



## Grazing induces direct and indirect shrub effects on soil nematode communities



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### ARTICLE INFO

#### Keywords:

Alpine meadow  
*Dasiphora fruticosa*  
 Nematode community composition  
 Structural equation model

### ABSTRACT

It is well established that aboveground-belowground interactions moderate ecosystem functioning. The direct and indirect effects of plants on belowground communities have been explored by many studies; however, few studies have considered how grazing moderate the direction and intensity of these effects. In this study, we explored how grazing by yak moderates the effect of the shrub *Dasiphora fruticosa* on nematode communities through a short-term shrub removal experiment in a grazed and ungrazed alpine meadow on the Tibetan plateau. We used structural equation modelling (SEM) to assess both the direct effects of *D. fruticosa* and indirect effects mediated by changes in understory vegetation composition and edaphic properties, on nematode communities. The presence of *D. fruticosa* had no significant impact on the abundance of nematodes in the ungrazed meadow. By contrast, *D. fruticosa* had a strong negative direct effect on nematode abundance, but also a positive indirect effect due to greater grass biomass, in the grazed meadow. The effect of *D. fruticosa* on nematode community composition was limited, with only a marginally significant direct effect on nematode community composition in the grazed meadow. Instead, nematode community composition was strongly related to soil water content and organic matter content in both grazing treatments, and soil pH in the grazed meadow. Our results indicate that grazing moderate aboveground-belowground linkages through direct and indirect shrub effects on nematode abundance, but have limited effects on nematode community composition.

### 1. Introduction

There is increasing recognition of the linkages between aboveground and belowground communities and how important they are in governing ecosystem functions (De Deyn et al., 2004; Wardle et al., 2004). For example, Eisenhauer et al. (2013) showed that plant diversity increases the biomass and activity of soil microorganism, which in turn moderate carbon and nitrogen cycling with feedbacks on the plant community. Grazing is known to impact vegetation structure and composition with potential consequences belowground (Bardgett et al., 1998). However, few studies have explicitly assessed the effect of grazing on soil organisms, such as nematodes, through changes in aboveground-belowground linkages (Bardgett and Wardle, 2003). The soil nematode community is an important component of the soil food web and changes in the plant community caused by grazing may modify soil nematode community structure and their contributions to ecosystem functioning (Yeates et al., 1993; Bradford et al., 2002).

Free-living soil nematodes are small (generally < 1 mm in length; Ingham et al., 2000) and represent multiple feeding habits including bacterivores, fungivores, plant feeders, omnivores and predators (Yeates et al., 1993). They occupy different trophic levels and therefore contribute to ecosystem function through several nodes of the soil food web. The microbial grazers (bacterial and fungal feeders) have for example been shown to influence organic matter decomposition and nutrient mineralization through their interactions with the microbial community (Ingham, 1996), while plant feeders affect plant productivity through grazing and contribute to organic matter decomposition by inducing root exudation and stimulating microbial growth (Denton et al., 1998). Furthermore, omnivores and predatory nematodes can regulate soil fauna at lower trophic levels thereby reducing the grazing pressure on microorganisms (Laakso and Setälä, 1999).

The soil nematode community is highly variable both spatially and temporally. This variability is driven in part by the spatiotemporal variability in edaphic properties (Norton, 1989; Neher, 1999; Ruan

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et al., 2012) and climate (Ruess et al., 1999; Sohlenius and Bostrom, 1999) as well as direct and indirect influences of vegetation composition (De Deyn et al., 2004; Kardol et al., 2010; Eisenhauer et al., 2011; Zhao et al., 2015). However, the influence of these drivers on nematode communities is context dependent and taxon specific. For example, Ruan et al. (2012) found that increased water content has a positive influence on the abundance of plant feeders, but decrease the abundance of bacterial feeders, omnivores and predators, and Sarathchandra et al. (2001) reported higher abundances of the plant feeding nematode genera *Pratylenchus* and *Paratylenchus* in soils with N fertilisation whereas the abundance of *Meloidogyne* was higher in unfertilised soils. The response of nematodes to climate is also variable; for example, warming increased the abundance of nematodes in an arctic ecosystem (Ruess et al., 1999), whereas warming had no effect on nematode abundance in a forested ecosystem (Jonathan et al., 2016).

Similarly, vegetation composition has contrasting impacts on the soil nematode community (van der Putten and van der Stoel, 1998; De Deyn et al., 2004). For instance, De Deyn et al. (2004) showed that the total abundance of plant-feeders was higher in the root zones of certain plant species, likely due to them being suitable hosts for plant-feeders. Plant identity further modifies nematode communities, with abundances of the plant parasitic nematodes *Heterodera schachtii*, *Globodera rostochiensis*, and *Rhadinaphelenchus cocophilus* differing between plant hosts (Yeates, 1999). Moreover, Diakhaté et al. (2013) reported that the abundance of plant feeding nematodes from the family Hoplolaimidae was lower in plots with the shrub *Piliostigma reticulatum* compared to that in plots without the shrub, possibly due to the production of nematocidal compounds, such as alkaloids and polyphenols by the shrub.

