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LETTER

Soil microbiome mediates positive plant diversity-productivity relationships in late successional grassland species

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Abstract

Which processes drive the productivity benefits of biodiversity remain a critical, but unanswered question in ecology. We tested whether the soil microbiome mediates the diversity-productivity relationships among late successional plant species. We found that productivity increased with plant richness in diverse soil communities, but not with low-diversity mixtures of arbuscular mycorrhizal fungi or in pasteurised soils. Diversity-interaction modelling revealed that pairwise interactions among species best explained the positive diversity-productivity relationships, and that transgressive overyielding resulting from positive complementarity was only observed with the late successional soil microbiome, which was both the most diverse and exhibited the strongest community differentiation among plant species. We found evidence that both dilution/suppression from host-specific pathogens and microbiome-mediated resource partitioning contributed to positive diversity-productivity relationships and overyielding. Our results suggest that re-establishment of a diverse, late successional soil microbiome may be critical to the restoration of the functional benefits of plant diversity following anthropogenic disturbance.

Keywords

Arbuscular mycorrhizal fungi, diversity-productivity relationships, late successional grassland, native prairie, post-agricultural, soil microbiome.

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INTRODUCTION

The value of diversity in providing ecosystem services is strongly supported (Cardinale *et al*. 2012; Brose & Hillebrand 2016), and higher diversity improves community efficiency in capturing resources and producing biomass (Tilman *et al*. 2014). This positive effect of diversity on productivity has been explained by complementarity and selection effects, largely thought to result from the differences in resource use (Loreau & Hector 2001). The complementarity effect refers to resource partitioning or facilitative interactions between species, whereas the selection effect is caused by species that are particularly productive and competitive for resources in plant mixtures (Loreau & Hector 2001). Recently, soil microbes, particularly symbionts and pathogens, have been suggested to be important in mediating diversity-productivity relationships in plant communities (van der Heijden *et al*. 2008; Maron *et al*. 2011; Schnitzer *et al*. 2011; Hodge & Fitter 2013). Besides, soil microbes affected complementarity and selection effects when associating with plant species (Jing *et al*. 2015; Wagg *et al*. 2015; Barry *et al*. 2019). Understanding the mechanism of microbially mediated community dynamics is necessary to generate predictions of benefits of plant diversity.

Mutualists are involved in soil biogeochemical cycles and plant nutrient uptake, which are important in regulating plant-plant interactions and productivity (van der Heijden *et al*. 2008, 2015). An underlying mechanism by which mutualists drive plant coexistence and productivity may be ascribed to resources partitioning (Bever *et al*. 2010), as plant resource acquisitions are determined in part by their associated mutualists. For example, symbiotic rhizobia mediate plant species coexistence between legumes and non-legumes (Schwinning & Parsons 1996; Cramer *et al*. 2010, see Fig. S1 in Appendix S1). Consistent with the importance of rhizobia-mediated N partitioning, inclusion of legumes has been shown to be instrumental in generating positive diversity-productivity relationships (Tilman *et al*. 2001; Hooper & Dukes 2004; Marquard *et al*. 2009). In forests, P partitioning induced by arbuscular mycorrhizal and ectomycorrhizal fungi may play an important role for tree species coexistence (Liu *et al*. 2018). In addition, asymmetric benefit delivery between plants and arbuscular mycorrhizal fungi (AMF) may favour less competitive plants and contribute to the plants coexistence and overyielding in mixture (Bever 2002; Walder *et al*. 2012). Moreover, microbial assemblages of symbionts like AMF and rhizobia could complement each other and increase plant productivity, diversity and nutrient acquisition (van der Heijden

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et al. 1998, 2016; Vogelsang *et al*. 2006). However, whether mutualist-induced complementarity effects on the plant diversity-productivity relationships will increase with higher mutualist diversity is not known.

Recent experimental work illustrates the important role of soil pathogens in driving the positive diversity-productivity relationships in biodiversity experiments (Maron *et al*. 2011; Schnitzer *et al*. 2011). This is mainly because conspecific plants suffer the most from their specific pathogens in monocultures while polycultures dilute or inhibit pathogenic effects (Hendriks *et al*. 2013; Mommer *et al*. 2018). These results are further supported by modelling work on biotic plant-soil feedbacks (PSFs) showing that plants with negative PSFs grow better in communities than in monoculture (i.e. overyielding) (Kulmatiski *et al*. 2012). Pathogens can also be important determinants of plant species coexistence and maintenance of diversity (Bagchi *et al*. 2014; Bever *et al*. 2015) because they generate negative frequency dependence (FD) of host plants and avoid competitive exclusion by the stronger competitor (Bever 2003; Eppinga *et al*. 2018). This limits individual plant species abundance and dominance (McPeek 2012), and consequently, microbial mechanisms that allow plant coexistence could generate complementarity and thereby induce overyielding. However, the effects of soil microbes on plants in isolation are not necessarily the same as in mixture (Casper & Castelli 2007; Lekberg *et al*. 2018), thus the extent to which PSFs and FD will generate overyielding in communities remains unknown.

The impact of pathogens and mutualists on the diversity-productivity relationship may change during succession. Studies show that early successional species tend to be more vulnerable to pathogens (Lutz & Halpern 2006; Kardol *et al*. 2007) and have more negative PSFs than middle and late successional species (Kardol *et al*. 2006; van de Voorde *et al*. 2011; Bauer *et al*. 2015). Since defending against pathogens is costly, plants selected for rapid growth and seed production that dominate early in succession are likely to be more poorly defended than longer-lived late successional plants (Rasmann *et al*. 2011; Bever *et al*. 2015). We would therefore expect soil pathogens and negative feedbacks to be important for generating positive plant diversity-productivity relationships for early successional species. Consistent with this, studies demonstrating an important role of pathogens in overyielding included early successional plant species (Maron *et al*. 2011; Schnitzer *et al*. 2011). In addition, negative feedbacks in early successional communities were found to influence the complementarity effects in mixtures, but not in mid successional plant communities (Jing *et al*. 2015).

