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**MYCORRHIZAL FUNGI AS DRIVERS AND
MODULATORS OF ECOSYSTEM PROCESSES****Arbuscular mycorrhizal fungi as mediators of ecosystem responses to nitrogen deposition: A trait-based predictive framework**Kathleen K. Treseder¹  | Edith B. Allen² | Louise M. Egerton-Warburton³ |
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Abstract

1. Anthropogenic nitrogen (N) deposition is exposing plants and their arbuscular mycorrhizal fungi (AMFs) to elevated N availability, often leading to shifts in communities of AMF. However, physiological trade-offs among AMF taxa in their response to N enrichment vs the ability to acquire other soil nutrients could have negative effects on plant and ecosystem productivity. It follows that information on the functional traits of AMF taxa can be used to generate predictions of their potential role in mediating ecosystem responses to N enrichment.
2. Arbuscular mycorrhizal fungi taxa that produce extensive networks of external hyphae should forage for N and phosphorus (P) more effectively, but these services incur greater carbon (C) costs to the plant. If N enrichment ameliorates plant nutrient limitation, then plants may reduce C available for AMF, which in turn could eliminate AMF taxa with large extensive external hyphae from the soil community. As a result, the remaining AMF taxa may confer less P benefit to their host plants.
3. Using a synthesis of data from the literature, we found that the ability of a taxon to persist in the face of increasing soil N availability was particularly high in isolates from the genus *Glomus*, but especially low among the Gigasporaceae. Across AMF genera, our data support the prediction that AMF with a tolerance for high soil N may confer a lower P benefit to their host plant. Relationships between high N tolerance and production of external hyphae were mixed.
4. *Synthesis.* If the relationship between N tolerance and plant P benefit is widespread, then shifts in arbuscular mycorrhizal fungi communities associated with N deposition could have negative consequences for the ability of plants to acquire P and possibly other nutrients via a mycorrhizal pathway. Based on this relationship, we predict that arbuscular mycorrhizal fungi responses could constrain net primary productivity in P-limited ecosystems exposed to N enrichment. This prediction could be tested in future empirical and modelling studies.

KEYWORDS

anthropogenic nitrogen deposition, arbuscular mycorrhizal fungal traits, external hyphae, Gigasporaceae, global change, *Glomus*, nitrogen association, phosphorus, physiological trade-offs, plant–soil (below-ground) interactions

1 | INTRODUCTION

Nitrogen (N) and phosphorus (P) are critical for plants, since they are required to construct proteins, nucleic acids, phospholipids and ATP (Elser, Dobberfuhl, MacKay, & Schampel, 1996). In many ecosystems, plants cannot access sufficient N or P, which limits their growth and function (Elser et al., 2007; Fay et al., 2015; Harpole et al., 2011; Vitousek & Howarth, 1991). To augment N and P uptake from soil, many plant species form symbiotic relationships with arbuscular mycorrhizal fungi (AMF; Newman & Reddell, 1987). These fungi transfer N and P to plants in exchange for carbon (C) from photosynthates (Smith & Read, 2008). In fact, AMFs represent a significant C investment—3%–20% of photosynthate can be allocated to AMF (e.g. Jakobsen & Rosendahl, 1990; Johnson, Leake, Ostle, Ineson, & Read, 2002; Johnson, Leake, & Read, 2002; Kucey & Paul, 1982). In return, AMF can boost plant growth by an average of 80% under ambient (unfertilized) conditions (Hoeksema et al., 2010). By improving net primary productivity (NPP) of plants in N- or P-limited ecosystems, AMF can facilitate the removal of CO₂ from the atmosphere. Thus, by using plant photosynthates, they can form a negative feedback on climate change (Orwin, Kirschbaum, St John, & Dickie, 2011).

The extent to which AMFs contribute to ecosystem C storage may change if soil N availability increases (Johnson, Angelard, Sanders, & Kiers, 2013). This is an important issue because N enrichment is becoming increasingly widespread owing to human activities such as cropland fertilization, legume cultivation and fossil fuel combustion (Galloway & Cowling, 2002; Galloway et al., 2008). In fact, these processes have essentially doubled the amount of fixed N available to most organisms world-wide (Vitousek et al., 1997). Numerous studies have amply demonstrated that AMFs are sensitive to anthropogenic N enrichment (Johnson et al., 2013; Mohan et al., 2014; Rillig, Treseder, & Allen, 2002). On average, AMF abundance (as root colonization, spore counts and external hyphal lengths) declines by about 24% in ecosystems exposed to inorganic N fertilization (Treseder, 2004). Ostensibly, this shift occurs because as plants become less N-limited, they direct C to above-ground growth instead of AMF (Read, 1991).

