

Using nematode traits to evaluate the effects of topography and grazing on the function of wet
grassland soils.

By

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CHAPTER 1: GENERAL INTRODUCTION

Livestock grazing is the world's most extensive agricultural activity, which occupies more than half of all land on the planet (Follet and Reed 2010). Grasslands support a large extent of the global grazing area and consequently face problems of habitat degradation as grazing expands and intensifies to meet global forage demands in a changing climate (Asner et al. 2004, Godde et al. 2018). Studying the effects of grazing on grasslands is essential in order to protect valuable habitats (Galvaneke and Lepš 2009), since grasslands, in addition to grazing and hay cultivation (Joyce et al. 2016), are recreationally significant as eco-tourism destinations (Barkmann and Zschiegner 2010); contribute to the production of global services such as clean air, water, and the regulation of pests and pathogens (Ferris et al. 2001, Yeates et al. 2009); and provide habitat for native flora and fauna, including rare, threatened, and endangered species (Askins et al. 2007, Junk et al. 2013, Santamarıa 2002). Aboveground effects of large herbivore grazing in grasslands are well documented, such as increases in annual and shorter plants characterized by prostrate structures and stoloniferous or rosette architectures (Dıaz et al. 2007a), patchiness, the removal of leaf litter, and the creation of microhabitats in open surfaces of mud and water (Biro et al. 2019). Despite this, knowledge surrounding the impacts of large herbivores on soil communities (Schrama et al. 2013, Andriuzzi and Wall 2017) and the consequence of these impacts on the function of grassland soils remains limited (Bardgett and van der Putten 2014, Yang et al. 2017).

Soil ecosystems in grasslands are dynamic with rapidly changing biotic interactions influencing, and being influenced by, abiotic soil properties (Nicholas 1984, Wardle et al. 2004, Bakker et al. 2013) and livestock grazing may directly and indirectly impact these habitat characteristics (Biro et al. 2009, Sanderson et al. 2010, McSherry and Ritchie 2013).

Consequently, understanding these potential impacts is an important research gap to address because grassland soil communities regulate ecosystem services that contribute to ecosystem function: primary production both above- and belowground, carbon sequestration, nutrient cycling, and the decomposition of organic matter (Wardle et al. 2004, Briones 2014, van den Hoogen et al. 2019). Belowground plant structures (roots and rhizomes) account for at least 50% of net primary production in temperate grasslands (Tierney and Fahey 2007, De Deyn et al. 2008). Plant roots give structure to the rhizosphere while the architecture, morphology, and chemistry of roots support soil food webs (Freschet et al. 2021, Wilschut and Geisen 2021). Soil biota associated with plant roots control the direction and quantity of energy flowing between plants and decomposers (Wardle et al. 2004). High heterogeneity of plant cover and litter accumulation in grasslands leads to spatial variation in soil organic matter quality and quantity (Burke et al. 1998). Microtopographic reliefs in grassland complexes provide variation in soil moisture levels and contribute to the development of resource islands that transform soil communities, including relative abundances (Burke et al. 1998, Liu et al. 2019) and traits of organisms (Leff et al. 2015).

Wet grassland complexes

One global response to meeting increasing forage demands as climate change limits growing conditions in upland rangelands is to graze wet grasslands earlier in the growing season and to increase their stocking rates (e.g., grazing intensity) (Joyce et al. 2016, Godde et al. 2018, Haigh et al. 2021). Wet grasslands are a type of grassland habitat which occur in shallow depressions, on flats with unconfined groundwater, or on the edges of deeper marshes (Galatowitsch et al. 2000, Ducks Unlimited Canada 2020). North American wet grasslands are included in a broad classification termed “emergent wetlands” along with marshes, meadows,

fens, prairie potholes, and sloughs (Cowardin et al. 1979, Warner and Rubec 1997). In the Great Plains, wet grasslands are gently sloping to depressional, occurring as ridge and swales (Pratt et al. 1961), sandhill meadows (Volesky et al. 2004), intermountain valleys (Jones et al. 2011), and playa lakes (Bolen et al. 1989). Wet grassland complexes provide a useful model for exploring the effects of grazing because of their wide distribution, distinct vegetation communities, and similar hydrologic systems and management practices (Brotherton and Joyce 2015). While wet grasslands, like all grasslands, depend on disturbances like grazing to maintain ecosystem function (Hobbs and Huenneke 1992, Fuhlendorf et al. 2009), changes in the timing and intensity of grazing can alter their diversity, composition, and function (Kauffman et al. 2004, Janeček et al. 2013, Otfinowski and Coffey 2022). Since wet grasslands are more sensitive to changes in hydrologic patterns resulting from climate change (Joyce et al. 2016), understanding the effects of grazing on soil function in wet grassland habitat is urgent.

Role of nematodes in soil function

Free-living soil nematodes dominate the soil food web in grassland ecosystems (Hodda et al. 2009, Wu et al. 2011, Thakur and Geisen 2019), including wet grasslands, and changes in their communities may provide valuable insight into changes in the function of wet grassland soils (Bongers 1990, Neher 2001). Food resources of soil nematodes include bacteria, fungi, plant roots, detritus, algae, and soil animals, including other nematodes (Yeates et al. 1993). When soil nematodes from all trophic levels consume food, the ingested carbon is used for respiration and assimilation, while nutrients (e.g., nitrogen, phosphorus, sulfur) are exclusively used for assimilation (Ferris 2010). Since the carbon:nutrient ratio of most soil nematodes, especially bacteria-feeding nematodes, is higher than that of their prey, excess nutrients are excreted in mineral or readily mineralizable forms such as amino acids, ammonium, and

phosphates (Ingham et al. 1985, Ferris and Venette 1998, Yeates et al. 2009). For example, bacteria-feeding nematodes in particular increase access to glutamate for plants (Brondani et al. 2022), which is an important amino acid in plant growth (Forde and Lea 2007). One product of phosphorus mineralization from nematodes is phytate (phytic acid) (Sterner and Elser 2002, Brondani et al. 2022), which is a compound that is responsible for up to 75% of seed phosphorus in plants (Raboy 2009). Communities of nematodes account for at least 25% of nitrogen mineralization in soil globally (Ferris et al. 2012) and up to 40% in some ecosystems where bacteria-feeding nematodes are abundant (de Ruiter et al. 1993). Fungus-feeding nematodes are associated with increased phosphorus mineralization (Ingham et al. 1985) and the ratio of bacteria-feeders to fungus-feeders reflects differences in decomposition pathways (Yeates 2003). While omnivorous and predatory soil nematodes are involved in direct nutrient mineralization, they also indirectly influence mineralization rates by regulating populations of other soil microorganisms (de Ruiter et al. 1993). Additionally, soil nematodes have been found to transport nitrogen-fixing microbes on their cuticle, further increasing nitrogen mineralization rates (Horiuchi et al. 2005).

Most nematodes are found in the top ten centimeters of soil, making nematode biomass in the global layer of topsoil roughly 0.3 Gt C (van den Hoogen et al. 2019). Within a global growing season, soil nematodes are responsible for a monthly carbon turnover of 0.14 Gt C and of that, 0.11 Gt C is returned into the atmosphere through respiration. Van den Hoogen et al. (2019) estimated that the amount of nematode-respired carbon is equivalent to ~15% of fossil fuel carbon emissions, revealing nematodes to be an important and under-recognized member of the carbon cycle. Therefore, as a result of their role in carbon and nutrient cycles, changes in nematode traits may impact soil function by altering the amount of carbon storage and rates of

nutrient mineralization in soil (Brose 2010, Andriuzzi and Wall 2018, Green et al. 2022) and in turn, affect soil bacterial populations (Xiao et al. 2014, Jiang et al. 2017) and plant performance (Gebremikael et al. 2016).

Soil nematode abundance and diversity

Nematodes are the most abundant soil animal, especially at northern latitudes, with >30,000 nematodes per kilogram of dry soil at some sites (van den Hoogen et al. 2019). Approximately four out of five multicellular animals on earth are nematodes (Bongers and Ferris 1999). An estimated one million extant species constitute the phylum Nematoda, only of which ~30,000 have been described (Kiontke and Fitch 2013). Three monophyletic clades (Chromadoria, Dorylaimia, and Enoplia) encompass at least 35 orders of nematodes that live in diverse habitats ranging from marine ecosystems and animal guts to soil microbiomes (Blaxter 2011). Nematode phylogenies constructed by rRNA sequencing place free-living soil nematodes across many orders within the phylum Nematoda (De Ley 2006, Blaxter 2011). Although high abundances of soil nematodes are associated with northern ecosystems and grasslands (van den Hoogen et al. 2019), perhaps due to the slower rate of decomposition and high root biomass (Tierney and Fahey 2007, Conant et al. 2017), no global trends of nematode diversity have been verified (Liu et al. 2019).

Trophic diversity of soil nematodes allows for classification into functional groups based on feeding habits: bacterivores, fungivores, herbivores, predators, omnivores, and algivores (Yeates et al. 1993). Mouth anatomy informs which functional group (feeding group) a soil nematode is classified, although variation in feeding preferences exist within one mouth anatomy (Yeates 2003, Neher 2001). Typically, bacterivores have setae or feathery labial extensions near the buccal cavity to sweep in bacterial prey, fungivores possess a thin hollow stylet for

puncturing hyphal cells, herbivores use a robust stylet to puncture plant root cells, predators have developed teeth (or denticles) to shred their prey, and omnivores use their lips for bacteria-feeding and a stylet for stabbing prey (Kiontke and Fitch 2013). Algivores are more common in brackish water habitats than in terrestrial soils, where algae are a prominent food source; these nematodes may possess small teeth in the buccal cavity for diatom feeding (Bouwman 1983, Warwick et al. 2002). Additionally, some animal parasitic nematodes spend part of their life cycle in soil waiting for ingestion by a host and these nematodes may or may not feed while in soil (Lee 2002).

Nematode biology

Although nematodes have evolved a diversity of mouth anatomies, they are phylogenetically constrained by their lack of appendages and have a relatively simple “tube in a tube” body plan (Kiontke and Fitch 2013). Nematodes are non-segmented invertebrates with a thread-like translucent body. Soil nematodes generally range in size between 0.1 and 2.5 mm in length but large predatory or omnivorous nematodes and animal parasitic nematodes may grow to be >5 cm long (Lee 2002). Nematode intestines and gonads are encased in a body wall surrounded by dorsal and ventral longitudinal muscles, which are further encased by the epidermis and cuticle (Basyoni and Rizk 2016). The pressure difference between the inner body cavity (pseudocoelom) and the outer cuticle creates a rigid hydrostatic skeleton that propels movement (White et al. 1986). All free-living soil nematodes are essentially aquatic since they depend on at least a thin film of moisture for function (Nicholas 1984). Locomotion through water films in soil pores is achieved through anterior-posterior (forward) or posterior-anterior (backward) flexes of the body, creating a sinusoidal wave-like motion as the nematode lies on one of its lateral sides (White et al. 1986). Lateral movement of the head adds some flexibility,

which is important for feeding in the soil microbiome. Soil moisture impacts the mobility of nematodes in wet grassland soils: nematodes dehydrate or desiccate where soil moisture is limiting and cannot anchor nor navigate between soil particles where soil moisture is excessive. Due to their size and limited range of motion, soil nematodes typically move at a pace of 10-100 cm per year (Bardgett and van der Putten 2014).

