



## RESEARCH ARTICLE

# Plant diversity but not productivity is associated with community mycorrhization in temperate grasslands

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## Abstract

**Aims:** Mycorrhizal symbiosis influences the performance of plant individuals. However, its impact on plant communities is less well understood. We used a database of plant mycorrhizal traits and investigated how community mycorrhization – the prevalence of mycorrhizal symbiosis in plant communities – is related to plant community productivity and diversity. We analysed: (a) how soil fertility affects community mycorrhization; (b) how plant productivity and diversity are related to community mycorrhization; and (c) whether community mycorrhization directly mediates the relationships between soil fertility and plant productivity and diversity.

**Location:** Twenty-nine semi-natural grasslands in the south of Estonia, representing a steep productivity gradient (80–500 g/m<sup>2</sup>).

**Methods:** We estimated the proportion of plant biomass associated with mycorrhizal symbiosis (arbuscular mycorrhization index, AMI). The relationships between soil fertility (soil nitrogen [N], phosphorus [P] and potassium [K], accounting for soil moisture and pH), AMI, plant diversity and productivity were analysed using model averaging and pairwise generalized linear models, and support for direct relationships was determined using path analysis.

**Results:** There was a positive linear relationship between soil nitrogen and AMI. In turn, plant biomass showed positive, and plant diversity negative linear relationships with AMI. Path analyses indicated that AMI mediates the relationship between soil nitrogen and plant diversity, but not the relationship between soil nitrogen and plant community productivity. Plant productivity and mycorrhization increased along the soil fertility gradient, but plant diversity decreased.

**Conclusion:** These results suggest that community mycorrhization, which is sensitive to soil fertility (N), can modulate community composition in temperate grasslands, probably by enhancing the most dominant plant species in the community.

## KEYWORDS

arbuscular mycorrhization index, grassland, plant diversity, plant mycorrhizal traits, richness, soil fertility, soil nitrogen

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## 1 | INTRODUCTION

Mycorrhizal symbiosis is a symbiotic relationship between fungi and plant roots, where fungi provide soil nutrients, mainly phosphorus (P) and nitrogen (N), to plants in return for carbon (C) (Smith & Read, 2008). In addition, mycorrhizae can improve water acquisition (Augé, 2001), protect roots against pathogens (Linderman, 2000; Veresoglou & Rillig, 2012) and mediate plant signalling about immediate threats (Gilbert & Johnson, 2017). Through the effect on plant survival and growth, mycorrhizae also affect plant community composition (Klironomos, 2011), and productivity (van der Heijden, et al., 2008a). Although experimental suppression of mycorrhizal symbiosis has been shown to affect plant communities (Klironomos, 2011), there are limited and contrasting results about how the occurrence of mycorrhizal symbiosis is related to plant diversity in natural systems. For instance, Bennett and Cahill (2016) showed that mycorrhizal symbiosis allows for the persistence of rarer species in temperate grasslands by modifying the establishment, growth, and competition of plant species, while in a similar ecosystem, Hartnett and Wilson (1999) found that mycorrhizal symbiosis is linked to diversity reductions. Further, Bennett et al. (2017) reported that arbuscular mycorrhizal (AM) symbiosis has the potential to reduce plant conspecific density dependence and thus enhance plant diversity. Indeed, AM may enhance plant species coexistence and hence increase plant diversity by amplifying intraspecific, and balancing interspecific, competition (Moora & Zobel, 2010; Bever et al., 2012). Although the exact mechanisms through which mycorrhizal symbiosis mediates community diversity responses are not well known (Tedesoo et al., 2020), host species' mycorrhizal response appears to be a key characteristic determining plant community structure.

A positive relationship between plant productivity and the occurrence of mycorrhizal symbiosis (van der Heijden et al., 2008b) may be due to enhancement of plant nutrient acquisition, but also indirectly through induced protection or by facilitation of soil aggregation and prevention of nutrient leaching (van der Heijden et al., 2008b; Delavaux et al., 2017). However, evidence for mycorrhizal symbiosis mediating plant productivity seems to be context-dependent: while suppression of mycorrhizal symbiosis reduces productivity in North American tallgrass prairies and old fields (Bentivenga & Hetrick, 1991; Allison et al., 2007; McCain et al., 2011), the opposite was found in Norwegian boreal grassland (Dhillon & Gardsjord, 2004). Moreover, suppression of mycorrhizal fungi using fungicides may be confounded by effects on fungal pathogens (Allison et al., 2007; van der Heijden et al., 2008b). Thus, it remains unclear how the occurrence of mycorrhizal symbiosis in plant communities is related to productivity, and the degree to which community mycorrhization (related to changes in community composition) might respond to soil fertility along a large productivity gradient.

