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Environmental drivers of grazing effects on arbuscular mycorrhizal fungi in grasslands

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Abstract

Arbuscular mycorrhizal fungi (AMF), common symbiotic root-associated soil biota, play a key role in maintaining ecosystem function and stability. However, how AMF are affected by livestock grazing in grassland ecosystem is variable, and this uncertainty in mycorrhizal responses to grazing is mainly due to the context-dependent nature of the AMF symbiosis association. The effects of grazing on AMF are through grazing-induced changes in the environment experienced by the mycorrhizal fungi and this includes both plant and soil-related factors. Here, we introduce a conceptual framework that highlights potential drivers and mechanistic pathways through which long-term grazing impacts AMF. We focus on known drivers of AMF abundance and diversity that are expected to be influenced by grazing including plant above-ground biomass and diversity, nutrient availability (soil available nitrogen and phosphorus) and edaphic properties (soil organic carbon, soil pH, soil bulk density and soil moisture). Given that the

identity and relative importance of each of these drivers may differ across different ecosystems, the application of our framework of potential environmental drivers allows us to generalize, organize and help formulate hypotheses for testing the impact of various grazing management approaches on AMF. We also argue the herbivory-AMF relationship can be moderated by climate, seasonality and topography. We reviewed the current state of knowledge of livestock grazing impacts on AMF and discussed some of the reasons behind conflicting results among empirical studies. We also provide suggestions for future research aimed at improving experimental design to unravel underlying mechanisms determining the impacts of grazing on AMF.

Key words: Mycorrhizal fungi, AMF-plant interactions, grazing, livestock, soil nutrients

1. Introduction

Arbuscular mycorrhizal fungi (AMF) are one of the most common root-associated soil biota, which influence plant productivity, sustain above- and below-ground biodiversity (Moora and Zobel, 2010; Chen *et al.*, 2016; Brundrett and Tedersoo, 2018; Yang *et al.*, 2018), and improve soil attributes vital for plant growth (Augé, 2004; Simard and Austin, 2010; Wagg *et al.*, 2014; Mardhiah *et al.*, 2016) in different ecosystems. Grasslands are among the most degraded ecosystems worldwide over the last 50 years, mainly due to excessive grazing which brought about widespread soil erosion, plant productivity and biodiversity loss, and a decline in ecosystem functioning and services (Conant, 2010; O'Mara, 2012; McSherry and Ritchie, 2013). However, how the ubiquitous symbiotic AMF are affected by livestock grazing remains unclear.

This lack of certainty on grazing impacts on mycorrhizas can be explained by the context-dependent nature of this symbiotic association (Hoeksema *et al.*, 2010; Smith *et al.*, 2010; Tao *et al.*, 2016; Alzarhani

et al., 2019). The indirect effects of grazing on AMF are through grazing-induced changes to the mycorrhizal environment, including both plant and soil related factors. Although previous studies cover a range of abiotic and biotic factors at different spatial and temporal scales (Ba *et al.*, 2012; Wang *et al.*, 2014; van der Heyde *et al.*, 2017), it is still difficult to generalize on the relative importance of drivers behind AMF community characteristics across different environments and grassland management systems. Moreover, the herbivory-AMF relationship may be moderated by climatic, seasonal and topographical effects (Soudzilovskaia *et al.*, 2015; Johnson *et al.*, 2016). Given that the identity and relative importance of each driver differs across different ecosystems (Alzarhani *et al.*, 2019), the suite of all interacting biotic and abiotic parameters which are affected by grazing and influence AMF community needs to be included in the analysis. This work will assist in providing further understanding of how the key drivers impact AMF and allow the development of models that generalize and help formulate hypotheses on the impacts of various grazing management approaches on AMF.

In this review, we present a conceptual framework to explain the indirect effects of long-term livestock grazing on AMF mediated by changes in mycorrhizal environment, thus providing insights into the potential environmental drivers and mechanistic pathways by which grazing alters AMF functioning. We focused on the current knowledge about the impact of grazing on AMF in long-term studies due to the time it takes for ecosystems to respond to environmental perturbations (McSherry and Ritchie, 2013). We also review current knowledge of livestock grazing effects on AMF and provide suggestions for future research aimed at improving experimental design and unravelling underlying mechanisms. This would assist in generalization and help produce a synthesis of the grazing effects on AMF, and identify different pathways through which grazing might alter AMF communities.

2. Conceptual framework and potential drivers of long-term livestock grazing effects on AMF

The context-dependent nature of the mycorrhizal symbiosis association suggests that the indirect effects of grazing on AMF occur through changes to the soil and root environment in which the AMF is found. Our framework proposes that the potential drivers of AMF which are expected to be influenced by grazing include plant community biomass and diversity, soil nutrient availability (here, soil available nitrogen (N) and phosphorus (P)) and edaphic properties (soil organic carbon, soil pH, soil bulk density and soil moisture). Moreover, the herbivory-AMF relationship can be moderated by climate, seasonality and topography effects (Figure 1). The framework defines the underlying mechanisms by which these potential drivers may be acting and explores their effects on AMF function and community structure (Table 1).