The digestive system of a nematode is a one-way track with three distinct regions: stomodaeum (foregut: lips, buccal cavity, and esophagus), mesenteron (midgut: long and non-muscular intestinal tube), and proctodeum (hindgut: rectum and anus in females, cloaca in males) (Freckman and Baldwin 1990, Basyoni and Rizk 2016). Food enters the mouth, travels through the esophagus, is pumped into the lumen of the intestine that is lined with microvilli, and is excreted through the anus on the ventral side (Albertson and Thomson 1976, White et al. 1986). The esophagus acts as a muscular tube that links the buccal cavity to the intestine and functions by expanding to draw in food from the mouth and when it relaxes, forces food into the intestine with a pumping motion (Nicholas 1984). The esophagus is bulbous in shape and prepares food for digestion by grinding, sieving, and filtering food particles before they enter the intestine (Freckman and Baldwin 1990). A valve, or cardia, is formed at the end of the esophagus from a cuticular elaboration of an esophageal bulb and prevents regurgitation of food from the intestine and sometimes acts mechanically on food as it passes (Nicholas 1984). Digestive enzymes from the subventral gland cells aid digestion of food near the opening of the intestinal lumen (Albertson and Thomson 1976). The intestine is a simple tube derived from the endoderm and lacks musculature; digestion is thought to be entirely extracellular (Nicholas 1984). The rectum is a cuticle-lined tube containing a muscular sphincter that closes the entrance to the intestine to

regulate the passage of waste and fluids, although some nematodes accomplish this action by apposition of cell membranes at the anus.

Nematodes reproduce exclusively by laying eggs (Nicholas 1984). Most nematodes reproduce through bisexual cross fertilization (amphimixis) but some have been observed to reproduce through bisexual pseudogamy, hermaphroditic pseudogamy, and thelytoky (Nicholas 1984, Singaravelu and Singson 2011). Although sex ratios are often dependent on the mode of reproduction, and sometimes on environmental factors such as temperature, females or hermaphrodites occur naturally in much higher abundances than males (Nicholas 1984, Freckman and Baldwin 1990). Nematodes exhibit sexual dimorphism with females larger than males. The male reproductive system contains testes, ducts, seminal vesicles, copulatory bursa, and spicules (Basyoni and Rizk 2016). Females have one or two ovaries, oviducts, and uteri, but only one vagina, and one gonopore (Bongers 1988, Basyoni and Rizk 2016). Uteri are the largest section of the female reproductive system and are filled with eggs at various stages of development. Females lay hundreds to thousands of eggs in a reproductive cycle, which may occur once (semelparous) or multiple times (iteroparous) depending on the taxa (Lee 2002). Nematodes begin life as an egg and molt through four larval (or “juvenile”) stages (L1-L4) until adulthood is reached, although variation in this general life cycle exists, such as entry into a Dauer larvae state (diapause) (**Figure 1.1**). Depending on life history traits and environmental conditions, free-living soil nematodes can live from days to years but typically have a lifespan between one and three months (Lee 2002).

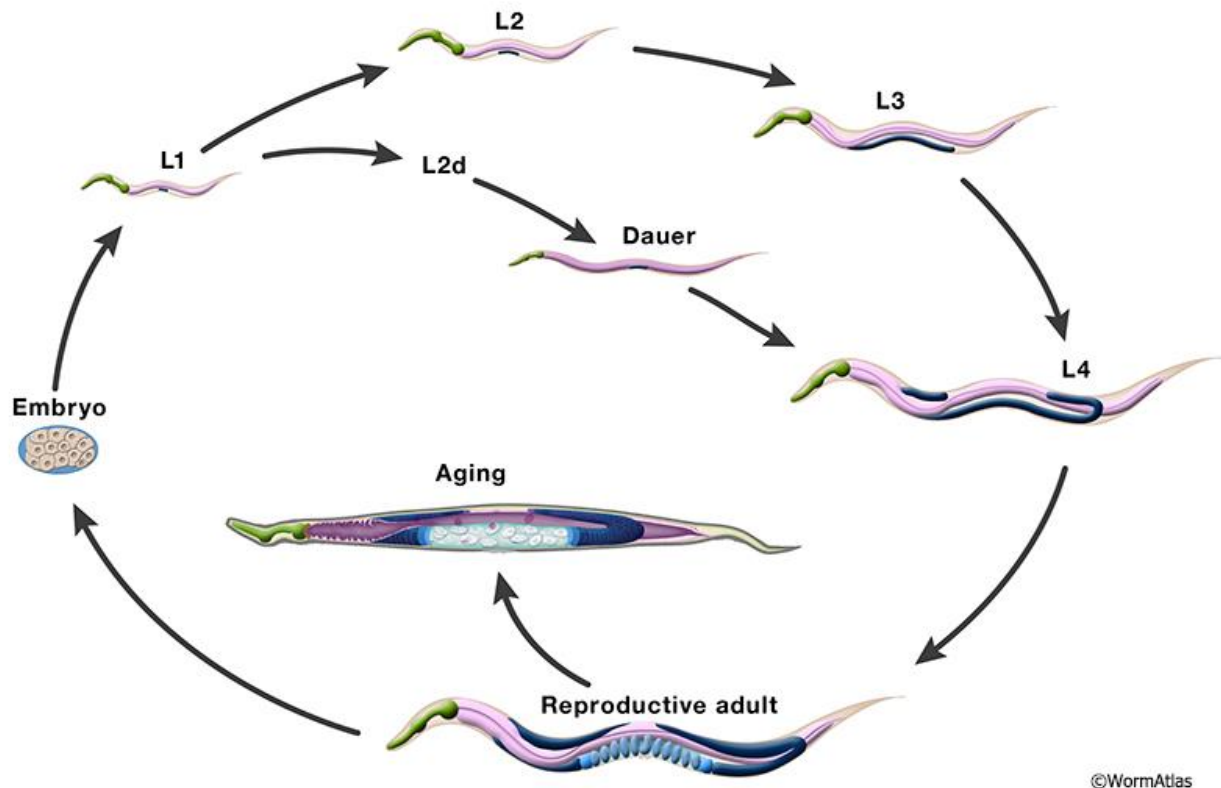


Figure 1.1. Life cycle of free-living soil nematode *Caenorhabditis elegans* from embryo through four larval stages (L1-L4) into a reproductive adult. In harsh environmental conditions, entry into a Dauer larvae state may follow L1 until more favorable conditions arise which trigger molting into the L4 stage and continuation through the rest of the life cycle. Figure from WormAtlas (Herndon et al. 2018).

Nematode indices

Soil nematodes serve as important bioindicators of soil health because they indicate changes in soil function but also drive those functions (Bongers 1990, Ferris and Venette 1998, Wilson and Kakouli-Duarte 2009). Several elements of nematode morphology and life history lend themselves well to their use as bioindicators of soil health: 1) possession of a permeable cuticle that allows for direct contact with the soil microenvironment; 2) limited mobility that inhibits long-distance travel, even under extreme environmental stress; 3) sensitivity to changes in environmental conditions; 4) distribution across all trophic levels of the soil food web; and 5)

mouth anatomy and esophagus morphology that provide a clear and direct relationship between structure and function (Bongers and Ferris 1999). Initially, research on soil nematodes as bioindicators was carried out in an agricultural context (Yeates 1984, Freckman and Caswell 1985), such as studying the effects of changing nematode diversity and abundance on crop growth following fertilization (Yeates and Bongers 1999, Hodda et al. 2009, Ferris et al. 2012). And while agricultural research still dominates the body of published work that uses nematodes as bioindicators, followed by experiments on land not in use, and also forestry studies, more recent trends have shifted focus towards the ecological role of free-living soil nematodes by examining their functional output relating to soil health in conservation and restoration (Du Preez et al. 2022). In particular, soil nematode communities may be used to evaluate soil health following environmental disturbances (Bongers 1990, Yeates 2003, Ferris et al. 2012).

A common approach when using soil nematode community composition to evaluate soil health, or the ability of soil to function, following a disturbance, beyond diversity and abundance measures, is the colonizer-persister scale (cp scale) (Bongers 1990, Du Preez et al. 2022). This approach uses assumed nematode feeding preferences, reproductive traits, and body size to group soil nematodes at the family level along a continuous cp scale (Ferris et al. 2001, Vonk et al. 2013). The cp scale largely follows the theory of r/K selection (MacArthur and Wilson 1967) and is similarly critiqued for over-generalizations and ambiguity (Stearns 1977), since nematodes, among other taxa, do not strictly follow the continuum that relates generation time to fecundity and body size (Neher 2001, Lee 2002, Vonk et al. 2013). Nonetheless, each nematode family is assigned a cp value (cp1-cp5) that reflects their general life strategy (Bongers 1990). For example, “colonizers,” are assigned a low cp value since they increase rapidly in population when resources become available. These nematodes tend to have short lifecycles, reproduce

early, and have many offspring (Ferris et al. 2001). In contrast, “persisters,” defined by their long lifecycles and few offspring, are assigned a high cp value. “Persisters” are also sensitive to environmental change and their presence may indicate stability in the soil food web. A healthy soil food web should support nematodes belonging to all trophic levels (Ferris et al. 2012).

Once a nematode community is assigned on the cp scale, a number of nematode indices may be calculated to make inferences about soil health (Bongers 1990, Yeates 2003, Ferris et al. 2001). The first semi-quantitative index that was developed using the cp scale for faunal analysis was the Maturity Index (MI) (Bongers 1990). The MI defines soil quality depending on soil nematode community composition following nutrient enrichment or a disturbance that results in increased nutrient availability in soil (Ferris et al. 2001). According to the MI, soil that has undergone such a disturbance is defined by a nematode community of generally small-bodied bacterivores (cp1). Over time, the nematode community may increase in fungivores and bacterivores (cp2) that dominate the community over large, slow-growing predators and omnivores. Soils that have not undergone nutrient enrichment nor disturbance are characterized by nematodes with large body sizes and a high trophic diversity (cp3 – cp5). As adults, nematodes in the lower cp classes tend to be ≤ 1 mm in length while nematodes in the upper cp classes are generally ≥ 1 mm in length, but body sizes are not consistent nor clearly defined across the MI (Bongers 1990. Vonk et al. 2013). Additionally, the MI excludes herbivores from calculations and therefore may fail to capture the full function of a soil nematode community following a disturbance (Yeates 1994). Thus, emerged the Sigma Maturity Index (Σ MI), which helped to link soil communities belowground to vegetation communities aboveground and more sufficiently evaluate soil health. Additional faunal indices were developed with the Σ MI: Structure Index (SI), Enrichment Index (EI), Channel Index (CI) and Basal Index (BI) (Ferris et

al. 2001). The SI describes the degree of trophic connections in a soil food web as it matures or degrades; the EI reflects nutrient enrichments and food availability; the CI distinguishes between bacterial and fungal decomposition pathways; and the BI is concerned with the basal components of the soil food web (Du Preez et al. 2022).

