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RESEARCH ARTICLE

Microbial mediators of plant community response to long-term N and P fertilization: Evidence of a role of plant responsiveness to mycorrhizal fungi

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Abstract

Climate changes and anthropogenic nutrient enrichment widely threaten plant diversity and ecosystem functions. Understanding the mechanisms governing plant species turnover across nutrient gradients is crucial to developing successful management and restoration strategies. We tested whether and how soil microbes, particularly arbuscular mycorrhizal fungi (AMF), could mediate plant community response to a 15 years long-term N (0, 4, 8, and 16 g N m^{-2} $year^{-1}$) and P (0 and 8 g N m^{-2} $year^{-1}$) enrichment in a grassland system. We found N and P enrichment resulted in plant community diversity decrease and composition change, in which perennial C_4 graminoids were dramatically reduced while annuals and perennial forbs increased. Metabarcoding analysis of soil fungal community showed that N and P changed fungal diversity and composition, of which only a cluster of AMF identified by the co-occurrence networks analysis was highly sensitive to P treatments and was negatively correlated with shifts in percentage cover of perennial C_4 graminoids. Moreover, by estimating the mycorrhizal responsiveness (MR) of 41 plant species in the field experiment from 264 independent tests, we found that the community weighted mean MR of the plant community was substantially reduced with nutrient enrichment and was positively correlated with C_4 graminoids percentage cover. Both analyses of covariance and structural equation modeling indicated that the shift in MR rather than AMF composition change was the primary predictor of the decline in perennial C_4 graminoids, suggesting that the energy cost invested by C_4 plants on those sensitive AMF might drive the inferior competitive abilities compared with other groups. Our results suggest that shifts in the competitive ability of mycorrhizal responsive plants can drive plant community change to anthropogenic eutrophication, suggesting a functional benefit of mycorrhizal mutualism in ecological restoration following climatic or anthropogenic degradation of soil communities.

KEYWORDS
fertilization, mycorrhizal responsiveness, nitrogen, phosphorus, plant community composition

1 | INTRODUCTION

Maintaining and protecting biodiversity is vital for the sustainable development of the earth's resources (Balvanera et al., 2006; Cardinale et al., 2012; Isbell et al., 2011). However, agricultural fertilization, heavy stocking densities, and human activities like fossil fuel combustion are threatening ecosystems across the globe with continuous N and P inputs (Guignard et al., 2017; Smith et al., 1999). Atmospheric N deposition has increased three times compared to pre-industrial levels in many parts of the world (Carpenter et al., 1998; Galloway et al., 2008; Ti et al., 2018), and remains high in the regions undergoing industrialization although declined in North America and Europe in recent years (Engardt et al., 2017; Gilliam et al., 2019). The atmospheric P deposition has increased 44.4% in the most recent two decades compared to the prior 40 years, in particular in Asia and Europe (Pan et al., 2021). Although elevated N and P could promote plant productivity as most natural terrestrial land areas are N and P limited (Du et al., 2020), soil N and P loadings threaten biodiversity and ecosystem functions important to human well-being (Tilman & Lehman, 2001). Plant diversity and plant community stability have been shown to decline with N (Han et al., 2019; Isbell et al., 2013; Reich, 2009; Simkin et al., 2016) and P accumulation (Ceulemans et al., 2014; Gilbert et al., 2009). Diversity loss in response to nutrient enrichment is often accompanied by changes in species composition, with native and perennial grassland species frequently showing greater vulnerability to decline than non-native or annual species (Avolio et al., 2014; Bai et al., 2010; Clark & Tilman, 2008; Flores-Moreno et al., 2016; Foster et al., 2011). Previous studies have attributed such changes in composition to the alteration of competitive relationships among functional groups driven by abiotic factors, including the direct effect of fertilization (Dean et al., 2014), indirect effects through changes in soil properties like heavy metal accumulation, and soil acidification (Kleijn et al., 2008; Stevens et al., 2004; Tian et al., 2016), responses of N:P ratios (Jiang et al., 2019) and light limitation (Hautier et al., 2009). However, how soil biotic factors mediate plant community composition changes in responses to N and P enrichment remains elusive.

As important engineers of soil nutrient transformation and elements cycling, the soil microbiome has drawn increasing attention as a driver of plant community dynamics (Bever et al., 2012; Van Der Heijden et al., 2008). As the most widely spread symbiont, AMF play a significant role in mediating interspecific interactions and population dynamics of plants (Bennett et al., 2017; Hiiesalu et al., 2014; Van der Heijden et al., 1998). However, AMF abundance and composition are also affected by nutrients, where both N and P enrichment generally have a negative influence on the abundance of mycorrhizal fungi, although the effect of P is larger than N (Han et al., 2020; Maitra et al., 2021; Treseder, 2004). Some investigations showed that high levels of N fertilization suppressed AMF biomass or abundance (Bradley et al., 2006; Jeske et al., 2018), while others found no significant effect (Tian et al., 2013; Williams et al., 2013). P fertilization has been shown to strongly suppress AMF abundance or diversity (Camenzind et al., 2014; Chen et al., 2014), while increased AMF abundance and biomass were also observed under P addition, as P addition has been shown to promote AMF growth and proliferation in soils that are strongly P limited (Grant et al., 2005; Treseder & Allen, 2002). As plants have trade-offs between nutrient acquisition and symbiotic associations, AMF-mediated plant interactions should be context-dependent (Johnson, 2010). For instance, plants have been shown to reduce their allocation to beneficial symbionts with P fertilization which is predicted to result in less-efficient symbionts dominating fertilized fields (Bever, 2015; Ji & Bever, 2016). Therefore, plants with high mycorrhizal responsiveness (MR) under P enrichment may weaken their competitive abilities due to carbon allocation into belowground compared with low responsive plants, resulting in the alternations of plant community dynamics. Thus, changes in AMF community composition or MR of plants could be potential mediators of shifts in plant community composition in response to different nutrient conditions.

Other fungal groups, like fungal pathogens (Schnitzer et al., 2011; Wang et al., 2019) and saprotrophic fungi (Veen et al., 2019) also impact plant diversity and plant community productivity. The composition and function of these fungi are affected by nutrients as well. Saprotrophic fungi are important decomposers of plant litter in terrestrial ecosystems, and several studies have found that N (Allison et al., 2009; van Diepen et al., 2017) and P (Xu et al., 2018) enrichment reduce the ability of saprotrophic fungi to decay organic litter. However, a recent study in 25 grasslands covering four continents found that N and P addition promoted a relative abundance of fungal pathogens while saprotrophs were not affected (Lekberg et al., 2021). The N effect on fungal pathogens is likely greater than P, as P addition can enhance plant health and tends to decrease susceptibility to pathogens (Veresoglou et al., 2013; Walters & Bingham, 2007). Such degradation or stimulation of fungal communities under nutrient additions could change their interactions with plants, resulting in shifts in plant community composition.