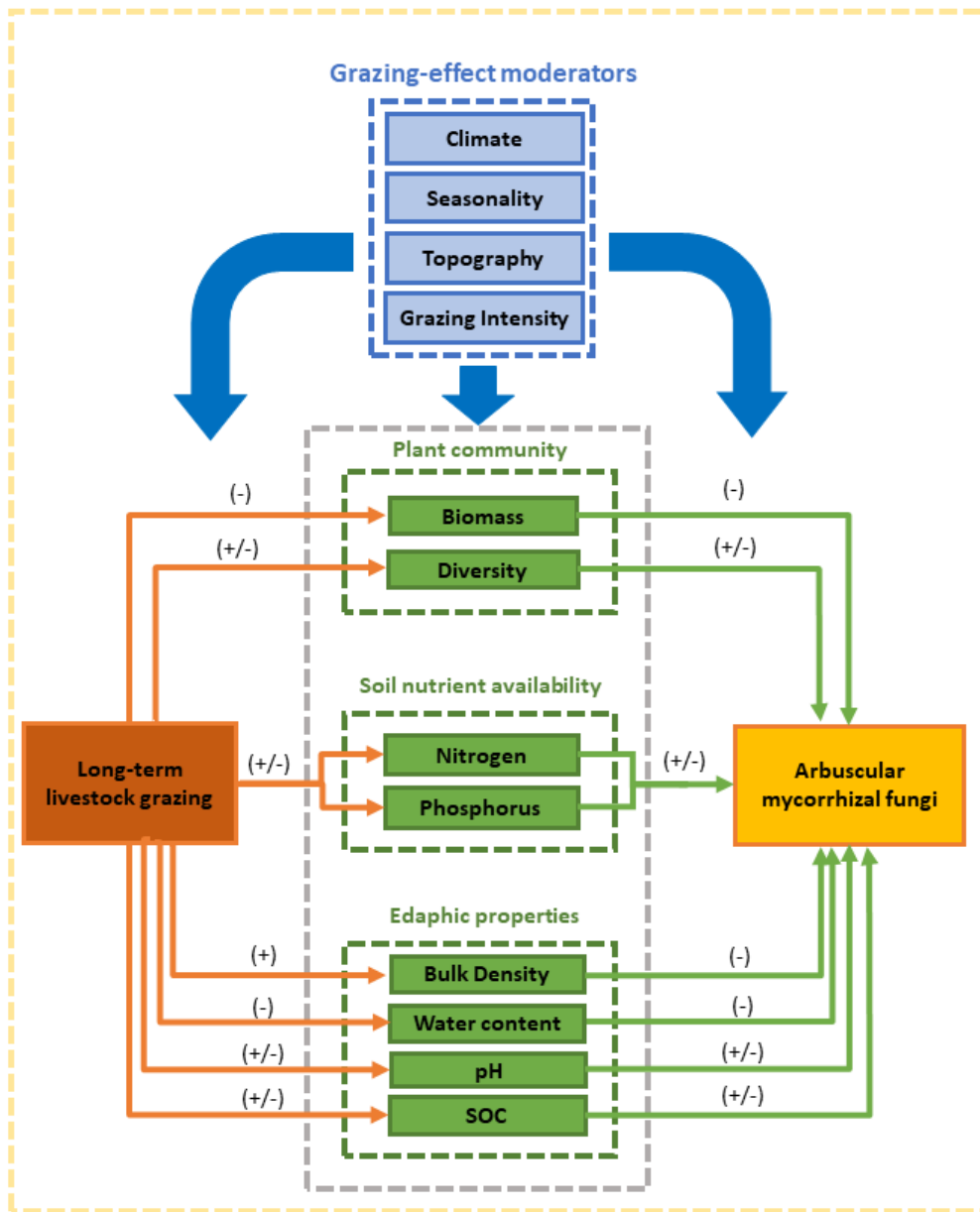


Figure 1 Conceptual framework of potential environmental drivers determining how long-term livestock grazing impacts arbuscular mycorrhizal fungi through changing the mycorrhizal environment. The possible outcome of grazing-induced change on plant community, soil nutrient availability, edaphic properties as well as AMF has been shown with + and – indicating the positive and negative effects respectively. The brown arrows indicate the direct effects of grazing on plant and soil related factors and green arrows indicate the indirect effect of grazing on AMF on each environmental variables. Blue arrows indicate the impacts of grazing-moderators (climate, seasonality, topography and grazing intensity) effects on interacting variables in the model. Dashed lines indicates that there is interaction among the variables within the boxes.

Table 1 Pathways, general outcomes and underlying mechanisms by which grazing impacts arbuscular mycorrhizal fungi (AMF) and their environment. The impacts of grazing on AMF are through the direct effects of grazing on plant community, soil nutrient availability and edaphic properties. One-way direction arrows show causal relation. + and - indicates the positive and negative effects respectively.

Pathway	Reported outcome	Potential underlying hypothesis	References
Long-term grazing effects on plant community biomass and diversity			
Grazing → Plant biomass	-	Clipping and removing the above-ground biomass, especially apical meristems, reduces the plant photosynthetic capacity, C capture and plant productivity.	(Schönbach <i>et al.</i> , 2011; Hao and He, 2019; Piñeiro <i>et al.</i> , 2010; Yan <i>et al.</i> , 2013)
	+	Grazing-induced increase in soil nutrient availability particularly soil nitrogen can enhance plant biomass and productivity.	(Medina-Roldán <i>et al.</i> , 2012; Veen <i>et al.</i> , 2014; Chen <i>et al.</i> , 2017)
Grazing → Plant diversity	-	Loss of grazing-sensitive rare species or removal of palatable dominant plant species from species pool under grazing may decrease plant biodiversity.	(Ba <i>et al.</i> , 2012; Li <i>et al.</i> , 2015; Epelde <i>et al.</i> , 2017; Ren <i>et al.</i> , 2018)
	+	Grazing may enhance plant community biodiversity at moderate level of grazing intensity through suppressing the domination of more competitive plant species with faster growth rates and promoting the coexistence of less competitive species with lower growth rates.	(Komac <i>et al.</i> , 2015; Pulungan <i>et al.</i> , 2019; Wan <i>et al.</i> , 2015)
Long-term grazing effects on soil nutrient availability			
Grazing → Soil nutrient availability	+	Adding dung and urine to the soil can enhance soil nutrient availability.	(Medina-Roldán <i>et al.</i> , 2012; Egan <i>et al.</i> , 2018; Vertès <i>et al.</i> , 2019)
	-	Grazing-caused defoliation, reduction in forage production, and litter accumulation is followed by further decreases in SOC and nutrient availability.	(Steffens <i>et al.</i> , 2008; Guo <i>et al.</i> , 2016; Hao and He, 2019)
Long-term grazing effects on edaphic variables			
Grazing → Bulk density	+	Livestock trampling and treading causes soil compaction and increases soil bulk density especially in the heavily grazed areas.	(Li <i>et al.</i> , 2012; Epelde <i>et al.</i> , 2017; Hao and He, 2019; Piñeiro <i>et al.</i> , 2010)
Grazing → Soil moisture	-	Soil compaction, diminishing plant shading effect, exposing soil to the air and increasing soil temperature reduces soil moisture and infiltration particularly in dry grasslands under grazing.	(Zhao <i>et al.</i> , 2007; Wiesmeier <i>et al.</i> , 2009; Ren <i>et al.</i> , 2018; Hao and He, 2019)
Grazing → pH	-	Gazing may decrease soil pH and causes soil acidification via urination and nitrification of urine-N, especially under high grazing pressure.	(Martins <i>et al.</i> , 2014; Ren <i>et al.</i> , 2018; Faghihinia <i>et al.</i> , 2020; Guo <i>et al.</i> , 2016)
	+	Grazing may increases soil pH and accelerating soil alkalization and salinization processes through loss of above-ground vegetation cover, increasing soil temperature, evaporation, and decomposition of soil organic matter.	(Kusakabe <i>et al.</i> , 2018; Hao and He, 2019)
Grazing → Soil organic carbon	-	Grazing may decrease SOC through reducing above-ground plant biomass, infiltration rates, enhancing soil compaction and SOC decomposition particularly in C3-dominated temperate grasslands.	(McSherry and Ritchie, 2013; Hao and He, 2019)
	+	Grazing may increase SOC via enhancing soil nitrogen stocks (SON), plant tissue deposition, and below-ground root litter deposition particularly in C4-dominated subtropical grasslands.	(McSherry and Ritchie, 2013; Wilson <i>et al.</i> , 2018)

