elsewhere (Hector, Loreau & Schmid 2002; Schmid *et al.* 2008; Turnbull *et al.* 2013). Briefly, the complementarity effect was calculated as $N \times \overline{\Delta RY} \times \bar{M}$, and the selection effect was calculated as $N \times \text{cov}(\Delta RY, M)$, where N is the number of species in the mixture (i.e. 3 in the plant mixture and 4 in the AM fungal mixture) and M is the yield of the species monoculture. The relative yield (RY) is the observed yield of a species in mixture (O) divided by the species monoculture yield (M) such that $RY = O/M$ (de Wit 1960). The ΔRY is then the difference in the RY of a species from its expected RY, which is $1/N$: the proportion in which the species were sown. The sum of the complementarity and selection effects is the net effect, which is the difference in the observed yield of the species mixture from the average of the species monocultures. The biodiversity effects were calculated for the plant mixture using plant species biomass and for the fungal mixture using the DNA abundance of each AM fungus.

DATA ANALYSES

All statistics were calculated using R for MAC OS X version 2.15.1 (R Development Core Team, 2011). To reduce heteroscedasticity, the biomass of *T. pratense* plants cube-root transformed. In addition, all measures of fungal abundance were $\log + 1$ transformed prior to analyses. In all ANOVA models, plant mortality was added as a covariate to counteract potential plant density effects. To assess the performance of individual plant and fungal species in their respective monocultures and mixtures, the data were standardized by the initial sown/inoculation density. Specifically, plant species biomass was assessed using species biomass per individual per microcosm and the abundance of each AM fungus was assessed as the number of DNA copies per mg of roots sampled per mg of AM fungal inoculum. This was performed to easily decipher monoculture and mixture effects on species performance independent of the initial intraspecific density and calculated. Therefore, no plant mixture vs. monoculture effect should be detected

in the ANOVA model if it performs similarly in both monoculture and mixture.

To assess our hypotheses (i) and (ii) with regards to plant community performance in relation AM fungal diversity, the plant community productivity and the biomass of individual plant species were assessed by ANOVA with the plant community and AM fungal community combinations as well as their interaction as sources of variation. Contrast terms were added to the ANOVA models to test first for the effect of the presence of AM fungi vs. the non-AM control plants. To explicitly test the hypothesis that a greater AM fungal diversity supports greater plant productivity (i), a contrast term was added to the model to compare plant productivity in the AM fungal mixture vs. the AM fungal monocultures. To test the hypothesis that greater AM fungal diversity improves complementarity among plants (ii), we assessed the plant biodiversity effects (complementarity, selection and net effects) separately by ANOVA for variation among AM fungal communities. The contrast terms testing for the effect of the presence of AM fungi and the mixture vs. monocultures of AM fungi were added to the model as was performed for assessing net productivity. The contrast of the AM fungal mixture against the AM fungal monocultures explicitly tests our hypothesis that greater AM fungal diversity alters the biodiversity effects within the mixed plant species community (ii).

Total AM fungal abundance and the abundance of individual AM fungi were assessed by ANOVA using plant and fungal community combinations as sources of variation. Contrast terms were added to the ANOVA model to assess whether AM fungal abundance in the plant mixture was greater than the plant monocultures thereby explicitly testing our hypothesis that greater plant diversity supports greater abundance of AM fungi (iii). Furthermore, AM biodiversity effects (complementarity, selection and net effects) were similarly assessed with the plant mixture vs. monoculture contrast term added to the model to test hypothesis as to whether greater plant richness improved complementarity in the abundance of AM fungi (iv).

