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Tidal flooding diminishes the effects of livestock grazing on soil micro-food webs in a coastal saltmarsh

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ABSTRACT

Livestock grazing not only has a direct impact on plant productivity but also exerts an indirect influence on soil biota via various pathways. However, little is known about the effects of livestock grazing on soil food webs in saltmarsh ecosystems that are subject to regular tidal inundation stress. By exclosure experiments established at a frequently inundated middle marsh and a less inundated high marsh of Chongming Island (China), the responses of soil micro-food web components (microorganisms, protozoa, and nematodes) to cattle grazing in intertidal marshes were investigated. In the high marsh, cattle grazing significantly increased the biomass of soil microorganisms, protozoa, and the abundance of total nematodes by 30.0%, 97.3% and 76.2%, respectively, but did not significantly affect their biomass or abundance in the middle marsh. For low-trophic-level nematodes, the abundance of bacterial-feeding and algal-feeding nematodes increased more in the high marsh than in the middle marsh, and that of plant-feeding nematodes decreased more in the high marsh than in the middle marsh under grazing. In contrast, carnivorous and omnivorous nematodes at high trophic levels did not respond to cattle grazing along an elevational gradient. The nematode maturity index and structure index based on nematode functional guilds significantly decreased under grazing along the elevational gradient, suggesting that cattle grazing caused a more simplified and unstable soil micro-food web structure. Overall, low trophic levels in soil micro-food webs were most vulnerable under grazing and the response was strongest in the less inundated high marsh. Thus, cattle grazing leads to different changes in soil ecosystem processes at different elevations. These results indicate that the strength of the biotic grazing effect on soil micro-food webs and ecological functions might also depend on local abiotic disturbance such as tidal inundations in the saltmarsh.

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1. Introduction

In terrestrial grasslands worldwide, livestock grazing has been a traditional land use for agricultural purposes (Doody, 2008). In general, grazing activities by livestock not only have a direct impact on plant shoot tissues but also exert an indirect influence on soil biota via various pathways, involving processes such as removal of plant biomass, dung and urine return, and trampling (Bardgett and Wardle, 2003; Chen et al., 2013). The removal of plant biomass and a reduced plant litter layer directly decreases plant material inputs into the soil (Ford and Grace, 1998; Lkhagva et al., 2013) while also possibly promoting root biomass and exudate production (Guitian and Bardgett, 2000). In turn, altered carbon resources from plants can positive or negative influence soil decomposer biomass and activity (Christensen et al., 2007; Kramer et al., 2012). Because grazing reduces the vegetation canopy, it affects soil temperature (Odriozola et al., 2014) and soil organisms (De Long et al., 2016). Inputs of dung and urine increase nutrient availability in the soil, which stimulates soil microbial activities (Bardgett et al., 1998). Trampling enhances soil compaction, i.e., it reduces soil pore size and increases soil waterlogging (limiting the availability of oxygen), thus it might negatively affect soil decomposers (Bardgett and Wardle, 2010). Overall, the effects of livestock grazing on soil biota are context dependent and vary depending on topographic conditions (Asner et al., 2009), ecosystem type (Bardgett et al., 1997), soil texture (Schrama et al., 2013b) and soil fertility (Sankaran and Augustine, 2004).

Soil micro-food webs are important trophic networks in belowground decomposer systems, largely including

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microorganisms (bacteria and fungi), microbivores (protozoa and low-trophic-level nematodes etc.) and micropredators (high-trophic-level nematodes etc.) (Wardle, 1995). The food sources of these trophic groups are mainly subjected to the bottom-up control of carbon resources that enter the soil (Scharroba et al., 2012), while protozoa and nematodes feed on microorganisms and eventually affect nutrient liberation for plant uptake (Bonkowski et al., 2000; Griffiths, 1994; Hunt et al., 1987). Soil nematode communities are often used as bioindicators in soil assessment because they involve taxa at diverse trophic levels in decomposer food webs and are susceptible to habitat changes (Wu et al., 2002; Yeates and Bongers, 1999).

Saltmarshes differ from other terrestrial ecosystems because of periodic tidal flooding that leads to high soil water contents and consequently limits oxygen penetration into the soil (Ford et al., 2013). In contrast to arid soils, where soil microbial activity is found to increase with higher water availability (Iovieno and Baath, 2008), microbial activity is lower in waterlogged soils since poorly drained soil diminishes the oxygen supply (Schinner, 1982). Surprisingly, microbial activity is found to be greater in waterlogged soils of grazed saltmarsh, containing increased available carbon, in the UK (Ford et al., 2013; Olsen et al., 2011). The abundance of soil macrofauna such as arthropods is, however, strongly reduced in grazed temperate saltmarshes (Schrama et al., 2013a; van Klink et al., 2015), probably because of a decrease in soil pore space for arthropod inhabitation. In saltmarshes, tidal inundation frequency is a significant factor affecting the distribution and development of vegetation (Bertness, 1991) and aboveground fauna such as spiders and insects (Andresen et al., 1990; Meyer et al., 1995). Despite some literature documenting the influence of livestock grazing on soil microbial activity in salt marshes (Ford et al., 2013; Olsen et al., 2011), it is unclear about livestock grazing interacts with tidal inundation in affecting the soil biota.