However, cp classes alone may not be sufficiently sensitive to detect changes in soil function after a disturbance across an environmental gradient (Neher 2001, Yeates 2003, Lazarova et al. 2021). For example, the cp scale does not completely capture variation in body size for soil nematodes, particularly families in class cp1 (Vonk et al. 2013). The cp scale also assumes fixed feeding strategies of nematodes throughout developmental stages and changing food resources, which leaves gaps in knowledge (Neher 2001). For instance, some juvenile nematodes feed on different food resources than their adult counterparts (Lee 2002). Furthermore, soil nematodes display phenotypic plasticity in mouth-form in response to changing environmental conditions (Renahan and Sommer 2021), resource availability (Susoy and Sommer 2016, Riebesell and Sommer 2017), and community context (Serobyán et al. 2013). Two mouth-forms have been observed in the omnivorous soil nematode *Pristionchus* sp. based on food availability: one mouth-morph is narrow for bacterial feeding while the other is wide and contains teeth for cutting open prey (Kiontke and Fitch 2013, Wilecki et al. 2015). *Tylenchus* sp. can be considered a fungus-feeder or plant-feeder depending on root abundance (Neher 2001). In many cases, the classification of soil nematode families into strict feeding groups was based on morphology rather than direct observation (Yeates et al. 1993). When experimentation on nematode feeding habits occurred, problems with small sample sizes and poor documentation lead investigators to make assumptions and extrapolations about feeding preferences, which created ambiguity in the cp assignment and in turn uncertainty in the application of cp classes

(Yeates 2003). Also, the cp scale focuses on “major taxonomic groups” of soil nematodes, leaving out lesser groups, and creating further gaps in knowledge (Briones 2014). Since a high level of expertise is required for nematode identification and because many naming inconsistencies exist for soil nematodes (Hedde et al. 2022), the cp scale becomes inefficient and error-prone (Yeates and Bongers 1999, Neher 2001, Yeates 2003). As a result of these shortcomings surrounding cp classes, more current approaches have supplemented taxonomic indices and faunal analysis with trait-based analysis (Mulder et al. 2008, George and Lindo 2015, Liu et al. 2015, Sechi et al. 2017, Andriuzzi and Wall 2018).

Nematode traits

Trait-based analysis is an approach in ecology stemming from the correlations between the frequency of observed phenotypic traits at the individual or the community level and environmental conditions (Southwood 1977, Green et al. 2022). In this approach, spatial and temporal habitat characteristics (abiotic and biotic factors) may filter traits of organisms (e.g., morphological, metabolic, reproductive) to form communities with similar sets of traits (Violle et al. 2007, Ristau et al. 2015). Trait-based analysis of nematodes has two major benefits over faunal analysis (cp classes): application to broad geographic regions (Statzner et al. 2001) and provision of a mechanistic understanding of community function along an environmental gradient (Sechi et al. 2017, Andriuzzi and Wall 2018). Research using trait-based analysis on birds, fish, herpetofauna, insects, mammals, and plants is widely used (Green et al. 2022). Some studies have conducted trait-based analysis using soil nematodes (Luan et al. 2020, Hou et al. 2023) including nematode responses to applications of agricultural pesticides (Sánchez-Moreno et al. 2010), fertilization (Liu et al. 2015), calcium-enriched wood ash post clear-cutting (George and Lindo 2015), and moderate-to-intensive grazing (Mills and Adl 2011, Andriuzzi and Wall

2018). However, little research has been done exploring the effects of disturbance on nematode traits across wet grassland topography (Wheeler et al. 2002, Kauffman et al. 2004, Vonk et al. 2013, Lazarova et al. 2021). This is an important research gap considering that nematodes may respond differently to grazing disturbances depending on grassland type (Zhou et al. 2023).

Exploring changes in the traits of soil nematodes provides a mechanistic understanding of soil function, including carbon storage, nutrient cycling, and the decomposition of organic matter (Sechi et al. 2017, Andriuzzi and Wall 2018). Body size is an important trait for soil nematodes (George and Lindo 2015) that can be used to indicate rates of carbon sequestration and nutrient mineralization (Ferris 2010, Lazarova et al. 2021). While nematode body size could be sensitive to temperature (Lindo 2015) and soil compaction (Mulder et al. 2008), nutrient enrichment may be more influential (Briar et al. 2011, Niu et al. 2015, Andriuzzi and Wall 2018, Hou et al. 2023). At the community level, soil nematode body size is positively correlated with soil organic carbon, total nitrogen, available phosphorus, and available potassium concentrations across wet and dry topographies in fertilized agroecosystems (Liu et al. 2015). Mills and Adl (2011) showed that soil nematodes in sandy loam soils increased in mean body length under grazing conditions and Vonk and Mulder (2013) demonstrated that soil nematode body size is negatively correlated with fungal biomass. Understanding the factors that affect body size is important because soil nematodes are directly and indirectly involved in carbon storage, nutrient mineralization, and the decomposition of organic matter when they feed (Ferris 2010, Lazarova et al. 2021). As a result, large-bodied nematodes may consume more food which can increase feeding rates in the soil food web and in turn increase rates of carbon and nutrient turnover in soil (Freckman and Baldwin 1990).

In addition to body size, b-ratio is another trait that could alter feeding rates for soil nematodes (Saunders and Burr 1978). B-ratio is determined by dividing body length (distance between lips and tail tip) by anterior length (distance between lips and esophageal-intestinal valve). Since the muscular esophagus constitutes a majority of the anterior measurement and is directly related to the generation of ATP for nematodes by grinding and sieving food (Lee 2002), b-ratio is interpreted as metabolic trait in this thesis. A higher b-ratio, or smaller esophagus relative to body length, may suggest a greater metabolic output by allowing a nematode to pump food through its body more quickly since less time may be needed to mechanically grind large complex food items before entry into the gut (Tita et al. 1999). An increase in feeding rates for nematode communities implies a greater ability to metabolize food and excrete mineral waste, potentially leading to greater nutrient mineralization and turnover in soil (Freckman and Baldwin 1990).

Objectives

The objective of my thesis was to evaluate the effects of topography and grazing on soil nematode communities and to examine how those potential effects may impact the function of wet grassland soils. To achieve this objective, my research examined soil nematode communities in two wet grassland complexes with similar topographic sequences and grazing prescriptions. In each wet grassland complex, I randomly sampled soil nematode communities in grazed and ungrazed upland prairies and wet meadows. I tested the hypothesis that topography and grazing affect soil nematode diversity, feeding composition, and traits. I began my research with traditional community ecology approaches by summarizing soil nematode abundances, calculating diversity indices, and analyzing proportions of feeding groups; I later supplemented these measures with trait-based analysis of dominant genera. By using trait-based analysis, I was

able to compare changes in the traits of soil nematode communities between upland prairies and wet meadows in grazed and ungrazed wet grasslands. Documenting changes in the traits of nematode communities allowed me to better understand the possible mechanisms underlying soil function in wet grasslands.

For my first hypothesis, I predicted that upland prairies (high topographic treatments) would have a higher soil nematode diversity than wet meadows (low topographic treatments); a potentially higher plant diversity in upland prairies aboveground could promote a higher diversity of nematodes belowground (Zak et al. 2003, Cortois et al. 2017, Dietrich et al. 2021). Even though upland prairies are typically less productive than wet meadows in terms of plant biomass, they are often more plant-diverse (Austin et al. 2007, Fayiah et al. 2019). I also predicted that grazed treatments would have a higher soil nematode diversity compared to ungrazed treatments due to light-moderate grazing potentially increasing plant diversity (Marty 2005, Gao and Carmel 2020, Otfinowski and Coffey 2022), which may cascade belowground to also increase nematode diversity (Bakker et al. 2019). Additionally, upland prairies and low intensity grazed soils may be associated with greater root biomass (McSherry and Ritchie 2013, Ma et al. 2022, Gong et al. 2023), which may also promote higher nematode diversity (De Deyn et al. 2004, Bardgett and van der Putten 2014).

For my second hypothesis, I predicted that wet meadows would have a higher proportion of bacterivores than upland prairies due to potential nutrient loading in wet meadow soils. Since wet meadows store water from surface run-off, rainfall, and snow-melt, they often retain higher concentrations of nutrients in their soils (Pennock et al. 2014), especially wet meadows near grazed pastures (Dunne et al. 2010). Specifically, wet meadows are typically higher in soil organic carbon (Manning et al. 2001), nitrogen (Aandahl 1949), and phosphorus (Florinsky et al.

2002), which may provide direct resources for substrate feeding by bacteria (Ingham et al. 1985). As a result, soil bacteria may increase in population and therefore provide additional food resources for bacteria-feeding nematodes. While both bacteria and fungi break down mineral substrates in soil, fungi tend to consume more complex substrates (e.g., lignin) and have a high carbon:nitrogen ratio (Hoorman 2011), whereas bacteria feed on simple sugars and cycle nutrients more quickly (Sterner and Elser 2002). Additionally, I predicted that grazed treatments would have a higher proportion of bacterivores compared to ungrazed treatments due to nutrient additions into soil by cattle via defecation and urination (Ferris et al. 2001, Sanderson et al. 2010). Potentially high soil nutrient levels in grazed soils may shift nematode communities towards a higher abundance of bacterivores since they have a higher metabolic rate and can cycle nutrients more quickly (Yeates 2003, Chen et al. 2013, Sanchez-Moreno et al. 2021). I am particularly interested in bacterivores because their assemblages reflect pathways of decomposition and rates of nitrogen mineralization when they feed (Ferris and Venette 1998, Yeates 2003).

For my third hypothesis, I predicted that wet meadows and grazed treatments would be characterized by soil nematodes with a larger body size, higher b-ratio, and more gonads (ovaries) compared to upland prairies and ungrazed treatments. I expected that potentially high soil nutrient levels in wet meadows (Aandahl 1949, Manning et al. 2001, Florinsky et al. 2002) and grazed treatments (Sanderson et al. 2010) would increase bacterial food resources (Ingham et al. 1985), and in turn allow for greater food consumption, which could lead to larger nematode bodies (Mulder et al. 2008, Ferris 2010, Andriuzzi and Wall 2018). Similarly, I predicted that wet meadows and grazed treatments would select for nematodes with a higher b-ratio (i.e., shorter esophagus relative to body length), which may allow nematodes to pump food more

quickly through the body (Tita et al. 1999). Lastly, I predicted that wet meadows and grazed treatments would select for a greater fecundity in soil nematodes by increasing the number of gonads (ovaries) present in the female reproductive tract. Since females can have one or two gonads (Bongers 1988, Basyoni and Rizk 2016), and since body mass positively covaries with egg production (Lee 2002), I expected that a potential increase in bacterial food availability would select for reproductive traits (i.e., more gonads) that could contribute to greater egg production and in turn increase overall abundance (Ferris 2010).

I used community-weighted means (CWM) and variances (CWV) to describe measured traits in soil nematodes and to make inferences about soil function in different treatments. This approach is commonly used in plant community ecology to interpret the relationship between environmental change, plant community composition, and ecosystem function (Díaz et al. 2007b, Lavorel et al. 2008, Sonnier et al. 2010). CWM, calculated by weighting each mean trait value by the relative abundance of each genus expressing that trait, is an aggregated metric that represents the expected trait value from a random sample of the community (Lavorel et al. 2008). This weighting method acts as an unbiased trait-based indicator and is useful for my research because wide disparities in size exist across diverse soil nematode communities (Liu et al. 2015). For example, a few large-bodied omnivores and predators (e.g., Dorylaimids) may influence a mean trait value more than many small-bodied bacterivores. Similarly, CWV defines the variability of a trait in the community by weighting the sum of squares for a genus with its relative abundance (Sonnier et al. 2010). Therefore, the CWM expresses the average trait value of a nematode in a community and the CWV expresses the variability of that trait value around the mean value (Sonnier et al. 2010). Since the community-weighted approach normalizes mean trait values and variances according to abundance, I was able to characterize soils in each

treatment with “dominant traits and variances” of nematodes that better reflect rates of carbon sequestration, nutrient mineralization, and decomposition in the soil community (Freckman and Baldwin 1990, Ferris et al. 2012, Vonk and Mulder 2013, Lazarova et al. 2021).