The phylum Glomeromycota (or subphylum Glomeromycotina, Spatafora et al., 2016) contains most currently described AMF taxa (Redecker et al., 2013). Within this phylum, there are four orders, 11 families and 25 genera (Redecker et al., 2013). By definition, all AMF taxa colonize plant roots (Smith & Read, 2008). Arbuscules or hyphal coils are the site of nutrient and carbon exchange between the fungus and plant. In addition, all AMF taxa grow external hyphae from the root into the soil, which they use to forage for N and P, and possibly other nutrients (Dodd, Boddington, Rodriguez, Gonzalez-Chavez,

& Mansur, 2000; Smith & Read, 2008). Nevertheless, AMF taxa vary in the extent to which they grow external hyphae, internal hyphae, arbuscules and other structures (Dodd et al., 2000; Hart & Reader, 2002; Koch, Antunes, Maherali, Hart, & Klironomos, 2017; Maherali & Klironomos, 2007; Powell et al., 2009). Broadly, taxa within the class Glomeraceae tend to allocate more biomass to intra-radical structures than to external hyphae, whereas those in the Gigasporaceae display the opposite tendency (reviewed in Chagnon, Bradley, Maherali, & Klironomos, 2013). The Acaulosporaceae produce low biomass both within and outside the root. However, these traits have not been as extensively measured or compared in other AMF families (Chagnon et al., 2013).

The composition of AMF taxa frequently changes in response to N enrichment (Egerton-Warburton & Allen, 2000; Eom, Hartnett, Wilson, & Figge, 1999; Kim et al., 2015; Treseder & Allen, 2002; Zheng et al., 2014). In general, the AMF community tends to shift from Gigasporaceae under low N availability to Glomeraceae under high N (Egerton-Warburton & Allen, 2000; Egerton-Warburton, Johnson, & Allen, 2007; Treseder & Allen, 2002). In other words, Glomeraceae tend to be associated with higher soil N availability than the Gigasporaceae. Hereafter, we will refer to the relationship between N availability and the prevalence of a given taxon as that taxon's "N association." For example, higher N associations indicate that the taxon is observed more often at relatively high N availability. A difference in N associations between the Glomeraceae and Gigasporaceae could result from differential demands for plant C. Members of the Gigasporaceae produce more extensive networks of external hyphae than do those of the Glomeraceae (Dodd et al., 2000; Hart & Reader, 2002; Klironomos, Ursic, Rillig, & Allen, 1998; Maherali & Klironomos, 2007; Powell et al., 2009). Therefore, Gigasporaceae could require more plant C to support the growth and maintenance of this network (Chagnon et al., 2013). Thus, as plants reduce their C investment in AMF under N enrichment, the abundance of Gigasporaceae may decline more strongly than Glomeraceae (Johnson, Rowland, Corkidi, Egerton-Warburton, & Allen, 2003). Similar relationships between external hyphae and N associations have been observed in ectomycorrhizal fungi (Lilleskov, Hobbie, & Horton, 2011). Furthermore, if N enrichment increases plant growth, shading by canopy plants could reduce the C status of understory plants, which could lead to reduced investment in AMF.

A shift towards high N-associated AMF with fewer external hyphae may have consequences for host plant P. Previous research has indicated that AMF taxa with less external hyphae tend to more weakly facilitate plant P uptake (Powell et al., 2009), ostensibly because they do not forage for soil P as effectively (Avio, Pellegrino,

Bonari, & Giovannetti, 2006; Chagnon et al., 2013; Dodd et al., 2000; Jansa, Mozafar, & Frossard, 2005; Smith, Dickson, & Smith, 2001). If N enrichment selects for AMF taxa with fewer external hyphae, perhaps P uptake by plants will decline accordingly. In P-limited ecosystems, this could decrease plant productivity and, in turn, cause a decline in CO₂ removal from the atmosphere.

Alternately, if plants become more P-limited following N enrichment, they may invest selectively in AMF taxa that acquire P effectively, such as the Gigasporaceae (Johnson et al., 2013). This is because excess N availability is expected to boost plant photosynthesis, making C for P trade less costly for the plant (Johnson, 2010). In this case, we would expect AMF taxa that confer greater plant P benefit to associate with high N availability.

We asked three questions relating the effects of N availability on AMF taxa to potential consequences for ecosystem function. First, how are N associations taxonomically distributed within AMF? Second, is the extent of external hyphae linked to N associations of AMF taxa? Third, is an AMF taxon's association with N enrichment related to its contributions to host plant P? We hypothesized that N enrichment favours AMF taxa with less extensive external hyphae, and that as a result AMF taxa with higher N associations may confer lower P acquisition benefit to their host plants. As an alternate hypothesis (e.g. Johnson, 2010), N enrichment may instead induce host plants to select for AMF taxa that provide greater P benefit, because N enrichment could induce plant P limitation.

We tested these hypotheses by examining relationships between N associations, quantity of external hyphae and plant P concentrations across AMF taxa. We estimated N associations of AMF taxa using data from previous studies: a regional-scale survey of AMF taxa along an N deposition gradient in Southern California (Egerton-Warburton & Allen, 2000), and a global survey of AMF taxa in 365 sites that varied in their levels of soil N (Tedersoo et al., 2014). We then compared the N associations of AMF taxa with published descriptions of their external hyphae and plant P benefit (Hart & Reader, 2002; Maherali & Klironomos, 2007).