Results

EFFECT OF AM FUNGAL COMMUNITIES ON PLANTS

Plant communities varied strongly in net productivity among both plant and AM fungal community combinations (Table 1,

Table 1. anova results for net plant community productivity (NPP) and the average biomass per plant harvested of each plant species. MS and the associated degrees of freedom are shown in parentheses for effect of the different plant communities (plant), arbuscular mycorrhizal fungal communities (AM) and their interaction (AM \times Plant). Indented terms indicate contrast terms where NM represents the differences between the non-AM control and the treatments with AM fungi. The Div term indicates the contrast between the mixture of AM fungi and the average of the four fungal monocultures (diversity effect of AM fungal richness on plant productivity)

	NPP		<i>Lolium multiflorum</i>		<i>Plantago lanceolata</i>		<i>Trifolium pratense</i>	
	MS	<i>F</i>	MS $\times 10^2$	<i>F</i>	MS $\times 10^2$	<i>F</i>	MS $\times 10^2$	<i>F</i>
Plant	20.4 (3)	19.5***	70.0 (1)	104.0***	4.01 (1)	14.8***	20.5 (1)	131.0***
NM	430.0 (1)	411.0***	0.56 (1)	0.84	56.5 (1)	208.0***	129.0 (1)	824.0***
Div	20.6 (1)	19.7***	0.22 (1)	0.32	3.17 (1)	11.7**	2.57 (1)	16.4***
AM	63.7 (3)	61.0***	4.67 (3)	6.95***	11.0 (3)	40.4***	6.64 (3)	42.2***
NM \times Plant	60.1 (3)	57.5***	2.27 (1)	3.38†	0.02 (1)	0.06	1.17 (1)	7.44**
Div \times Plant	2.14 (3)	2.05	1.37 (1)	2.04	0.02 (1)	0.05	0.04 (1)	0.27
AM \times Plant	5.86 (9)	5.61***	2.38 (3)	3.54*	2.18 (3)	8.00***	0.24 (3)	1.51
Residual	1.04 (166)		0.67 (83)		0.27 (82)		0.16 (83)	

MS, mean squares; *F*, *F* statistic.

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fig. 2a). The overall presence of AM fungi increased the productivity of the plant mixture and of the *P. lanceolata* and *T. pratense* monocultures, while the productivity of the *L. multiflorum* monoculture was generally not affected by the presence of AM fungi (Table 1, Fig. 2a). Plant communities also had greater net productivity with the mixture of all four AM fungi than the average of the fungal monocultures, as indicated by the contrast between the AM fungal mixture and the average of the AM fungal monocultures (Table 1, Fig. 1a: AM fungal community M vs. the average of F, R, C and D fungal treatments). The productivity of the *P. lanceolata* and *T. pratense* monocultures, as well as the plant mixture, all generally benefited from the inoculation of the individual AM fungal monocultures (Fig. 1a). However, *F. mosseae* had the lowest beneficial effect on the *P. lanceolata* and *T. pratense* monocultures and had no beneficial effect on the plant mixture (Fig. 1a). In addition, the productivity of the *L. multiflorum* monoculture varied little among the AM fungal monocultures. This differential response in productivity of