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CHAPTER 2: USING NEMATODE TRAITS TO EVALUATE THE EFFECTS OF TOPOGRAPHY AND GRAZING ON THE FUNCTION OF WET GRASSLAND SOILS

Abstract

Understanding belowground impacts of livestock in rangelands is critical to developing sustainable grazing practices. This is particularly the case in wet grasslands, which face increased pressures in the timing and intensity of grazing in a changing climate. To understand the coupled effects of topography and grazing on wet grassland soils, I examined the generic diversity, feeding composition, and traits of soil nematode communities. I collected nematodes from grazed and ungrazed upland prairies and wet meadows in southern and central Manitoba. Nematodes were extracted from fresh soil cores, counted, identified to the genus level, and assigned to feeding groups. I measured morphological, metabolic, and reproductive traits for a subset of dominant nematode genera and calculated community-weighted means and variances of five nematode traits (length, greatest body diameter, mass, b-ratio, average number of gonads). Topography and grazing did not affect the alpha and beta diversity of nematode genera. However, wet meadows and grazed treatments were characterized by a higher proportion of bacteria-feeding nematodes. On average, larger nematodes with lower b-ratios (i.e., longer esophagus relative to body length) dominated wet meadow soils compared to upland prairie soils. Grazing significantly interacted with topography to result in community-weighted means and variances of nematode traits that were similar across topography. The observed changes in nematode feeding composition and traits suggest that topography and grazing may alter rates of carbon and nutrient cycling in wet grassland soils. This study reinforces the ability of nematode communities, particularly their traits, to serve as valuable bioindicators of soil function in changing environments.

Introduction

Understanding the impacts of grazing animals in rangelands is critical to developing land management practices that will support growing forage demands while simultaneously decreasing negative impacts on the environment (Guyader et al. 2016, Godde et al. 2018). Therefore, it is necessary to study both above- and belowground effects of grazing animals in order to implement and maintain sustainable grazing practices that improve ecosystem function (Wardle et al. 2004, Fuhlendorf et al. 2012). This is especially true in wet grasslands (Johnson et al. 2005), which face increased pressure in the timing and intensity of grazing as a result of climate change reducing the ability of upland rangelands to provide adequate forage material for livestock (Joyce et al. 2016, Godde et al. 2018, Haigh et al. 2021). However, changes in the timing and intensity of grazing in wet grasslands can alter their diversity, composition, and function (Kauffman et al. 2004, Janeček et al. 2013, Otfinowski and Coffey 2022). The effects of grazing on aboveground vegetation are well-documented: increased heterogeneity, suppression of tall plants, and the removal of leaf litter (Díaz et al. 2007, Biró et al. 2019). However, few studies have examined the effects of grazing on soil communities across wet grassland topography (Schrama et al. 2013, Andriuzzi and Wall 2017) and the impact of those potential effects on soil function (Bardgett and van der Putten 2014, Yang et al. 2017).

Among soil organisms, nematodes are the most abundant (van den Hoogen et al. 2019); they are diverse taxonomically (Bongers 1988) and functionally (Yeates et al. 1993). Soil nematodes can be used as bioindicators of soil health because they have a permeable cuticle, respond rapidly to changes in environmental conditions, have limited mobility, occupy all trophic levels of the soil food web, and their mouth morphology provides a clear and direct relationship between structure and function (Bongers and Ferris 1999). Due to their ability to

process organic nutrients, control soil microorganism populations, and regulate nutrient and carbon cycles (van den Hoogen et al. 2019), soil nematodes can be used to assess soil quality in response to changes in ecology and land use (Bongers 1990, Neher 2001, Vink et al. 2020). The use of nematodes as bioindicators of soil health has been tested in temperate forests (Sun et al. 2013), wheat pastures (Yeates and Bird 1994), mowed or burned tall grass prairies (Todd 1996), and coastal grasslands (Vink et al. 2020); however, research is limited for wet grasslands (Frank et al. 2002, Kauffman et al. 2004, Schrama et al. 2013, Leff et al. 2015).

Much of the existing research on soil nematodes as bioindicators relies on taxonomically driven diversity indices and faunal indices to evaluate soil health (Du Preez et al. 2022). Faunal indices group soil nematodes at the family level along a colonizer-persister scale (cp scale) based on assumed feeding habits, reproductive traits, and body size (Bongers 1990, Ferris et al. 2001). While these traditional approaches are useful for beginning to characterize nematode communities in soil, they fail to capture the phenotypic variability of nematode genera and therefore may not be sufficiently sensitive to capture changes in soil function across a disturbed landscape (Neher 2001, Yeates 2003, Lazarova et al. 2021). Moreover, the cp scale does not completely capture variation in nematode body size (Vonk et al. 2013), it assumes fixed feeding strategies of soil nematodes (Ferris et al. 2001, Neher 2001), and original cp assignments were often based on morphology rather than direct observation (Yeates 2003). For example, a single nematode genus can deploy multiple feeding strategies during development and as an adult, therefore occupying multiple trophic levels in the soil food web throughout its lifecycle (Lee 2002). As a result of these limitations, more current approaches have supplemented taxonomic and faunal analysis of nematode communities with trait-based analysis (Mulder et al. 2008, George and Lindo 2015, Liu et al. 2015, Sechi et al. 2017, Andriuzzi and Wall 2018).

Trait-based analysis of nematode communities explores potential correlations between changes in the frequency of observed traits (e.g., morphological, metabolic, reproductive) and environmental conditions (e.g., abiotic, biotic) (Southwood 1977, Green et al. 2022) to search for patterns related to generalizable ecological strategies of nematodes in a changing environment (Liu et al. 2015). This approach provides a mechanistic understanding of nematode community function along a disturbed environmental gradient (Liess et al. 2008, Sechi et al. 2017). For soil nematodes, body size is an important trait (George and Lindo 2015) that can be used to indicate rates of carbon sequestration, nutrient mineralization, and the decomposition of organic matter in a soil ecosystem (Ferris 2010, Lazarova et al. 2021). Since the carbon:nutrient ratio of most soil nematodes is higher than that of their prey, excess nutrients are excreted in mineral or readily mineralizable forms such as amino acids, ammonium, and phosphates (Ingham et al. 1985, Ferris and Venette 1998). While not all carbon and nutrients mineralized by nematodes becomes available to plants and other soil organisms (Cotrufo et al. 2013), larger nematodes that consume more prey may still increase rates of carbon and nutrient cycling in soil (Freckman and Baldwin 1990, Ferris 2010, Lazarova et al. 2021). Additionally, b-ratio (body length:anterior length) may also impact feeding rates in the soil food web by altering the rate at which food is pumped through the nematode body (Saunders and Burr 1978, Freckman and Baldwin 1990, Tita et al. 1999). Despite the connection between soil nematode traits and their functional impact in carbon sequestration and nutrient mineralization, few studies have explored how grazing across wet grassland topography affects soil nematode traits (Andriuzzi and Wall 2017, Mulder and Maas 2017).

I examined the effects of topography and grazing on the generic diversity, feeding composition, and traits of soil nematode communities and how those potential effects may

impact the function of wet grassland soils. I used trait-based analysis because of its ability to provide a mechanistic understanding of community function by connecting nematode morphology to function, and consequently soil health. My three hypotheses are that changes in topography and grazing will affect 1) soil nematode diversity, 2) soil nematode feeding composition, and 3) soil nematode traits. Studying the impacts of topography and grazing on the diversity, feeding composition, and traits of soil nematode communities provides an important belowground perspective to understanding the flow of carbon, nitrogen, phosphorus, and other nutrients through wet grassland ecosystems (George and Lindo 2015, Luan et al. 2020). Incorporating a belowground perspective in rangeland management is crucial for the protection of wet grassland habitat and consequently the provision of important ecosystem services (Wardle et al. 2004, Fuhlendorf et al. 2012). This research helps to establish a link between grazing, the health of rangeland habitats, and the function of their soils by using nematodes, particularly their traits, as bioindicators of soil function.

Methods

Study area

Research was conducted in two Nature Conservancy of Canada properties within the Tall Grass Ecoregion of Manitoba, Canada (Thorpe 2014). The experiment was set up in locations where grazed and ungrazed wet grassland complexes were present: Tall Grass Prairie Preserve (49°08' N, 96°39' W) and East Shoal Lake Property (50°17' N, 97°31' W). However, East Shoal Lake Property was exclusively ungrazed, therefore, Lake Ranch Property provided a grazed comparison along the same wet grassland complex and is considered part of the East Shoal Lake Property site. Grazed treatments have stocking rates <1.1 AUM/ac (<2.75 AUM/ha) and are therefore considered lightly grazed by cattle (Thorpe 2014). Study sites were selected to avoid

historically disturbed soils (e.g., clear-cut, hayed); however, the ungrazed treatments at Tall Grass Prairie Preserve were last burned in 2014. Daily mean temperatures at these sites range from -16.2°C in January to 19.3°C in July with an average annual precipitation of 565.7 mm (1981-2010) (Environment Canada 2011) (**Appendix A**). Precipitation was high across the study area during the sampling year (2022) (Manitoba Agricultural Staff 2022); by November 2022, soil moisture remained at 80-100% of holding capacity in the top 30 cm of soil (Manitoba Agriculture 2022). The main soil type at Tall Grass Prairie Preserve belongs to the Gray Luvisol Great Group, which is comprised of a thin to very thin sandy mantle (up to 15 inches in depth) on gravel, cobble, or stony lens developed over calcareous till (Ehrlich et al. 1953, Soil Classification Working Group 1998). The main soil types at East Shoal Lake Property belong to the Black Chernozem and Gleysol Great Groups, which are comprised of thin to very thin loamy or lacustrine sediments (up to 15 inches in depth) over stony, extremely calcareous till or clay (Pratt et al. 1961, Soil Classification Working Group 1998).

Wet grasslands at these sites support species of ecological importance such as grassland birds, butterflies, amphibians, and mammals, including endangered, threatened, and uncommon or provincially rare species (Environment Canada 2012, Neufeld 2013, Borkowsky 2014, Hamel 2015, Nature Conservancy of Canada 2020). The experiment was set up in two contrasting topographic positions (**Appendix B**). High topographic treatments have distinct vegetation communities that are not adapted to the presence of prolonged soil moisture, such as grasses (e.g., *Andropogon gerardi*, *Elymus trachycaulus*, *Panicum virgatum*, *Schizachyrium scoparium*), forbs (e.g., *Symphiotrichum* sp., *Campanula rotundifolia*, *Rudbeckia hirta*, *Solidago canadensis*, *Solidago* sp.), and shrubs (e.g., *Prunus virginiana*, *Symphoricarpos occidentali*). Low topographic treatments flood annually for 2-6 weeks depending on rainfall and snowmelt (Ducks

Unlimited Canada 2020) but vegetation communities are still not adapted to prolonged soil moisture; representative plants are grasses (e.g., *Calamagrostis canadensis*, *Calamagrostis stricta*, *Spartina pectinata*), sedges (e.g., *Carex pellita*, *Carex praegracilis*, *Carex* spp.), rushes (e.g., *Juncus balticus*), forbs (e.g., *Cirsium arvense*, *Lycopus americanus*, *Potentilla anserina*, *Symphyotrichum ericoides*), and shrubs (e.g., *Salix* sp.). In this thesis, the two topographic positions are referred to as upland prairie and wet meadow respectively and their vegetation communities were used to indicate topographic positioning.