2 | MATERIALS AND METHODS

2.1 | Datasets

Many studies have examined shifts in AMF communities in response to N availability, or have documented external hyphal production or plant P benefit across multiple AMF taxa (see above). For our analysis, however, we selected studies that included a broad phylogenetic distribution of AMF taxa that were identified at a relatively fine taxonomic level (genus, species or operational taxonomic unit [OTU]). We used these two criteria because together they allowed us to broadly quantify variation in N associations at multiple taxonomic ranks (i.e. order, family or genus). Specifically, each of the selected studies included representatives of at least seven genera distributed across four families and three orders.

To test our hypotheses, we assessed four traits that covaried among AMF taxa: relationship to N deposition from Egerton-Warburton and

Allen (2000), relationships to soil N availability from Tedersoo et al. (2014), external hyphal length from Hart and Reader (2002) and Maherali and Klironomos (2007), and plant P benefit from Maherali and Klironomos (2007). These studies differed in the taxonomic resolution at which they examined these traits. For example, Hart and Reader (2002) reported data for isolates within AMF species. Then again, Tedersoo et al. (2014) defined OTUs as sequences with $\geq 98\%$ sequence similarity within the ITS rRNA gene region. Most of these OTUs were conservatively identified to genus, not species. Thus, for all tests of correlations between traits, we used genus as the common taxonomic rank and statistical unit. To achieve this, for each dataset, we calculated average trait values for each genus as detailed below. Functional traits of AMF taxa tend to be phylogenetically conserved at the genus to family levels (Powell et al., 2009), and N associations were no exception (see "Nitrogen associations" in Section 3). This means that for practical purposes, we could bin taxa within genera and still preserve much of their variation in functional traits (Treseder & Lennon, 2015).

To assess N associations of AMF taxa, we selected Egerton-Warburton and Allen (2000) as a regional-scale study, because their field sites spanned an existing gradient of anthropogenic N deposition. The gradient was located in Southern California, and its sites were exposed to total N deposition rates of about 8 to $>22 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (Fenn et al., 2010). For comparison, Galloway et al. (2008) estimated that by 2050, many terrestrial regions around the world will receive N deposition rates within this range. These rates are much higher than those observed in ecosystems without anthropogenic N deposition ($\leq 0.5 \text{ kg N ha}^{-1} \text{ year}^{-1}$; Dentener et al., 2006). Nitrogen limits plant growth at the low end of the N deposition gradient, but not at the high end (Allen, Padgett, Bytnerowicz, & Minnich, 1998). Where anthropogenic N deposition is high, other resources such as P, light or water might limit plant growth instead.

The Egerton-Warburton and Allen (2000) sites spanned 85 km. All sites occurred on granitic parent materials with relatively high P concentrations (15–30 $\mu\text{g P/g}$) and experienced similar climate. Mean annual precipitation at the sites ranged between 244 and 357 mm per year, and mean annual temperature was 18–20°C (weather.gov, accessed 9/2015).

Egerton-Warburton and Allen (2000) extracted AMF spores from soils at each site, and then identified them to species (where possible) based on morphology and cell wall characters. They reported relative abundance (% of total spore number) of each taxon in each site (table 2 of Egerton-Warburton & Allen, 2000). For our purposes, this study represented a well-constrained regional sampling of shifts in AMF taxa along N deposition levels that mimic future scenarios of global change. Taxa that were more abundant in sites with higher N deposition than in those with lower N deposition were considered to have higher N associations.

We also examined shifts in AMF taxa with N availability at a global scale. To do so, we selected a study by Tedersoo et al. (2014), because it represents an extensive global sampling of soils that range widely in soil fertility. In this study, soils were collected from 365 ecosystems across the world and from every continent except Antarctica. For each sample, a number of soil characteristics were measured including soil

C:N ratios. At high soil C:N ratios, saprotrophic microbes immobilize N in their tissues. Conversely, at low C:N ratios, N is available in excess, so microbes secrete N into surrounding soil where it is available to other organisms (Chapin, Matson, Vitousek, & Chapin, 2011). Thus, soil C:N ratios have often been used as a coarse indicator of N availability, with lower ratios indicating higher N availability (*sensu* Aber et al., 2003; Enriquez, Duarte, & Sand-Jensen, 1993; Lovett, Weathers, & Arthur, 2002; McGill, Hunt, Woodmansee, & Reuss, 1981; Soudzilovskaia et al., 2015). By contrast, total N concentrations in soil is a less robust indicator of N availability, as the N could exist in unavailable forms such as aromatic rings (Chapin et al., 2011). In Tedersoo et al. (2014), soil C:N ratios ranged between 10.4 (in a grassland/shrubland) and 53.0 (in a boreal forest), with a median of 18.5. For context, Chapin et al. (2011) note that a soil C:N ratio of 25:1 is often considered a threshold, below which a net N release by microbes is more likely to occur.