The effect of local environmental conditions, such as soil moisture, pH and especially soil fertility, is well known to affect mycorrhizal associations (Atkinson, 2003; Smith & Read, 2008; Bennett & Cahill, 2016). In line with the functional equilibrium hypothesis, which states that plant photosynthates are preferentially allocated

towards structures that acquire limiting resources, the allocation of photosynthates to mycorrhizae should decrease under high-fertility conditions (Johnson et al., 2003). However, field evidence has shown that the effect of fertilization on plant AM colonization is inconsistent, showing either no change (Wang et al., 2018) or a variable decrease in the root colonization rate (Liu et al., 2012; Verbruggen et al., 2013; Camenzind et al., 2014; Chen et al., 2014). This variation seems to be dependent on the community composition of AM fungi, the specific nutrient under investigation – mainly soil phosphorus (P) or nitrogen (N) (Liu et al., 2012; Chen et al., 2014) – and on the initial nutrient concentration in the soil (Treseder & Allen, 2002). Similarly, soil fertility has showed variable effects on the prevalence of mycorrhizal plant species (Peat & Fitter, 1993; Hempel et al., 2013). Indeed, the few studies specifically analysing the relationship between soil fertility and the prevalence of mycorrhizal or non-mycorrhizal plants have reported a negative relationship in central Europe (Hempel et al., 2013) but no clear relationship in the UK (Fitter et al. 1992). Therefore, the response of plant community mycorrhization to soil fertility might vary depending on the local environmental conditions.

To analyse the relationships between mycorrhizal symbiosis and key plant community properties, such as fertility, diversity and productivity, incorporation of plant individual- or species-based mycorrhizal traits can be an effective approach (Moora, 2014). However, when characterizing plant individuals on the basis of root mycorrhizal colonization, a large variety of factors must be taken into account. For example, mycorrhizal colonization of host plants depends on plant individual fitness and resources, currently available fungal partners, and seasonal effects of local biotic and abiotic factors (Hart & Reader, 2002; Treseder, 2013). Besides, mycorrhizal colonization levels are highly variable in time and space; yet, analysing it in plant individuals is a destructive measure, hampering temporal monitoring. By contrast, plant mycorrhizal traits measured at the species level are stable measurements shown to consistently capture key changes in plant community characteristics related to mycorrhizal symbiosis (Moora, 2014; Gerz et al., 2016). For instance, plant mycorrhizal status – whether the roots of a plant species are consistently (obligately mycorrhizal, OM), sometimes (facultatively mycorrhizal, FM) or never (non-mycorrhizal, NM) colonized by mycorrhizal fungi (Smith & Read, 2008; Moora, 2014) – is an effective stable trait sensitive to changes in habitat characteristics, such as fertility or plant diversity (Gerz, 2016; Porazinska et al., 2018). Thus, community mycorrhization shows how the prevalence of mycorrhizal symbiosis in plant communities changes along ecological gradients (Smith & Read, 2008; Moora, 2014). Previous studies estimating community mycorrhization or the relative abundance of mycorrhizal vs non-mycorrhizal species, found that both community mycorrhization and arbuscular community mycorrhization decreased with increasing soil fertility in temperate grasslands (Gerz et al., 2016), suggesting a lesser role of mycorrhizas in fertile habitats. Besides, no relationship was found between community mycorrhization and plant diversity. By contrast, Porazinska et al. (2018) reported a positive relationship between mycorrhization and diversity, with plant community richness positively related to the

abundance of mycorrhizal species and negatively related to that of non-mycorrhizal species.

In this study, we aimed to evaluate how plant community mycorrhization is related to soil fertility, plant productivity and plant richness in temperate grassland communities. Based on previous knowledge, we hypothesized that: (a) there is a negative relationship between community mycorrhization and soil nutrient content; but that (b) mycorrhization is positively related to plant community productivity; and (c) mycorrhization could be positively or negatively related to richness. Finally, we hypothesized that (d) soil fertility may indirectly drive plant richness and community productivity by regulating mycorrhizal symbioses in communities (Figure 1).

## 2 | METHODS

### 2.1 | Study sites

We selected 29 sites within an approximately 800-km<sup>2</sup> region south of Tartu, Estonia (58.07–58.35° N; 26.14–26.97° E), with a minimum distance of 1.2 km among sites. Plant productivity, richness, and soil data were sampled at all sites along a productivity gradient (80–500 g/m<sup>2</sup> of shoot biomass), representing a considerable fraction of the productivity range in grasslands worldwide (Fraser et al., 2015). The data were collected from open sites within semi-natural grassland habitats. At each site, 15 adjacent subplots of 0.5 m × 0.5 m, forming an extensive site plot of 1.5 m × 2.5 m, were established

during the summer of 2014. During the summer of 2015, the identity and cover of all plant species was estimated in each subplot and then averaged at the plot level.

### 2.2 | Soil abiotic factors

We characterized soil abiotic factors by analysing soil data collected from the field. Soil samples were pooled from three individual soil subsamples (10 cm × 10 cm × 10 cm) per site, from the area immediately surrounding each plot. Samples were analysed for total nitrogen and carbon, extractable phosphorus and soil-extractable potassium, using standard analyses, developed in the Estonian University of Life Sciences (Bennett & Cahill, 2016).