Sampling design

Aerial imagery (Google Earth version 7.3.2.5776, 2021), in-person site visits, and vegetation, management, and property maps were used to confirm boundaries of grazing paddocks and vegetation communities at Tall Grass Prairie Preserve and East Shoal Lake Property. Treatment polygons were drawn representing upland prairies and wet meadows in grazed and ungrazed wet grasslands at both sites using QGIS (version 3.18.3) (QGIS Association 2021) (**Figure 2.1**). A buffer of three meters was maintained around each treatment polygon to account for edge effects from fences, roads, and community transitions. I placed a 3 x 3 m grid over each treatment polygon and randomly selected three grid cells per treatment using a random cell selector. The coordinates for each grid cell were loaded into a handheld GPS (Garmin inReach GPSMAP 66i, Garmin International Inc., Olathe, KS, USA, position accuracy = 3 meters). Each 3 x 3m grid cell contained nine possible 1m² quadrats, only one of which was selected for sampling soil nematodes in the field. To choose the sampling quadrat, I positioned myself in the southeast corner of the grid cell oriented northerly. If the first 1m² quadrat did not meet the target topographic position or was too stony, I moved to the next quadrat in the same grid cell. A soil core (10 cm deep, 7.5 cm diameter) was collected from the center of each 1m²

quadrat. Three soil cores per treatment were collected in the first sampling period (August 2022) and three additional samples were collected in each treatment during the second sampling period (September 2022) by moving four meters west and eight meters north from the initial random point of the first survey.

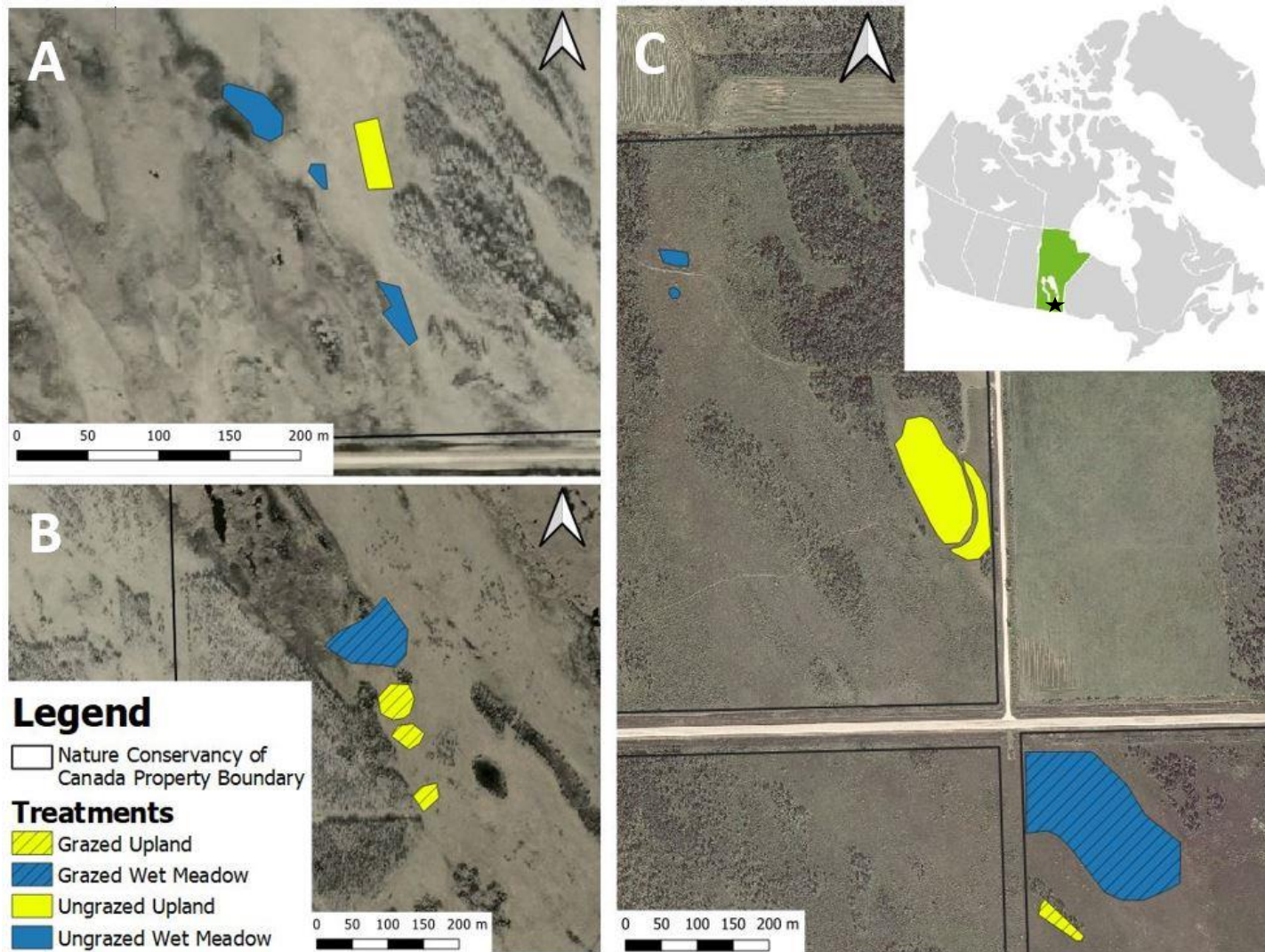


Figure 2.1. Distribution of treatment polygons used to evaluate the effects of topography and grazing on soil nematode communities across wet grasslands in Manitoba, Canada. Four treatments, denoted by topographical positioning and by grazing presence, are illustrated above for two sites (see legend). Quadrats (1 x 1 m) were randomly selected using a grid overlay to sample soil nematodes from each treatment: A) ungrazed treatment polygons at East Shoal Lake Property, B) grazed treatment polygons at East Shoal Lake Property, and C) grazed and ungrazed treatment polygons at Tall Grass Prairie Preserve.

Soil nematode communities

I collected a total of 48 soil cores (7.5 cm diameter) from the top ten centimeters of mineral soil using a root auger (Royal Eijkelkamp, Giesbeek, The Netherlands) (2 sites x 2 grazing treatments x 2 topographic positions x 3 samples x 2 sampling periods; $n = 48$). Soil cores were immediately placed into plastic bags, sealed, and stored in a cooler (8°C) for transport back to the laboratory. Soil cores were transferred to an environmental chamber (4°C) within eight hours of collection and analyzed within three weeks. Soil cores were homogenized by hand in a 9 x 13-inch glass dish, plant roots were cut into 1-cm segments, and large stones were removed. Soil nematodes were extracted from a subsample (50-100 g) of each homogenized soil core using the improved centrifugal floatation method (Barker et al. 1985). In this method, fine mesh sieves (149 μm , 37 μm) were used to separate nematodes from plant roots, large soil particles, and large arthropods. After sieving, samples were centrifuged (1.9 RPM x 1000 for 300 s) to concentrate nematodes and the resulting supernatant was replaced with sucrose solution (0.454 mL/g) (Kimpinski 1993). The samples were re-centrifuged (1.1 RPM x 1000 for 80 s) to separate nematodes from the soil particles and the supernatant was sieved (25 μm), washed with deionized water, and stored (4°C). Extracted nematodes were analyzed within 24 hours.

Soil nematodes from each extraction were counted on a 2-mm gridded Petri dish using a stereoscopic dissecting microscope (Nikon SMZ800N, 40-80x). After counting, the soil nematodes were re-centrifuged (2.2 RPM x 1000 for 300 s) and dropped onto a glass microscope slide (50 x 22 mm cover slip) for identification using a light compound microscope (Leica DM2500, 100-630x) with differential interference contrast optics (DIC). The first live 100 soil nematodes were identified to the genus level following Jairajpuri and Ahmad (1992) for the order Dorylaimida and Bongers (1988) for all other orders. I used the number of each identified

nematode genus in the sample of 100 to estimate the population of the entire sample. High resolution images (8MB) were taken of the first ten adult females of dominant genera to measure traits (pco.panda 4.2 camera, 16-bit sCMOS monochrome sensor with 2048 x 2048-pixel resolution) using Volocity Software (version 6.3) (Volocity 2021) (**Appendix C**). Only adult females were selected for trait-based analysis due to the higher natural abundance of females compared to males (Freckman and Baldwin 1990) and to control for sexual dimorphism. An adult female was defined by the presence of any reproductive trait (e.g., vulva, vagina, ovaries). Images of nematodes were taken in multiple planes of focus to accurately capture all parts of the body. Images were calibrated in Volocity according to microscope magnification (100-630x) and measurements were drawn directly onto images in Volocity that were later stored inside a PostgreSQL database (version 11) (PostgreSQL Global Development Group 2019). To standardize nematode abundances by dry weight of soil, gravimetric moisture content (GMC) was calculated for all 48 samples. Ten grams of homogenized soil from each sample were weighed and placed into a preheated oven (105°C, 24h) and re-weighed to calculate the GMC (Gardner 1986).

I calculated the proportional abundance of each genus at each site by dividing the percent cover of a single genus in a particular treatment by the total cover of all nematodes in that treatment. I determined that 26 out of 98 genera comprised 70% abundance in the community across all treatments at both sites (Cornelissen et al. 2003). For the first ten adult females of the top 26 genera, body length (μm) was measured by drawing a line down the center of the nematode from the lips to the tail tip on high resolution images (**Figure 2.2**). Anterior length (μm) was measured by drawing a line from the lips to the esophageal-intestinal valve to calculate b-ratio (body length:anterior length). The greatest body diameter (GBD, μm) was measured

perpendicular to the center line at the nematode's widest point. Since nematodes are cylindrical but taper at both ends, the body was treated as three volumetric regions: anterior frustum (head region), core, and posterior frustum (tail region) (Brown et al. 2016). Volume was calculated for each region of the body ($v = \frac{\pi h}{3}(r_1^2 + r_1 r_2 + r_2^2)$) where h = length of center line within each region, r_1 = major diameter, and r_2 = minor diameter. The resulting volumes were summed for total volume (μm^3), converted to cubic centimeters (cm^3), and used to calculate mass (g) ($m = sv$) using the nematode specific gravity (s) of 1.084 (Andrássy 1956). I used published literature to determine the number of gonads for each genus: Jairajpuri and Ahmad (1992) for the order Dorylaimida; Mai and Mullin (1996) for *Filenchus* and *Tylenchus*; and Bongers (1988) for the remaining genera.