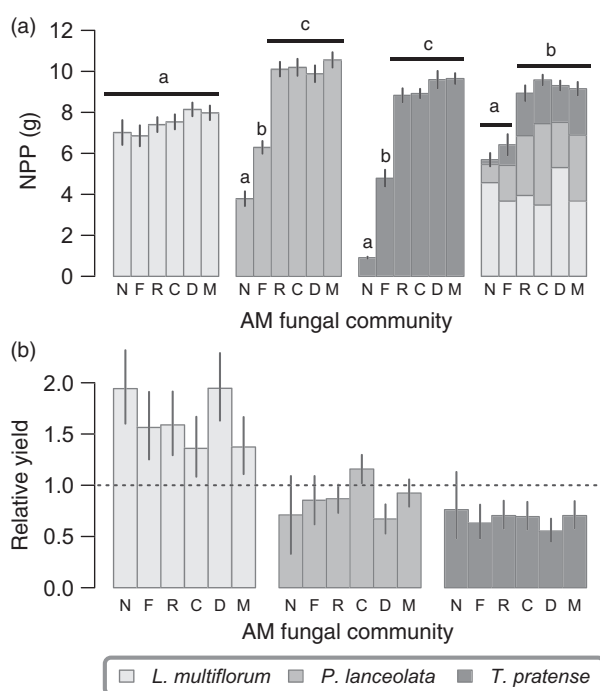


Fig. 2. Mean net plant productivity (NPP) with standard errors for each plant and arbuscular mycorrhizal (AM) fungal community combination is shown in (a). Different lowercase letters indicate differences in net productivity among AM fungal treatments for each plant community (Tukey's HSD, $P < 0.05$). The mean performance of each plant species per sown density in mixture relative to the monoculture is expressed as a relative yield (RY) in (b) with 95% confidence intervals for the difference from monoculture (indicated by the dotted line). Note the standardizing of yields by sown density means monoculture and mixture yields are equal when the RY = 1). Shading indicates different plant species, such that the stacked bars in (a) is the biomass of each plant species within the plant mixture (also see Figure S1). The AM fungal community composition is indicated by uppercase letters on the x-axis: N = non-AM control, F = *Funneliformis mosseae*, R = *Rhizoglossum irregulare*, C = *Claroideoglossum claroideum*, D = *Diversispora celata* and M = AM fungal mixture.

L. multiflorum from the other two plant monocultures to the various AM fungal monocultures resulted in a significant plant community by AM fungal treatment interaction term (Table 1). Overall, the lower productivity of plant communities with the *F. mosseae* monoculture contributed to the lower average effect of AM fungal monocultures on plant productivity relative to the AM fungal mixture.

All plant species varied in their individual performance depending on the AM fungal community and whether they were grown in monoculture or in mixture (Table 1, Figure S1). Overall, the grass *L. multiflorum* performed better in the plant mixture than in the plant monoculture (Table 1, Fig. 1b). Of the AM fungal monocultures, *L. multiflorum* performed best in the plant mixture with the *D. celata* monoculture resulting in significant AM by plant interaction (Table 1, Fig. 1a, b). *P. lanceolata* performed better in the plant mixture when inoculated with *C. claroideum* and worse when inoculated with *D. celata* resulting in the AM fungal by plant community interaction (Table 1, Fig. 1b). *Trifolium pratense* performed better when grown as a plant monoculture in all AM fungal communities, although the difference between monoculture and mixture performance of *T. pratense* was not strongly significant in the non-AM control treatment (Fig. 1b).

AM FUNGAL DIVERSITY INFLUENCE ON PLANT COMPLEMENTARITY AND SELECTION EFFECTS

As a result of the strong performance of *L. multiflorum* in both plant monocultures and mixtures and the poor performance of the other two plant species when AM fungi were absent, the plant species mixture out-performed the average of the plant monocultures indicated by a positive net biodiversity effect (Table 2, Fig. 3: AM fungal community N). Since in the absence of AM fungi *L. multiflorum* was the most productive species in both monoculture and mixture relative to *P. lanceolata* and *T. pratense* (Fig. 2a), the positive net effect was largely driven by the selection biodiversity effect, which contributed 72% of the net effect (Fig. 3). Overall, the net

Table 2. anova results for the complementarity effect (CE) selection effect (SE) and the net effect (NE) in the plant mixture. MS and the associated degrees of freedom are shown in parentheses. Indented terms indicate contrast terms where NM is the contrast between the non-arbuscular mycorrhizal (AM) control and the treatments with AM fungi and Div is the contrast between the AM fungal mixture and the average of the AM fungal monocultures

	d.f.	SE		CE		NE	
		MS	F	MS	F	MS	F
NM	1	13.9	203.0***	0.80	0.08	16.1	16.0***
Div	1	0.09	1.24	1.04	1.06	1.71	1.70
AM	3	1.03	15.0***	0.62	0.64	0.59	0.58
Residual	4	0.07		0.97		1.01	

MS, mean squares; d.f., degrees of freedom; F, F statistic.
 $\dagger P < 0.1$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