Mutualists may be more important to plant-plant interactions and diversity-productivity relationships in late successional plant species. Late successional plant species, for example, are more AMF-responsive (Kardol *et al*. 2006; Koziol & Bever 2015; Bauer *et al*. 2018) and more sensitive to AMF identity (Koziol & Bever 2016), perhaps contributing to observations of positive feedback in late successional species (Bauer *et al*. 2015). Late successional legume species can also be very responsive to rhizobia (Larimer *et al*. 2014), suggesting that microbial mediation of resource partitioning might be important. As soil microbial communities change during succession, including increasing microbial biomass (Allison *et al*. 2007; Jangid *et al*. 2011) and shifting towards a fungal-dominated community (Maharning *et al*. 2009; Susyan *et al*. 2011), the performance of late successional plant species relative to early successional plants may be altered. The recovery of mycorrhizal fungal community following abandonment of agricultural land (Johnson *et al*. 2003; Treseder 2004), for example, may improve establishment of late successional native plants (Koziol *et al*. 2018). Pathogens may remain important in late successional communities, as meta-analyses have shown PSFs differ among plant functional groups and tend to be negative in graminoids (Kulmatiski *et al*. 2008; Baxendale *et al*. 2014; Cortois *et al*. 2016). Whether the importance of soil microbes in general, and of different microbial groups in particular, in mediating complementarity and selection effects on the plant diversity-productivity relationships changes during succession is not known.

Here, we used three late successional plants: grass *Andropogon gerardii* (Johnson *et al*. 2010; Herzberger *et al*. 2015), legume *Amorpha canescens* and forb *Liatris pycnostachya* (Koziol & Bever 2016) to test how plant interactions and community productivity are influenced by soil microbiota (sterile, AMF culture, post-agricultural and late successional native prairie). By creating different combinations of plant species, we first tested if there was a positive diversity-productivity relationship for late successional plant communities, and whether the relationship was influenced by complementarity or selection effects and whether these results depended on the soil microbiome. We then supplemented these analyses using diversity-interaction (DI) modelling (Kirwan *et al*. 2009) to investigate species interaction patterns and their dependence on the soil microbiome. We expected the most positive diversity-productivity relationships with the most diverse soil microbial community and with the late successional soil community. Then, we tested the PSFs using soils from the first experiment to explore conspecific or heterospecific soil microbial effects. We expected to observe the largest negative PSF effects and FD with the full complement of native pathogens in the late successional prairie soil community. As all three species are mycorrhiza-responsive (Johnson *et al*. 2010; Koziol & Bever 2016) and the legume has been shown to respond synergistically to native AMF and native rhizobia (Larimer *et al*. 2014), microbial resource partitioning may also be important amongst these species. Therefore, we hypothesised that: (1) productivity benefits of plant diversity will be the strongest in late successional, native prairie soil microbial communities; (2) overyielding will be determined by species suffering from negative FD with better performance in mixture and negative PSFs with pathogen dilution/suppression in heterospecific soils; and/or (3) microbially mediated resource dynamics will affect plant interactions and productivity.

MATERIALS AND METHODS

Experiment 1: plant diversity-productivity test

A replacement design was used with three plant species forming 15 plant combinations with consistent plant density (four

individuals per pot) but different frequency ratio (4 : 0 : 0, 3 : 1 : 0, 2 : 2 : 0, 2 : 1 : 1, see Fig. 1 and Table S1 in Appendix S2). Thus, four plant diversity types (monoculture, 3 : 1, 2 : 2 and 2 : 1 : 1 mixture) were formed and there were four plant frequencies (25, 50, 75 and 100%) for each species. Each combination was planted into mesocosms inoculated with one of the four soil inocula treatments: (1) native AMF community, which includes 22 AMF isolates (Table S2 in Appendix S2) from native prairie sites located in Kansas and Missouri, USA; (2) post-agricultural whole soil, collected from old farm land (*c*. 6 ha) that has been abandoned for *c*. 15 years located at the University of Kansas Field Station (KUFS); (3) native prairie whole soil, collected from a remnant prairie area (*c*. 4 ha) with over 200 native prairie plant species (Rockefeller Prairie at the KUFS); (4) sterile soil, which was autoclaved background soil. All pots were arranged in a randomised block design, with eight replicates for plant monocultures and four replicates for the mixtures, 288 pots in total. After 5.5 months, plants were harvested, shoot dry mass was measured, plant tissue was collected for N and P content analyses and soil was collected for analyses of fungal and mycorrhizal fungal composition and structure, or as inocula for Experiment 2. See details in Appendix S2.

Experiment 2: soil feedback test

Soils collected in Experiment 1 were used as inocula to test both conspecific (from the same plant species) and heterospecific (from other species or mixtures) soil feedback

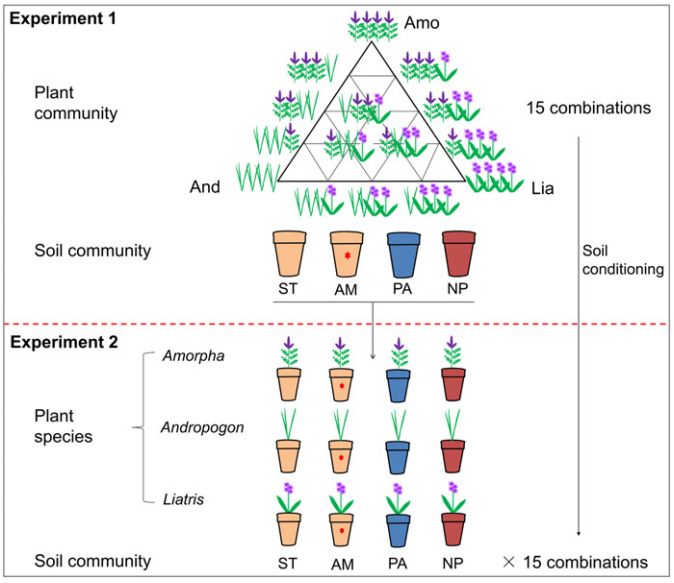

Figure 1 Schematic diagram for experimental design. In Experiment 1, three plant species formed a full 15 plant combinations with consistent plant density (four individuals per pot) but different frequency ratio (4 : 0 : 0, 3 : 1 : 0, 2 : 2 : 0 and 2 : 1 : 1). With four soil treatments, 60 different soil communities conditioned in Experiment 1 were used as inocula in Experiment 2. Inocula from each pot were separated into three part and planted three species again. 'ST', 'AM', 'PA' and 'NP' represent sterile, AMF, post-agricultural and native prairie soils respectively. 'Amo', 'And' and 'Lia' represent *Amorpha canescens*, *Andropogon gerardii* and *Liatris pycnostachya* respectively.

effects (Fig. 1). We divided the soil of each pot from Experiment 1 into three parts to the three species used in Experiment 1. The same background sterile soil as in the Experiment 1 was used. Each deepot was filled with 500 mL soil into three layers: 175 mL sterile soil at the bottom, 150 mL inoculum in the middle and another 175 mL sterile soil on the top. One individual of each species was planted in each deepot, 864 deepots in total. Plants were harvested after 9 weeks, shoots and roots dry mass were collected separately. In order to detect rhizobial effect on *Amorpha*, nodules were counted on *Amorpha* monoculture roots in three non-sterile soils conditioned by conspecifics and the other two species.