To determine whether topography and grazing significantly affected the traits of dominant genera of soil nematodes, I calculated community-weighted means (CWM) and variances (CWV) for five nematode traits: length, greatest body diameter (GBD), mass, b-ratio (body length:anterior length), and number of gonads. CWM is defined as the mean community trait value weighted by the relative abundance of each nematode genus expressing that trait in the community ($\text{CWM} = \sum_{i=1}^n p_i \times \text{trait}_i$), where p_i represents the proportional abundance of genus i and trait_i represents the mean trait value of genus i (Lavorel et al. 2008). CWV defines variability of a trait in the community by weighting the sum of squares for genus i with its relative abundance ($\text{CWV} = \sum_{i=1}^n p_i (\text{trait}_i - \text{CWM})^2$) (Sonnier et al. 2010). Therefore, the CWM expresses the average trait value of a dominant nematode in a community and the CWV expresses the variability of that trait value around the mean value (Sonnier et al. 2010).

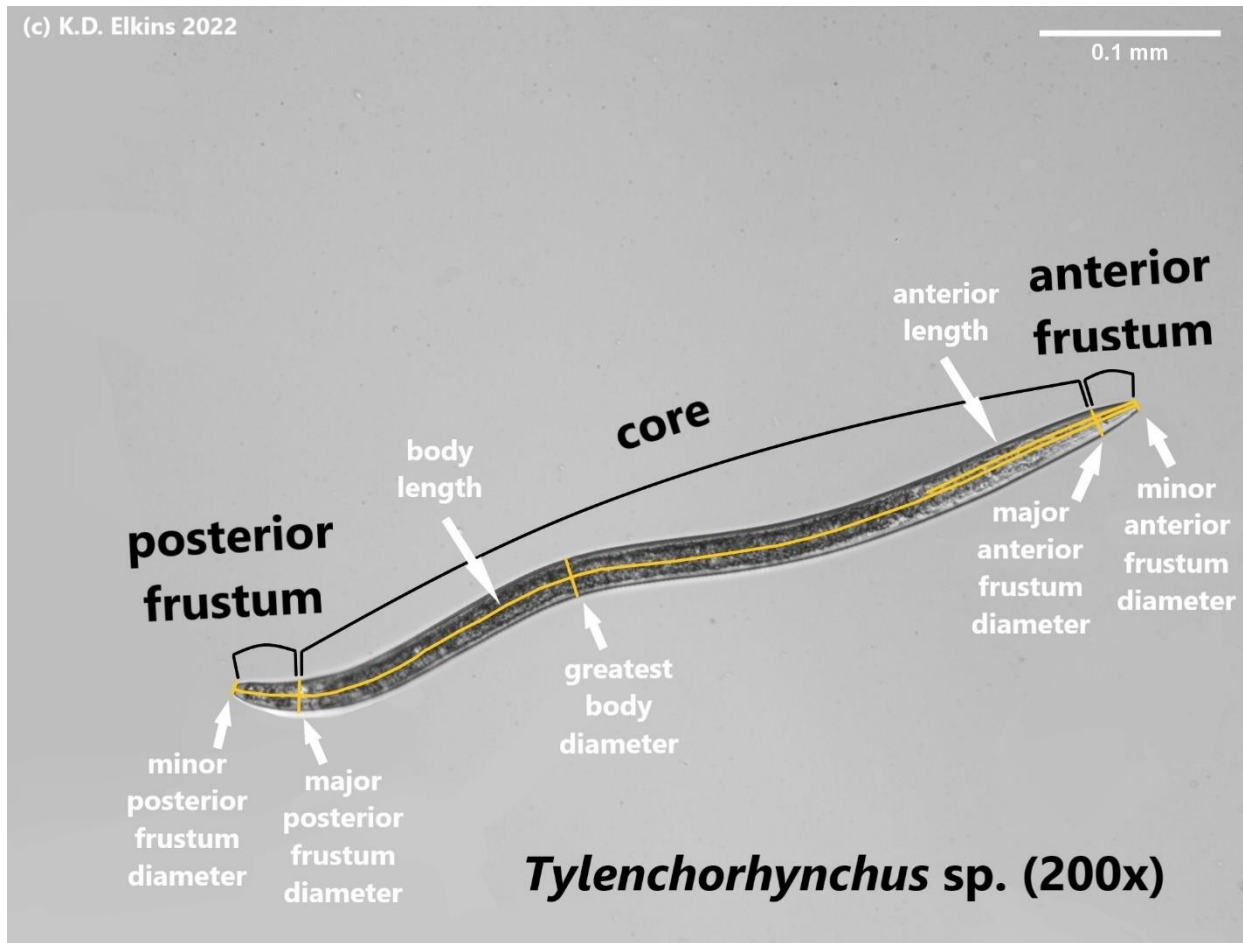


Figure 2.2. Image of a plant-feeding nematode (*Tylenchorhynchus* sp., 200x) taken from an ungrazed upland prairie at Tall Grass Prairie Preserve, near Vita, Manitoba, Canada. Morphological traits are illustrated above including greatest body diameter (μm); anterior frustum, core, and posterior frustum diameters (μm); and body and anterior lengths (μm) using Volocity software (version 6.3).

Statistical analyses

I evaluated the hypotheses that topography and grazing affect soil nematode diversity, feeding composition, and trait profiles of dominant genera by comparing nematodes in grazed and ungrazed upland prairies and wet meadows. To measure alpha diversity (diversity within a sample), I calculated nematode generic richness (s), effective richness ($e^H = e^{-\sum_{i=1}^s p_i \log(p_i)}$), and concentration (inverse Simpson, $D_2 = \frac{1}{\sum_{i=1}^s p_i^2}$) for each sample (Hill 1973, Legendre and Legendre 2012). To measure beta diversity (diversity between samples within a treatment), I calculated average pairwise distance for each sample using the Jaccard's similarity index ($J_{ij} = \frac{a}{(a+b+c)}$), where a represents shared genera of samples i and j , b represents unique genera of sample i , and c represents unique genera of sample j . I also calculated average pairwise distance between quadrats using the Bray-Curtis dissimilarity index ($BC_{ij} = 1 - \frac{2C_{ij}}{S_i + S_j}$), where C_{ij} represents the sum of the lesser values for genera found in samples i and j , S_i represents the total number of genera in sample i , and S_j represents the total number of genera in sample j . I selected generic richness and Jaccard's distance to highlight uniqueness of soil nematode genera in or between samples because it uses presence/absence data whereas effective richness, concentration, and Bray-Curtis distance were used to describe the composition of nematodes in the community because it considers relative abundances of genera and therefore gives greater emphasis to dominant genera (Legendre and Legendre 2012). I used a two-way analysis of variance (ANOVA) and Tukey's post-hoc tests on log-transformed values for each diversity index to determine if differences in the mean of each diversity index exist among treatments. I used log-transformations to normalize the distribution of diversity data prior to analysis in order to meet statistical assumptions for parametric tests (Legendre and Legendre 2012).

To test if topography and grazing affected soil nematode feeding composition, I assigned each soil nematode genus into one of six different feeding groups according to Yeates et al. (1993): bacterivores, fungivores, herbivores, predators, omnivores, and algivores. Ambiguity exists surrounding the feeding strategy of *Tobrilus* sp. (Yeates et al. 1993, Okada et al. 2011), since this genus may consume algae in freshwater ecosystems (Traunspurger 1995); however, in this study, *Tobrilus* sp. was classified as a predator similar to Liu et al. (2008). I calculated the mean proportion of each feeding group using abundances per kilogram of dry soil for each sample. I also performed a two-way ANOVA and Tukey's post hoc tests on arcsine-transformed mean proportions of each feeding group to determine if differences in mean proportions exist among treatments. I used arcsine-transformed proportions to normalize the distribution of the data prior to analysis since the abundances of many nematode genera in the samples may be close to zero (Sokal and Rohlf 1995). Finally, I tested whether topography and grazing affected soil nematode traits using a two-way ANOVA and Tukey's post hoc tests on each log-transformed CWM and CWV trait value to determine if differences in the means and variances of nematode traits exist among treatments. Residual analysis was used to determine the validity of each ANOVA with Shapiro-Wilk tests ($W=0.93-0.99$, $p>0.01$) and quantile-quantile plots for assessing normality and Levene's tests ($F_{1,22}=0.003-3.15$, $p>0.05$) and residuals-versus-fitted scatter plots for assessing homogeneity of variance.

I also performed principal component analysis (PCA) to analyze potential covariances among the CWM and CWV of nematode traits in order to determine which nematode traits contributed the highest proportion of variance in the soil nematode community and in which treatments. I used redundancy analysis (RDA) to test the results from my PCA models in order to determine if topography and grazing could explain any observed covariance in nematode traits

across treatments. RDA is a multivariate statistical model that acts as an extension of multiple linear regression by using eigenvector analysis to determine what proportion of variation in a set of continuous response variables (CWM and CWV) is explained by variation in a set of continuous predictor variables (topography and grazing) (Legendre and Legendre 2012). Since the predictors in this study are binary, I used dummy variables (k-1) to represent topography and grazing in the RDA models. Monte Carlo permutations ($n = 999$) were used to test RDA results for statistical significance ($p \leq 0.05$) to determine if the observed variation explained by each RDA axis was higher than the randomized permutations generated of the soil nematode trait data along each axis (Oksanen et al. 2020).

Statistical tests were performed in R software version 4.1.0 (R Core Team, 2020) using the R “stats” package (version 4.4.0) and the “tidyverse” package (version 4.1.3) (Wickham et al. 2019). Diversity indices, principal component analysis, and redundancy analysis were performed using the R “vegan” package (version 4.1.3) using standardized trait variables (Oksanen et al. 2020).

Results

I identified 98 genera of nematodes across 50 families (20 orders) in the existing soil nematode community at two research sites within two sampling periods. I found that 26 genera constituted the top 70% proportional abundance of nematodes in the community (**Table 2.1**). Common nematodes included bacterivores (e.g., *Prismatolaimus*, *Euteratocephalus*, *Plectus*), fungivores (e.g., *Nothotylenchus*, *Tylencholaimellus*, *Pseudhalenchus*), herbivores (e.g., *Helicotylenchus*, *Ecphyadophora*, *Filenchus*), predators (e.g., *Tripyla*, *Paratripyla*, *Eudorylaimus*), and omnivores (e.g., *Microdorylaimus*, *Thornenema*, *Epidorylaimus*). In this study, *Paracyatholaimus* was the only genus that represented the algivorous feeding group and

was found in 11 out of 48 soil nematode samples in low abundances, generally in wet meadows at Tall Grass Prairie Preserve and in upland prairies at East Shoal Lake Property.

Topography and grazing did not affect the diversity of nematode genera. There was no difference in the alpha diversity of nematodes between upland prairies and wet meadows nor between grazed and ungrazed treatments ($F_{1,43}=0.00-3.96$, $p=0.053-0.997$) (**Table 2.2**). Beta diversity, or the heterogeneity of nematode genera between samples, also did not differ across wet grasslands based on topography or grazing ($F_{1,43}=0.02-2.81$, $p=0.101-0.890$) (**Table 2.2**). Topography and grazing also did not affect total nematode abundance per kilogram of dry soil ($F_{1,43}=0.01-2.53$, $p=0.119-0.934$) (**Table 2.2**).