Table continued

Long-term grazing effects on AMF through impact on plant community			
Grazing → Plant biomass → AMF	-	Grazing-caused reduction in standing vegetation cover and plant photosynthetic capability reduces below-ground C allocation to root associate AMF.	(Ren <i>et al.</i> , 2018; van der Heyde <i>et al.</i> , 2017)
Grazing → Plant diversity → AMF	+	Grazing-caused promotion in plant biodiversity, particularly at intermediate intensity, may provide AMF with wide range of below-ground root exudates for AMF spores germination, hyphal extension. Further, greater diversity of host plants for AMF may facilitate the establishment of some host-specific AMF species and enhance AMF diversity.	(Ba <i>et al.</i> , 2012; Stover <i>et al.</i> , 2018)
	-	Grazing-caused reduction in plant diversity decreases the range of below-ground plant root types and root exudates and consequently decreases the abundance and variability of the soil/root resources for AMF.	(Ba <i>et al.</i> , 2012; Epelde <i>et al.</i> , 2017)
Long-term grazing effects on AMF through impact on soil nutrient availability			
Grazing → Soil nutrient availability → AMF	+	As a general pattern, grazing-induced negative impact on relative availability of soil nutrients may cause higher plant nutrient demands for regrowth and to compensate for tissue loss, leading to more investment in AMF mutualisms to obtain additional nutrients.	(Hoeksema <i>et al.</i> , 2010; Yang <i>et al.</i> , 2016; Guo <i>et al.</i> , 2016)
	-	As a general pattern, grazing-induced positive impact on relative availability of soil nutrients may limit the plant investment in symbionts and result in less below-ground C allocation to AMF.	(Hoeksema <i>et al.</i> , 2010; Yang <i>et al.</i> , 2016)
Long-term grazing effects on AMF through impact on edaphic properties			
Grazing → pH → AMF	+	Grazing-caused positive impact on soil pH may provide a niche space for external hyphal extension.	(Mendoza <i>et al.</i> , 2011a; Hu <i>et al.</i> , 2013; Soudzilovskaia <i>et al.</i> , 2015; Guo <i>et al.</i> , 2016)
Grazing → pH → AMF	-	Soil acidification and decreasing pH under grazing condition can suppress microbial activities and growth including AMF. Further, AMF species with greater optimal pH range could disappear under soil acidic condition leading to decrease in AMF diversity	(Xu <i>et al.</i> , 2016)
Grazing → Bulk density → AMF	-	Grazing-induced soil compaction disrupts AMF hyphal networks.	(van der Heyde <i>et al.</i> , 2017; Faghihinia <i>et al.</i> , 2020)
Grazing → Soil moisture → AMF	+	Grazing-caused water limitation may constrain plant photosynthesis and primary production resulting in lower N and P demand from the plant and lower availability of photosynthate C for allocation to fungal partners	(Murray <i>et al.</i> , 2010; Mendoza <i>et al.</i> , 2011)
Grazing → Soil organic carbon → AMF	+	Grazing-induced increase in root carbon allocation, fine root exudation and SOC/SON stocks could reduce the AMF functioning.	(McSherry and Ritchie, 2013; Wilson <i>et al.</i> , 2018)
	-	Grazing-caused decrease in lower carbon allocation to roots, root and microbial biomass, and lower SOC/SON stocks could negatively impact the AMF abundance and activity.	(McSherry and Ritchie, 2013; Hao and He, 2019)

2.1. Plant community (biomass and diversity)

Obligate AMF depend upon their host plant for receiving photosynthetic carbon and in return they provide a wide range of beneficial services for their associated plants (Moora and Zobel, 2010; Powell and Rillig, 2018). The effect of herbivory on mycorrhizal fungi can be predicted, based on how grazing influences plant above-ground biomass and diversity (Figure 1). Since there is a close link between above- and below-ground parts of ecosystems (Yang *et al.*, 2018), direct effects of grazing events on the above-ground plant community would explain the indirect effects of livestock herbivory on AMF abundance and diversity. Here, we discuss the impact of long-term livestock grazing on AMF brought about by changes in plant biomass and diversity.

2.1.1. Plant biomass

Long-term grazing generally reduces plant above-ground biomass by removing parts of the standing biomass, and thus reducing total plant photosynthetic capacity (Schönbach *et al.*, 2011; Veen *et al.*, 2014; van der Heyde *et al.*, 2017; Hao and He, 2019). Although many studies report that long-term livestock grazing decreases plant biomass and productivity, a few, mainly lab experiments, report a positive grazing impact (Table 1). A meta-analysis (n=251 datasets) in China showed grazing decreased total biomass and above-ground biomass by 58% (95% CI: -72%~-38%) and 43% (95% Confidence Interval: -49%~-36%) respectively (Yan *et al.*, 2013). These results have recently been supported by the results of another meta-analysis of 140 study, where total biomass and above-ground biomass decreased by 28% and 45% respectively as grazing intensity increased during growing seasons in grazed Chinese grasslands (Hao and He, 2019). On the other hand, the reported positive impact was due to different plant species composition (Wan *et al.*, 2011), grazing in the non-growing season (Hao and He, 2019) and grazing-induced change in soil resource availability, particularly providing greater soil available nitrogen especially under stimulated grazing (Medina-Roldán *et al.*, 2012; Veen *et al.*, 2014; Chen *et al.*, 2017).

Either negative or positive grazing impacts on plant biomass and productivity will lead to changes in the AMF community and function, since AMF depend upon the symbiotic relationship with their host plants. Broadly speaking, the indirect impacts of grazing on AMF through changes in plant biomass and productivity can be explained by the fact that grazing-caused defoliation leads to a reduction in plant photosynthetic capacity and below-ground carbon allocation, which in turn reduce the abundance of plant AMF symbionts (Gehring and Whitham, 2002; Piñeiro *et al.*, 2010). Consistent with this, Ren *et al.* (2018) found significant negative impacts of grazing intensity on above-ground net primary productivity and its positive correlation with soil hyphal length density in a long-term manipulated experimental site with seven levels of grazing intensity in a temperate grassland in north of China. Bai *et al.* (2013) found that both above-ground plant biomass and AMF root colonization were greater where grazing had been stopped for 60 days compared to continuous grazing, thus showing the positive impact of AMF symbiosis on plant productivity. Ba *et al.* (2012) showed that AMF diversity was greater under light- to moderate-grazing intensity and declined under intense-grazing pressures, and that 38% of the variation in AMF diversity was associated with the above-ground biomass in a meadow steppe.