The microbial-mediated feedback effects on plant growth and composition changes are related to plant functional traits and successional position (Cortois et al., 2016; Wilschut et al., 2019). For example, fine root (≤2 mm in diameter) plants have a larger root surface area for nutrient absorption and utilization, and they tend to have a lower mycorrhizal infection rate than coarse root (>2 mm in diameter) plants (Cortois et al., 2016; Wen et al., 2019), but with higher susceptibility to pathogen colonization (Emmett et al., 2014). Slow-growing and late-successional, plants, usually have a higher dependence and responsiveness to mycorrhizal fungi than fast-growing plants (Koziol & Bever, 2015), as fast-growing plants are more likely to use available soil nutrients via direct uptake. Moreover, early successional plant species are less sensitive to changes in AMF identity, while changes in AMF composition can have large effects on late-successional plant species (Cheeke et al., 2019). With the trade-off between resource acquisition and defense, early successional plants are often subjected to negative plant-soil feedback resulting from the accumulation of host pathogens (Bauer et al., 2015; Kardol et al., 2006), while also being subject to positive plant-soil feedback (PSF) resulting

from tissue decomposition by saprotrophs (Zhang et al., 2016). Therefore, how soil fungi affect individual plant performance and consequent community composition under nutrient addition should be species-specific and depend on which microbes are sensitive to nutrients.

While the microbial-dependent effects are better understood to explain plant community dynamics, a major challenge is to link microbial composition to function. The capacity of soil microbial functions is not the sum of its individual components, as microbial species strongly and frequently interact with each other and form a complex network (van der Heijden & Hartmann, 2016). These interactions potentially influence plant-plant interaction via direct consequences of relative fitness changes of different microbial taxa. Microbial taxa that frequently co-occur with other taxa as keystone species may play a key role within the microbiome as they might interact with other taxa (Banerjee et al., 2018; van der Heijden & Hartmann, 2016), which potentially has a larger regulatory effect on the plant community. However, some other studies have found that rare microbial taxa play a more important role in influencing ecosystem functions under changes in environmental conditions (Kurm et al., 2019; Yachi & Loreau, 1999). Therefore, it is unclear which microbial guilds with specific ecological clusters are sensitive to nutrients and how they contribute to changes in plant community composition with nutrient enrichment.

Using a long-term field experiment conducted in temperate grassland, we investigated the impact of N and P enrichment on plant community composition and evaluated the potential for the soil fungi to mediate the observed changes. We evaluated AMF and non-symbiotic fungal communities using amplicon and co-occurrence network analysis, to explicitly understand whether and how soil microbiome components predict the shift of plant community composition in response to the nutrients addition. We specially ask: (1) Which plant and microbial functional groups are sensitive to N and P enrichment? (2) Which kind of sensitive microbes are potential mediators of plant community changes in response to N and P addition? Finally, we used analysis of covariance and structural equation modeling to test the hypothesis that changes in microbiome composition mediate the plant community response to N and P enrichment.

2 | MATERIALS AND METHODS

2.1 | Field experiment and soil sampling

The long-term field experiment was established in 2001 at the University of Kansas Field Station (39°02'56" N, 95°11'35" W), which is located in eastern Kansas, USA (Foster et al., 2011). The field site has a long history of tillage but had been abandoned from hay production for a number of years and was dominated by introduced cool-season grasses just prior to the establishment of the experiment. Climate is humid continental with a mean annual temperature of 12.9°C and mean annual precipitation of 93.0 cm. Precipitation is unimodal, peaking in June. Soils are moderately productive Pawnee clay loam and Grundy silty clay loam (Kettle & Whittemore, 1991). The total N deposition in this region is about 9.38 kg ha^{-1} $year^{-1}$ (U.S. Environmental Protection Agency, 2019). Previous work at the site has shown that plant species composition and community dynamics are highly responsive to N enrichment and that plant productivity is generally more limited by N than P (Dickson & Foster, 2008; Foster et al., 2011).

Starting in 2002, fertilizer treatments were applied annually to a set of 4 × 5 m plots distributed equally among six experimental blocks. Fertilizer treatments included four levels of nitrogen (0, 4, 8, and 16 g N m^{-2} $year^{-1}$) crossed factorially with two levels of phosphorus (0 and 8 g P m^{-2} $year^{-1}$). Soil samples (0–20 cm) were collected in February 2017 from each plot for DNA sequencing and physiochemical analysis. See details in Appendix.

2.2 | Vegetation percentage cover survey and coefficients of conservatism

We conducted percentage cover surveys of vegetation during the mid-growing season (late June–early July 2017). This was done by taking ocular estimates of percentage cover for each species rooted within two permanently marked 1 × 1 m sampling quadrats in each plot. Plant composition for each plot was determined by combining data from each quadrat, constructing a species list for the plot, and then calculating the mean cover of each species across the two quadrats. For each plot, we standardized percentage cover estimates to 100%.

Coefficients of conservatism (hereafter Cc value) was developed as an indicator of a species' sensitivity to anthropogenic disturbance and is used in Floristic Quality Assessment as a means of assessing the ecological value of an area (Bauer et al., 2018). It is likely that these values reflect a plant species' life history, with low Cc values expected for ruderal species and high Cc values expected for late-successional competitive or stress-tolerant species (Taft et al., 1997). Therefore, the Cc value could be effective in predicting plant community composition changes in responses to different N and P gradients. The Cc values were assigned to the flora of Kansas (Freeman & Morse, 2002).

2.3 | MR meta-data collection

We evaluated the MR of plant species based on six previous experimental or meta-analysis studies (Bauer et al., 2018; Chaudhary et al., 2016; Cheeke et al., 2019; Koziol & Bever, 2015, 2016; Wilson & Hartnett, 1998), and one unpublished work done by our group (Dataset S1). MR for each plant/fungal isolate combination was determined using the following equation:

$$MR = \ln \frac{\text{average plant biomass with AMF inoculation}}{\text{average plant biomass without inoculation}} \quad (1)$$

In the database, plants must be grown in monoculture and have a growth response (shoot or total biomass) with isolates of AMF and uninoculated controls. If there were more than one plant species or AMF isolate tested in the paper, the experiments were analyzed separately as independent studies. For each study, plant biomass of inoculated and control treatments was taken directly from the manuscript or requested from the authors. After collection, we filtered out 41 plant species reported in 264 independent studies that overlapped with the plants in the field experiment. We extracted the estimated mean responsiveness from each of these 41 plant species using a mixed model meta-analysis that identified the study as a random effect in Metafor in R (Viechtbauer, 2010). These 41 species represent on average 82.2% of the plant cover in the plots. We then analyzed the correlations between MR and percentage cover of different species under different N and P levels.