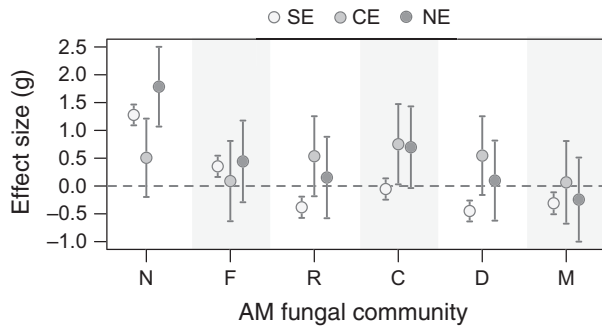


Fig. 3. Plant biodiversity effects are shown for each arbuscular mycorrhizal (AM) fungal treatment. Points indicate means and error bars indicate 95% confidence intervals for a difference from 0 (dashed line – no biodiversity effect) for the selection (SE = open points), complementarity (CE = lightly shaded points) and the net (NE = darkly shaded points) effects. The AM fungal communities are indicated on the x-axis by N = non-AM control, F = *Funneliformis mosseae*, R = *Rhizoglyphus irregularis*, C = *Claroideoglomus claroideum*, D = *Diversispora celata* and M = AM fungal mixture.

and selection biodiversity effects in the plant species mixture were greatest in the non-AM plant community than in the presence of AM fungi (Table 2, Fig. 3).

In the presence of AM fungi, the selection effect in the plant community did not differ between the AM fungal mixture and the average of the AM fungal monocultures (Table 2). However, the selection effect in the plant mixture was dependent upon the identity of the AM fungal monocultures (Table 2), which was largely due to *F. mosseae* resulting in a positive selection effect while *R. irregularis* and *D. celata* resulted in a negative selection effect in the plant mixture (Fig. 3).

Overall, the plant net biodiversity effect did not vary greatly among the AM fungal treatments (Table 2) and did not differ strongly from 0 in all treatments where AM fungi were present (Fig. 3). Although the complementarity effect in the plant community was generally positive, it varied little among AM fungal community treatments (Table 2) and generally did not differ from 0, with the exception of the

C. claroideum AM fungal monoculture (Fig. 3). With the *C. claroideum* AM fungal monoculture, the plant complementarity effect was significantly positive. With this AM fungal monoculture, the plant complementarity effect was 93% of the net biodiversity effect in the plant mixture (Fig. 3 – AM fungal community C).

EFFECT OF PLANT COMMUNITIES ON AM FUNGI

We found the total AM fungal abundance was not greater in the plant mixture relative to the average of the plant monocultures (Table 3, Fig. 4a). The total abundance of AM fungi was generally more dependent on the plant species comprising the plant community (Table 3, Fig. 4a). This resulted from the low detection of AM fungi within the *L. multiflorum* monoculture while the *P. lanceolata* and *T. pratense* monocultures supported the highest levels of AM fungal abundance (Fig. 3). However, a significant plant community by AM fungal community interaction was detected (Table 3; Fig. 4a).

As with the total AM fungal abundance, the abundance of each of the AM fungi was lowest in the *L. multiflorum* monoculture and generally greatest with the *P. lanceolata* and *T. pratense* monocultures (Table 3, also see Figure S2). The abundance of individual AM fungi, however, did not differ between the plant mixture and the average of the plant monocultures, with the exception of *R. irregularis* where its abundance was lower in the plant species mixture than the average of the plant monocultures (Table 3, Figure S2). There was little difference in general in the performance of individual AM fungi in monoculture and mixture (Table 3, Fig. 4b, Figure S2). However, *F. mosseae* performed marginally better in the AM fungal mixtures, and *C. claroideum* performed worse in the AM fungal mixtures overall (Table 3, Fig. 4b).

PLANT DIVERSITY INFLUENCE ON AM FUNGAL COMPLEMENTARITY AND SELECTION EFFECTS

The plant communities had little impact on the selection, complementarity and net biodiversity effects when assessed

Table 3. anova results for total log + 1-transformed arbuscular mycorrhizal (AM) fungal abundance and the abundance of each fungal species. MS and the associated degrees of freedom are shown in parentheses for effect of the different plant communities (plant), AM fungal communities (AM) and their interaction (AM × Plant). Indented terms (Div and Div × AMF) indicate contrast terms for assessing the difference between the plant mixture and average of the plant monocultures (diversity effect of plant species richness on total fungal community abundance)