In contrast, defoliation by grazing can stimulate and increase below-ground carbon allocation (Wilson *et al.*, 2018) which could lead to an increase in the abundance and activity of AMF symbionts. In a C4-dominated sub-tropical grassland, greater below-ground carbon allocation, root biomass, root exudates and microbial biomass were observed in grazed plots compared to ungrazed ones (Wilson *et al.*, 2018). We are, however, unaware of any field evidence that shows any effects of long-term grazing on AMF through defoliation-caused positive effects on plant community biomass. Current knowledge suggests that the possible outcomes of plant-AMF interactions in response to grazing should be explained in the context of environmental variables. For example, in an effort to elucidate the effect of grazing on AMF root colonization of common plant species in a Rocky-mountain grassland in the US, two bunchgrasses and an invasive forb, with or without AMF, were subjected to simulated grazing (75% removal of above-

ground material) (Walling and Zabinski, 2006). The results showed that after clipping, AMF plants were smaller than non-AMF plants. However, greater concentrations of N and P were found in AMF-plants tissues (Walling and Zabinski, 2006). This findings suggests that the AMF benefits for plants under grazing can be through providing other ecological services, such as improving the plant nutritional status and chemical defenses against herbivory rather than maintaining plant productivity *per se*, especially over the shorter term.

2.1.2. Plant diversity

Long-term livestock grazing can decrease overall plant species diversity via loss of grazing-sensitive rare species which can be exacerbated by grazing pressure (Table 1) (Ba *et al.*, 2012; Li *et al.*, 2017). In a manipulated grazing experiment with seven grazing intensities, Li *et al.* (2017) showed that plant species richness significantly decreased up to 50% at higher grazing intensities (greater than 4.5 ewes (female sheep) ha⁻¹) suggesting that grazing intensity should not exceed this threshold in order to maintain plant biodiversity at their experimental site. The negative effect of grazing on plant species diversity may be also caused by the removal of palatable dominant plant species from the species pool (Table 1) (Wan *et al.*, 2011; Li *et al.*, 2017). Wan *et al.* (2015) reported a U-shaped relationship between plant species diversity and grazing intensity and a severe loss of palatable plant species at intermediate levels of grazing intensity. However, the abundance of low palatable plant species remained unaffected by grazing intensity (Wan *et al.*, 2015).

Loss of plant diversity leads to a decline in the range of below-ground plant root types and root exudates and consequently decreases the variability of the soil/root resources for soil micro-organisms including AM root associated fungi (Ba *et al.*, 2012; Epelde *et al.*, 2017). Indeed, AMF spores germination, hyphal extension and root infection take place in the presence of root and root exudates (Smith and Read, 2008;

Tahat *et al.*, 2010). In addition, it has been reported that root exudates change soil nutrient availability by priming decomposition of soil organic matter (Lambers *et al.*, 2008; Smith and Read, 2008). Given that AMF species have distinct nutrient absorption strategies (Mendoza *et al.*, 2011a; Guo *et al.*, 2016; Powell and Rillig, 2018), and that grazing can alter both plant below-ground biomass and soil resource availability (Hao and He, 2019), the abundance and composition of AMF would be expected to change in response to grazing (Ba *et al.*, 2012).

Grazing, on the other hand, may enhance plant community biodiversity at moderate level of grazing intensity by suppressing dominance by the more competitive plant species with faster growth rates and thus promoting the coexistence of less competitive species with lower growth rates (Komac *et al.*, 2015; Pulungan *et al.*, 2019). Highest levels of plant diversity has been suggested as a consequence of intermediate levels of grazing intensity where the plant community is dominated by palatable species with sub-dominant unpalatable plant species (Wan *et al.*, 2015).

Interestingly, it has been shown that grazing is likely to have a positive feedback on the strength of the association between AMF and plant community under light- to moderate-grazing, but with a negative impact under heavy-grazing pressures (Ba *et al.*, 2012). A conceptual model proposed by Ba *et al.* (2012) suggested under light to moderate grazing a positive feedback on AMF-plant associations would occur through improved photosynthetic and regrowth capability of the plants followed by increased below-ground carbon allocation to mycorrhizal fungi. In contrast, under heavy grazing, considerable above-ground biomass loss and below-ground carbon limitation could lead to less mutualistic benefits between AMF and plant. However, the AMF-plant community composition interactions under real grazing conditions, particularly at the large scale, have not been sufficiently investigated. Experiments at the local scale showed either positive effects (Ren *et al.*, 2018) or no relationship (van der Heyde *et al.*, 2017) between AMF and plant biodiversity in grazed grasslands. The underlying mechanisms are unclear,

however, a couple of factors can explain the possible positive or negative outcomes of the grazing impact on the interaction between plant and AMF, including:

- I. **Host plant identity:** Grazing reduced mycorrhizal root colonization significantly, and the greatest reduction was observed for the most preferred grasses compared with the least preferred ones in a sheep grazed site in the Patagonian steppe (Cavagnaro *et al.*, 2019). Similarly, grazing and host-plant species explained most variation in AMF spore community composition at different sites in Yellowstone National Park, USA (Mendoza *et al.*, 2011b). Likewise, the intra-radical AMF community composition was significantly shaped by interactive effects of host plant identity and grazing in grasslands in central Germany (Vályi *et al.*, 2015). Moreover, a greater diversity of host plants for AMF may facilitate the establishment of some host-specific AMF species, enhancing AMF diversity (Stover *et al.*, 2018). These finding suggests that grazing and host plant identity impact interactively on the abundance and community composition of mycorrhizal fungi.
- II. **Plant functional diversity:** it has been suggested that C4 grasses, non-nitrogen-fixing herbaceous dicotyledonous and woody plants are more responsive to mycorrhizal colonization compared with C3 grasses and plants associated with nitrogen-fixing bacteria (Hoeksema *et al.*, 2010). Furthermore, Lin *et al.* (2015) showed a significant increase in the competitive ability of N-fixing forbs and significant decrease in that of C3 grasses after AMF inoculation by synthesizing the results of 304 studies. Additionally, there is evidence that loss of plant functional groups reduced the abundance or biomass of below-ground community components in temperate grasslands (Chen *et al.*, 2016). Thus, plant functional diversity almost certainly plays an important role in determining the effects of grazing on AMF.
- III. **Mycorrhizal dependence of dominant and sub-dominant plant species:** AMF in a plant community with mycorrhizal-dominant plant species decreases plant diversity by increasing competitiveness of the dominant plant species. In contrast, AMF can exert positive impacts on

plant diversity in a community with sub-dominant mycorrhizal plant species (Mendoza *et al.*, 2011a; Ba *et al.*, 2012; Lin *et al.*, 2015; Yang *et al.*, 2018). Grazing effects on, either dominant, or sub-dominant, mycorrhizal plant species could, therefore, differentially impact on AMF communities.