To test the contributions of MR to plant community, community-weighted mean (CWM) values were calculated using data from each plot under N and P addition treatments (Garnier et al., 2004):

$$\mathrm{CWM} = \sum_{i=1}^{n} P_i \times \mathrm{MR}_i \quad (2)$$

where P_i is the percentage cover of species i in the plant community, n is the number of species in each plot, and MR_i is the value of species i. While there is interspecific variation between species, CWMs are likely to capture traits variations at the community level with significant species turnover over large environmental gradients (Boeddinghaus et al., 2019). In addition, CWM-Cc values were also calculated to assess the plant life-history changes along N and P levels.

2.4 | DNA extraction, sequencing, and processing

Subsamples of each plot were thoroughly mixed and 0.25 g was used for DNA extraction. The fungal primers fITS7/ITS4 (Ihrmark et al., 2012) and mycorrhizal fungal primers fLROR/FLR2 (House & Bever, 2018) were amplified and barcoded, respectively. Sequencing was performed by Illumina MiSeq v3 PE300 Next-Gen Sequencer in Genome Sequencing Core of University of Kansas, and sequences were submitted to the NCBI Sequence Read Archive (SRA) under the accession number of PRJNA749886. After sequencing, barcodes and primer sequences were removed, and paired amplicons were subjected to additional quality filtering using QIIME v.1.3.1 (Caporaso et al., 2010; Magoč & Salzberg, 2011) and chimera removal was done by UCHIME (Edgar et al., 2011). Quality sequences were clustered into operational taxonomic units (OTUs) at ≥97% similarity using the UCLUST algorithm (Edgar et al., 2011), followed by molecular identification of fungi and AM fungi based on the UNITE (Kõljalg et al., 2013) and MaarjAM database (Öpik et al., 2010), respectively. The OTUs with only one sequence (singletons) were discarded to preclude the inclusion of sequences from potential contamination or sequencing errors. The most abundant sequence in each cluster was designated as the representative sequence and taxonomic assignment was conducted in QIIME using the BLAST option. FUNGuild was used to annotate fungal OTUs into groups of pathogens and saprotrophs (Nguyen et al., 2016). Only OTUs with trophic mode as "Pathotroph" and Guild with "Plant Pathotroph" were used as fungal pathogens and with trophic mode as "Saprotroph" for the subsequent analysis. Details of DNA extraction, PCR conditions, and sequences processing were provided in the Appendix.

2.5 | Statistical analysis

Shannon diversity and richness of the whole plant community in each plot were calculated using the diversity function in the *vegan* package (Oksanen et al., 2017) in R (version 3.5.1). We separated the vegetation into eight functional guilds to examine N and P effects on the plant community composition: annual graminoids; annual forbs; biennials; perennial C_3 graminoids; perennial C_4 graminoids; perennial forbs; perennial legumes; woody plants. Annual graminoids and forbs were combined to one guild for simplicity, and biennials and woody plants were not included in the subsequent analysis due to low abundance overall (0.055% and 1.74% on average, respectively). We analyzed Shannon diversity and richness of the whole plant community, percentage cover of each functional guild, CWM-Cc values using a mixed model with N, P and their interactions as fixed effects, and with block as random effects (SAS Institute, 2009). To compare how MR mediated the outcomes of perennial graminoids and legumes percentage cover to N and P additions, analysis of covariance (ANCOVA) was conducted in R based on Type II sum of squares, with CWM-MR as covariates. We analyzed mean MR using a mixed model with plant species as a fixed effect and independent study ("Last_name" in Dataset S1) as a random effect. Within these models, the estimated MR of each plant species was used for establishing correlations with percentage cover. The regression coefficients and the functions' significance were obtained with the *lm* function in R (version 3.5.1). Additionally, we assessed correlations between CWM-MR values and percentage cover of perennial C_4 graminoids as well as CWM-MR values.

Shannon-Wiener diversity and richness of mycorrhizal fungi, total fungi, fungal pathogen, and saprotroph communities for each sample were calculated using the *diversity* function in R. Relative abundance of fungi and AMF at the genus level among different nutrient treatments were calculated and compared. Relative abundance and diversity were analyzed and compared among different N and P using the *lm* function in R for the ANOVA test, and their relationships with percentage cover of perennial C_4 graminoids were constructed. Principal coordinates analysis (PCoA) was done in R with the Bray-Curtis distance matrix. Permutational multivariate analysis of variance (PERMANOVA, *adonis* function in vegan package) with 1000 permutations were conducted to test whether soil microbial communities were significantly affected by N and P fertilization.

Given the responses of OTUs to N and P, fertilization was variable, we used two complementary approaches to identify those

OTUs that were significantly affected by N and P fertilization (Hartman et al., 2018). First, we used indicator species analysis to assess the degree of preference and significance of each OUT for the association to one or a combination of N and P treatments using the *multipatt* function in the *indicspecies* R package (De Cáceres et al., 2010) The analysis was conducted with 10^4 permutations and considered significant at $p < .05$. Additionally, the *edgeR* package (Robinson et al., 2010) was used for differential OTU analysis, by creating an object with the *DGEList* function for different N and P treatments. OTUs whose abundances were identified as differing between N and P treatment at a false discovery rate (FDR) corrected value of $p < .05$ were considered to be N and P responsive. OTUs that were confirmed by both indicator species and *edgeR* analyses as N and P sensitive OTUs (sOTUs).

To understand which microbes are sensitive to N and P enrichment and whether they possess specific network properties, we constructed the AMF, fungal pathogen, and saprotroph networks to detect the correlations between the relevant OTUs and visualize the sOTUs within the networks. For AMF, fungal pathogen, and saprotroph, 1241, 167, and 814 OTUs were used, respectively, to construct each network. First, the quality OTU sequences were normalized using the "trimmed means of M-values" (TMM) method with the BioConductor package *edgeR* (10), and the normalized OTU counts were expressed as relative abundance counts per million (CPM) (Hartman et al., 2018). For all networks, Spearman rank correlations between OTUs were calculated with a coefficient larger than 0.7 and the significance *p*-value smaller than .001. We identified network modules (ecological clusters) by implementing the cluster_fast_greedy function (Clauset et al., 2004). The modules are soil taxa strongly interacting with each other within groups than between them, which is a way to explore community structure within the microbial networks. We calculated the relative abundance of sOTUs by averaging the standardized CPM with each module. In addition, keystone OTUs were chosen from the networks and defined as those nodes within the top 1% of node degree values (Hartman et al., 2018). All co-occurrence networks were also visualized in igraph (Csardi & Nepusz, 2006) by implementing the FruchtermanReingold layout with 10^4 permutations.