DNA extraction and sequencing processing

Fungal and AM fungal DNA were extracted from the three non-sterile soil treatments. Subsamples of each pot collected in Experiment 1 were thoroughly mixed and 0.4 g was used for DNA extraction. The fungal primers fITS7/ITS4 (Ihrmark *et al*. 2012) and mycorrhizal fungal primers fLROR/FLR2 (House & Bever 2018) targeting the internal transcribed spacer (ITC) and large subunit (LSU) region were amplified respectively. Amplicons were barcoded and sequenced on Illumina MiSeq v3 PE300 platform, and sequences were submitted to the NCBI Sequence Read Archive (SRA) under the accession number PRJNA509037 for fungi and PRJNA530825 for mycorrhizal fungi.

After sequencing, reads of both fungal and mycorrhizal fungal communities were paired and paired amplicons were subjected to additional quality filtering using QIIME v.1.3.1 (Caporaso *et al*. 2010; Magoč & Salzberg 2011). Chimeric sequences were removed using a combination of *de novo* and reference-based Chimera checking using the program UCHIME (Edgar *et al*. 2011). Quality sequences were clustered into operational taxonomic units (OTUs) at ≥ 97% sequence similarity using the UCLUST algorithm (Edgar *et al*. 2011). The UNITE database was used as reference centroids (Kõljalg *et al*. 2013) for fungi and the MaarjAM database (Öpik *et al*. 2010) was used for mycorrhizal fungi. The most abundant sequence in each cluster was designated as the representative sequence and given a taxonomic assignment using BLAST option in QIIME. The mycorrhizal fungal database was further examined to discard sequences falling outside the AM fungal clade with *Mortierella elongata* as an outgroup (House & Bever 2018). Putative pathogens from fungal community were categorised based on the FUNGuild database (Nguyen *et al*. 2016) and the RDP naïve Bayesian classifier with a > 70% confidence threshold (Wang *et al*. 2007). Only OTUs with tropic mode as 'Pathotroph' and Guild as 'Plant Pathotroph' were used for the subsequent analysis (Dataset S1). Details of DNA extraction, PCR conditions and sequencing data processing are described in the Appendix S3.

Statistical analysis

In Experiment 1, we analysed mean biomass of individuals in per pot using a mixed model with plant diversity (monoculture, 3 : 1, 2 : 2 and 2 : 2 : 1 mixture), plant combinations, soil inoculation and their interactions as fixed effects, and

with block and pot ID as random effects (SAS Institute Inc. 2009). In order to test plant frequency dependence on biomass of individual plant species, soil inoculations and proportion of that plant species were used as fixed effects. Plant biomass was log-transformed to improve homoscedasticity. Within these models, we also performed orthogonal, *a priori* contrasts (live vs. sterile, AMF vs. sterile, whole soil vs. AMF and native prairie vs. post-agricultural) to separately test the overall effects when the soil effect was significant. 'Live vs. sterile' and 'AMF vs. sterile' contrasts tested the net soil biota and AMF effect respectively. Similarly, 'whole soil vs. AMF' compared other soil biota effect with AMF culture, and 'native prairie vs. post-agricultural' compared native and disturbed soil biota effect.

The net diversity effect in the mixtures in Experiment 1 was partitioned into selection and complementarity effects using the additive partitioning diversity effect equations (Loreau & Hector 2001, Appendix S4). We also used DI models to test alternative hypotheses about the contribution of individual species and interactions of species pairs to changes in productivity of plant communities (Kirwan *et al.* 2009; Kuebbing *et al.* 2015). The species identity model (M1) tests individual plant species' effects on productivity (β_i), but not their interactions (Table 1). The interaction coefficients estimate the following: the average interaction effect across all species pairs (δ_{avg}; M2), the individual interaction effect for each species pair (δ_{ij}; M3) or the contribution of a single species in an interaction, independently of its neighbour's identity (λ_i; M4). By comparing the goodness-of-fit of model (using the corrected Akaike information criteria, AICc), we assessed which model was best for explaining diversity-productivity patterns (see Table 1 Appendix S4). The best model for each soil treatment was plotted with ternary plots in OriginPro, by interpolating a smooth surface across estimates resulting from 10 000 different combinations with different frequency ratios of three species.

After identification of OTUs, Shannon-Wiener diversity index and richness of fungal, mycorrhizal fungi and putative pathogen communities for each sample were calculated using the *diversity* function in vegan package (Oksanen *et al.* 2017) in R (version 3.5.1). As the negative PSFs were only observed for *Andropogon* in post-agricultural and native prairie soils, analyses of pathogen community were only conducted in these two soil treatments. Relative abundance of fungal (at the phylum level) and pathogen communities among different plant diversity treatments or three species monocultures was calculated and compared. Relative abundance of *Fusarium* and *Rhizoctonia* genera among different *Andropogon* frequencies was also compared as these two genera were shown to infect *Andropogon* (Holah & Alexander 1999; Lofgren *et al.* 2018). Relative abundance and diversities were analysed using mixed models as above. For the relative abundances of pathogen community, *Fusarium* and *Rhizoctonia* genera, orthogonal contrasts were conducted to compare the effects between plant monoculture and mixtures. Non-metric multidimensional scaling (NMDS) was done using the *metaMDS* function in R with Bray-Curtis distance matrix. Permutational multivariate analysis (*adonis*) with 1000 permutations was used to test whether soil microbial community was significantly affected by plant species. Significant difference of soil communities between two plant species were also compared using the *adonis* function.

In Experiment 2, we compared soil feedback effects of each species with changes in plant frequency using the Proc mixed model, with initial plant proportion (IPP) per pot and soil inoculations from Experiment 1 as fixed effects and block as the random effect. Orthogonal contrasts were performed to compare different soil inoculation effects and interactions with IPP.