Table 2.1: Mean nematode abundance (count per kilogram of dry soil \pm S.D.) of the top 26 genera of nematodes (70% proportional community abundance) across a topographic gradient in grazed and ungrazed wet grasslands at A) Tall Grass Prairie Preserve and B) East Shoal Lake Property in Manitoba, Canada. Superscripts indicate feeding groups of nematodes according to Yeates et al. (1993): B=bacterivore, F=fungivore, H=herbivore, P=predator, O=omnivore.

UPLAND PRAIRIE						WET MEADOW					
Grazed			Ungrazed			Grazed			Ungrazed		
Genus	Count/kg	SD	Genus	Count/kg	SD	Genus	Count/kg	SD	Genus	Count/kg	SD
<i>A) Tall Grass Prairie Preserve</i>											
<i>Coslenchus</i> ^H	1,185	1,568	<i>Filenchus</i> ^H	2,236	1,987	<i>Filenchus</i> ^H	2,992	1,910	<i>Helicotylenchus</i> ^H	4,093	2,357
<i>Filenchus</i> ^H	1,143	1,021	<i>Hemicyclophora</i> ^H	1,949	2,232	<i>Euteratocephalus</i> ^B	2,560	2,830	<i>Prismatolaimus</i> ^B	1,520	805
<i>Merlinius</i> ^H	972	1,002	<i>Ecphyadophora</i> ^H	1,648	1,330	<i>Merlinius</i> ^H	2,384	4,182	<i>Filenchus</i> ^H	1,486	832
<i>Tylenchus</i> ^H	933	856	<i>Coslenchus</i> ^H	1,390	1,055	<i>Plectus</i> ^B	1,595	782	<i>Criconemella</i> ^H	1,074	739
<i>Prismatolaimus</i> ^B	927	529	<i>Tylencholaimellus</i> ^F	1,043	1,141	<i>Tripyla</i> ^P	1,120	1,233	<i>Euteratocephalus</i> ^B	897	346
<i>Euteratocephalus</i> ^B	654	420	<i>Nothotylenchus</i> ^F	897	710	<i>Eumonhystera</i> ^B	1,070	992	<i>Tripyla</i> ^P	660	320
<i>Tylencholaimellus</i> ^F	609	525	<i>Plectus</i> ^B	876	403	<i>Coslenchus</i> ^H	984	1,724	<i>Cephalobus</i> ^B	627	584
<i>Cephalobus</i> ^B	548	399	<i>Prismatolaimus</i> ^B	791	569	<i>Prismatolaimus</i> ^B	962	799	<i>Panagrobelus</i> ^B	543	319
<i>Tylenchorhynchus</i> ^H	495	330	<i>Microdorylaimus</i> ^O	786	835	<i>Tylenchus</i> ^H	958	425	<i>Plectus</i> ^B	540	262
<i>Plectus</i> ^B	433	286	<i>Tylenchorhynchus</i> ^P	758	707	<i>Panagrobelus</i> ^B	876	1,122	<i>Teratocephalus</i> ^B	523	518
<i>Monhystera</i> ^B	413	367				<i>Teratocephalus</i> ^B	826	494	<i>Eumonhystera</i> ^B	520	254
<i>Microdorylaimus</i> ^O	381	189				<i>Cephalobus</i> ^B	662	212	<i>Merlinius</i> ^H	435	362
<i>Epidorylaimus</i> ^O	278	209									
TOTAL	12,534	4,366		17,050	6,166		22,153	11,139		18,748	5,655
<i>B) East Shoal Lake</i>											
<i>Helicotylenchus</i> ^H	12,526	14,253	<i>Ecphyadophora</i> ^H	6,793	5,827	<i>Filenchus</i> ^H	2,732	2,086	<i>Prismatolaimus</i> ^B	5,553	3,318
<i>Filenchus</i> ^H	3,100	1,781	<i>Helicotylenchus</i> ^H	4,790	3,197	<i>Panagrobelus</i> ^B	1,808	1,482	<i>Merlinius</i> ^H	3,435	4,832
<i>Merlinius</i> ^H	2,899	3,229	<i>Filenchus</i> ^H	2,666	1,770	<i>Eumonhystera</i> ^B	1,784	1,932	<i>Panagrobelus</i> ^B	1,356	934
<i>Acrobeles</i> ^B	2,304	261	<i>Tylenchus</i> ^H	2,315	1,717	<i>Plectus</i> ^B	1,403	702	<i>Thornenema</i> ^O	1,289	1,267
<i>Tylencholaimellus</i> ^F	1,492	1,600	<i>Nothotylenchus</i> ^F	2,091	1,112	<i>Coslenchus</i> ^H	1,374	948	<i>Eumonhystera</i> ^B	1,244	862
<i>Plectus</i> ^B	1,457	1,854	<i>Prismatolaimus</i> ^B	1,610	1,715	<i>Microdorylaimus</i> ^O	1,297	608	<i>Tylenchorhynchus</i> ^H	1,209	1,125
<i>Prismatolaimus</i> ^B	1,291	1,106	<i>Merlinius</i> ^H	1,374	1,795	<i>Tylenchus</i> ^H	792	783	<i>Plectus</i> ^B	1,190	825
<i>Nothotylenchus</i> ^F	1,035	907				<i>Prismatolaimus</i> ^B	734	346			
<i>Tylenchorhynchus</i> ^H	897	728									
<i>Diplogasteritus</i> ^B	727	853									
<i>Pseudhalenchus</i> ^F	641	545									
TOTAL	25,527	14,261		27,795	10,022		14,940	5,451		22,807	7,380

Table 2.2: Mean (\pm S.D.) generic richness, effective richness, concentration (A), pairwise Jaccard distance, pairwise Bray-Curtis distance (B), and abundance (C) of soil nematodes across a topographic gradient in grazed and ungrazed wet grasslands in Manitoba, Canada. Variance from site (Tall Grass Prairie Preserve and East Shoal Lake Property) was controlled in the analysis of variance of log-transformed values for each diversity index and abundance ($n=48$, DOF=1,43).

	UPLAND PRAIRIE		WET MEADOW		Topography		Grazing		Topography: Grazing	
	Grazed	Ungrazed	Grazed	Ungrazed	F-Value	p-Value	F-Value	p-Value	F-Value	p-Value
<i>A) Alpha Diversity</i>										
Generic richness (s)	24 \pm 3	21 \pm 4	22 \pm 6	22 \pm 7	0.66	0.421	2.35	0.132	1.64	0.207
Effective richness (e^H)	15 \pm 3	12 \pm 4	14 \pm 4	14 \pm 5	0.05	0.832	3.96	0.053	0.74	0.394
Concentration (D_2)	10.62 \pm 3.32	8.72 \pm 3.33	10.16 \pm 2.92	9.21 \pm 4.00	0.00	0.997	3.82	0.057	0.12	0.733
<i>B) Beta Diversity</i>										
Jaccard similarity	0.31 \pm 0.02	0.29 \pm 0.03	0.29 \pm 0.04	0.30 \pm 0.03	0.38	0.539	1.21	0.278	2.70	0.108
Bray-Curtis dissimilarity	0.67 \pm 0.03	0.68 \pm 0.03	0.68 \pm 0.04	0.70 \pm 0.04	0.87	0.357	2.81	0.101	0.02	0.890
<i>C) Abundance</i>										
Total abundance (kg^{-1} dry soil)	19,030 \pm 12,130	22,423 \pm 9,717	18,546 \pm 9,170	20,777 \pm 6,617	0.01	0.934	2.53	0.119	0.05	0.828

Observed nematode genera represented all feeding strategies: bacterivores, fungivores, herbivores, predators, omnivores, and algivores. Both topography and grazing affected the feeding composition of soil nematodes. The mean proportion of bacterivores was higher in wet meadows compared to upland prairies ($F_{1,43}=71.86$, $p<0.01$) and higher in grazed treatments compared to ungrazed treatments ($F_{1,43}=9.98$, $p<0.01$) (**Table 2.3**). However, topography removed the effect of grazing on the mean proportion of bacterivores in wet meadows ($F_{1,43}=5.70$, $p<0.05$) (**Table 2.3**). The mean proportion of fungivores ($F_{1,43}=24.25$, $p<0.01$) and herbivores ($F_{1,43}=29.02$, $p<0.01$) was higher in upland prairies (**Table 2.3**). Grazing decreased the mean proportion of herbivores in upland prairies ($F_{1,43}=5.71$, $p<0.05$) but did not significantly affect the mean proportion of fungivores ($F_{1,43}=0.03$, $p=0.869$). Soils in upland prairies and wet meadows did not differ in their composition of predators and omnivores (**Table 2.3**). Lastly, the interaction of topography and grazing did not affect mean proportions of fungivores, herbivores, predators, and omnivores (**Table 2.3**).

Table 2.3. Mean proportion (\pm S.D.) of soil nematode feeding groups by mean abundance (per kg of dry soil) across a topographic gradient in grazed and ungrazed wet grasslands in Manitoba, Canada. Feeding groups were assigned according to Yeates et al. (1993). Variance from site (Tall Grass Prairie Preserve and East Shoal Lake Property) was controlled in the analysis of variance on the arcsine-transformed mean proportion for each feeding group ($n=48$, DOF=1,43). Tukey's post-hoc test results on mean treatment proportions are indicated by superscript letters where each letter represents a group that does not significantly differ at the $p<0.05$ confidence level.

	UPLAND PRAIRIE		WET MEADOW		Topography		Grazing		Topography:Grazing	
	Grazed	Ungrazed	Grazed	Ungrazed	F-Value	p-Value	F-Value	p-Value	F-Value	p-Value
Bacterivore	0.32 \pm 0.10 ^a	0.17 \pm 0.07 ^b	0.50 \pm 0.09 ^c	0.48 \pm 0.14 ^c	71.86	<0.01	9.98	<0.01	5.70	<0.05
Fungivore	0.13 \pm 0.07 ^a	0.14 \pm 0.07 ^a	0.05 \pm 0.04 ^b	0.04 \pm 0.03 ^b	24.25	<0.01	0.03	0.869	0.23	0.631
Herbivore	0.46 \pm 0.12 ^a	0.62 \pm 0.10 ^b	0.32 \pm 0.09 ^a	0.35 \pm 0.17 ^a	29.02	<0.01	5.71	<0.05	3.31	0.076
Predator	0.03 \pm 0.03	0.02 \pm 0.03	0.05 \pm 0.04	0.03 \pm 0.04	1.43	0.238	2.78	0.103	0.27	0.609
Omnivore	0.06 \pm 0.04	0.05 \pm 0.05	0.07 \pm 0.06	0.09 \pm 0.07	3.18	0.082	0.05	0.821	2.15	0.150
Algivore	\leq 0.01	\leq 0.01	\leq 0.01	\leq 0.01	N/A	N/A	N/A	N/A	N/A	N/A