The structural equation model (SEM) was constructed to investigate the possible causal relationships among N, P, sensitive AMF OTUs, and MR which were determined to affect perennial C_4 graminoids. The model was constructed in AMOS 21.0 (Arbuckle, 2006). We tested the fitness of the model with the data using the maximum likelihood estimation, with Chi-square (χ^2), root mean square error of approximation (RMSEA), goodness of fit index (GFI), comparative fit index (CFI), Tucker-Lewis Index (TLI), Akaike information criterion (AIC), and Bayes information criterion (BIC) used to evaluate model fit based on the Bollen-Stine bootstrap test. The model had a good fit when the CFI value was close to 1 and the *p* values of the statistics were high (traditionally > .05). With a good model fit, we were able to interpret the path coefficients of the model and their associated *p*-values. A path coefficient is analogous to the partial correlation coefficient and describes the strength and sign of the relationship between two variables.

3 | RESULTS

3.1 | Plant community responses to N and P enrichment

Both N and P addition increased soil N and P concentration, respectively, while no significant effect was found on soil pH and organic matter (Figure S1). Nutrient enrichment decreased Shannon diversity and richness of the plant community at the highest nutrient level (N16P8) (Figure S2). Nutrient enrichment decreased perennial plant cover, in particular the perennial C_4 graminoids, which was negatively affected by both N ($F_{3,35} = 13.0$, $p < .001$) and P ($F_{3,35} = 11.6$, $p = .0016$) individually but without interaction ($F_{3,35} = 1.64$, $p = .20$, Figure 1). Additionally, perennial legumes also showed decreasing cover with N addition, however, N addition increased percent coverage of annuals and perennial forbs (Figure 1).

3.2 | Microbial community responses to N and P enrichment

N and P enrichment did not significantly affect OTU richness of the AMF, fungal, and fungal saprotroph communities (Figure S3a,b, Figure S4a,b, Figure S5a,b), but increased fungal pathogen richness (Figure S6a,b). For Shannon diversity, the N effect was not significant in general while P increased the AMF and fungal pathogen diversity (Figure S3c,d, Figure S6c,d) but decreased total fungal and fungal saprotroph diversity in P8 compared to P0 (Figure S4c,d, Figure S5c,d). Similarly, AMF, total fungal community and fungal saprotroph composition were significantly affected by P but not N (Figure 2a,b, Figure S7a,b, Figure S8c,d) while fungal pathogen composition was influenced by both N and P (Figure S8a,b). For the AMF community at genera level, N increased *Glomus* ($F_{3,35} = 4.91$, $p = .006$) but decreased *Claroideoglomus* ($F_{3,35} = 3.42$, $p = .027$) relative abundance (Figure 2c). P increased *Paraglomus* ($F_{1,35} = 27.4$, $p < .001$) but decreased *Rhizophagus* ($F_{1,35} = 12.4$, $p = .001$) relative abundance (Figure 2d). For the fungal community, N increased the relative abundance of *Delicatula* ($F_{3,35} = 7.26$, $p < .001$) while P decreased *Delicatula* ($F_{1,35} = 10.4$, $p = .003$) and *Leohumicola* ($F_{1,35} = 43.6$, $p < .001$) relative abundance (Figure S7c,d).

3.3 | AMF sOTUs negatively correlated with percentage cover of perennial C_4 graminoids

No significant correlations between percentage cover of perennial C_4 graminoids and relative abundance, Shannon diversity, and richness of three microbial groups (AMF, fungal pathogens, and saprotrophs) were found (Figure S9). We further identified the sensitive

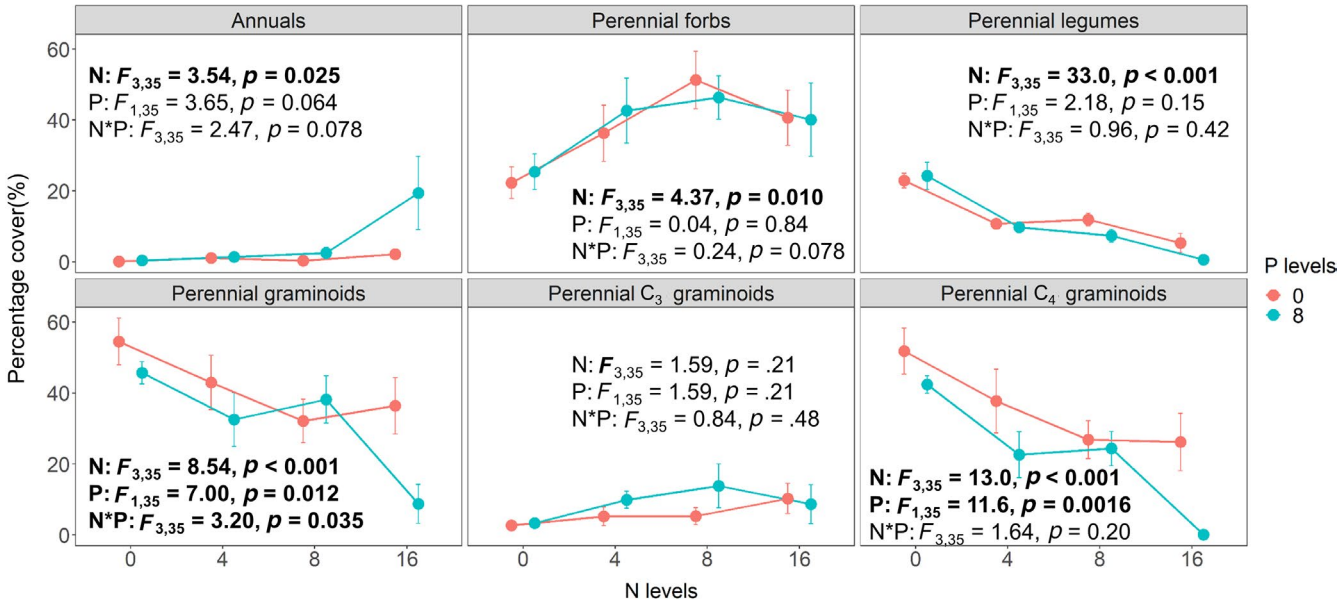


FIGURE 1 Percentage coverage of plant functional guilds in different N and P levels. Values represent mean ± SE ($n = 6$). p-values of ANOVA analyses of N and P effects were shown in each plot, and significant effects ($p < .05$) are noted with bold font. R^2 represents the proportion of the variance for the percentage cover of different functional guilds that is explained by the N and P effect in the linear regression model