Tedersoo et al. (2014) used 454 pyrosequencing of the ITS2 region to assign fungi to OTUs and provided identification from genus to phylum level. From this dataset, we extracted all Glomeromycota OTUs that were identified at least to genus. Taxa that were detected in sites with relatively low soil C:N were considered to have higher N associations than those detected in sites with higher soil C:N.

To characterize external hyphal production and plant P benefit from AMF taxa, we synthesized data from two publications. In Hart and Reader (2002), four plant species were each inoculated with one of 21 AMF isolates and grown in sterile, low P potting soil and silica sand. External hyphal production was measured in six harvests spanning 70 days. We used data from the final harvest. In Maherali and Klironomos (2007), individuals of *Plantago lanceolata* were grown for 1 year in sterilized field soil. Each individual was inoculated with one of 20 AMF species. Maherali and Klironomos (2007) also reported external AMF hyphal lengths in soil and leaf %P. Previously, Powell et al. (2009) synthesized the data from Hart and Reader (2002) and Maherali and Klironomos (2007) and reported that external hyphal length and leaf % P were positively related across taxa.

The taxonomy of AMF has been extensively revised in recent years (Redecker et al., 2013; Schüßler & Walker, 2010). Accordingly, we updated species names from these previous publications to match current names listed in Index Fungorum (<http://www.indexfungorum.org/>, accessed 9/2015). In Egerton-Warburton and Allen (2000), five *Glomus* morphotypes and one *Entrophospora* morphotype could not be identified to species. Since 2000, *Glomus* has been reorganized into several genera (Schüßler & Walker, 2010), and many species of *Entrophospora* have been transferred to *Acaulospora* (Oehl et al., 2011). Since we could not be certain of the current genus classification of these morphotypes, we excluded them from further analysis.

2.2 | Calculation of N associations

We calculated N associations for each AMF species (for Egerton-Warburton & Allen, 2000) or OTU (for Tedersoo et al., 2014). Egerton-Warburton and Allen (2000) ranked their sites by N deposition rate, based on atmospheric nitrate and ammonium concentrations, and soil nitrate concentrations measured during peak N loads.

We used the same site rankings, with higher values indicating higher N deposition. We used the same site rankings, with higher values indicating higher N deposition. We then calculated an “N association index” for each species as a weighted average of site rankings at which it was present:

$$\text{N association index} = \frac{\sum_{\text{site}=1}^9 \text{Abundance} \times \text{site rank}}{\sum_{\text{site}=1}^9 \text{Abundance}}$$

where “Abundance” is % total spores at that site represented by the species. We calculated the N association index for each of 18 AMF species (Figure S1). We also calculated an “alternate N association index” based on best-fit polynomials of abundance vs site rank (see Figure S2 for details).

To describe N associations for AMF OTUs in the global dataset, we calculated the average soil C:N of all sites in which a given OTU was detected. We refer to this value as the “observed soil C:N” for an OTU, and it is akin to realized niche space. Essentially, OTUs with lower values of observed soil C:N were considered to have relatively high N associations. Observed soil C:N was calculated for the 58 most common OTUs that were taxonomically assigned at the genus level (Figure S3). Finally, to determine genus-level traits, we calculated unweighted average values of the N association index and observed soil C:N for each genus.

2.3 | Taxonomic distributions of N associations

To examine whether N associations varied most among orders, families or genera, we used a hierarchical linear mixed model with residual/restricted maximum likelihood as the estimation method (SPSS, 2009). The dependent variable was either N association index or observed soil C:N. This test partitioned the variance in N associations among the three taxonomic ranks. Specifically, order, family and genus were included as three hierarchical random factors. In addition, the model applied post hoc one-sample *t*-tests to each taxonomic group (e.g. *Glomus*) to determine if the mean value of that group departed significantly from the mean value across all taxonomic groups (e.g. the mean of all genera). Replicates were species or OTUs, respectively.

2.4 | Calculation of external hyphal production

Hart and Reader (2002) and Maherali and Klironomos (2007) reported similar patterns in external hyphal production across AMF taxa (Powell et al., 2009). Therefore, we combined the data from both studies into composite indices. First, we calculated average values for each AMF genus in the Hart and Reader (2002) dataset. Then, we repeated these steps for the Maherali and Klironomos (2007) dataset.

Seven genera were common to both studies, so we determined composite indices for these genera. Hart and Reader (2002) reported external hyphal lengths per unit soil volume, whereas Maherali and Klironomos (2007) reported them per unit soil mass. Thus, we converted the data to rankings so we could combine the studies in a common index. For each study, we ranked the AMF genera by hyphal

length; lower rankings were associated with less external hyphae. For each genus, we then took the average of the Hart and Reader (2002) ranking and the Maherali and Klironomos (2007) ranking (Table S1).