RESULTS

Plant diversity-productivity relationships and interspecific interactions depend on soil microbiome

Soils with mycorrhizal fungi significantly improved plant biomass compared with sterile soil (Figs 2a and 3). A positive

Table 1 Diversity-interaction models and corrected Akaike information criteria (AICc) for four soil treatments

Model	Functions	AICc			
		Sterile	AMF	Post-agricultural	Native prairie
Null model (M0)	$y = \beta + \varepsilon$	−234.4	250.7	250.3	241.4
Species identity model (M1)	$y = \sum_{i=1}^{3} \beta_i P_i + \varepsilon$	**−255.0**	255.3	188.9	203.5
Average pairwise interactions model (M2)	$y = \sum_{i=1}^{3} \beta_i P_i + \delta_{avg} \sum_{i<j}^{3} P_i P_j + \varepsilon$	−250.4	251.0	178.6	181.7
All pairwise interactions model (M3)	$y = \sum_{i=1}^{3} \beta_i P_i + \sum_{i=1}^{3} \delta_{ij}(P_i P_j) + \varepsilon$	−242.5	**244.3**	**170.8**	**166.0**
Additive species-specific pairwise interactions model (M4)	$y = \sum_{i=1}^{3} \beta_i P_i + \sum_{i=1}^{3} \lambda_i(P_i(1-P_i)) + \varepsilon$	−241.1	245.8	172.2	167.3

The smaller of AICc value, the better the model fits to the data and the differences in AICc (> 2) indicated that the models are significantly different between each other. The best model for each soil treatment was noted with bold font.

'β' and 'δ' refer to fitted species-specific and interspecific interaction coefficients separately. The identity effect of each species i ($\beta_i P_i$) is a function of the productivity of each species in monoculture (β_i) weighted by its proportion (P_i) in the community, and interactions between two species (i and j) are modelled as the product of their proportions ($P_i P_j$).

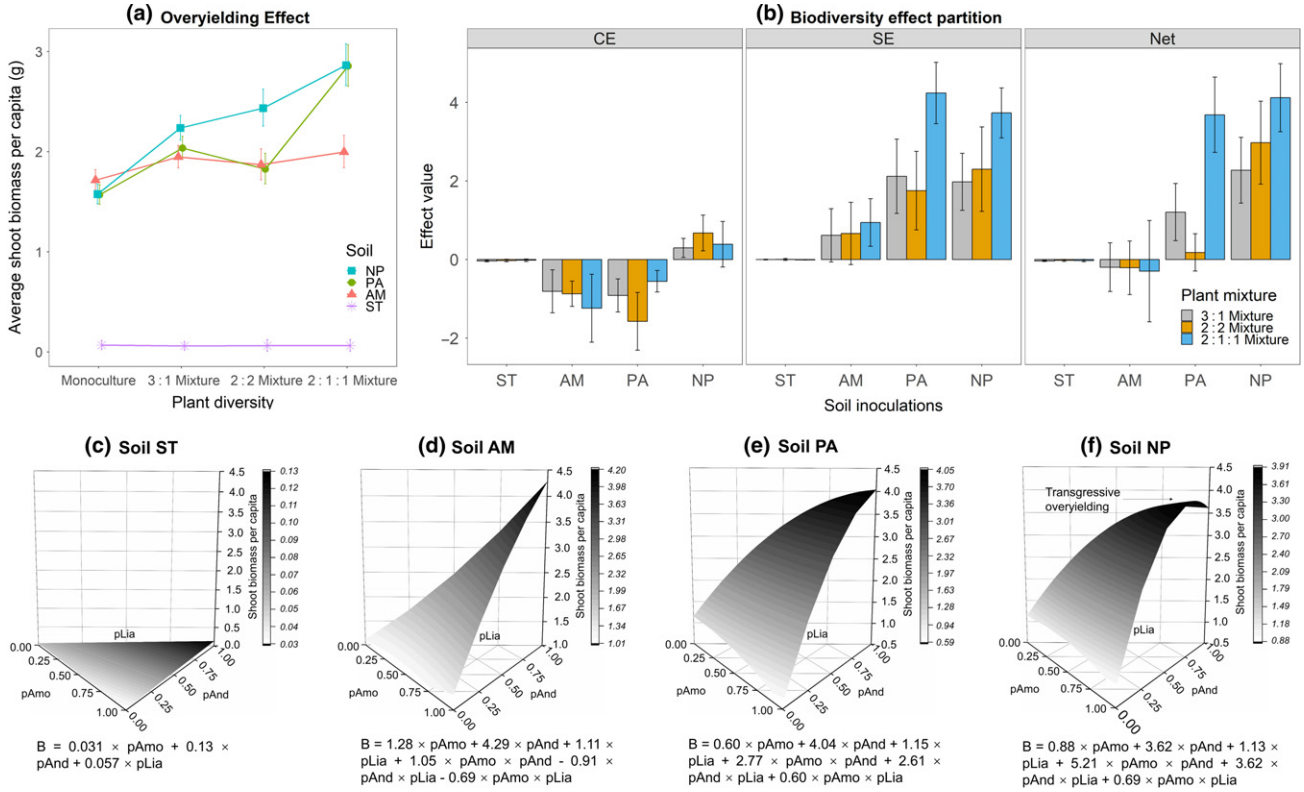

Figure 2 Average productivity (mean ± SE) of different plant community diversity (a) and the additive partition of biodiversity effects (b) in Experiment 1. 'CE', 'SE' and 'Net', respectively, represent complementarity effect, selection effect and net diversity effect. Plots c-f show how individual species and pairwise interactions between species contribute to changes of plant community shoot biomass with different combinations of plant proportions according to the diversity-interaction models. For sterile soil (ST), the best fit model (see Table 1) is the plant identity model, for AMF (AM), post-agricultural (PA) and native prairie (NP), the best fit models are the all pairwise interactions model. 'pAmo', 'pAnd' and 'pLia' represent respective proportion (0, 0.25, 0.5, 0.75 and 1) of *Amorpha canescens*, *Andropogon gerardii* and *Liatris pycnostachya* in each pot. Equations of the models are shown on the bottom of plots and 'B' represents biomass. Transgressive overyielding in plot f occurs when plant mixture yields more than any monoculture of the component species.