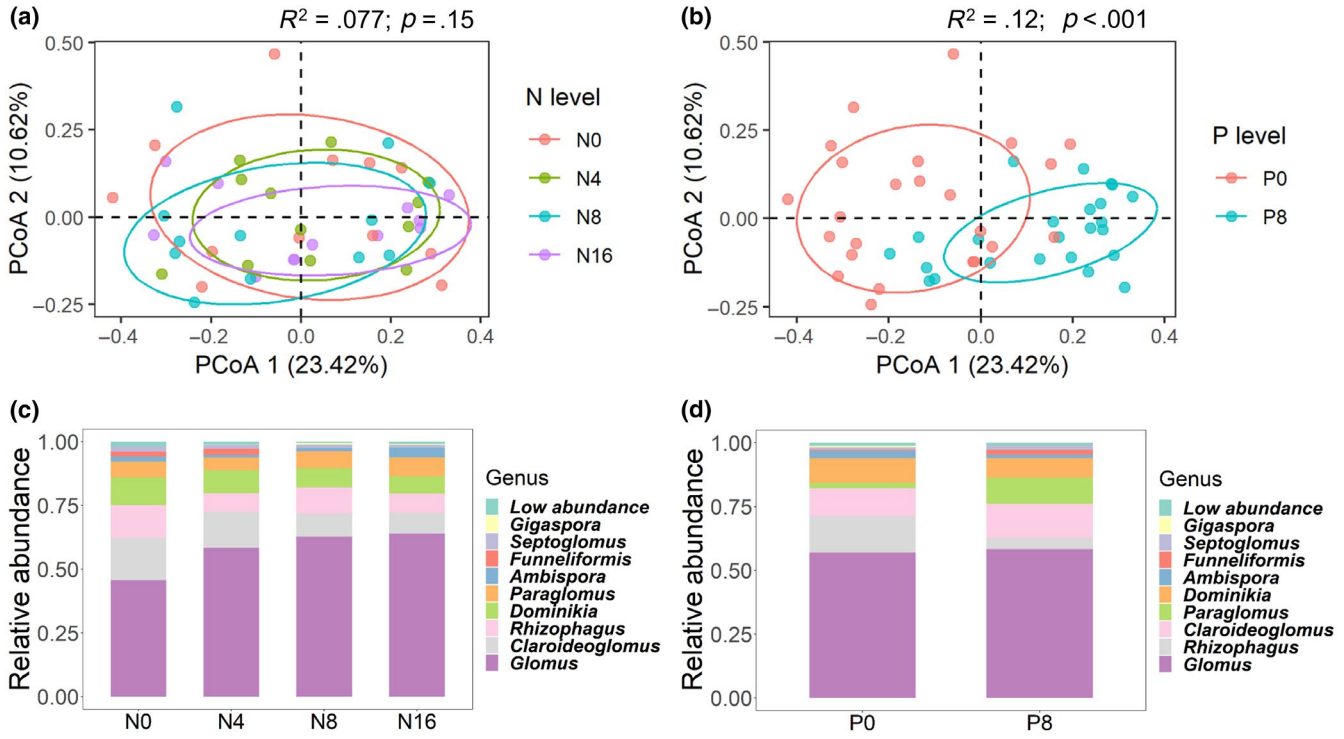


FIGURE 2 Principal coordinate analysis (PCoA) of AMF community structure based on the Bray-Curtis distances (a, b) and the relative abundance of genera within the AMF community (c, d) in response to N and P enrichment. In PCoA plots, the percentage of the total variance explained by each PC is indicated in parentheses. Only the top nine genera with the highest relative abundance are shown, and the others are represented by "low abundance" in the legends

species of these three microbial groups that were responsive to changes of N and P level. Within the top 10 most populated modules for the microbial co-occurrence networks, four, one, and three modules that contained the sOTUs of AMF, fungal pathogen, and fungal saprotroph communities that are readily affected by N and P addition were shown in the co-occurrence networks, respectively

(Figure 3a,b, Figure S10a,b, Figure S11a,b). For fungal pathogens and saprotroph, no significant relationships between sOTUs and the percentage of perennial C_4 graminoids were found (Figure S10c, Figure S11c). However, for the AMF community, we identified a total of 42 sOTUs belonging to seven genera accounting for 4.52% of the total soil community sequences (Dataset S2, Figure S12a, Figure S13). The relative abundance of sOTUs in aggregate was significantly increased by P ($F_{3,35} = 0.73$, $p = .54$) but unaffected N ($F_{3,35} = 7.91$, $p = .008$) fertilization (Figure S12b). In particular, Module 1 showed the largest proportion of sOTUs to increase in abundance by P ($F_{1,35} = 41.1$, $p < .001$) addition (Figure 3b, Figure S14), which partially reflected the diversity and composition changes caused by P enrichment (Figure 2b, Figure S3d). Furthermore, the percentage cover of perennial C_4 graminoids showed significantly negative correlations with the cumulative relative abundance of AMF sOTUs in Module 1 but not other Modules (Figure 4). However, all of the keystone OTUs from two genera of *Claroideoglomus* and *Glomus* were not sensitive to N and P fertilization, namely without overlap with sensitive OTUs (Dataset S2).

3.4 | The role of mycorrhizal fungi on plant community response

Further analysis showed that when including community weighted mean MR (CWM-MR) as a covariate, the N and P effects on C_4 graminoid percentage cover became non-significant, consistent with CWM-MR being a major predictor of this change in plant composition to N and P enrichment (Table S1). The inclusion of CWM-MR as a covariate did not remove the significance of the N effect on perennial legume cover (Table S2), indicating that legume cover change was not entirely mediated by CWM-MR. An important role of MR was also indicated by significant or marginally significant positive relationships between percentage cover of individual species and their MRs observed in the N0P0, N4P0, and N8P0 treatments, but not in N16P0 treatment (Figure S15a). With increased N, the slope of these positive relationships tended to decrease. A similar pattern occurred in response to P enrichment, where the N0P8 treatment showed a lower coefficient than the N0P0 treatment (Figure S15b). The N and P interactions were more remarkable, with the most positive correlations in N0P0, followed by positive but not significant correlations in N4P8 and N8P8, and no correlation was found in N16P8 treatment (Figure S15c).

CWM-MR was also negatively affected by N ($F_{3,35} = 15.8$, $p < .001$) and P ($F_{1,35} = 15.4$, $p < .001$) enrichment individually (Figure 5a), and there was a significant positive correlation between percentage cover of perennial C_4 graminoids and CWM-MR of the plant community (Figure 5b) and between CWM-MR and CWM-Cc values (Figure 5c), suggesting that the response of C_4 graminoids was an indicator of overall community response via MR. Similarly, N ($F_{3,35} = 6.84$, $p < .001$) and P ($F_{1,35} = 4.99$, $p = .032$) showed significantly negative effects on CWM-Cc values (Figure S16).