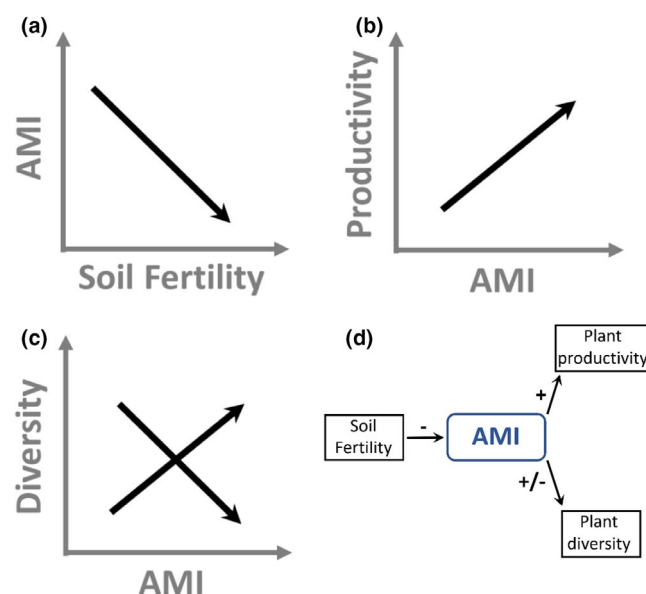
### 2.3 | Community mycorrhization index

To estimate community mycorrhization for each plot, we used community mycorrhization indices (Moora, 2014; Gerz et al., 2016). We first assigned plant mycorrhizal types and statuses to all plant species present in the plots. The assignment was based on all available empirical mycorrhizal information for each plant species (Bueno et al., 2019). Plant mycorrhizal type assignments reflect the identities of associated plant and fungal taxa, and the mycorrhizal structures present in plant roots. The plant mycorrhizal types distinguished were arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), ericoid mycorrhizal (ERM), orchid mycorrhizal (ORM), and dual mycorrhizal (AM + ECM) plants. Plant mycorrhizal status indicates the frequency of occurrence of mycorrhizal symbiosis; whether a plant species is always (obligately mycorrhizal; OM), sometimes (facultatively mycorrhizal; FM) or never (non-mycorrhizal; NM), associated with mycorrhizal fungi in their roots (Smith & Read, 2008).

For each site, we calculated both AMI and an overall mycorrhization index (MI; Moora, 2014; Gerz et al., 2016). Due to the very low representation of other plant mycorrhizal types (2% of ECM, 1% of ERM and 0.3% of ORM), we only present AMI results, as no differences between AMI and MI were apparent in the results. For both indices, a mycorrhizal status coefficient was first estimated for all plant species. The coefficient ranges from 0 (completely non-mycorrhizal) to 1 (completely mycorrhizal) and it is estimated as the number of observations of mycorrhizal plant individuals divided by the total number of plant individual observations per species (Moora, 2014; Gerz et al., 2016). We estimated mycorrhization indices as the average of the mycorrhizal status coefficients (*msc*) of all plant species in a plot, weighted by the relative cover of the plant species in the plot, and expressed as logit functions:

$$(A)MI = \ln \left( \frac{\sum (p_i \times msc_i)}{1 - \sum (p_i \times msc_i)} \right)$$

where  $p_i$  represents the proportional cover of species  $i$  in each plot and  $msc_i$  is the numerical coefficient of the mycorrhizal status of species  $i$



**FIGURE 1** Working hypotheses about the mediating role of community mycorrhization in relation to soil fertility, plant diversity and productivity: (a) there is a negative relationship between the arbuscular mycorrhization index (AMI) and soil fertility (measured as total soil nitrogen); (b) AMI is positively related to with plant community productivity; (c) AMI could be positively or negatively related to richness; and (d) soil fertility may indirectly drive plant richness and community productivity by regulating AMI

(Gerz et al., 2016). For full examples of the calculation of community mycorrhization see Moora (2014) and Gerz et al. (2016).

To assign mycorrhizal status, we used an updated version of the most recently published empirical mycorrhizal database (Bueno et al., 2017; Appendix S1). Three abundant plant species had no available mycorrhizal information in the literature (*Carex ornithopoda*, *Medicago × varia* and *Melampyrum nemorosum*), so we collected root samples around the study sites during the spring and summer of 2018. For each species, we collected up to 15 plant individuals: five plant individuals in three different sites. To estimate plant mycorrhizal traits in the lab, we selected young roots from the whole root system, for a total of approximately 1 g per plant. These roots were cleaned and dried in an oven at 40°C for 24 h, and then stored in dry conditions at room temperature. To clean and remove mineral particles, we left the roots overnight in KOH 2.5%. We then followed the microwave root-staining protocol (Dalpé & Séguin, 2013). The stain used was trypan blue at 0.05%. To remove excess stain, we left samples overnight in lactoglycerol. The percentages of root colonization and fungal structures in root samples were determined using the grid line-intersect approach (Newman, 1966; Tennant, 1975; supporting information Appendices S2, S3).

The community MI represents an estimate of a community property, indicating the dependence on mycorrhizal symbiosis of the community as a whole. In this study, the measure was used to understand relationships between mycorrhization and other community-level ecological properties (i.e. productivity, fertility, etc), regardless of the evolutionary relationships of their component plant species. Therefore, phylogenetic and evolutionary aspects (i.e. phylogenetic signal) were not considered in this study; for a detailed explanation of appropriate complementary phylogenetic analyses see de Bello et al. (2015).

## 2.4 | Plant productivity and richness

Plant productivity was estimated as the shoot, root, and leaf litter biomass from two 0.1 m × 1.0 m plots at each site, see Bennett et al. (2017) for details. The community composition of vascular plants was estimated between late June and early July 2015 for each of the 0.5 m × 0.5 m subplots. Species richness was then calculated for each site as the number of unique species found across all subplots.