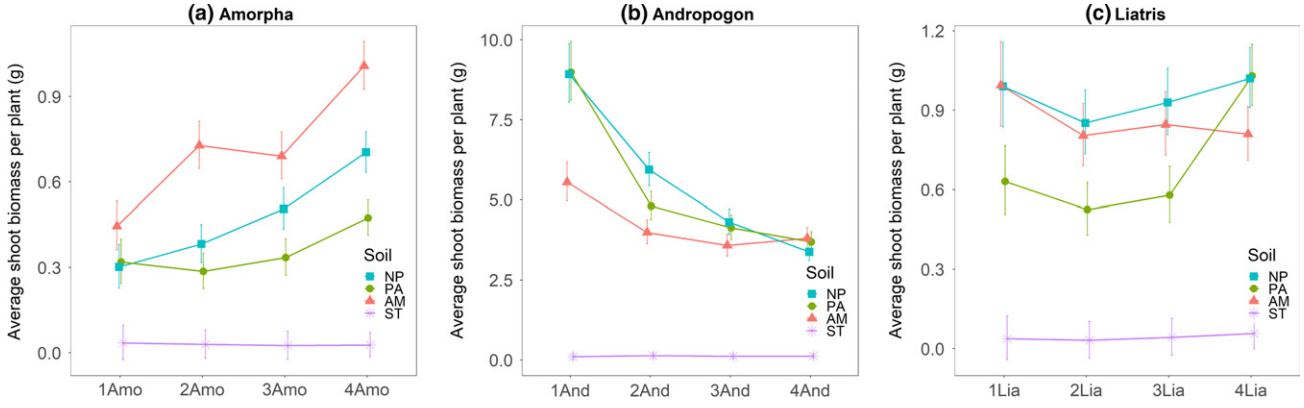

Figure 3 Average shoot biomass (mean ± SE) of *Amorpha canescens* (a), *Andropogon gerardii* (b) and *Liatris pycnostachya* (c) in Experiment 1 with increasing plant frequency in four soil treatments (e.g. panel A represents *Amorpha* growing in pots including 1, 2, 3 and 4 individuals respectively). 'ST', 'AM', 'PA' and 'NP' represent sterile, AMF, post-agricultural and native prairie soils respectively.

plant diversity-productivity relationship (overyielding) was observed in whole soil (post-agricultural and native prairie) inocula, but not in soils with AMF alone or sterile soil (Fig. 2a, Table S8). Positive net diversity effects were observed in whole soils, but not in sterile or AMF only treatments (Fig. 2b). Positive diversity effects resulted mainly from selection effects rather than complementarity effects, and positive complementarity effects were only observed when inoculated with native prairie soil (Fig. 2b). Soil microbes were important drivers of plant-plant interactions, as interspecific

interactions in the DI models only existed in live soil treatments. Diversity-productivity patterns of AMF, post-agricultural and native prairie were best explained by the all pairwise interactions model (M3), while sterile treatment only showed plant identity effects (M1) (Fig. 2c–f, Table 1). While the best model for the AMF culture treatment included both positive and negative interactive effects (Fig. 2b), the best models for the whole soil communities only included positive interactive effects, with transgressive overyielding only being predicted for native prairie soil (Fig. 2e and f).

Plant species had different responses when growing alone or interacting with other species. *Andropogon* showed negative FD (decreasing biomass with increasing own frequency) (Fig. 3b) and the effect was significantly stronger in the two whole soil treatments compared to the AMF treatment (Table S9). In contrast, *Amorpha* showed positive FD (Fig. 3a, Table S9), while *Liatris* in general did not show significant FD effect (Fig. 3c, Table S9). More subtly, *Andropogon* growth (Fig. S2), N, P concentration and uptake (Fig. S3, Fig. S4) benefited from living together with *Amorpha* and *Liatris*, while growth of the latter two species was suppressed by *Andropogon* (Fig. S2a,c). Although *Amorpha* and *Liatris* did not show many interactions in growth (Fig. S2), there was competition for N and P between them, showing a facilitation effect for *Liatris* when growing with *Amorpha* and an opposite effect for *Amorpha* in mixture with *Liatris* (Fig. S3, Fig. S4).

Fungal and mycorrhizal fungal community composition and structure

Native prairie soil showed the highest Shannon-Wiener diversity index and richness for both fungi and mycorrhizal fungi, followed by post-agricultural soil, and the AMF treatment (Fig. S5). The mycorrhizal fungal richness and diversity (Shannon-Wiener index) increased with plant diversity (Fig. S5b and d) and the increase in the Shannon-Wiener index with diversity was stronger in the two whole soils than in the AMF treatment (Fig. S5b, Table S10). The relative abundance of pathogens, in general, and of *Fusarium*, in particular, in the fungal community tended to be lower in plant mixtures than monocultures (Fig. S6a and d). The Shannon-Wiener index of fungal pathogens was significantly higher in plant monoculture relative to mixtures (Fig. S6b). The effect of plant diversity and species identity on fungal phylum composition differed between the soil treatments (Fig. S7). Basidiomycota was the dominant fungal phylum in the AMF treatment, while Mucoromycota was dominant in the whole soil treatments (Fig. S7a–c). The relative abundance of fungal phyla varied significantly among plant species in the native prairie soil treatment (Wilks' lambda $F_{8,30} = 3.96$, $P = 0.003$), but not in the AMF or post-agricultural soil treatments (Fig. S7d–f).

Soil fungal and mycorrhizal community differentiation with planting treatments occurred in the two whole soils, but not in the AMF treatments (Fig. 4). Moreover, more variance was explained by planting treatment in the native prairie than in the post-agricultural soil treatment. All pairwise comparisons of fungal and mycorrhizal communities between plant species were significantly different in native prairie soil (Fig. 4c and f), but fungal communities between *Amorpha* and *Liatris*, and mycorrhizal fungal community between *Andropogon* and *Liatris*, showed no significant difference in post-agricultural soil (Fig. 4b and e), However, for putative pathogen community, significant differentiation only occurred between *Amorpha* and *Andropogon* (Fig. 4g and h).