	Total		<i>Funneliformis mosseae</i>		<i>Rhizoglyphus irregularis</i>		<i>Claroideoglomus claroideum</i>		<i>Diversispora celata</i>	
	MS	F	MS × 10 ¹	F	MS	F	MS × 10 ¹	F	MS × 10 ¹	F
Div	0.54 (1)	0.13	1.22 (1)	0.14	3.76 (1)	5.66*	6.63 (1)	2.87 [†]	0.94 (1)	0.38
Plant	255. (2)	59.2***	75.3 (2)	8.58***	11.3 (2)	17.0***	50.1 (2)	21.7***	24.1 (2)	9.69***
AM	3.08 (4)	0.72	26.3 (1)	3.00 [†]	0.41 (1)	0.62	10.9 (1)	4.72*	1.50 (1)	0.60
Div × AM	4.02 (4)	0.93	0.02 (1)	<0.00	0.14 (1)	0.21	1.09 (1)	0.47	3.95 (1)	1.58
Plant × AM	10.5 (8)	2.44*	2.85 (2)	0.32	0.13 (2)	0.20	4.07 (2)	1.76	3.76 (2)	1.51
Residual	4.31 (139)		8.77 (55)		0.66 (55)		2.31 (55)		2.49 (55)	

MS, mean squares; F, F statistic.

[†]P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.

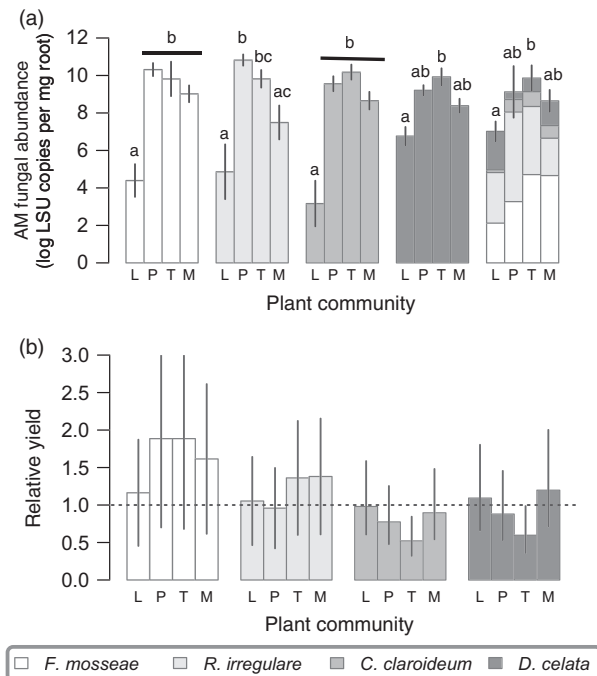


Fig. 4. Mean arbuscular mycorrhizal (AM) fungal abundance (log transformed) with standard errors for each plant and AM fungal community combination is shown in (a). Different lowercase letters indicate differences in AM fungal abundance among plant communities within each AM fungal treatment (Tukey's HSD, $P < 0.05$). The mean performance of each AM fungi per inoculum volume in mixture relative to the monoculture is shown in (b) and is expressed as the relative yield (RY) with 95% confidence intervals for the difference from the fungal monoculture (indicated by the dotted line). Note the standardizing of AMF abundance by inoculum volume means monoculture and mixture yields are equal when the RY = 1). Shading indicates the different AM fungi, such that the stacked bars in (a) indicate the proportional abundance of each AM fungus in the AM fungal mixture (also see Figure S2). The plant community composition is indicated by different uppercase letters on the x-axis where L = *Lolium multiflorum*, P = *Plantago lanceolata*, T = *Trifolium pratense* and M = plant species mixture.

using the AM fungal abundances. Neither did the biodiversity effects differ significantly from 0 (Table 4, Fig. 5). The plant species mixture also showed no difference from the average of the plant monocultures in its impact on the AM fungal biodiversity effects with regards to AM fungal abundance (Table 4).