## 2.5 | Statistical analyses

To test the influence of soil fertility on plant community arbuscular mycorrhization (AMI), we used a model averaging approach, based on the average of the best generalized linear models (GLMs), defined using the models representing the 95% confidence interval of the deviance explained by all models, (Delta AIC [Akaike information criterion] 95% confidence interval; Burnham & Anderson, 2003). The full models were built with AMI as the response variable and soil N, P and K, as well as soil moisture and pH, as predictor

variables. All predictors were standardized before modelling to avoid scaling issues (Burnham & Anderson, 2003). Soil P was log-transformed to avoid modelling with a skewed P distribution due to the presence of two extreme values. Model assumptions (homoscedasticity and normality) were visually checked on the full models and met validation criteria (Zuur et al., 2009). Collinearity was checked using the Pearson correlation coefficient and variance inflation factor (VIF) among variables. Collinearity issues were not found ( $r < 0.6$  and  $VIF < 3$ ; Zuur et al., 2009) either in the GLMs or the path analysis.

To test the influence of AMI on plant productivity and richness, GLMs were used, as the relationships were linear. Plant productivity and richness were the response variables, and AMI the predictor variable. A Gaussian GLM was used for the plant productivity model, as the model residuals were normally distributed and homoscedastic; richness was modelled with a negative binomial error distribution and a log-link function, to meet model assumptions (Zuur et al., 2009). All these analyses were performed using R: Model averaging was done using the *MUMIn* package; the plant richness model was fitted using the function “glm.nb” from the *MASS* package (Venables & Ripley, 2002).

### 2.5.1 | Path analysis

We used path analysis to evaluate direct and indirect relationships among plant productivity, richness, soil fertility and AMI. Path analysis is particularly useful in community-scale studies, as it allows direct and indirect effects of predictors to be distinguished (Shipley, 2016). Our theoretical model was based on prior knowledge. We expected soil N (as a proxy of fertility) to directly affect AMI due to the potential inhibitory effect of fertile conditions on mycorrhizal colonization, and to indirectly affect plant richness and community productivity (through modulation of AMI). If a community becomes less mycorrhizal in fertile conditions, it may be dominated by few, productive plant species, which lowers plant richness and increases community productivity.

The hypothesized path analysis was built and tested using the R package *lavaan*. The model was fitted with robust standard errors using a Satorra–Bentler-scaled (mean-adjusted) test statistic to account for possible non-multi-variate normality of the data. To account for the relatively small sample size ( $n = 28$ ), we used a Monte Carlo method and simulated 20,000 datasets with the same degree of freedoms, sample size and chi-square ( $\chi^2$ ) as the fitted model using the “MCX2” function in the R package *CauseAndCorrelation* (Shipley, 2016). If the  $\chi^2$  values obtained from the simulation are significant using a theoretical  $\chi^2$  distribution, then the results can be considered ambiguous.

The tested model was not rejected ( $\chi^2 = 5.734$ ;  $p$ -value = 0.125) and it was also robust to multi-variate non-normality, but the Monte Carlo simulation was only marginally significant ( $p = 0.062$ ). We therefore further tested the model using the function “psem” in the R package *piecewiseSEM* (Lefcheck, 2016), which has the advantage



of testing the main  $d$  separation claims (conditional dependence/independence between variables, Shipley, 2016) for the model being tested. We found an unaccounted link between N and total biomass and formulated a new model including this path. Since no other  $d$  separation claim was significant, we considered the model to be definitive.

To analyse the relationship between dominant plants, diversity and AMI, we used non-metric multi-dimensional scaling analysis (NMDS), and we fit plant richness and AMI gradients using the function “envfit”, while NMDS analysis was performed using the function “metaMDS”, both from the R package *vegan*. Selection of abundant plants followed the dominance candidate index (DCI) with a criterion of  $DCI > 0.2$  (Avolio et al., 2019).

### 3 | RESULTS

#### 3.1 | Community mycorrhization relationships with soil fertility, plant productivity and richness

We identified a positive linear relationship between AMI index and total soil nitrogen (N; Figure 2c). We found no appreciable relationships between AMI index and other soil properties (P, K, soil moisture and pH; Figure 2a–b).

AMI had a significant positive relationship with productivity (Figure 3a;  $F = 5.19$   $p = 0.031$ ), and a significant negative relationship with richness (Figure 3b;  $F = 4.13$ ,  $p = 0.042$ ; Appendix S4).

The hypothesized path (Figure 1d) fitted the data (Table 1 for model statistics) only when the link between AMI and total biomass was removed from the final model. Soil N positively affected total biomass and AMI, which, in turn, negatively affected species richness. The model explained 21%, 27% and 12% of the variance in AMI, total biomass and species richness, (Figure 4). Overall, path analysis suggested that soil fertility directly correlates with AMI and productivity and that AMI directly relates with plant diversity (Figure 4).