- IV. **AMF isolates and functional diversity (mycorrhizal traits):** AMF species are different in terms of their functions and traits; for example some AMF species are better at defending their host plant against pathogens, whereas others are better at improving plant productivity through nutrient uptake (van der Heijden *et al.*, 2006; Hoeksema *et al.*, 2010; Yang *et al.*, 2017; Ferlian *et al.*, 2018; Powell and Rillig, 2018). Grazing impacts would in this case favor those plant-AMF associations best-placed to respond positively to any competitive release caused by grazing.

Taken together, changes in plant community diversity caused by grazing would impact AMF functioning via a range of pathways. The possible outcome of this grazing effect can be explained in the context of factors including host plant and AMF species identity, grazing intensity and environmental conditions. For example, grazing can enhance forbs with low net primary productivity and thereby reduce soil carbon input in one region while it can increase encroachment by shrubs with high net primary productivity and increase soil carbon input in another region (Piñeiro *et al.*, 2010). In both cases, changing the above-ground plant community composition would alter the interconnected below-ground soil biota, thus affecting soil ecosystem functioning and the soil carbon cycle.

2.2. Soil nutrient availability

Soil nutrient availability can be influenced positively by livestock grazing (van der Heyde *et al.*, 2017; Egan *et al.*, 2018) via dung and urine addition (Vertès *et al.*, 2019). Dung is rich in carbon and phosphorus and urine is rich in nitrogen and potassium. However, negative effects of grazing on soil resources (Steffens *et*

et al., 2008; Wiesmeier *et al.*, 2009; Guo *et al.*, 2016) and null effects (Li *et al.*, 2008; Burke *et al.*, 2019), depending on the balance between inputs and outputs in the system, have been also reported (Table 1). For example, in a recent meta-analysis conducted in manipulated field grazing experiments in Chinese grasslands, Hao and He (2019) showed that grazing reduced soil total N and P by 3.9% and 9.4% respectively. Negative impacts of herbivory on soil resource availability occurs via defoliation, reduction in forage production, litter accumulation, followed by further decreases in soil carbon and nitrogen availability (Piñeiro *et al.*, 2010).

Both positive and negative impacts of livestock grazing on soil nutrient content change mycorrhizal behavior and activities since the obligate symbiotic AMF rely on plants for their C in exchange for nutrients such as P and to a minor extent N (Figure 1). Indeed, strong correlations between abundance and diversity of AMF and soil nutrient availability, including N (Birgander *et al.*, 2014; Soudzilovskaia *et al.*, 2015; Binet *et al.*, 2017; Soka and Ritchie, 2018), P (Wang *et al.*, 2014; Guo *et al.*, 2016; Faghihinia *et al.*, 2020), and their interactions (Chen *et al.*, 2014) have been reported in grazed grassland ecosystems. Therefore, grazing-induced change in soil nutrient availability is expected to affect AMF by changing the mycorrhizal environment. However, the mechanisms and pathways of long-term grazing impacts on AMF community through altering soil stoichiometry are unclear due to the many reported conflicting results. For example, a long-term grazing-induced reduction in soil N and P was significantly positively correlated with AMF diversity in typical meadow steppe in north of China (Guo *et al.*, 2016), whereas the grazing-induced positive effects on soil N and P was not related to AMF abundance and diversity in grazed prairies in Canada (van der Heyde *et al.*, 2017). Conflicting results can be partly explained by relative availability of soil resources. It has been suggested that the relative availability of soil nutrients, particularly N and P, determines the outcome of plant-AMF interaction (Hoeksema *et al.*, 2010; Yang *et al.*, 2016). Positive mutualisms and higher rate of AMF colonization in nutrient limited grasslands is expected due to greater host nutrient demands for regrowth and to compensate for tissue loss caused by grazing (Guo *et al.*, 2016;

Faghihinia *et al.*, 2020). Meanwhile, decreases AMF colonization was reported at very low nutrient availability due to apparent competition with the host plant for the limited resources (Piippo *et al.*, 2011). Grazing effects on AMF through the altering of soil resource availability may also depend on which nutrient is most limiting in the ecosystem. The findings of a meta-analysis of mycorrhizal inoculation experiments are consistent with the hypothesis that AMF inoculation is most beneficial to plant growth in P-limited systems (tissue N:P > 16 in non-inoculated plants) rather than N-limited (tissue N:P < 14 in non-inoculated plants) (Hoeksema *et al.*, 2010) (Table 1). Given that different grasslands types located in different climate zones differ in terms of N (Piñeiro *et al.*, 2010) and P availability (Zhou *et al.*, 2017), variable AMF responses to grazing in different ecosystems must be expected. For example, low values of AMF root colonization has been reported in the lowland equatorial zone (–15° and 15° latitudes) with low soil P availability due to the evolutionary strategy of plants to cope with P limitation through cluster root development (Soudzilovskaia *et al.*, 2015). In contrast, AMF root colonization intensity was greatest at sites with high soil nitrogen availability and with a continental climate at the global scale (Soudzilovskaia *et al.*, 2015). Further field investigations at the global scale are needed to test these hypotheses and provide more insight into the underlying mechanisms of grazing impacts.

Soil fertility expressed as a C:N ratio may be another important predictor which could be affected by grazing (Piñeiro *et al.*, 2010; Mendoza *et al.*, 2011a) and translate to changes in the AMF community (Soudzilovskaia *et al.*, 2015). As a general global pattern, Piñeiro *et al.* (2010) reported increased C:N ratios in grazed compared to ungrazed sites. Interestingly, in a global review across 233 sites an unimodal relationship was described between soil C:N and intensity of root colonization by AMF, peaking in moderately-fertile soils with a soil C:N ratio of 11.8 followed by a decreasing trend (Soudzilovskaia *et al.*, 2015).

2.3. Edaphic properties

Grazing can impact the edaphic properties of the mycorrhizal environment. For example, as a general pattern, grazing increases soil bulk density and decreases soil moisture, permeability and hence water available for plant growth (Wiesmeier *et al.*, 2009; Piñeiro *et al.*, 2010; Hao and He, 2019; Tang *et al.*, 2019b); this occurs where livestock trampling and treading leads to soil compaction, especially in dry grasslands with lower water and nutrient availability. Moreover, by reducing the plant shading effect, grazing exposes soil to the air, increasing soil temperature and reducing the water content (Table 1). Considering the important role of soil water content in the plant-AMF relationship (Smith *et al.*, 2010; Augé *et al.*, 2015), adverse effects of grazing on soil moisture will impact on AMF functioning. Indeed, strong positive relationships between soil water content and AMF spore richness (Murray *et al.*, 2010; Mendoza *et al.*, 2011b), AMF root colonization (Faghihinia *et al.*, 2020) and external hyphal density (Ren *et al.*, 2018; Soka and Ritchie, 2018) have all been reported for grazing experiments. Grazing-induced water limitation may reduce plant photosynthesis rates, and hence primary production, resulting in lower N and P demands by the plant and lower availability of photosynthate C for allocation to fungal partners (Mendoza *et al.*, 2011b).