2.5 | Relationships among traits of AMF genera

We hypothesized that AMF taxa are associated with N enrichment tend to have less extensive external hyphae and confer lower P benefit to their host plant. To test this hypothesis, we used the “nlme” version 3.1-128 of R to conduct a series of hierarchical mixed regressions between N association index or observed soil C:N vs external hyphal lengths or leaf %P associated with AMF genera (Pineiro, Bates, DebRoy, & Sarkar, 2017). Genus was nested within family. We used a nested model because it allowed us to account for the potential influence of taxonomy on trait relationships (Ricklefs & Starck, 1996). This approach is appropriate when traits are taxonomically structured. We nested replicates within family because the observed soil C:N varied most at the family level (Table S2, see “Section 3”). In comparison, variance was minimal at the order level for all of the N association traits, so we did not nest within orders.

We weighted each genus as follows:

$$\text{weight} = \frac{\sum_{\text{taxon}=1}^n \text{sites}}{\text{CV}}$$

where n is the number of taxa represented within the genus, sites is the number of sites in which a given taxon was detected, and CV is the coefficient of variation for the genus (i.e. SD/M). This approach accounted for a higher confidence in N association values for genera that: (1) were more comprehensively sampled, because they were detected in more sites and/or were represented by more taxa; and (2) displayed consistent N associations, as indicated by lower coefficients of variation. Genera that were represented by one taxon were assigned a weight of 1.

To avoid undue influence of outliers, we ranked all data. For all statistical tests, relationships were considered significant when two-tailed $p < .05$ and marginally significant when $p < .10$. On one hand, our hypothesis would be supported by significant negative relationships between N association index vs external hyphal lengths or leaf %P and significant positive relationships between observed soil C:N vs external hyphal lengths or leaf %P. On the other hand, our alternative hypothesis would be supported by a significant positive relationship between N association index and leaf %P and a significant negative relationship between the observed soil C:N and leaf %P.

3 | RESULTS

3.1 | Nitrogen associations

In the study by Egerton-Warburton and Allen (2000), the N association index varied more at the genus level than the family or order level (Figure 1, Table S2), primarily owing to a marginally significantly large N association index of *Glomus* compared with other genera ($t = 2.249$, $df = 8$, $p = .056$). In the Tedersoo et al. (2014) study, the observed soil C:N ratios varied more among families than genera or orders (Figure 1, Table S2). Specifically, the Gigasporaceae were associated with especially low N availability ($t = 2.086$, $df = 47$, $p = .042$).

Genera with higher values of the N association index also displayed lower observed soil C:N ratios (Figure 2). Specifically, the N association index and observed soil C:N were significantly negatively related with one another across genera (Table 1). In other words, the two measures of N associations were consistent with one another. The alternate N association index, which we calculated for the Southern California N deposition gradient, yielded similar results to the primary N association index for all trait relationships (Figure S4).

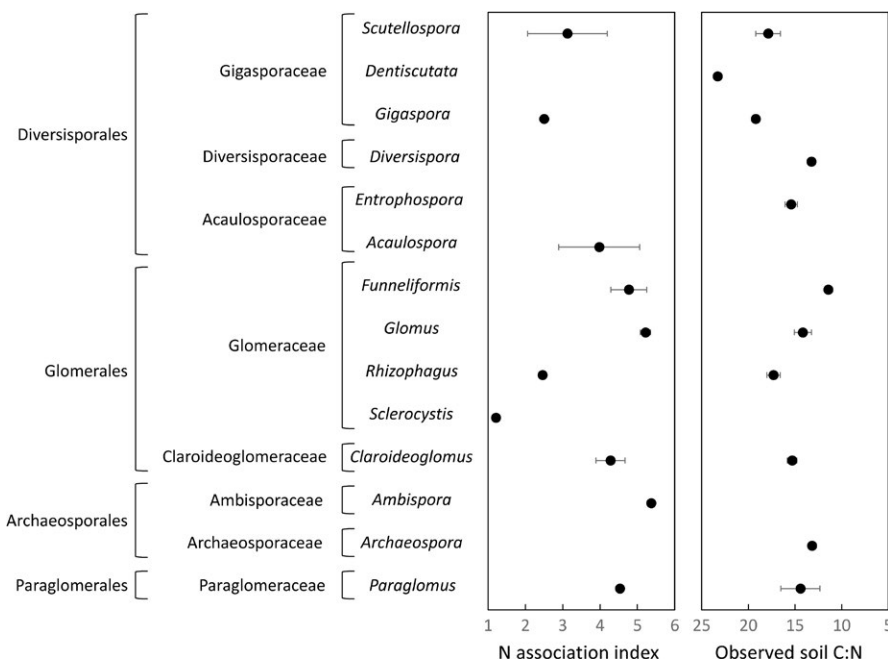


FIGURE 1 Taxonomic distribution of the N association index (calculated from Egerton-Warburton & Allen, 2000) and observed soil C:N (calculated from Tedersoo et al., 2014) across arbuscular mycorrhizal fungi (AMF) taxa. Bars are $M + 1$ SE of species (N association index) or operational taxonomic unit (OTUs) (observed soil C:N). Note that the x-axis is reversed for observed soil C:N