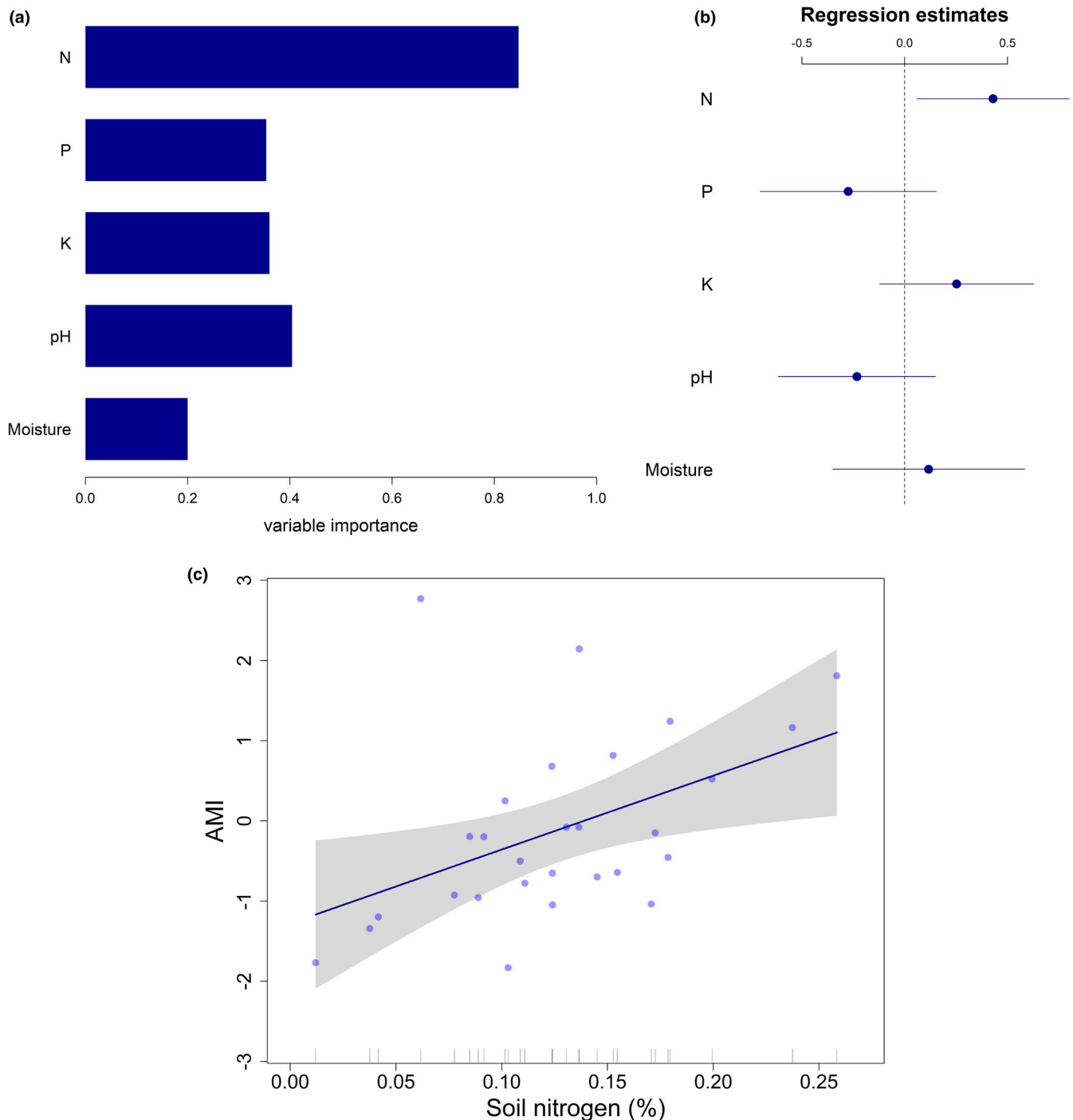
We found that dominant plant species, in particular *Cirsium arvense*, *Anthriscus sylvestris*, *Lupinus polyphyllus*, and *Equisetum arvense*, tended to have a high value of the mycorrhizal status coefficient ( $m_{sc}$ ) and occur in plant communities with higher AMI and lower values of plant richness (Figure 5). According to Grime's strategy classification (Saugier, 2001) all of them are considered competitors. Although plant strategy information was not available for *Lupinus polyphyllus*, we consider it a competitor, given its tall stature, fast growth and high LAI. Grime's model of plant strategies (Saugier, 2001), defines all plant species following a degree of specialization on three main aspects: competitiveness, stress tolerance and ruderality, which are related to key plant ecological characteristics. These characteristics are in turn associated with different ecological contexts and processes, for instance the successional stage or the regeneration ability of a plant community after a disturbance.

## 4 | DISCUSSION

Theoretical reviews have often concluded that mycorrhizal symbiosis may affect plant community structure and function (Bever et al., 2010; Bever et al., 2012; Atkinson, 2003), yet there remains a scarcity of empirical evidence (particularly in relation to support for these theories). We addressed the relationships between plant community arbuscular mycorrhization index (AMI), soil fertility, and plant productivity and diversity in temperate grasslands. Our results showed that AMI is positively related to soil fertility (N) and plant community productivity; unexpectedly, we found a negative relationship between AMI and plant richness. Evaluation of direct links between the variables indicated that higher AMI levels tend to suppress plant richness, suggesting that mycorrhizal symbiosis favours a small number of dominant species. At the same time, no direct relationship between AMI and productivity was identified, indicating that the relationship between AMI and productivity is explained by soil fertility and is not mediated by community mycorrhization.