In this study, the impact of livestock grazing and tidal inundation on selective soil biota groups (microorganisms, protozoa and nematodes) that are essential components in the soil food web was investigated. By conducting an exclusion experiment in a coastal saltmarsh at Dongtan, Chongming Island, China, we aimed to assess the influence of dual-disturbance on the structure of soil micro-food webs in an experiment by comparing grazed and ungrazed treatments at two marsh elevations. Grazing often changes vegetation biomass or structure more intensively in the high marsh than in the middle marsh because it is subjected to less environmental stress, such as tidal inundation (Di Bella et al., 2014; Fariña et al., 2016), and the vegetation change exerts considerable influence on the organisms at lower trophic levels more directly than at higher trophic levels (Bardgett and Wardle, 2003; Scharroba et al., 2012). Therefore, we hypothesized that (1) under grazing, low trophic levels in soil micro-food webs are most vulnerable, as their main carbon resources are directly affected by grazing; and (2) grazing effects on soil organisms (microbial and protozoan biomass, nematode abundance) are stronger in the high marsh than in the middle marsh because of less frequent tidal inundation.

2. Materials and methods

2.1. Site description

The study site was in the Dongtan saltmarsh (31°28′N, 121°56′E) of Chongming Island, which is located in the estuary of the Yangtze River, China. The climate is subtropical monsoon with mean annual temperature of 15.3 °C and precipitation of 1022 mm. Since the 1950s, the saltmarsh has been regularly and pervasively grazed by cattle. In the last decade after the reserve was established, cattle grazing was restricted to a 600 ha southeastern area of the Dongtan saltmarsh, which led to increased grazing intensity and an increased risk of ecosystem degradation (Yang et al., 2008). This area is grazed by approximately 1 cattle ha^{-1} from early April to late October each year. In the Dongtan marsh, the tides are irregularly semidiurnal with the range of two successive tides being unequal. The average tidal range is 2.5 m and around 3.5 m during spring tides; the highest astronomical tide is up to 5.2 m above the lowest astronomical tide (Yang et al., 2008). For the terms of the marsh, we follow the definition of Redfield (1972): the high marsh lies at approximately the mean high water level between spring tide and neap tide and the middle marsh lies below the mean high water and low water level of neap tide. In our study, the dominant plant species in the high marsh are *Phragmites australis* and *Carex scabrifolia*, while the middle marsh is dominated by sedges *Scirpus mariqueter* and *C. scabrifolia*.

2.2. Experimental design

A grazing-exclusion experiment was established in the grazed area of the Dongtan saltmarsh in April 2014. The experimental plots were set up in 12 blocks, with half in the high marsh and the other half in the middle marsh, respectively (Fig. 1). In our study area, the width of the grazed salt marsh (from marsh edge to seawall) is approximately 1.5 km and has a gentle slope. Based on this situation, the distance between the high and middle marsh blocks was chosen as long as possible to achieve a distinct discrimination between tidal regimes (inundation frequency and duration). The mean elevation is 380 cm above sea level for high-marsh blocks and 330 cm for middle-marsh blocks. Tidal inundations are relatively infrequent at the high marsh, with a frequency of 17 times on average and an accumulative duration of 43 h per month. At the middle marsh, tidal inundations are more frequent with around 39 inundations and an accumulative duration of 127 h per month. Based on the observation on cattle activity and the counting of fresh cattle dungs, the stock cattle densities between the high and middle marsh were similar. Within both the high and middle marsh sites, we aimed to have all replicates on a similar elevation within a ±10 cm to ensure consistency of tidal inundation at a site and homogeneous soil environment. Therefore, in the high or middle marsh site, there is 50–100 m distance apart between every two blocks. Each block contained three experimental plots (15 × 15 m) that were assigned to one of three treatments: grazed without fence, grazed with short fence (the fence height is 50 cm) or ungrazed with tall fence (the fence height is 150 cm and the entire plot was surrounded with barbed wire). The distance was about 5 m between each two plots of all the three treatments. The grazed with short fence plots were used to eliminate the effects of the fence *per se* on soil biota.

2.3. Soil and plant characteristics

In September 2015, two growing seasons after the fences were established, soil pH, temperature and oxidation reduction potential (ORP) were measured *in situ* using a multiple meter (IQ Scientific Instruments, CA, USA). Soil conductivity was determined *in situ* as a proxy for salinity using a soil electrical conductivity (EC) meter (2265FS, Spectrum Technologies, Inc., IL, USA). Soil samples were collected to determine soil porosity and organic matter content using a splittable soil corer to take intact soil cores of 3.2 cm diameter and 15 cm depth. The entire core was dried at 70 °C for 72 h to determine soil bulk density. The specific gravity of soil was estimated using the density bottle method (Prakash et al., 2012). Soil porosity was calculated using the following formula (1−ratio of bulk density and specific gravity). Loss-on-ignition (550 °C for 5 h) method was used for determining soil organic

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