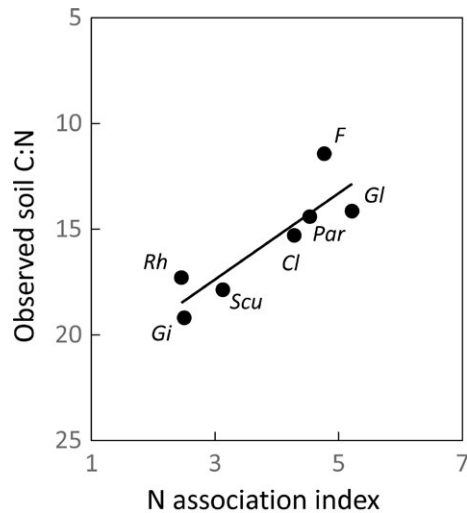


FIGURE 2 Relationship between observed soil C:N and N association index across arbuscular mycorrhizal fungi (AMF) genera. The two N association traits were significantly related to one another (Table 1, $p = .022$). Statistical analyses were performed on ranked data. Line is best fit. Symbols are means for each genus. Cl = *Claroideoglomus*, F = *Funneliformis*, Gi = *Gigaspora*, Gl = *Glomus*, Par = *Paraglomus*, Rh = *Rhizophagus* and Scu = *Scutellospora*. Values are calculated from data in Egerton-Warburton and Allen (2000) and Tedersoo et al. (2014). Note that the y-axis is reversed

TABLE 1 Relationships between traits of arbuscular mycorrhizal fungal genera

Trait 1 vs trait 2	Hierarchical linear mixed effects model ^a
Observed soil C:N vs N association index	$t = -6.590, p = .022$
Observed soil C:N vs external hyphal length	$t = 4.356, p = .049$
Observed soil C:N vs leaf %P	$t = 3.406, p = .077$
N association index vs external hyphal length	$t = -0.227, p = .842$
N association index vs leaf %P	$t = -4.534, p = .045$

^aGenera nested within family.

3.2 | Relationships among traits of AMF genera

Our hypothesis that high N-associated AMF should produce less extensive external hyphae and confer smaller plant P benefit was partially supported. Across AMF genera, external hyphal length (from Hart & Reader, 2002; Maherali & Klironomos, 2007) was significantly and positively correlated with the observed soil C:N, but not with the N association index (Figure 3, Table 1). Furthermore, AMF genera that increased %P in *P. lanceolata* leaves in Maherali and Klironomos (2007) also tended to occur in sites with higher soil C:N in Tedersoo et al. (2014), and lower N deposition in Egerton-Warburton and Allen (2000) (Figure 3, Table 1). By the same token, we rejected our alternative hypothesis that N enrichment should select for AMF taxa that contribute larger P benefits to host plants.

4 | DISCUSSION

Our results provide the first evidence for functional differences among AMF taxa in their association with N enrichment. We can use this information to predict AMF functioning under current and future N-pollution scenarios. We found that N associations varied most at the genus and family level and were higher in *Glomus* than genera in the *Gigasporaceae* (Figure 1). Moreover, N associations of AMF taxa were consistent whether measured in a regional-scale N deposition gradient using spores or a global scale survey using molecular methods. Specifically, genera that were more locally abundant at higher N deposition levels were detected more often in globally distributed sites with higher N availability (i.e. lower soil C:N ratio; Figure 2). Furthermore, N associations were linked to a key AMF trait—improvement of host plant P. Specifically, high N-associated genera did not tend to augment host plant P as well as other genera (Figure 3). Nevertheless, we found mixed evidence that high N-associated genera lacked the foraging capacity conferred by extensive external hyphae. For instance, genera with less external hyphae tended to inhabit soils with lower soil C:N (Figure 3). However, there was no significant relationship between N deposition association and external hyphal length (Figure 3). Taken together, our findings predict that selection for certain AMF genera by N enrichment may have consequences for ecosystem dynamics, by potentially constraining NPP where plant growth is limited by P. We note that plant P benefits were determined on one plant species in a greenhouse setting, so independent assessments of this trait in field settings would be especially valuable in testing this prediction.

Our quantification of N associations of AMF genera also provides valuable insights into the functional differences among AMF. Nitrogen associations were generally consistent with other observations of shifts in AMF communities following N fertilization. In this study, *Glomus* and *Funneliformis* ranked high in their N associations, whereas *Scutellospora* and *Gigaspora* were especially low. Other studies have noted that N augmentation increases the abundance of Glomeraceae taxa in general (Klironomos et al., 1997; Treseder & Allen, 2002), and *Funneliformis* in particular (Eom et al., 1999). Likewise, Gigasporaceae species may decline under N enrichment (Antoninka, Reich, & Johnson, 2011; Egerton-Warburton et al., 2007; Johnson et al., 2003; Treseder & Allen, 2002).