#### 4.1 | Community mycorrhization and soil fertility

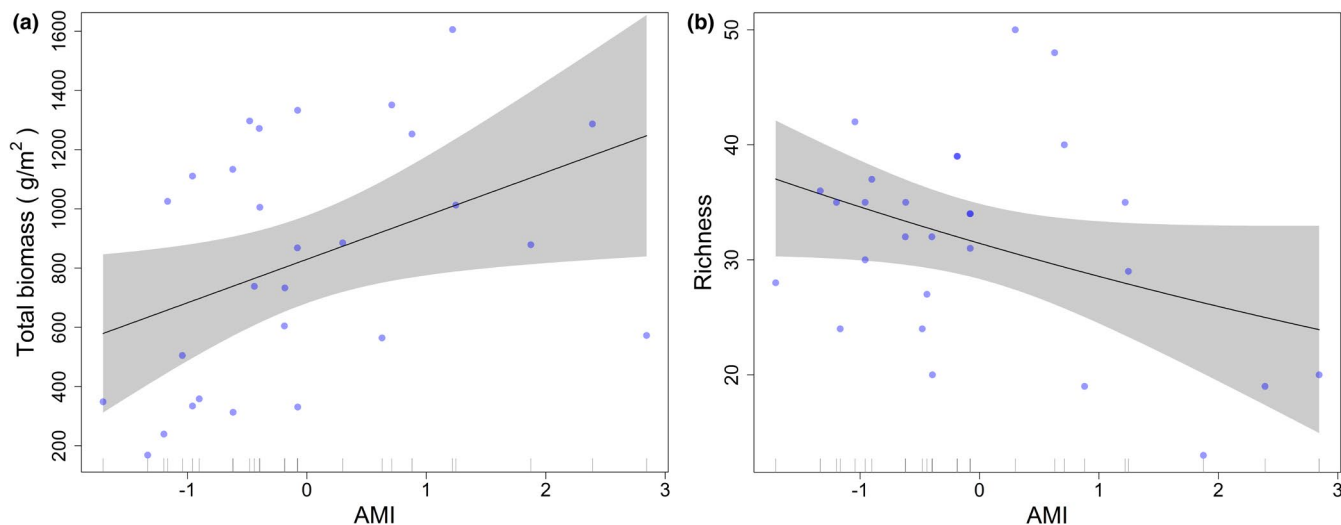
We found a positive linear relationship between soil nitrogen and community mycorrhization, which is contrary to our initial hypothesis. We expected that higher levels of soil fertility would limit the occurrence of mycorrhizal plant species, as mycorrhizal fungi might not be needed for plant nutrient uptake in an apparent unlimited nutrient context. Hempel et al. (2013) found that the prevalence of mycorrhizal symbiosis in the European flora was lower in species whose realized niche optimum was in fertile soil conditions, while Peat and Fitter (1993) found no relationship between soil fertility and the occurrence of mycorrhizal plant species. Further, experimental studies indicate that in moderately fertile soils, N fertilization reduces the abundance of AM fungal structures in roots and soil, but increases them when either N or P is limited (Treseder & Allen, 2002; Johnson et al., 2003; Jiang et al., 2018). This dependency on soil fertility suggests a role of the nutrient stoichiometry of plant and fungi, which can turn the mycorrhizal mutualism into a parasitic relationship, on the scale of both the plant individual (Johnson et al., 2014) as well as at the whole plant community (Jiang et al., 2018). Mechanistically, low levels of soil N may lead to fungi and plants competing for N (Hodge et al., 2010; Johnson et al., 2010). Indeed, Johnson et al. (2014) showed that AM mutualistic phenotypes are most likely in P-limited environments, so in high-N environments P is more likely to be limiting, thereby increasing the benefit of mycorrhization for plants. The mechanism proposed by these authors followed the *Law of the Minimum* between symbionts; while fungi depend mostly on N, plants are mainly limited by P. The availability of N and P could thus determine whether mycorrhizal benefits offset their cost. In temperate grasslands the availability of N may satisfy the requirements of the fungi and, in turn, enhance the performance of AM plants. This in turn may lead to a more prominent



**FIGURE 2** Variable importance (a) and coefficient estimates (b), describing the best predictors of the arbuscular mycorrhizal index (AMI) among soil nitrogen (N), phosphorus (P), potassium (K), moisture and pH. For regression estimates, we used one confidence interval, and we performed model-averaging using a delta Akaike information criterion (AIC) of 95% confidence intervals of the explained deviance of all models. The importance of each predictor was estimated as the sum of the Akaike weights for all the models where each variable is present. Variable importance is used to rank the relevance of the predictors, indicating the predictor's relative probability of belonging to the best model set. P was log-transformed to normalize its distribution. (c) Only N was significantly related to AMI with a positive relationship between AMI and N ( $F = 6.66$ ,  $p = 0.016$ )

role of mycorrhizal symbioses in shaping plant community structure than might be expected in fertile habitats. Our result suggests that, at the community level, favourable soil nutrient conditions are important for the establishment of AM associations.

Besides the nutrient stoichiometry of plants and AM fungi, other unmeasured factors might also explain the positive correlation between soil N and community mycorrhization. In fact, according to some reports, N and P fertilization, alone or combined, may elicit either a



**FIGURE 3** Relationships between arbuscular mycorrhization index (AMI) and (a) total biomass (indicating plant productivity) and (b) plant species richness