Discussion

It is often observed that greater AM fungal diversity can enhance the productivity of plant communities (van der Heijden *et al.* 1998; Wagg *et al.* 2011a). In conjunction, it has been observed that greater plant diversity can be associated with greater AM fungal abundance and richness (De Deyn, Quirk & Bardgett 2011; Hiiesalu *et al.* 2014). Yet, whether greater species diversity in either the plant or fungal community allows for greater functional complementarity among species in the other is not understood. Here, we hypothesized that (i) greater AM fungal diversity would

improve plant productivity paralleling past studies and (ii) if greater AM fungal diversity improves plant productivity by reducing niche overlap among plant species, then greater AM fungal diversity should lead to greater plant complementarity. As in past studies, we did observe that greater AM fungal diversity generally resulted in a greater plant productivity compared to the average of the AM fungal monocultures in support of our hypothesis (i). In addition, we found the overall presence of AM fungi reduced the selection effect in the plant community indicating that the productivity of the plant community was less dependent on a particularly productive plant species when AM fungi are present. In contrast to our hypothesis, (ii) greater AM fungal diversity did not improve the complementarity effect in the plant species mixture more than the AM fungi in monoculture average. In addition, the complementarity effect in the plant community varied little from 0 (no effect). However, plant complementarity was only significantly positive in the presence of a single AM fungus,

Table 4. Anova results for the complementarity effect (CE) selection effect (SE) and the net effect (NE) in the arbuscular mycorrhizal (AM) fungal mixture. MS and the associated degrees of freedom are shown in parentheses. The indented term Div is the contrast between the plant mixture and the average of the plant monocultures

	d.f.	SE		CE		NE	
		MS	F	MS	F	MS	F
Div	1	0.04	0.002	6.85	0.79	65.3	0.74
Plant	2	43.7	2.63	4.31	0.50	14.7	1.66
Residual	27	16.6		8.68		8.86	

MS, mean squares; d.f., degrees of freedom; F, F statistic. MS values are $\times 10^7$.

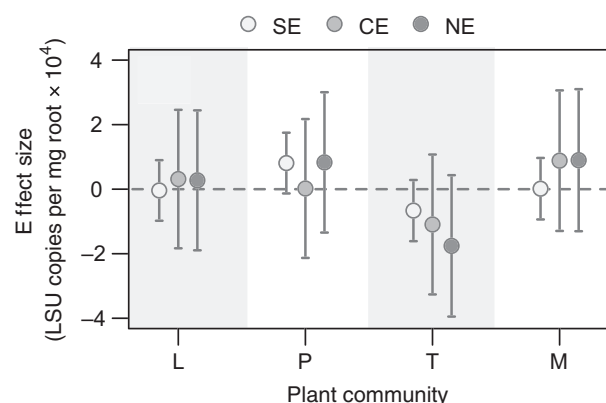


Fig. 5. Arbuscular mycorrhizal (AM) fungal biodiversity effects on the total abundance of AM fungi are shown for each plant community treatment. Points indicate means and error bars indicate 95% confidence intervals for a difference from 0 (dashed line – no effect) for the selection (SE = open points), complementarity (CE = lightly shaded points) and the net (NE = darkly shaded points) effects. The plant communities are indicated on the x-axis by L = *Lolium multiflorum*, P = *Plantago lanceolata*, T = *Trifolium pratense* and M = plant species mixture.

C. claroideum, indicating the identity of the plant–AM fungal association may be a key determinant in plant community complementarity effects.

On the fungal side, greater plant diversity did not improve the overall abundance of AM fungi detected within plant roots, in contrast to our hypothesis (iii). Neither the net nor complementarity biodiversity effects of the AM fungi were greatest in the plant species mixture. This provides little empirical evidence to support our hypothesis (iv) that greater plant diversity reduces niche overlap among AM fungi. Instead, we found no evidence for AM fungal biodiversity effects based on AM fungal abundance overall.