Grazing can also exert either negative or positive effects on soil pH which also impacts on the mycorrhizal environment (Table 1). Grazing may cause increases in soil pH via accelerating soil alkalization and salinization processes through loss of above-ground vegetation cover, increasing soil temperature, evaporation, and decomposition of soil organic matter (Kusakabe *et al.*, 2018). In contrast, grazing may also cause soil acidification and decreases in soil pH via urination and nitrification of urine-N, especially under high grazing pressure (Martins *et al.*, 2014).

Changes in soil pH influences the soil carbon and nutrient cycles (particularly N) thereby affecting the activities of soil microorganisms involved in the transformations of compounds containing these two

elements (Kunhikrishnan *et al.*, 2016). Indeed, field evidence for positive relationships between pH and AMF spore density (Mendoza *et al.*, 2011a; Birgander *et al.*, 2014; Soka and Ritchie, 2018), soil hyphal length density (Hu *et al.*, 2013; Ren *et al.*, 2018) and AMF Shannon diversity in soil and root (Guo *et al.*, 2016) have been recently documented in grasslands.

At high soil pH, P can precipitate with calcium forming calcium phosphates and thus become unavailable for plant uptake directly or via their associated microorganisms (Gupta *et al.*, 2008). Low soil pH, on the other hand, has been frequently shown to drive AM fungal community structure (Mendoza *et al.*, 2011a; Chagnon *et al.*, 2013). However, low pH, beyond a certain threshold, can cause P immobilization due to fixation by aluminum and iron ions, also reducing its availability to plants, and thus increasing plant requirement for interactions with AMF (Zhu *et al.*, 2007; Klichowska *et al.*, 2019).

Additionally, AMF species differ in terms of their optimal pH ranges (An *et al.*, 2008; Chagnon *et al.*, 2013) and grazing-caused changes in AMF niche space could impact the abundance and community composition of the mycorrhizal fungi (Wang *et al.*, 2014; Xu *et al.*, 2016). For example, a strong negative correlation between AMF richness and phylogenetic diversity and pH was reported along a 5000-km transect at 47 sites with mostly alkaline soils and four different vegetation types including meadow, typical steppe, desert steppe and desert in northern China (Xu *et al.*, 2016). The strong negative correlation were attributed to disappearance of some AMF species under extreme soil alkaline condition (Xu *et al.*, 2016).

Grazing has also been suggested to impact on SOC content via three main pathways simultaneously, by altering: (1) plant net primary productivity, (2) soil nitrogen stocks (SON), and (3) SOM decomposition (Piñeiro *et al.*, 2010). Grazing may decrease SOC by reducing above-ground plant biomass, infiltration rates, enhancing soil compaction and SOC decomposition particularly in C3-dominated temperate grasslands (McSherry and Ritchie, 2013; Hao and He, 2019) (Table 1). Conversely, grazing may increase SOC via enhancing soil nitrogen stocks (SON), plant tissue deposition, and below-ground root litter

deposition, particularly in C4-dominated subtropical grasslands (McSherry and Ritchie, 2013; Wilson *et al.*, 2018). In either case, carbon allocation to roots and root exudates, and the abundance and activity of soil micro-organisms including AMF, would be affected by grazing (Wilson *et al.*, 2018). In general, the dynamic of grazing effects on AMF through changes in SOC, below-ground carbon allocation or root exudation has not been addressed adequately in previous studies. However, it can be hypothesized that lower carbon allocation to roots, root and microbial biomass, and lower SOC/SON stocks would negatively impact the AMF abundance and activity under grazing. In contrast, grazing-induced increase in root carbon allocation, fine root exudation and SOC/SON stocks could reduce AMF functioning. Having said that, the effects of grazing on SOC is controlled by plant community productivity and composition, soil nutrient content and precipitation (Piñeiro *et al.*, 2010; McSherry and Ritchie, 2013; Wilson *et al.*, 2018) suggesting that all these factors, interacting together, will also influence the soil microbial processes.

Taken together, these findings demonstrate that changes in the edaphic properties is another pathway through which livestock can influence the environment experienced by mycorrhizas. It is worth, therefore, considering that all grazing-caused changes in physical and chemical properties occur simultaneously and that including them in frameworks and models could help to unravel the co-occurring mechanisms affecting mycorrhizal communities in different environments and better understand the grazing effects on below-ground processes.

2.4. Grazing-effects moderators

There is evidence that grazing effects on AMF community can be moderated by climate (Dickie *et al.*, 2013; Soudzilovskaia *et al.*, 2015; Zhang *et al.*, 2019), seasonality (Lingfei *et al.*, 2005; Regan *et al.*, 2014), topography (Ren *et al.*, 2018; Faghihinia *et al.*, 2020) and grazing intensity (Mendoza *et al.*, 2011b; Ba *et al.*, 2012; Ren *et al.*, 2018).

2.4.1. Climate

The latitudinal gradients in climate variables, mainly temperature and precipitation, has generated various types of grasslands with distinct floristic composition and abiotic features in different climatic zones (Faber-Langendoen *et al.*, 2012; Dixon *et al.*, 2014). Therefore, the possible outcomes of interacting effects of climate and grazing on above- and below-ground communities would likely lead to different results depending on ecosystem type. For example, in a review study of 67 paired comparisons at the global scale, Piñeiro *et al.* (2010) revealed that below-ground root biomass and SOC were greater in grazed compared with ungrazed sites at the driest and wettest sites, but were lower at sites with intermediate precipitation (400 mm to 850 mm). Moreover, it has been demonstrated that grazing can buffer (Wang *et al.*, 2019) or exacerbate (Tang *et al.*, 2019a) the response of plant communities to climatic variation due to its important influences on plant biomass, community composition and soil nutrient dynamics.

Despite a great deal of effort in investigating the effects of climatic variables and grazing on above-ground community and nutrient cycling (Post and Pedersen, 2008; Tang *et al.*, 2019a; Wang *et al.*, 2019; Lv *et al.*, 2020), little is known about their interacting effects on the below-ground community, particularly at the global scale. Much of the work has been primarily conducted in mesocosm experiments through the manipulation of temperature (Hawkes *et al.*, 2008; Zhang *et al.*, 2019), rainfall (Deveautour *et al.*, 2019), or both (Sun *et al.*, 2013) at very local scales. Data collected from 233 sites worldwide revealed the key role of climate in explaining the global pattern of AMF root colonization (Soudzilovskaia *et al.*, 2015), for example, showing that plant root colonization by AMF peaked at sites with warm growing season temperatures and declined at sites with cooler or hotter growing seasons. However, how AMF are influenced by grazing and climate in conjunction remains unclear. Given that grazing is a common practice in almost all climatic zones, gaining an insight into how climate interacts with grazing impacts on AMF

functioning has essential implications for sustainable grassland managements and predicting the consequences of the future climate change scenarios.