Our hypothesized SEM fit well with the data with 70% of the variance for percentage cover of C_4 graminoids explained by the N and P effect. Regarding the total effects, CWM-MR was the strongest predictor for perennial C_4 graminoids with positive direct effects (Figure 6), while N, P, and AMF sOTUs showed total negative effects, mainly contributed by the indirect effects mediated by CWM-MR. Both N and P showed significant negative effects on CWM-MR while the P effect was positive on AMF sOTUs.

4 | DISCUSSION

Eutrophication of terrestrial systems due to anthropogenic inputs of N and P drives diversity loss across many systems. We show that these changes can be mediated by shifting relationships with the soil microbiome, with mycorrhizal fungi being particularly important.

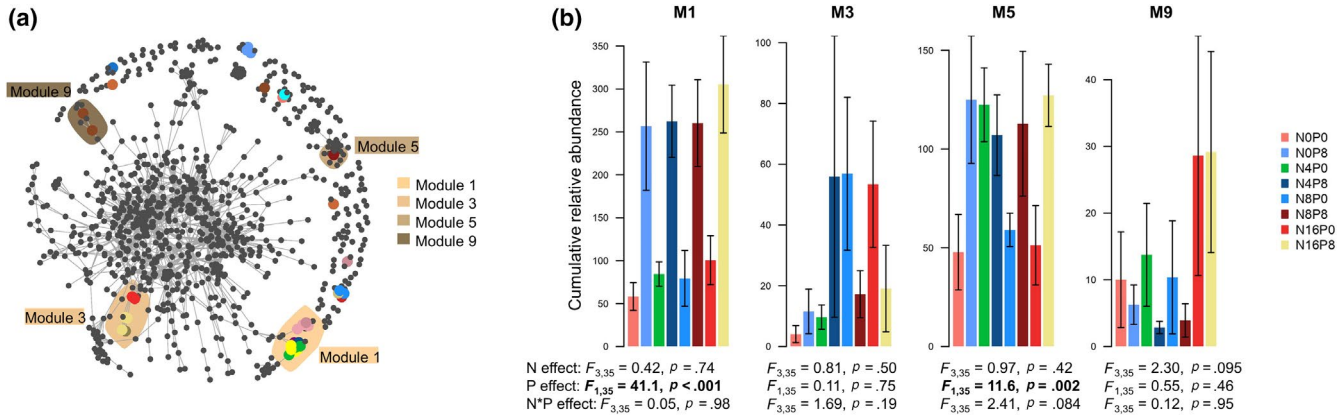


FIGURE 3 AMF co-occurrence network (a) and relative abundance of each module in different N and P treatments (b). Co-occurrence networks were visualized by significant correlations (Spearman correlation coefficient > 0.7, $p < .001$; indicated with gray lines) between OTUs within AMF communities. OTUs were colored by their association to the different N and P treatments (Figures S10 and S11; gray OTUs are insensitive to N and P fertilization). Shaded areas represent the network modules containing sOTUs as defined in Figure S12. The cumulative relative abundance (mean ± SE, $n = 6$) indicates the overall response of sensitive modules to the different N and P treatments. "M1," "M2," "M5," and "M9" represent "Module 1," "Module 3," "Module 5," and "Module 9," respectively

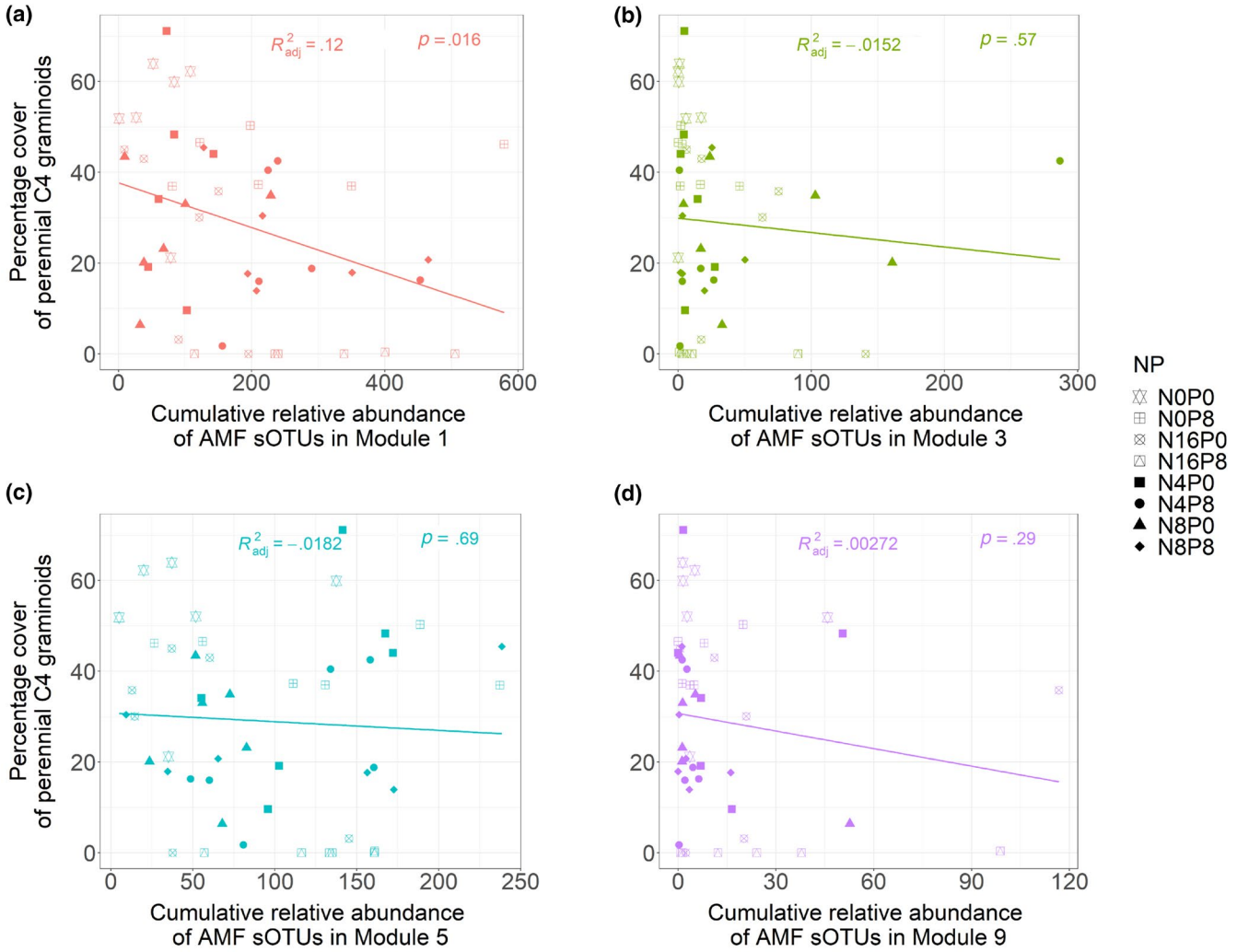


FIGURE 4 Correlations between AMF sensitive OTUs in each module and percentage cover of perennial C_4 graminoids under different N and P treatments. Adjusted determination coefficients (R_{adj}^2) and *p*-values of each module were presented in the plot with different colors and significant effects ($p < .05$) are noted with bold font