Plants can also impact the soil nematode community indirectly. For example, dominant plant species can facilitate or suppress specific understory plant species (Michalet et al., 2015), and thereby induce changes in the soil nematode community due to changes in plant hosts and resource inputs (van der Putten and van der Stoel, 1998). Similarly, dominant plant species in particular can affect soil properties, which in turn impact the soil nematode community (Chałańska et al., 2016; Fitoussi et al., 2016). For example, Chałańska et al. (2016) found that the distribution of *Pratylenchus* spp. was related to changes in soil pH and organic carbon induced by the presence of shrubs and trees. Similarly, Fitoussi et al. (2016) showed that changes in soil properties, specifically  $\text{Ca}_2^+$ ,  $\text{K}^+$  and soil organic carbon content, induced by an invasive shrub influenced soil nematode community composition. Moreover, Shao et al. (2015) showed that the presence of the shrub *Illicium verum* changed nematode abundance through changing soil carbon and nitrogen content.

Herbivory is known to induce belowground effects through changes in the vegetation composition, with ecosystem specific effects on soil nematode communities (Andriuzzi and Wall, 2017; Bardgett and Wardle, 2003). For example, grazing increased the abundance of omnivores and predators in a humid grassland (Wang et al., 2006), while fungal feeding nematodes increased in an arid steppe (Freckman and Huang, 1998). Recently, Andriuzzi and Wall (2017) conducted a literature review to consolidate our knowledge of belowground impacts of large grazers and found that the responses differ among taxa. In particular, predators and root-feeders were more abundant without herbivores, whereas fungivores, bacterivores and omnivores show no response to grazing. Moreover, grazing intensity differentially effect nematode communities; for instance, Hu et al. (2015) showed that heavy grazing increased nematode diversity and abundance compared to low grazing intensity. As grazing effects on nematode communities are dependent on vegetation structure (Freckman and Huang, 1998; Wang et al., 2006; Veen et al., 2010), more studies are needed to disentangle grazing effects on nematode community.

Although many studies have explored the direct and indirect effects of dominant plant species on soil nematode communities, few have considered how the direction and intensity of these effects change in response to altered grazing regimes. We used a grazing exclusion x

plant removal method that has previously been used successfully to assess the shrub effects on understory species (Xu et al., 2010; Michalet et al., 2015). In this study, we explored the effect of a dominant shrub, *Dasiphora fruticosa*, on the soil nematode community through a removal experiment in both ungrazed and grazed alpine meadow on the Tibetan plateau. We applied structural equation modelling (SEM) to assess both the direct effect of *D. fruticosa* and its indirect effect on nematodes through changes in the understory plant community as well as edaphic properties. We hypothesized that i) shrubs influence nematode communities directly and indirectly through changes in the understory plant community and soil properties; but ii) that grazing will modify the direction and intensity of indirect effects of *D. fruticosa* on the soil nematode community as shrub presence may favor certain understory plant species and biomass in the grazed relative to the ungrazed meadow.

## 2. Method

### 2.1. Study site

The experiment was conducted in a relatively flat alpine meadow of the Research Station of the Alpine Meadow and Wetland Ecosystems of Lanzhou University (Azi Branch Station) in Maqu (33°40' N, 101°51' E), Gansu, China. The site is located on the eastern Tibetan Plateau at 3500 m above sea level. The mean monthly temperature ranges from  $-10^\circ\text{C}$  in January to  $11.7^\circ\text{C}$  in July, and the mean annual temperature is  $1.2^\circ\text{C}$ , with approximately 270 frost days per year. The annual precipitation (620 mm) measured over the last 35 years falls mainly during the short, cool summer. There are approximately 2580 h of cloud-free solar radiation annually. The vegetation is dominated by *Kobresia* spp. (Cyperaceae), *Elymus nutans* (Poaceae), *Agrostis* spp. (Poaceae), *Festuca ovina* (Poaceae), *Poa* spp. (Poaceae) and the shrub *Dasiphora fruticosa* (Rosaceae). The study area has been grazed by yak at a density of 1.6 head  $\text{ha}^{-1}$  since 1999 (Hu et al., 2015).

### 2.2. Experimental design

Herbivores were excluded from a representative area of meadow (measuring 35 by 35 m) with more than 250 individuals of the shrub *D. fruticosa* using barbed wire fence in June 2014. In early June 2015, we randomly allocated 30 plots inside the fenced area (hereafter 'ungrazed meadow') and 30 plots outside the fence (hereafter 'grazed meadow') each containing a shrub, respectively, with shrubs of similar size in both areas. Then, we randomly assigned the plots to one of two treatments: with and without shrub. The aboveground parts of the shrubs were removed at ground level from the 'without shrub' treatment and no resprouting was observed during the experiment. While there may still be some effects of leaving the dying roots in the ground, although this method has been used successfully in other studies (Xu et al., 2010; Michalet et al., 2015). We left dying roots in the ground, because the removal of dying roots may be potentially destructive to the soil. Thus, we have four treatments: ungrazed with shrub, ungrazed without shrub, grazed with shrub and grazed without shrub. At the center of each of the 60 plots, we delimited a 30 cm by 30 cm area for assessing understory plant species biomass. During harvest, the height and width were recorded for each shrub individual to calculate the size of shrub.

### 2.3. Measurements

At the end of the growing season (the end of August 2015), the aboveground parts of each understory species was collected separately from each of the 30 × 30 cm plots and oven-dried for three days at  $80^\circ\text{C}$  before weighting. We then collected a composite sample in each plot comprised of three randomly allocated soil samples (4 cm diameter, 20 cm depth) using a soil auger. Each composite soil sample was mixed well and stones were removed by hand. The composite soil

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