Our results confirm that greater AM fungal diversity can lead to greater plant community performance. However, the greater plant community performance does not necessarily indicate that greater AM fungal diversity reduces niche overlap among plants to improve plant species complementarity. In addition, there was little evidence to suggest that greater plant diversity reduced niche overlap among AM fungi. It is important to consider, however, that our experiment occurred within a relatively short time frame (12 weeks) and biodiversity effects are known to change and develop over time (e.g. Fargione *et al.* 2007; Marquard *et al.* 2009; Reich *et al.* 2012). It is likely in our study that the effects of plant and AM fungal diversity on each other may also change through time as the plants and fungi utilize more of the available biotope and their interactions strengthen. Therefore, the biodiversity effects in our study are perhaps underestimated due to the short experimental time frame. Generally, our findings highlight that although changes in species diversity in one group of organisms may impact the functioning of species diversity in an associated group of organisms, it would seem the identity of the species comprising both communities is perhaps a key determinant of vertical diversity effects (Duffy *et al.* 2007; Eisenhauer 2012; Eisenhauer, Reich & Isbell 2012).

AM FUNGAL MEDIATED PLANT COMMUNITY PERFORMANCE

We did not find greater AM fungal diversity improved plant complementarity. Instead, the complementarity effect in the plant community was only positive and contributed the most to the net biodiversity effect (93%) when the AM fungus *C. claroideum* was present as a monoculture. Therefore, an AM fungal community identity effect rather than an AM fungal diversity effect was relatively more influential on plant complementarity. In general, the effect of the AM fungal monocultures and mixture on plant performance in plant species mixtures parallels our previous findings (Wagg *et al.* 2011b) where the RY total of plant mixtures [RYT, which is analogous to the complementarity effect (Loreau & Hector 2001)] was greater with the monoculture of a particular AM fungus rather than a mixture of AM fungi. Similar presence and compositional effects of organisms on the functioning of plant diversity have recently been observed by Eisenhauer, Reich & Isbell (2012) who found the plant complementarity effect was driven more by the absence and presence of groups

of soil decomposers and not necessarily by their diversity. Together, our results provide support for the argument that community composition, and not necessarily the diversity, of soil organisms determines the functioning of plant communities.

The large net biodiversity effect in the absence of AM fungi was largely driven by a positive selection effect, which is determined by species performing strongly in both monocultures and mixtures (Loreau & Hector 2001). In our study, the selection effect was caused by the strong productivity of *L. multiflorum* in the absence of AM fungi, as both *P. lanceolata* and *T. pratense* are typically known to depend on AM fungal associations for biomass production (van der Heijden *et al.* 1998; Klironomos 2003; Wagg *et al.* 2011a,b). The increased growth in *P. lanceolata* and *T. pratense* and little variation in the performance of *L. multiflorum* in the presence of AM fungi reduced the differences among the plant monoculture performances. This in turn reduced the selection effect. Therefore, the AM fungal communities likely played a stronger role in expanding the available resource niche of *P. lanceolata* and *T. pratense* rather than reducing niche overlap among the plants *per se*. Moreover, competitive interactions were not strongly evident in our study as implied by the species RYs. However, in the AM fungal community treatments where *L. multiflorum* exhibited a somewhat lower performance in the plant mixture, *P. lanceolata* performed relatively better suggesting a plant–plant competitive shift mediated by the AM fungal communities. Such altered plant–plant competitive interactions as a result of AM fungal associations parallel many past studies that have also found the presence and diversity of AM fungi to mitigate competitive differences among plants (Fitter 1977; van der Heijden, Wiemken & Sanders 2003; Urcelay & Díaz 2003; Scheublin, van Logtestijn & van der Heijden 2007; Collins & Foster 2009; Wagg *et al.* 2011b). This may suggest that the AM fungal communities play some role in resource partitioning among plant species.