4.1 | MR is the proximate driver of plant community changes

This study provides a novel link in explaining the shift of plant community composition via MR of the plant species rather than changes in AMF composition *per se* (Figure 6), indicating that the direct associations between plants and mycorrhizal fungi could predict the growth response and plant community dynamics under the N and P enrichment (2nd question proposed). The AMF mediated plant community dynamics are context-dependent, as soil nutrient availabilities and C allocation from plants to extraradical hyphae determine the relationships between plants and symbiotic partners (Walder & van der Heijden, 2015). Many previous studies have found that mycorrhizal fungi mediate competitive abilities between plant species and alter plant community structure under different nutrient conditions (Lin et al., 2015; Scheublin et al., 2007; Thakur et al., 2019; Wagg et al., 2011). Under low nutrient conditions, plants with high mycorrhizal responses can be facilitated by AMF to gain a competitive advantage. However, under high nutrient conditions, plants that are highly dependent on AMF may be less competitive due to their investment in AMF. These trade-offs in resource acquisition through symbiosis with AMF versus directly through plant root acquisition of nutrients might be an important driver in community changes because of the shift in competitive abilities.

In this study, the positive correlations between percentage cover of perennial C_4 graminoids and CWM-Cc with CWM-MR values (Figure 5b,c) indicate that late-successional grasses are highly dependent on mycorrhizae, which is consistent with other studies (Koziol & Bever, 2015). The high cost of investment in AMF by perennial C_4 graminoids under fertilization likely weakens the competitive ability of this functional group. Based on the microbial coexistence network, we identified sOTUs clustered into different modules were strongly affected by P fertilization, and negative correlations between perennial C_4 graminoids and these sOTUs were

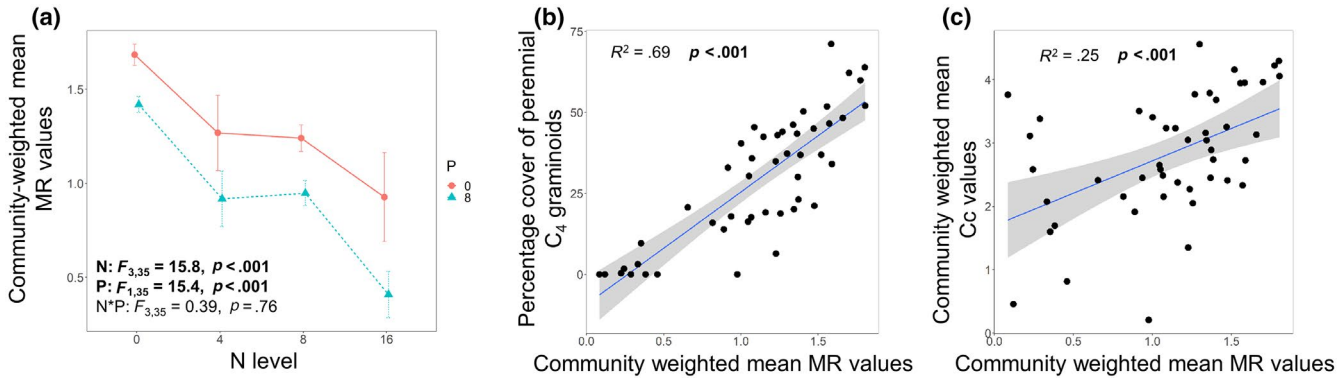
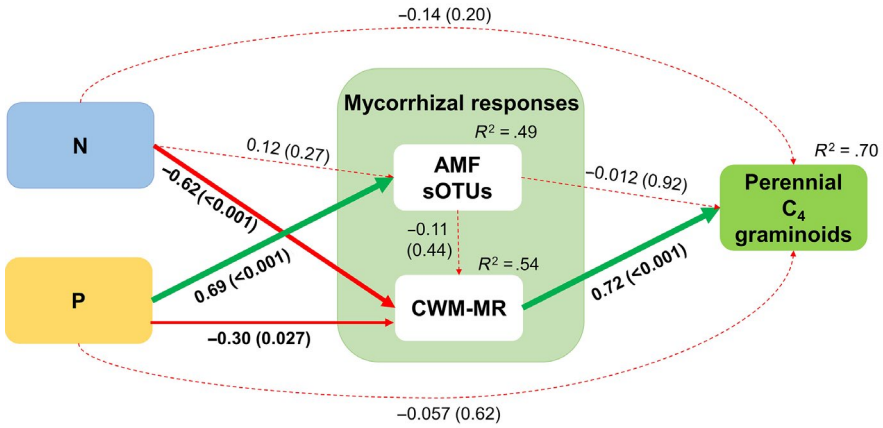


FIGURE 5 Community weighted mean MR (CWM-MR) values respond strongly to N and P fertilization treatment (a) and are strongly correlated with the percentage cover of perennial C_4 graminoids (b) and coefficients of conservatism (Cc) values of the plant community (c). Values in (a) represent mean ± SE (n = 6). Analysis of variance (ANOVA) results and correlation significance were shown in plot (a) and (b), respectively, and significant effects (p < .05) are noted with bold font



χ^2 = 0.98; df = 1; RMSEA < 0.001; GFI = 0.99; CFI = 1.00; TLI = 1.00; AIC = 29.0; BIC = 55.2

	Direct effect	Indirect effect	Total effect
N	–0.138	–0.454	–0.591
P	–0.057	–0.279	–0.336
AMF sOTUs	–0.012	–0.076	–0.088
CWM-MR	0.72	0	0.72

FIGURE 6 Effects of four variables on percentage coverage of perennial C_4 graminoids. Bold and dashed lines indicate significant ($p \leq .05$) and non-significant ($p > .05$) pathways, respectively. The numbers along the arrows indicate path coefficients and p-values. The width of arrows indicates the strength of the causal effect, while arrow colored with green and red indicates positive and negative coefficients. R^2 values represent the proportion of the variance explained for each variable. Sensitive OTUs from Module 1 were used as "AMF sOTUs" because of significant effects based on the result of Figure 5. CWM-MR represents community weighted mean mycorrhizal responsiveness. Direct, indirect, and total effect coefficients of each variable on percentage coverage of perennial C_4 graminoids were shown. "χ^2," "df," "RMSEA," "GFI," "CFI," "TLI," "AIC," and "BIC" represent Chi-square, degree of freedom, root mean square error of approximation, goodness of fit index, comparative fit index, Tucker-Lewis Index, Akaike information criterion and Bayes information criterion, respectively

found (Figures 3 and 4), indicating that microbial guilds the specific ecological networks have the potential regulatory effect on plant community dynamics. This pattern also suggests that sOTUs may be potential AMF cheaters, utilizing plant carbon while providing little benefit to their plant hosts (Bever et al., 2009), which is consistent with previous studies found that AMF could induce antagonism under P addition conditions (Grman, 2012; Grman & Robinson, 2013; Yang et al., 2014).