**TABLE 1** Model statistics for the path analysis

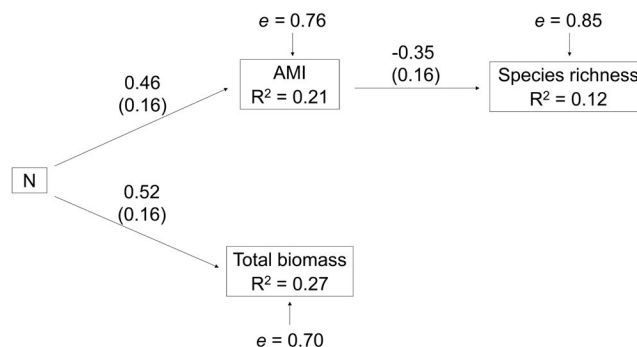
Model	df	$\chi^2$	p-value	AIC
1 (Richness)	3	1.970 (2.294)	0.579 (0.514; 0.390)	228.067

Degrees of freedom (*df*), maximum-likelihood-estimated chi-square statistic ( $\chi^2$ ), and *p*-value are shown. Values in parentheses are robust estimates of model statistics. The *p*-values in parentheses refer to the *p*-value range obtained from the Monte Carlo simulation (see *Methods*). AIC, Akaike Information Criterion.

pronounced change (Liu et al., 2012; Camenzind et al., 2014; Chen et al., 2014) or no change at all (Wang et al., 2018) in the mycorrhizal colonization of plants. Thus, it is unclear whether fertility and fertilization themselves or the type of nutrient, and degree and context of application, systematically affect fungal root colonization and, ultimately, mycorrhizal functioning in plants and plant communities. In our study, we might hypothesize that other symbiotic fungi, such as pathogenic fungi, could negatively influence the plants weakly colonized by mycorrhizal fungi, and thus favour the fast-growing species. This would be consistent with observations that mycorrhizal colonization is effective in plant defence against pathogens (Veresoglou & Rillig, 2012; Fernández et al., 2019), while pathogen occurrence is often related to low plant diversity conditions (Bever et al., 2015), such as in high-fertility environments. Furthermore, other unmeasured soil elements could directly influence the nutrient trade-offs. For instance, greater aluminium and calcium content tends to increase P fixation in soil, which is likely to reduce the availability of P to plants and fungi (Penn & Camberato, 2019).

## 4.2 | Community mycorrhization and plant productivity

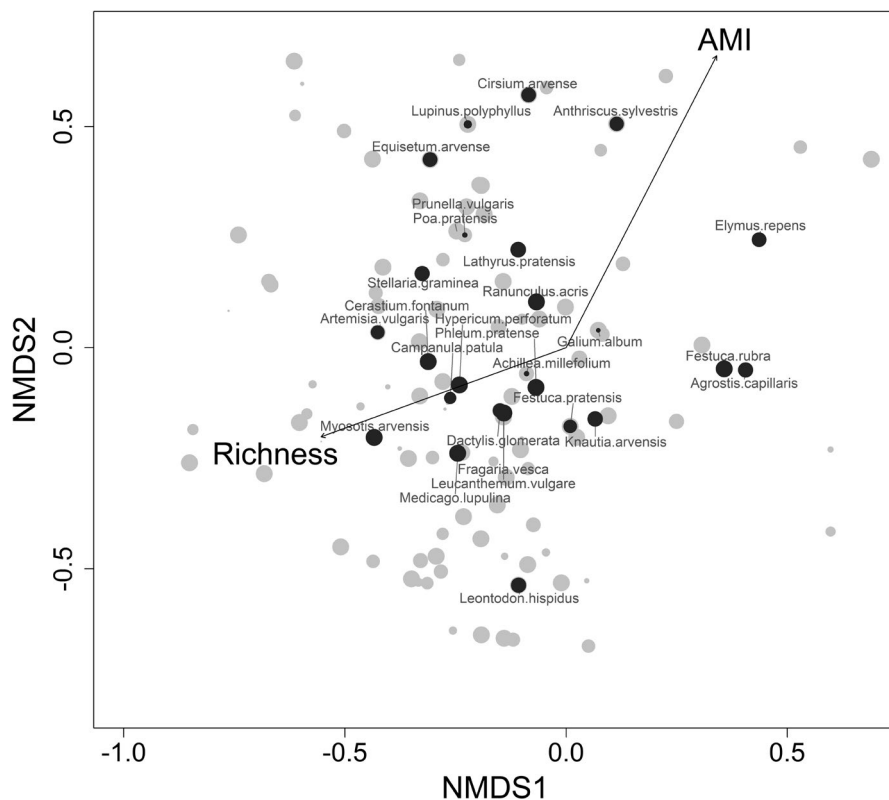
We hypothesized that mycorrhizal fungi could ameliorate plant nutrient limitation, subsequently increasing plant biomass and



**FIGURE 4** Path analysis model describing causal links between fertility, productivity, arbuscular mycorrhizal index (AMI) and species richness. Path coefficients, their standard errors, residual variances (*e*) and the percentage of explained variance ( $R^2$ ) for endogenous variables are shown. Model statistics are shown in Table 1. N, soil total nitrogen content; AMI, arbuscular mycorrhization index

productivity, so an increase in plant community mycorrhization would lead to an increase in plant community productivity. Indeed, we found a positive relationship between community mycorrhization and productivity. However, the communities with the highest AMI and productivity were in high-fertility sites, which does not support the explanation that higher productivity was due to amelioration of a nutrient deficit via mycorrhizal symbiosis.