PLANT-MEDIATED AM FUNGAL COMMUNITY PERFORMANCE

In line with previous studies demonstrating that plant species differ in their influence on AM fungi (Bever 2002; Johnson *et al.* 2003; De Deyn, Quirk & Bardgett 2011; Koch, Antunes & Klironomos 2012), we found the composition of the various plant communities had a strong influence on the abundance of AM fungi within the roots of the plants. Specifically, AM fungal abundance was consistently lower in the *L. multiflorum* monoculture than in all other plant communities. Our results compare with some previous findings that although AM fungal abundance may be associated with greater plant diversity, AM fungal abundance is likely driven more by the presence of particular plants species (De Deyn, Quirk & Bardgett 2011; Koch, Antunes & Klironomos 2012). Such findings would indicate that greater plant host diversity does not necessarily offer the AM fungi a greater opportunity to increase AM fungal abundance and reduce niche overlap.

Instead, it suggests that the resource pool available to AM fungi is largely influenced by particular plant species rather than host diversity.

It is possible, however, that niche overlap among AM fungi is reduced by colonizing different plant hosts, as plant host preference by AM fungi has been observed in a number of studies (Eom, Hartnett & Wilson 2000; Bever 2002; Burrows & Pfleger 2002; Johnson *et al.* 2003; Vandenkoornhuyse *et al.* 2003; Croll *et al.* 2008). Moreover, spatial segregation among competing AM fungi has been observed to improve the beneficial effect of AM fungi on host plants (Bennett & Bever 2009; Bever *et al.* 2009). In our study, however, as the complementarity effect in the AM fungal mixture was not improved by greater plant host diversity, we find no evidence to support the concept that spatial segregation through differential host preference among fungi occurred. Moreover, more diverse AM fungal communities are more often thought to influence plant communities through their variation in function, from improving nutrient acquisition to pathogen protection (Newsham, Fitter & Watkinson 1995; Koide 2000; Powell *et al.* 2009). In addition, AM fungi have been shown to differ in their hyphal growth strategies and spatial foraging for soil phosphorus (Hart & Reader 2002; Jansa, Mozafar & Frossard 2005; Thonar *et al.* 2011). Therefore, spatial niche segregation within the soil matrix, rather than host plant associations, may be relatively more important for facilitating reduced niche overlap among AM fungi.

Conclusions

Overall, the presence and diversity of AM fungi improved the productivity in the plant communities. However, it did not necessarily increase the complementarity in the plant species mixture. This indicates that greater AM fungal diversity may not improve the net plant community productivity by reducing niche overlap among plant species. Instead, the presence and to a lesser extent, the identity of the AM fungi influenced the biodiversity effects in the plant community by expanding the resource niche available to the forb and legume to reduce the plant selection effect. On the fungal side, the abundance of AM fungi was heavily influenced by a particular plant species and not by plant diversity indicating that a greater plant host diversity does not necessarily and always reduce AM fungal niche overlap.

Here, the lack of strong effects of plant or AM fungal diversity on the community functioning of the other guild does not support our hypotheses (ii) and (iv). However, the weak differences in the abundance of AM fungi between the AM fungal mixture and monocultures, coupled with the generally weak plant biodiversity effects in the plant community in the presence of AM fungi, could indicate that the plant and AM fungal communities were still in the early stages of establishment. This may be due to the larger below-ground rooting volume and shorter time frame than our previous studies (e.g. Jansa, Smith & Smith 2008; Wagg *et al.* 2011a) such that the short time frame used here did not allow for the fungi and plants to fully proliferate, establish and interact

within our system. Furthermore, our model system does not represent a broad gradient of diversity in either plant or fungal communities that may have also contributed to the generally low biodiversity effects. Therefore, it will be important to assess a broader depth of species diversity as well as the temporal development of the plant–AM fungal diversity interaction in the future.

Generally, our results reinforce that the functioning of a more diverse community does not only depend upon its interactions with neighbouring species of the same guild, but also on the composition of associating guilds of organisms (Duffy *et al.* 2007; Eisenhauer 2012; Eisenhauer, Reich & Isbell 2012). Therefore, changes in species compositions in either or both plant and soil communities may be key components to understanding the effect of species losses on the overall functioning of the ecosystem (van der Putten 2012; Hodge & Fitter 2013).

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Data accessibility

Data are available at: doi: 10.5061/dryad.g464v.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Biomass and mean survival of individual plant species.

Figure S2. Abundances of individual AM fungi.