4.2 | AMF OTUs were sensitive to P rather than N fertilization

Interestingly, our results showed that AMF sOTUs were mainly affected by P fertilization rather than by N (1st question, Figure 3b, Figure S12b), which is partially consistent with previous studies showing that AMF were directly influenced by P but not by N fertilization in both grassland and forest ecosystems

(He et al., 2016; Maitra et al., 2021). The efficiency of mutualists could be degraded due to mineral fertilizers application, as P would have a direct negative influence on the abundance of mycorrhizal fungi (Bradley et al., 2006; Jeske et al., 2018; Treseder, 2004), or plants allocate less carbohydrate to roots which limit the C resources necessary for AMF growth and proliferation (Camenzind et al., 2014; Chen et al., 2014; Ji & Bever, 2016; Olsson et al., 1997). However, opposite results have been observed where fertilization with NPK significantly increases total mycorrhizal abundance and growth (Nijjer et al., 2010), perhaps reflecting the proliferation of non-beneficial AMF (Grant et al., 2005; Nijjer et al., 2010; Treseder & Allen, 2002). Consistent with this, AMF Shannon diversity rather than richness was increased with P enrichment in the current study (Figure S3d), indicating that P fertilization influences AMF relative abundance and evenness. In particular, we observed the relative abundance of sOTUs from two genera of *Paraglomus* and *Claroideoglomous* was increased by P addition (Figure S13), partly consistent with previous studies showing that some species from these genera were positively responsive to P fertilizer (Lang et al., 2022). We found that the AMF responded positively to P enrichment were associated with loss of mycorrhizal responsive plants (Figure 4), suggesting that they were non-beneficial AMF. Based on the module-based analysis, our results provide novel links between specific clusters in the microbial networks and ecological functions, driven mainly by P. However, the variability was also observed as some individual sOTUs were affected by N or interactions between N and P (Figure 3b, Figure S13), and further studies need to investigate whether such microbial composition can be linked to predict plant performance, by combing with current rapidly developed molecular tools like culturomics, metagenomics, etc.

Our results are consistent with previous studies showing that N and P enrichment increased the richness of fungal pathogens (Lekberg et al., 2021). While fungal pathogens have been shown to be important to plant species coexistence (Bever et al., 2015; Crawford et al., 2019; Mody et al., 2015), no significant relationship was found between fungal pathogen diversity and percentage coverage of C_4 plant species (Figure S9). This indicates that the overall fungal pathogen diversity might be not the causal driver of plant community response to N and P enrichment (Benítez et al., 2013). Early successional plant species with fast growth rates typically show negative PSF induced by potential pathogens (Bauer et al., 2015; Kardol et al., 2006), while late-successional species tend to associate with AMF and demonstrate positive PSF (Koziol & Bever, 2017, 2019). As a result, the accumulation of host-specific pathogens and AMF during succession may both inhibit early successional species and facilitate late-successional species. We found positive correlations between CWM-Cc and CWM-MR values (Figure 5c), indicating MR could be a predictive indicator of plant succession dynamics. However, N and P addition may delay or disturb the natural succession process by promoting the growth of annual or early successional plant species while influencing the association between native or late-successional plant species and AMF.

4.3 | The potential mechanisms of plant community changes in response to N fertilization

Although the AMF community was not significantly affected by N, perennial C_4 graminoids and legumes were negatively responsive to N enrichment (Figure 1). As for legumes, their exposure to high soil N may disrupt their physiological processes due to suppression of rhizobia fixation or the nitrogenase activity, which may explain the decreased effect with the increase in N levels (Tian et al., 2020). In addition, a number of theories or hypotheses related to environmental conditions have been proposed to explain plant community dynamics in response to N enrichment, like soil acidification (Barlow et al., 2020; Horswill et al., 2008) and ionic toxicity induced by acidification (Bowman et al., 2008; Tian et al., 2016, 2020). However, in our study, we did not observe a significant pH decrease probably due to the soil buffering capacity (Figure S1c). Another popular explanation is that N enrichment improves the light competition among species and results in competition exclusion (Hautier et al., 2009). However, this light manipulation study was conducted in the glasshouse and the light density was much lower than the field and the processes occurring in the field were more complex. One previous study in the same site as our current study showed that fertilization decreased plant biodiversity even when the light was not limiting (Dickson & Foster, 2011). This light effect might be related to soil temperature as a significant positive correlation with plant species richness was observed, suggesting that soil temperature would confound the effects of the light manipulation treatments on species richness. Another reason could be affected by the precipitation variability caused by the interannual effect, as low light levels only inhibited plant richness when water availability did not severely limit plant survival (Dickson & Foster, 2011). Therefore, except for the microbial mediations, the confounding abiotic effects of light, temperature, and annual precipitation interacting with fertilization need to be disentangled in future studies.

5 | CONCLUSION

This study showed that N and P enrichment decreased plant community diversity and resulted in composition changes, including a major loss of perennial C_4 graminoids and a decline in the average conservation value of the plant community. Moreover, N and P enrichment changed the soil microbial composition, with increased richness and altered composition of fungal pathogens in response to both N and P enrichment, while P enrichment increased the diversity and altered the composition of AMF, but decreased fungal and fungal saprotroph diversity and altered their compositions. Of these changes in the soil microbiome, only the changes in the

composition of AMF taxa sensitive to fertilization was correlated with the changes in the plant community, suggesting that changes in AMF composition were an important driver of plant community change reflected by the reduction of competitive abilities of C_4 plants compared with other groups. Further analyses identified the average MR of plant species mediated by AMF rather than the change in AMF composition *per se*, is the most likely proximate driver of plant community change. More work is necessary to test the generality of microbiome mediation of plant community response to global change drivers.

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AUTHOR CONTRIBUTION

GW, BLF, and JDB designed the project and GW performed experiments and collected data. All authors performed statistical analyses, and GW wrote the first draft of the manuscript, followed by substantial contributions from all authors to manuscript revisions.

DATA AVAILABILITY STATEMENT

The data used in this study are available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.15063213.

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