We suggest that this increase in plant productivity and fertility with higher values of community mycorrhization could be primarily related to the abundance of soil N, which can drive above-ground net primary productivity (Fay et al., 2015). In such conditions, there is no N limitation for AM fungi, which might result in a higher abundance of fungi (Treseder & Allen, 2002). In principle, fungi can favour plants by means other than nutrition (Delavaux et al., 2017) such as pathogen protection (Bennett et al., 2009; Cameron et al., 2013; Chen et al., 2018). However, these functions were not necessarily



**FIGURE 5** Non-metric multi-dimensional scaling two-dimensional analysis (NMDS) to visualize the ordination of dominant plants, arbuscular mycorrhization index (AMI) and richness. The dot size represents frequency of plant species being mycorrhizal, measured with the numerical coefficient of the species' mycorrhizal status (msc). Black dots highlight the dominant species, defined by values of the Dominance candidate index (DCI) > 0.2. All highlighted species (black dots) are classified as competitors following Grime's plant strategy classification

important in our study system because the high availability of soil nitrogen alone can independently influence productivity and AMI, as indicated by our path analyses (Figure 4; Appendix S5).

### 4.3 | Community mycorrhization and richness

We expected that higher AMI would be associated with higher plant richness. Although theoretical papers have described mechanisms by which AM could facilitate coexistence (Hart et al., 2003; Bever et al., 2010), empirical evidence is limited and confusing (e.g. Klironomos et al., 2011). For instance, Porazinska et al. (2018) found a positive relationship between plant richness and community mycorrhization in alpine plant communities, while Gerz et al. (2016) found no clear relationship when analysing different communities of temperate grassland. However, our results showed that richness was negatively related to community mycorrhization. This suggests that in some circumstances AM may not enhance the development of diverse plant communities. So it is possible that in highly heterogeneous habitats plants tend to develop different strategies to obtain resources (Klironomos et al., 2000). A diversity of resource acquisition strategies may thus directly decrease the incidence of plants that rely solely on AM. In addition, there may be mechanisms by which the mutualism restricts plant coexistence, such as by favouring the performance of dominant species, or by initiating positive feedback loops between mutualistic partners (Chomicki et al., 2019). Indeed, there is experimental evidence that suppressing mycorrhizal symbiosis in the field with fungicide can increase diversity because community dominants are mycorrhizal, and reduction of

mycorrhizal fungi decreases their competitive ability (Hartnett & Wilson, 1999; Smith et al., 1999; McCain et al., 2011). Thus, in our study, high values of community mycorrhization associated with low plant species richness, which can indicate that mycorrhizal symbiosis supports dominant species. This, in turn, may enhance fitness differences with their plant neighbours ultimately leading to the potential competitive exclusion of non-mycorrhizal or facultatively mycorrhizal species. These findings differ from Saugier (2001) suggestion that competitive plants represent an acquisitive strategy and thus are less dependent on mycorrhizal symbiosis. Rather, our results are consistent with those of Betekhtina and Veselkin (2011) and Hempel et al. (2013), who showed that competitors tend to be mycorrhizal more frequently than ruderals or stress-tolerant species (Betekhtina & Veselkin, 2011; Hempel et al., 2013). Being mycorrhizal thus tends to support competitors in implementing an acquisitive strategy.

Given our still incomplete understanding of plant mycorrhizal status and community mycorrhization, we cannot rule out the possibility that new discoveries of relationships with other plant traits could help to explain the patterns reported here. Further research on the relationships between community mycorrhization and other plant and fungal functional traits and ecosystem properties deserves future attention.

## 5 | CONCLUSION

Overall, we found that productive plant communities in highly fertile soil harbour low plant diversity and exhibit high community mycorrhization (higher prevalence of mycorrhizal plant species), suggesting

on one hand that fertile soil is favourable for both mycorrhizal plants and fungi, and on the other hand that competitively dominant plant species may tend to require AMF.

In many grassland ecosystems, the highest species richness is observed in moderately low soil fertility, while increasing fertility is associated with lower diversity (Fraser et al., 2015). However, this relationship can be modulated by soil biota (Luo et al., 2017). Future studies should disentangle the mechanism underlying the negative relationship between AMI and plant richness, and investigate potential non-nutritional benefits of mycorrhizal symbiosis for dominant plants in species-poor yet fertile and productive communities.

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## AUTHOR CONTRIBUTIONS

CGB, MZ, MM and DL conceived the main research idea; JB, KR, CGB, DL collected and processed data; CGB, GP and DL performed statistical analyses; DL, CGB, MZ and MM wrote the paper; DL, CGB, MZ and MM discussed the methods and results; all the authors commented on the manuscript.

## DATA AVAILABILITY STATEMENT

Supporting information data are available on figshare (<https://doi.org/10.6084/m9.figshare.17169077>).

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

### Appendix S1 Mycorrhizal traits from all species and their references:

Type of mycorrhizal association reported: arbuscular mycorrhiza (AM), ectomycorrhiza (ECM), ericoid mycorrhiza (ERM), orchid mycorrhiza (ORM)

### Appendix S2 Mycorrhizal colonization data from *Carex ornithopoda*, *Medicago x varia* and *Melampyrum nemorosum*

Appendix S3 Pictures of arbuscular mycorrhizal fungi structures (vesicles, hyphae and spores inside of roots of a) *Carex ornithopoda*, b) *Medicago x varia* c) *Melampyrum nemorosum*

### Appendix S4 Structural equation models describing causal links between fertility, productivity, AMI and evenness

Appendix S5 Model statistics for the generalized linear models relating the effect of a) AMI to plant community productivity and plant b) richness

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