Soil feedback test

Live soil significantly increased plant shoot and root biomass (Fig. 5, Table S11). *Amorpha* showed positive feedback, as its biomass increased with *Amorpha* frequency in the mesocosms, and the effect was more significant in two whole soils compared with AMF, particularly for shoot biomass (Fig. 5a and b, Table S11). We also found more rhizobial nodules in pots inoculated with soil from *Amorpha* monocultures than monocultures from other species (Fig. S8, $P = 0.006$).

Andropogon showed negative feedback, as its shoot biomass declined with its frequency in the mesocosms in all three live soil types, and the effect was more significant in whole soils compared with AMF (Fig. 5c, Table S11). In contrast, root biomass was not affected by changes in composition of the mesocosms (Fig. 5d, Table S11).

In general, *Liatris* showed no difference in its growth with changes of its frequency in the mesocosms (Fig. 5e,f, Table S11).

DISCUSSION

This study identifies the importance of soil microbes in mediating plant-plant interactions and community productivity. We found that soil microbes were not only critical to the growth of late successional plants, but that more diverse and late successional soil communities drove stronger positive plant diversity-productivity relationships, which support our first hypothesis (Fig. 2a). While AMF played major roles in promoting growth of late successional plant species, AMF alone did not generate positive plant diversity-productivity relationships (Fig. 2a and b). The more complex microbial communities in post-agricultural and late successional, native prairie soils generated a positive diversity effect, largely through a strong selection effect (Fig. 2a and b). The selection effect has been shown to be dominant in the first growing season (Cardinale *et al.* 2007; Fargione *et al.* 2007; Mori *et al.* 2017). Our results suggest that the plant-microbe relationships of the dominant plant species (*Andropogon*) drove the increase in production and overyielding (Fig. 3). *Andropogon* usually produced high biomass and was a strong competitor in the presence of native mycorrhizal fungi (Wilson & Hartnett 1997; Koziol & Bever 2015), and has been involved in selection effect in previous field trials (Tilman *et al.* 2001; Fargione *et al.* 2007).

Positive complementarity, resulting in transgressive overyielding, was only observed in mesocosms inoculated with native prairie soils (Fig. 2b and f), which contained the most diverse fungal and mycorrhizal fungal communities (Fig. S5) and the fungal communities that differentiated most strongly in monocultures of the three plant species (Fig. 4, Fig. S7). Composition shifts between plant species with higher diversity

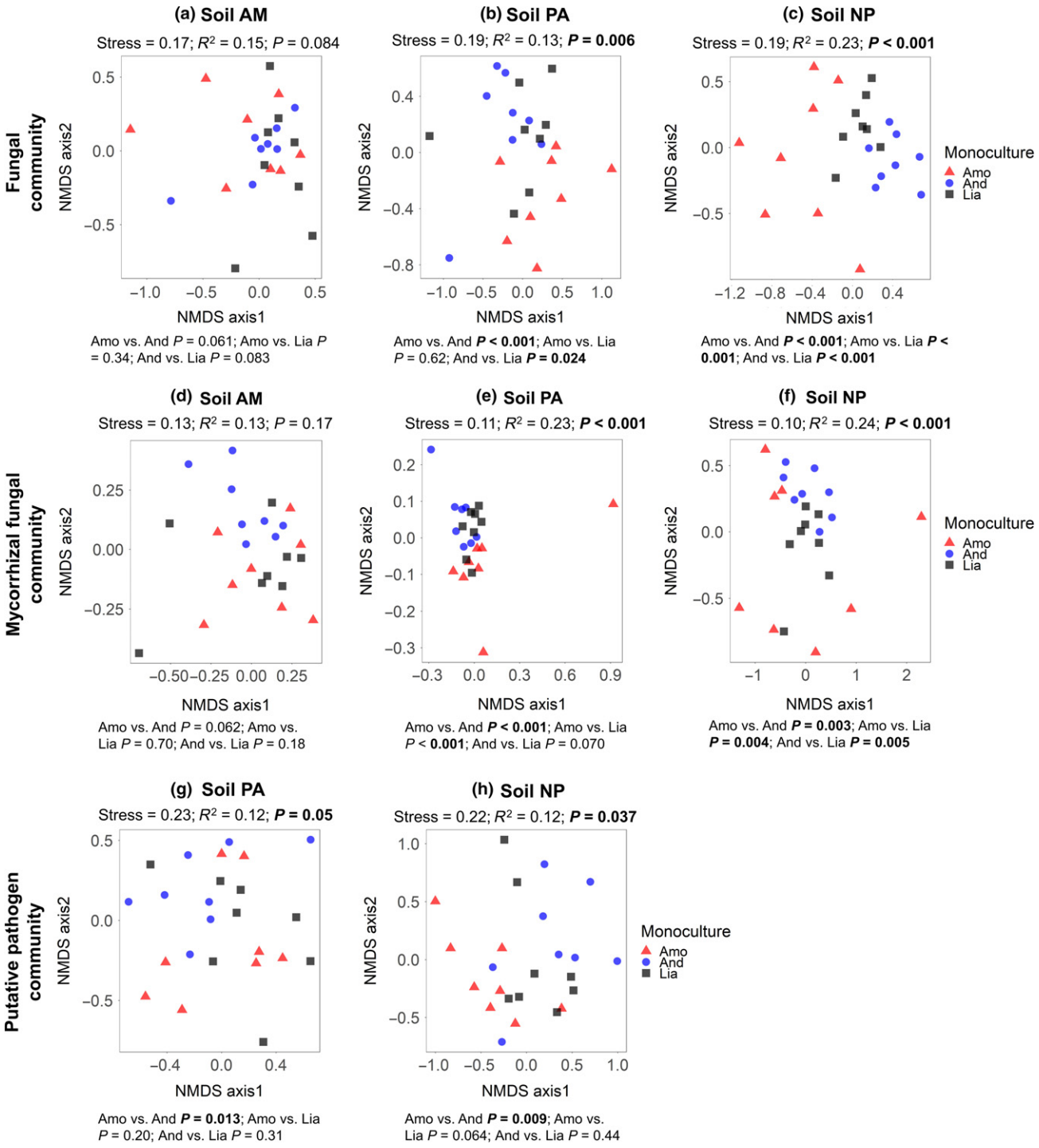

Figure 4 Non-metric multidimensional scaling (NMDS) ordinations, based on Bray-Curtis distance of fungal (a, b and c), mycorrhizal fungal (d, e and f) and putative pathogen (g and h) communities in soils conditioned by *Amorpha canescens* (Amo), *Andropogon gerardii* (And) and *Liatris pycnostachya* (Lia) monoculture. The statistical significance of plant species on soil microbial community composition is given on the top of each plot, and the statistical significance between plant species pairs is given at the bottom of each plot. Each dot corresponds to an individual sample, coloured by plant species. 'AM', 'PA' and 'NP' represent AMF, post-agricultural and native prairie inoculation treatments.