2.4.2. Seasonality

In addition to annual variations in climatic factors, climatic seasonality is also expected to moderate the grazing effects on above- and below ground community as a result of inter-annual variations in temperature and precipitation (He *et al.*, 2010; Li *et al.*, 2010; Ramos-Zapata *et al.*, 2011; Omirou *et al.*, 2013; Wang *et al.*, 2014), vegetation growth and plant phenology (Sánchez-Castro *et al.*, 2012), plant nutritional quality (Mysterud *et al.*, 2011) and nutrient availability (Smith and Smith, 2011; Wang *et al.*, 2014).

Despite the major changes that seasonal variation causes to plant phenological development and soil nutrient status, the interaction of seasonality and grazing effects on mycorrhizal fungi has not been addressed sufficiently, and the underlying mechanisms remain poorly understood. Many studies addressed the response of AMF to grazing at a single seasonal time point (Bai *et al.*, 2013; van der Heyde *et al.*, 2017). However, there appears to be a pronounced seasonal pattern in AMF responses to grazing, particularly in temperate systems; this has been described for mycorrhizal root colonization (Lekberg *et al.*, 2013; Hazard *et al.*, 2014; Regan *et al.*, 2014; Wang *et al.*, 2014; Cavagnaro *et al.*, 2018), fungal hyphal length density (Staddon *et al.*, 2003; Wang *et al.*, 2014) and AMF spore density (Bever *et al.*, 2001; Wang *et al.*, 2014). Additionally, Wang *et al.* (2014) found a significant interaction between grazing management and seasonality on AMF abundance and community composition.

AM fungal abundance and activity is expected to peak in summer because of the greater plant nutrient demand, rapid vegetative growth and root production. In addition, plants may need more nutrients to fund shoot regrowth, thus invest more in AM fungi during summer when grazing is usually most intense

(Cavagnaro *et al.*, 2018). Consistent with this hypothesis, Cavagnaro *et al.* (2018) observed that AMF root colonization of both sheep preferred and non-preferred grass species was significantly higher in summer compared with autumn in a steppe grassland in Argentina. Similarly, Staddon *et al.*, (2003), Mandyam and Jumpponen (2008) and Wang *et al.* (2014) reported greater mycorrhizal root colonization in the summer, and lower during the autumn in grassland ecosystems. The same seasonal pattern has been reported for fungal hyphal length density in a grassland soil (Staddon *et al.*, 2003). However, no seasonal variation in AMF colonization has also been reported between summer and winter in a coastal- sandy, temperate-grassland in Denmark (Lekberg *et al.*, 2013). Further research is needed to explain these different observations.

Together, the current knowledge suggests that the impact of grazing on AMF community may not be particularly representative at a given seasonal time point. Therefore, if we are to understand the mechanisms underlying grazing effect on AMF, seasonality should not be overlooked in studies of grazing on AMF. This could have large implications for grassland management in term of the timing of grazing within the growing season and helping with management decisions aimed at maintaining sustainable grassland productivity and soil biodiversity.

2.4.3. Topography

Topographic relief influences habitat conditions via the creation of gradients in soil water and nutrient availability and solar exposure (Schowalter, 2016). Furthermore, topography impacts animal behavior and their distribution leading to an heterogeneous grazing intensity (Johnson *et al.*, 2016). Lower lying areas tend to be grazed more heavily with deposition of greater loads of dung and urine. Areas at higher elevation, in contrast, experience low- to moderate-grazing intensity with less nutrient deposition

(Johnson *et al.*, 2016). Therefore, topography, even at the local scale, alters soil resource availability (e.g. soil moisture, soil organic carbon and total nitrogen stocks) thereby affecting plant community structure leading to changes in soil microbial biomass and composition (Murray *et al.*, 2010; Zhang *et al.*, 2013; Ren *et al.*, 2018).

Given that the plant-AM fungi association is fundamentally a symbiotic relationship based on nutrient exchange (Johnson *et al.*, 2015; Powell and Rillig, 2018), topographic gradients of moisture and nutrient availability will almost certainly interact with grazing to influence AM fungi. For example, significant negative correlations between topographic-induced changes in soil nutrient availability and mycorrhizal root colonization (Faghihinia *et al.*, 2020), extra-radical hyphal production (Ren *et al.*, 2018) and AMF spore community composition (Murray *et al.*, 2010) under grazing have been reported suggesting topography moderates the impacts of grazing on AMF. AMF may enhance plant grazing tolerance through acquisition of more nutrients in more upland areas, where low- to moderate-grazing occurs and nutrients are often limited. On the other hand, AMF can be less beneficial in lower lying areas where grazing is more intense and competition between plant and AMF is probable due to limited photosynthetic carbon (Johnson *et al.*, 2016). Consistent with this hypothesis, Faghihinia *et al.* (2020) found a greater intensity and frequency of mycorrhizal root colonization under grazing in sloped sites with limited nutrient availability compared to flat sites with greater nutrient availability in a temperate grassland experimental system. Similarly, Bueno de Mesquita *et al.* (2018) found greater AMF root colonization at lower elevations with lower availability of soil N and P in a mountain grassland.

2.4.4. Grazing intensity

Given that the number of livestock per unit area strongly impacts above- and below-ground productivity and diversity (Yan *et al.*, 2013), it would be reasonable to assume that the extent of the grazing impact on

AMF function and community structure would largely depend on grazing intensity. Whilst overgrazing has destructive and irreversible negative impacts on plant community and soil properties, undergrazing can be just as harmful to grassland biodiversity and functioning through less stimulation of plant growth and loss of grazing-dependent legumes and grasses (Metera *et al.*, 2010). Having said that, undergrazing is not a common practice worldwide. On the other hand, moderate grazing has been identified as a benefit to grassland plant and soil conditions through natural fertilization, seed dispersal, making space for annual and bi-annual plant species growth and expansion, and periodic above-ground defoliation which helps to regulate succession in plant communities (Metera *et al.*, 2010). However, the effects of different grazing intensities on AMF is still largely unknown.