Which physiological traits might determine the N associations of a given AMF genus? We examined production of external hyphae as one possibility. We surmised that an extensive hyphal network improves soil foraging and can be advantageous when soil nutrient availability is low (Johnson et al., 2003, 2013). On the other hand, a large mycelium may be too costly if C transfer from host plants declines under N enrichment (Johnson et al., 2003; Treseder, 2005). We specifically looked for evidence that this trade-off could select for AMF taxa with more external hyphae when N availability is low and against them when N availability is high. We found mixed support for this idea. On one hand, AMF genera that inhabited ecosystems with lower C:N ratios (i.e. higher N availability) also tended to produce less external hyphae (Figure 3). On the other hand, there was no discernible relationship between external hyphal production and association with

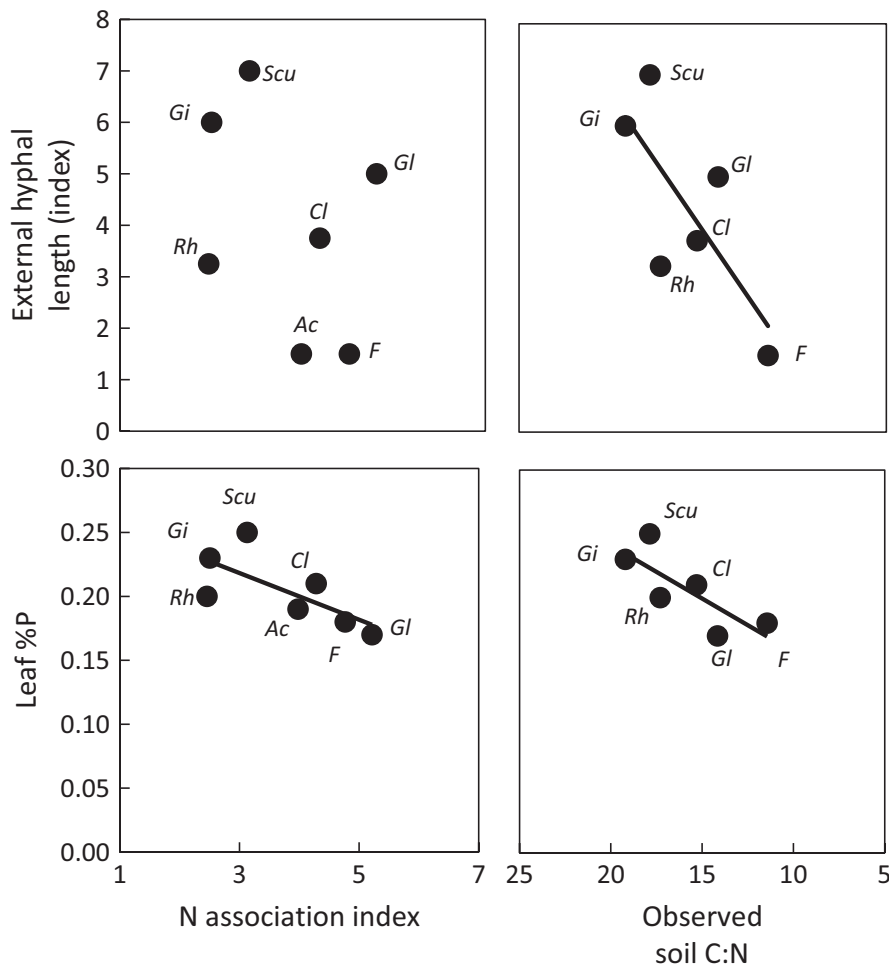


FIGURE 3 Relationships between N association traits vs external hyphal production and host plant P. Line is best fit for significant relationships (Table 1). Leaf %P was measured in plants grown in common media. Observed soil C:N was significantly related to external hyphal length ($p = .049$) and marginally significantly related to leaf %P ($p = .077$). The N association index was significantly related to total leaf %P ($p = .045$), but not external hyphal length ($p = .842$). Statistical analyses were performed on ranked data. Symbols are means for each genus. Ac = *Acaulospora*, Cl = *Claroideoglomus*, F = *Funneliformis*, Gi = *Gigaspora*, Gl = *Glomus*, Rh = *Rhizophagus* and Scu = *Scutellospora*. Data are from Egerton-Warburton and Allen (2000), Hart and Reader (2002), Maherali and Klironomos (2007) and Tedersoo et al. (2014). Note that the x-axis is reversed for observed soil C:N

N deposition in the Southern California gradient (Figure 3). Perhaps, other traits are more critical for N associations of AMF genera. AMF genera may, for example, vary in their sensitivity to changes in soil moisture, osmotic potentials, soil pH and aluminium toxicity, each of which can occur under N enrichment (Baath, Lundgren, & Soderstrom, 1981; Broadbent, 1965; Vitousek et al., 1997).