and richness in native prairie soil provided more possibilities of complementarity than competition when associating with different plant species in mixture, while the lower diversity and richness of soil microbes in post-agricultural might intensify the competition among species and resulted in only selection effect. The microbially mediated positive complementarity was likely due to host-specific pathogen dilution/suppression, which was supported by observations of reduced pathogen diversity and relative abundance in plant mixtures (Fig. S6a,c and d) as well as microbial mediation of resource

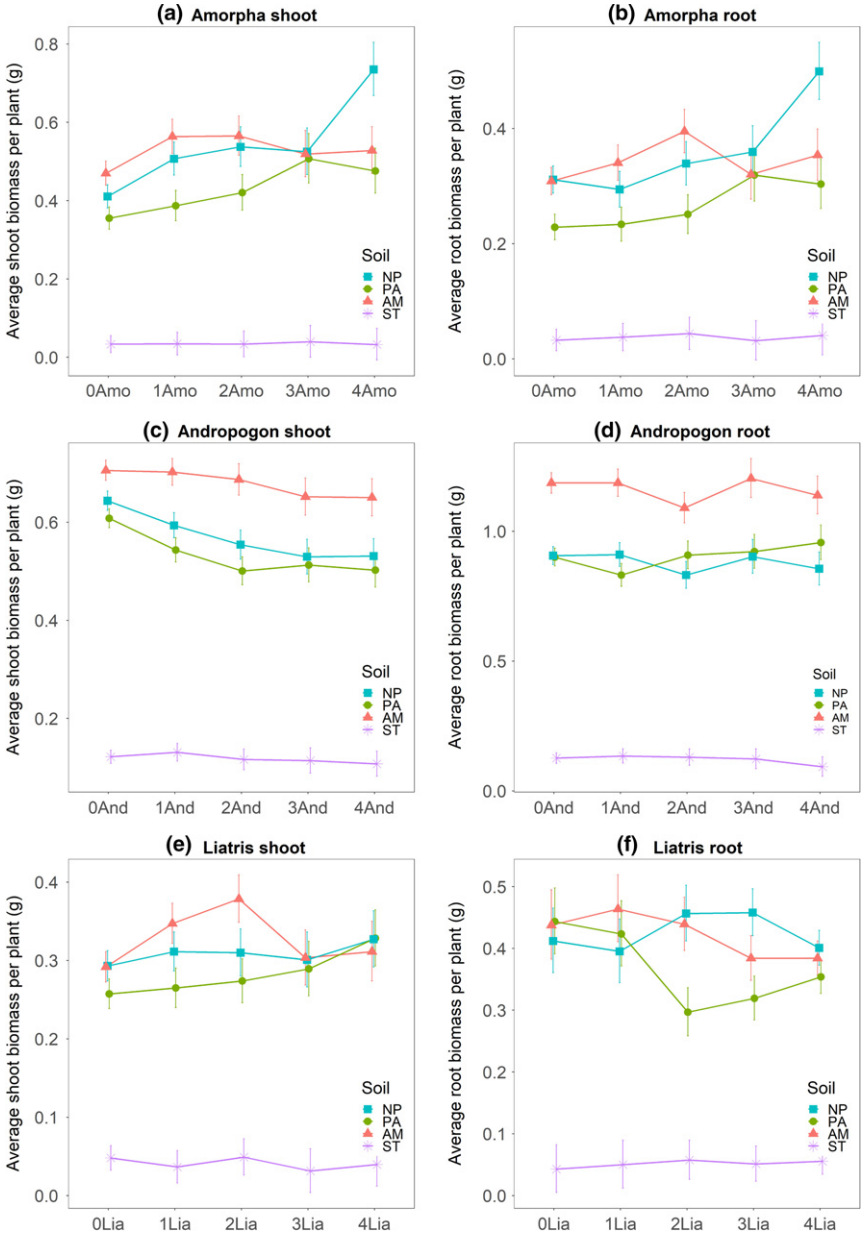

Figure 5 Shoot and root biomass (mean ± SE) of *Amorpha canescens* (a and b), *Andropogon gerardii* (c and d) and *Liatris pycnostachya* (e and f) in Experiment 2. Soils used in this experiment were conditioned in Experiment 1 by different planting combinations with increase of plant frequency (e.g. five treatments in *x*-axis of plot A represent soils conditioned in Experiment 1 planted with 0, 1, 2, 3 and 4 *Amorpha* individuals respectively). 'ST', 'AM', 'PA' and 'NP' represent sterile, AMF, post-agricultural and native prairie soils respectively.

partitioning via nitrogen fixation (Figs S3 and S4). This supports previous evidence of the importance of these two microbial mechanisms (Hooper & Dukes 2004; Marquard *et al.* 2009; Maron *et al.* 2011; Schnitzer *et al.* 2011; Barry *et al.* 2019). Interestingly, the biggest differences between post-agricultural and native prairie soils occurred in the 2 : 2 mixture (Fig. 2a), suggesting that plant evenness played a critical role in microbial-mediated productivity benefit. This result adds to the evidence of the importance of plant evenness on diversity-productivity relationships (Wilsey & Potvin 2000; Kirwan *et al.* 2007). Our observation of the strongest complementarity effects when combining late successional plant species with late successional soil communities is also consistent with the observations of positive complementarity increasing with time since the establishment of experiments (Cardinale *et al.* 2007; Fargione *et al.* 2007; Mori *et al.* 2017).