Most studies compared the effects of grazing on AMF abundance and diversity in grazed and ungrazed plots (Murray *et al.*, 2010; Guo *et al.*, 2016; van der Heyde *et al.*, 2017), with very few assessing impacts along a gradient of grazing intensity such as that ranging from light-grazing to overgrazing (Mendoza *et al.*, 2011b; Ba *et al.*, 2012; Ren *et al.*, 2018). There is some evidence of unimodality in which the response of AMF abundance to herbivory peaks at an intermediate level of grazing intensity. For examples, AMF spore density increased from light to moderate grazing and decreased from moderate to extremely heavy grazing in a natural meadow steppe in China (Ba *et al.*, 2012). Furthermore, an unimodal relationship between the ratio of external (hyphal length density in soil) to internal AM fungal structures (mycorrhizal root intensity) and grazing intensity was detected in a typical steppe grassland (Faghihinia *et al.*, 2020). Given that moderate grazing can enhance plant community biomass and biodiversity (Komac *et al.*, 2015; Pulungan *et al.*, 2019), positive feedbacks on below-ground root associated AMF would be expected (Ba *et al.*, 2012). The impact of different grazing intensities on AMF requires further testing in different ecosystems and with different AMF variables in order to determine the threshold of grazing intensity that significantly alters below-ground soil microbial community composition and function in grasslands ecosystems.

3. Variations among empirical studies

Results of studies investigating the response of AMF to long-term herbivory are contradictory. For example, the response of AMF root colonization to grazing is variable with either positive (Eom *et al.*, 2001; Hokka *et al.*, 2004; Techau *et al.*, 2004; Wearn and Gange, 2007; Nishida *et al.*, 2009), negative (Wardle *et al.*, 2002; Ba *et al.*, 2012; Barber *et al.*, 2012; Birhane *et al.*, 2017; Cavagnaro *et al.*, 2018; Soka and Ritchie, 2018) or neutral effects (Yang *et al.*, 2013; van der Heyde *et al.*, 2017). Grazing has been shown to stimulate AMF sporulation (van der Heyde *et al.*, 2017), however, negative (Mendoza *et al.*, 2011a; Birhane *et al.*, 2017) and null grazing effects (Burke *et al.*, 2019) on AM fungal spore density have also been documented. We suggest that in addition to the potential environmental drivers of grazing impacts on AMF communities, which were discussed in this paper, the inconsistent results among studies may also be due to differences in AMF variable measures.

AMF variables appear to respond to herbivory in different ways; while soil hyphal length density is generally negatively impacted by grazing (Wang *et al.*, 2014; van der Heyde *et al.*, 2017; Ren *et al.*, 2018; Vowles *et al.*, 2018), but the response of mycorrhizal root colonization (van der Heyde *et al.*, 2017) and spore density to grazing is very variable (Barto and Rillig, 2010; Mendoza *et al.*, 2011a; Ba *et al.*, 2012; Wang *et al.*, 2014; van der Heyde *et al.*, 2017).

Hence, each AMF measure has its own limitation in terms of measurement and potential for yielding useful insights. For example, intensity of plant root colonized by AMF is usually quantified as percent root colonization. This is a relative measure, and may remain unchanged while total length of root colonized may decrease following herbivory (van der Heyde *et al.*, 2017). Although classical approaches for estimating percent root length colonization provide greater resolution of AMF structures, they fail to describe the amount of AMF in a whole root system as they do not account for the total root length (Hart

and Reader, 2002), particularly in studies on individual plant species. In addition, percent root length colonization does not account for how many structures were observed at each intersection meaning AMF biomass deductions cannot be made. Likewise, given that spores and sporocarps are long-term survival structures with the capacity of dispersal by wind and water, or locally through animal activities, with wide range of age and dormancy or quiescence status, and in addition some AMF species have never been detected as spores (Merryweather and Fitter, 1998a). The density of the spores in soil is unlikely to give a meaningful picture of mycorrhizal community and activity.

Overall, differences in AMF measures in response to herbivory suggests that measuring a single variable is not sufficient to elucidate this relationship and underlying mechanisms (van der Heyde *et al.*, 2019). Research in this field may be advanced by including various mycorrhizal variables, especially a combination of internal colonization and extra-radical hyphae, for measurement when assessing impacts of environmental variables or perturbation, including grazing, on mycorrhizal communities.

There are also other factors which have been suggested to be influential on the magnitude and direction of grazing effects on AMF. However, these factors were not sufficiently addressed in previous studies and require further investigation in order to improve the management of grassland ecosystems and maintain the above- and below-ground biodiversity. These include the type of herbivores due to their differences in terms of browsing strategies, diet and preferential grazing of different plant species (Metera *et al.*, 2010). The age and body size of the grazers are also important in determining grazing preferences. Young grazers and pregnant or lactating females prefer higher nutritive forages and so browse more selectively when grazing (Rook *et al.*, 2004). Smaller herbivores have been shown to graze more selectively than larger ones due to their small gut capacity and higher energy demands (Rook *et al.*, 2004).

Furthermore, the wide range of grassland management practices (e.g. mono- or mixed grazing, seasonal grazing, selective grazing, application of fertilizers and lime, etc.) applied in many places showed shifts in

the plant community and soil environmental conditions (Mettera *et al.*, 2010). However, how these management practices affects below-ground soil biota is less clear. Further research on grazing practices such as mixed- and co-grazing in conservation and management of grassland biodiversity and their impact on AMF community will be interesting areas for future work.

4. Conclusions and future challenges

Current knowledge of the impacts of livestock grazing on mycorrhizal fungal function is inconsistent and inadequate, which is mainly because of the context-dependent nature of the plant-AMF symbiosis. Here we discussed a suite of biotic and abiotic drivers that regulate the response of AMF abundance and community structure to grazing. Developing models, based on our framework, that integrate all of these variables would be helpful to understand how the abiotic and biotic environment determines the response of the plant-AMF relationship to grazing. Application of our framework of potential environmental drivers allows us to make sense of the complexity and generalize on the likely impacts of various grazing management approaches on AMF communities. Conducting a meta-analysis to integrate the available data would be helpful to account for the variation among studies, provide quantitative estimates for grazing impacts on root-associated mycorrhizal fungi and additionally to check the relative importance of each biotic and abiotic variables in outcomes of the mycorrhizal symbiosis across different landscapes. We also suggest that developing new investigation approaches that integrate the effect of climate and grazing simultaneously, particularly at larger scales, would help to better understand the degree and magnitude of grazing impact on AMF communities across climatic zones.

We further suggest the need for more research focusing on the impacts of different grazing intensities. Understanding the response of AMF to different grazing intensities and identifying the threshold of grazing intensity that significantly alters below-ground AMF would contribute to improved sustainable

food and forage production on grasslands by improving plant health and soil fertility. In addition, we suggest that measuring a single variable is not sufficient to explain the response of AMF to grazing and that the research field may be advanced by including various mycorrhizal variables for measurement. Finally, and crucially, seasonality needs to be included in studies if we are to understand the mechanisms underlying grazing effect on AMF and their functioning over the whole growing season. The challenge for the future will be to improve knowledge and gain new insights to predict the effects of grazing on plant-AMF interaction in the context of global environmental changes, with the aim to restore degraded grasslands, enhance food and feed production, and maintain grassland sustainability.

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