Moreover, in the global sampling, other environmental characteristics like dominant vegetation co-varied with soil C:N (Tedersoo et al., 2014). These other characteristics may have influenced our assessment of N associations of AMF taxa. For comparison, climate and soil types were constrained across the Southern Californian N deposition gradient. By the same token, results from the N deposition gradient are less generalizable outside the Southern Californian region. We note, in particular, that the Southern Californian sites were located on relatively P-rich soils (Egerton-Warburton & Allen, 2000), whereas P concentrations varied widely in soils from the global survey (Tedersoo et al., 2014). We used data from both studies, because each has its own strengths and caveats with respect to N associations.

It is possible that shifts in the AMF community under N deposition could reduce P uptake by host plants. Since AMF genera associated with higher N availabilities also tended to contribute less to host plant P, this mechanism might explain why AMF inoculation does not generally improve plant growth when N fertilizer has been added, as reported in the meta-analysis of Hoeksema et al. (2010). If P uptake by

plants is constrained because beneficial AMF decline under N enrichment, then what are the potential consequences for ecosystem function? If plants are primarily N-limited, there may not be a discernable effect on NPP, since P availability would be sufficient to meet plant demands. However, in ecosystems where plants are P-limited, a decrease in P supply from AMF may further reduce NPP and, in turn, C inputs into ecosystems may decline.

Based on the observed linkages between AMF traits, we predict that N enrichment would generally reduce the abundance of AMF taxa with greater plant P benefit (e.g. *Scutellospora* or *Gigaspora*). This finding is not in line with the prediction of Johnson (2010) based on ecological stoichiometry. In this framework, N enrichment improves host plants' photosynthetic capacity, increasing the availability of C for transfer to AMF symbionts. At the same time, N enrichment may accentuate P limitation of host plant growth. In this case, as N availability increases, host plants are expected to allocate more C to AMF to obtain P. Essentially, the trade-off between plant P benefit and C cost of external hyphae could be reduced. In this scenario, AMF taxa with more extensive external hyphae and better plant P benefit should be associated with higher N availability. Since our results indicated the opposite trend, we cannot accept the alternate hypothesis derived from Johnson (2010). Nonetheless, evidence that this mechanism could influence AMF communities has been documented in other ecosystems, such as the temperate grasslands examined in Johnson

et al. (2003) and Egerton-Warburton et al. (2007), and in a greenhouse experiment by Puschel et al. (2016). In contrast to our findings, the latter investigators suggested that competition for N between AMF and their host plants may reduce plant P benefits where N is scarce, but that N fertilization could alleviate this constraint (Puschel et al., 2016).

Owing to logistical constraints, our analysis focused on trade-offs associated with traits among genera. Variation in N associations, external hyphal production and plant P benefit was greatest at the genus or family levels (Table S2 and Powell et al., 2009), so our approach took into account much of the taxonomic variation associated with these traits. Nevertheless, these traits also vary among and within species of AMF (Figures S1 and S3, Hart & Reader, 2002; Koch et al., 2017; Maherali & Klironomos, 2007; Mensah et al., 2015; Powell et al., 2009). As such, it is possible that these trade-offs could also occur at smaller taxonomic scales. For example, Jansa et al. (2005) recorded positive relationships between mycelium extent and P uptake among *Glomus* species. As high-throughput sequencing more common, so should information regarding the responses of AMF species/genotypes to N in the environment (Morgan & Egerton-Warburton, 2017). In addition, we synthesized trait data from disparate studies, and study-specific differences in experimental design and growth conditions could have influenced the patterns we observed. We look forward to the opportunity to examine relationships between N associations and functional traits with finer taxonomic resolution, especially by measuring multiple traits on common samples. Finally, hyphal lengths and plant P benefits were measured on plants inoculated with single AMF isolates, whereas in natural ecosystems, plants are often colonized by multiple AMF taxa (e.g. Clapp, Young, Merryweather, & Fitter, 1995).

In summary, we quantified associations of AMF taxa with N availability along an N deposition gradient and in a global survey, and we compared these responses to previously determined traits of the same taxa: external hyphal production and P benefit to host plants. We found that N associations varied most among families and genera—isolates within *Glomus* declined least under high N deposition, but those in the Gigasporaceae were associated with low N availability. Moreover, high N-associated taxa tended to contribute less to host plant P. These traits can affect ecosystem processes, since facilitation of plant P uptake might increase NPP where P is limiting. Altogether, we predict that N deposition can shift the AMF community towards taxa that contribute less to ecosystem C inputs. We emphasize that this is a tentative prediction based on relationships between AMF traits. The next step is to test this prediction, either empirically via field or greenhouse studies or theoretically via trait-based ecosystem models (Treseder, 2016).

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AUTHORS' CONTRIBUTIONS

K.K.T. conceived the ideas, compiled and analysed data, and led the writing of the manuscript; E.B.A., L.M.E.W., M.M.H., J.N.K., H.M. and L.T. supplied data, collaborated on the ideas, and contributed critically to the drafts. All authors gave the final approval for publication.

DATA ACCESSIBILITY

Data from this synthesis are available on figshare <https://doi.org/10.6084/m9.figshare.5517013.v1> (Treseder et al., 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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