This work supports our second hypothesis and previous results suggesting that negative PSFs drive positive plant diversity-productivity relationships, as pathogenic effects are diluted or suppressed in higher-diversity communities, thus contributing to overyielding (Maron *et al.* 2011; Schnitzer *et al.* 2011; Kulmatiski *et al.* 2012). In this study, *Andropogon* experienced negative FD and PSFs (Fig. 3b, Fig. 5c), which resulted in more biomass per plant in polyculture than

monoculture and in soils conditioned by other species than by its monoculture. Negative feedbacks in *Andropogon* were also reported in other studies (Casper & Castelli 2007; Herzberger *et al*. 2015) and fungal pathogens have been previously isolated and identified from *Andropogon* roots (Holah & Alexander 1999; Lofgren *et al*. 2018). *Andropogon* had the highest relative growth rate and competitive ability in our study (Fig. 3, Fig. S2), and its sensitivity to pathogens is consistent with a trade-off between resource acquisition and defence against consumers for plant growth (Lind *et al*. 2013; Bever *et al*. 2015). However, the negative pathogenic effects could be reduced when growing with heterospecific plants or in heterospecific soils due to dilution or suppression of pathogens by differentiation of soil communities (Fig. 4, Fig. S7). This dilution effect was partly supported by the relatively reduced relative abundance of pathogens and *Fusarium* in the fungal community in soil conditioned by plant mixtures compared with monoculture (Fig. S6a and d). The decrease in diversity of pathogens in plant mixtures (Fig. S6b) is consistent with pathogen suppression by a more complex microbial community (Fig. S5). As accumulation of pathogens on plants is time-dependent (Mitchell *et al*. 2010), we expect that the pathogen dilution/suppression effect would become more important in increasing plant diversity effects on productivity with time (Eisenhauer *et al*. 2012).

Consistent with the third hypothesis, our evidence of an important role of microbial mediations of resource partitioning in generating overyielding comes from multiple sources. *Amorpha* as a legume, might rely more on atmospheric N_2, reducing competition for soil N with *Andropogon* and *Liatris* (Figs S3 and S4). *Andropogon* and *Liatris* could also indirectly benefit from *Amorpha*'s N-fixation through root decomposition or leakage (Mulder *et al*. 2002; Temperton *et al*. 2007; Mueller *et al*. 2013). In this scenario, the stronger the *Amorpha*-rhizobia symbiosis, the greater potential benefits of resource facilitation. We observed significant positive FD and PSFs for *Amorpha*, particularly with native, late successional soil communities (Figs 3a and 5a,b), which were consistent with reinforcement of beneficial rhizobial communities following conditioning by *Amorpha* (Fig. S8). While positive FD and PSFs themselves would generate negative diversity-productivity relationships (i.e. underyielding), the strengthening of the rhizobia mutualism may enhance resource partitioning and facilitation through increased N availability. Consistent with this possibility, we found higher N concentration and uptake in *Amorpha* tissue when grown in monoculture than in mixture (Fig. S3a, Fig. S4a). Additionally, we also found higher N concentration and uptake in *Andropogon* and *Liatris* when grown in mixture with *Amorpha* than in monoculture (Figs S3 and S4). *Andropogon* might have also benefited from facilitation via shared mycorrhizal fungi community in mixture, in particular with *Liatris* (Fig. 4e and f), with potentially intensifying N and P supplement (panel c,d in Fig. S3, Fig. S4). The N and P uptake are usually promoted mutually, as N is very dependent on P due to the high ATP requirement per mole N fixed (Vance *et al*. 2003) and P uptake can be very demanding of N as mycorrhizal fungi have a 10 : 1 C: N ratio that needs to be invested by plants (Johnson 2010). Our observation of increased diversity of mycorrhizal fungi with increasing plant diversity also provides a qualitative connection between positive productivity responses to plant diversity, as shown here, and previous work showing positive plant productivity responses to increasing mycorrhizal fungal richness (van der Heijden *et al*. 1998; Vogelsang *et al*. 2006). Thus, rhizobia and AMF regulated resources uptake can result in enhanced plant growth, in particular for *Andropogon*, and further drive overyielding.

Though our study was of mesocosms, the positive diversity-productivity relationships we found were consistent with other studies, including field studies, suggesting that resources partitioning (Hooper & Dukes 2004; Marquard *et al*. 2009) and negative PSFs (Maron *et al*. 2011; Schnitzer *et al*. 2011) caused by symbionts and pathogens, respectively, contribute to the observed outcomes. Negative soil feedbacks and strong pathogen effects were previously observed in *Andropogon* (Casper & Castelli 2007; Herzberger *et al*. 2015). Positive feedback observed in *Amorpha* is consistent with positive responses to late successional AMF in lab and field studies (Koziol & Bever 2016, 2017) and with previous studies of late successional species in general (Kardol *et al*. 2006; Bauer *et al*. 2015). Furthermore, previous observations of synergism in growth of *Amorpha* in association with native rhizobia and native mycorrhizal fungi are consistent with positive feedback (Larimer *et al*. 2014).

We found support for microbial mechanisms that would mediate plant species coexistence. The importance of negative FD for coexistence in species-rich communities has been well reported (Petermann *et al*. 2008; Comita *et al*. 2010; Mangan *et al*. 2010; Eppinga *et al*. 2018). Here in this study, although *Andropogon* showed higher growth rate and higher competitive ability than the other two species, negative FD can allow other plants to coexist. Other studies have also shown that pathogens having more detrimental effects on dominant plants than on subordinates can increase plant diversity (Bagchi *et al*. 2014; Bever *et al*. 2015; Laliberté *et al*. 2015). In this study, we also provide evidence of resource facilitation of *Andropogon* when grown with the other two species. As both negative PSFs and microbially mediated resources partitioning can mediate plant species coexistence (Bever *et al*. 2010), we show support for a consistency between mechanisms potentially driving coexistence and those driving positive diversity-productivity relationships.

In conclusion, our research suggests that positive diversity-productivity relationships in late successional plant community occur with higher soil microbial diversity and richness, and that this context dependence results from the operation of two microbial mechanisms: pathogen dilution/suppression and microbially mediated resources partitioning, each of which was strongest in the most diverse community. We found a correspondence of the direction and magnitude between PSFs and FD, which varied with plant species, with overyielding resulting from negative PSFs and negative FD. Given the critical role that we found both for microbial diversity and late successional microbiome composition in generating overyielding in late successional plant communities, our results identify a functional benefit of restoration of soil microbial composition following anthropogenic degradation of soil communities.

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AUTHORSHIP

GW, PS and JDB designed the project and GW performed experiments and collected data. GW, AT and JDB performed statistical analyses, with substantial input from JZ and FZ on data interpretations. GW wrote the first draft of the manuscript. All authors contributed substantially to manuscript revisions.

DATA ACCESSIBILITY STATEMENT

The data used in this study are available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.7441343.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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