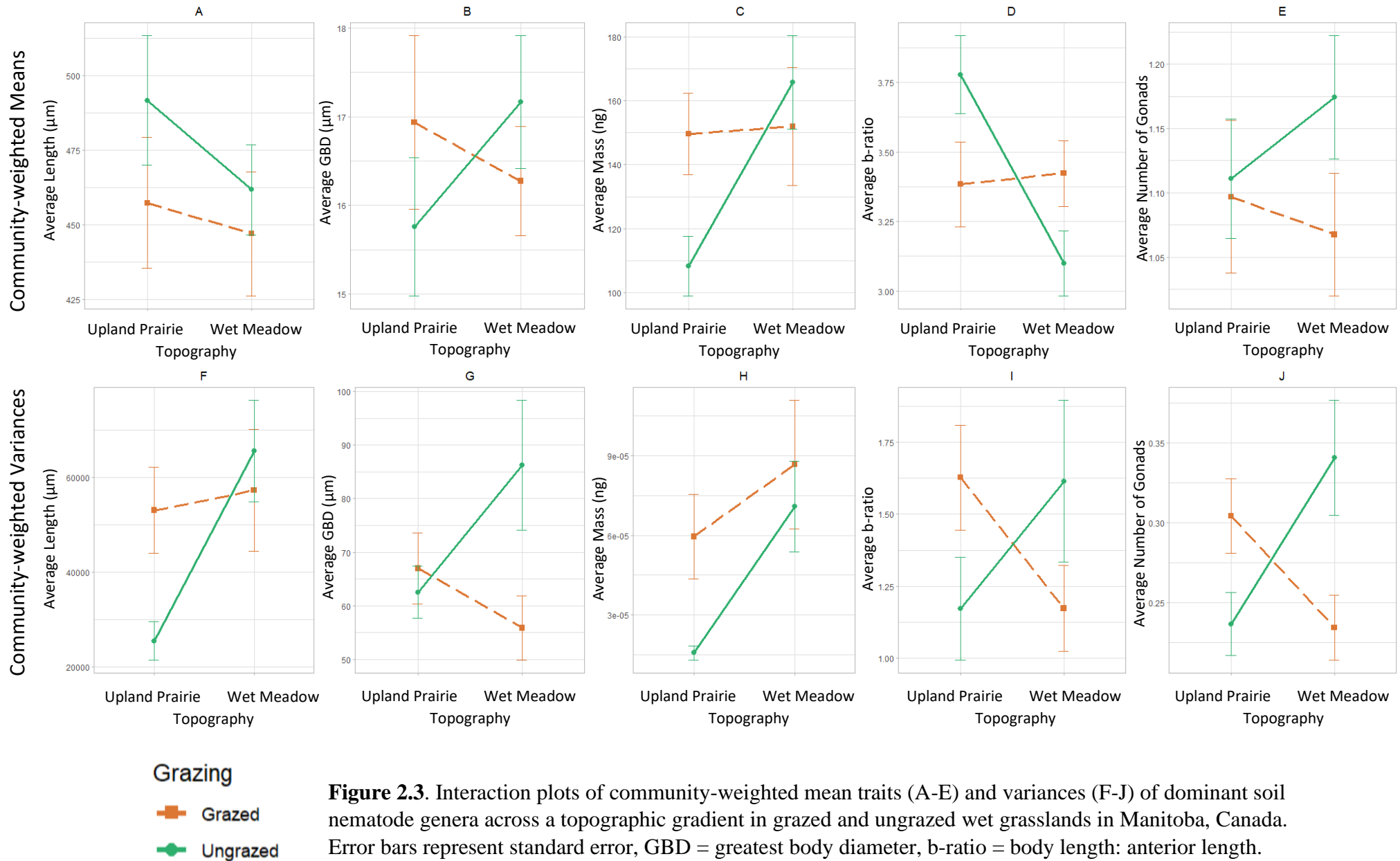
Topography and grazing affected the community-weighted means and variances of traits of dominant nematode genera. Soil nematodes in wet meadows had a greater CWM of mass ($F_{1,43}=5.51$, $p<0.05$) (**Table 2.4A**) (**Figure 2.3C**) and a lower CWM of b-ratio (i.e., bigger esophagus relative to body length) ($F_{1,43}=5.66$, $p<0.05$) (**Figure 2.3D**). While grazing alone did not significantly impact mass ($F_{1,43}=1.44$, $p=0.236$) nor b-ratio ($F_{1,43}=0.03$, $p=0.876$), the introduction of grazing in upland prairies removed the effect of topography on mass ($F_{1,43}=6.30$, $p<0.05$) and b-ratio ($F_{1,43}=7.80$, $p<0.01$) (**Table 2.4A**). The CWM of length, GBD, and average number of gonads (**Table 2.4A**) (**Figure 2.3A,B,E**) was similar in grazed and ungrazed upland prairies and wet meadows.

The CWV of length ($F_{1,43}=9.15$, $p<0.01$) (**Table 2.4B**) (**Figure 2.3F**) and mass ($F_{1,43}=15.07$, $p<0.01$) (**Figure 2.3H**) was greater in wet meadows compared to upland prairies. Ungrazed upland prairies had the lowest CWV of length and mass but the introduction of grazing to upland soils increased the variance of length ($F_{1,43}=9.44$, $p<0.01$) and mass ($F_{1,43}=4.31$, $p<0.05$) (**Table 2.4B**). Even though grazing interacted with topography to impact the CWV of GBD ($F_{1,43}=4.33$, $p<0.05$) (**Figure 2.3G**) and b-ratio ($F_{1,43}=6.01$, $p<0.05$) (**Figure 2.3I**), there were no significant differences in variance between topographic positions nor between grazing treatments for GBD and b-ratio. Additionally, the CWV for the average number of gonads was the greatest in ungrazed wet meadows but the introduction of grazing decreased variance ($F_{1,43}=12.65$, $p<0.01$) (**Table 2.4B**) (**Figure 2.3J**). Grazing and topography alone did not impact the CWV of GBD, b-ratio, or the average number of gonads (**Table 2.4B**).

Table 2.4: Community-weighted means (\pm S.D.) (A) and community-weighted variances (\pm S.D.) (B) of morphological, metabolic, and reproductive traits of dominant nematode genera across a topographic gradient in grazed and ungrazed wet grasslands in Manitoba, Canada. Variance from site (Tall Grass Prairie Preserve and East Shoal Lake Property) was controlled in the analysis of variance for each log-transformed trait value ($n=48$, $DOF=1,43$). Tukey's post-hoc test results on mean trait values are indicated by superscript letters where each letter represents a group that does not significantly differ at the $p<0.05$ confidence level and p-values are indicated by asterisks: * = $p<0.05$.

	UPLAND PRAIRIE		WET MEADOW		Topography F-Value	Grazing F-Value	Topography: Grazing F-Value
	Grazed	Ungrazed	Grazed	Ungrazed			
<i>A) Community-weighted means (CWM)</i>							
Average length (μm)	457.36 \pm 75.94	491.70 \pm 75.07	447.03 \pm 72.12	461.77 \pm 52.39	0.86	1.69	0.18
Average GBD ¹ (μm)	16.94 \pm 3.38	15.76 \pm 2.70	16.27 \pm 2.14	17.17 \pm 2.59	0.36	0.03	1.57
Average mass (ng)	149.54 \pm 43.97 ^{ab}	108.29 \pm 32.26 ^a	151.94 \pm 63.68 ^{ab}	165.66 \pm 50.75 ^b	5.51*	1.44	6.30*
Average b-ratio ¹	3.38 \pm 0.53 ^{ab}	3.78 \pm 0.49 ^a	3.42 \pm 0.41 ^{ab}	3.10 \pm 0.41 ^b	5.66*	0.03	7.80*
Average number of gonads	1.10 \pm 0.21	1.07 \pm 0.17	1.11 \pm 0.16	1.17 \pm 0.17	0.13	1.71	0.78
<i>B) Community-weighted variances (CWV)</i>							
Average length (μm)	53,049.50 \pm 31,470.33 ^a	25,505.51 \pm 13,954.40 ^b	57,309.58 \pm 44,480.12 ^a	65,578.92 \pm 36,932.35 ^a	9.15*	2.78	9.44*
Average GBD ¹ (μm)	66.99 \pm 23.13	62.53 \pm 16.79	55.86 \pm 20.77	86.24 \pm 41.97	0.06	2.19	4.33*
Average mass (ng)	5.95e-5 \pm 5.50e-5 ^a	1.56e-5 \pm 9.26e-6 ^b	8.67e-5 \pm 8.38e-5 ^a	7.10e-5 \pm 5.93e-5 ^a	15.07*	9.10*	4.31*
Average b-ratio ¹	1.63 \pm 0.63	1.17 \pm 0.62	1.17 \pm 0.51	1.62 \pm 0.97	0.00	0.09	6.01*
Average number of gonads	0.30 \pm 0.08 ^{ab}	0.23 \pm 0.07 ^a	0.24 \pm 0.07 ^a	0.34 \pm 0.12 ^b	0.22	0.38	12.65*

¹ GBD = greatest body diameter, b-ratio = body length: anterior length.

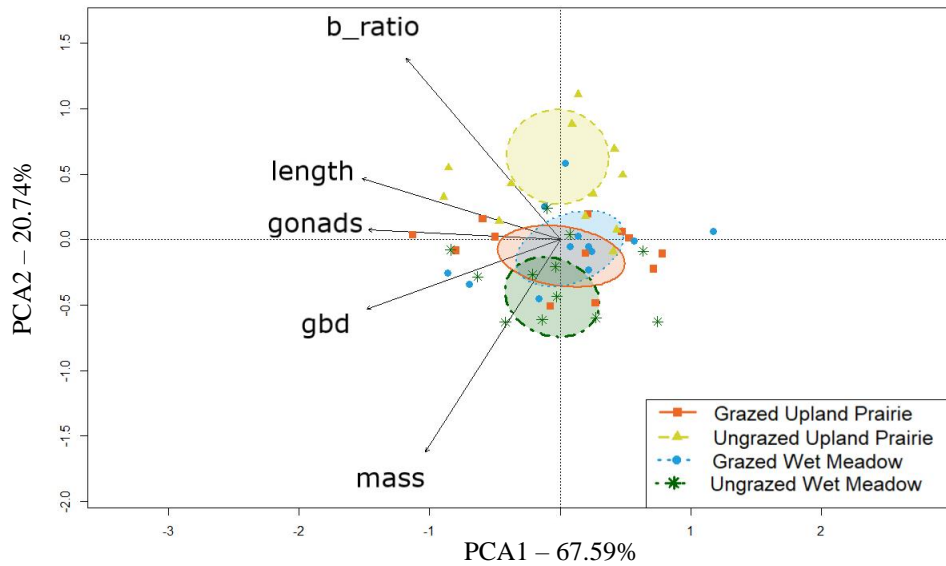


All measured traits of nematode genera were highly correlated and the first two principal component axes accounted for 88.33% of the variance in CWM traits of nematodes (**Figure 2.4A**). The first axis (PCA1) captured 67.59% of the total variation in nematode CWM traits and separated quadrats with higher values of all nematode traits without any separation among topography or grazing treatments. The first ordination axis also accounted for covariances among length and GBD, which were relevant in determining mass and b-ratio. The second axis (PCA2) captured an additional 20.74% of the total variation in nematode traits and separated samples based on grazing and topography. Communities of nematodes in ungrazed upland prairies were associated with higher CWM of b-ratios while nematodes in ungrazed wet meadows were most associated with greater CWM of mass. The overlapping ellipses of grazed treatments show that nematodes in grazed samples were more homogenous in their trait profiles than in ungrazed samples.

As with community-weighted means, the mean variances of nematode traits were also highly correlated and the first two principal component axes accounted for 82.35% of the variation in weighted trait variances (**Figure 2.4B**). PCA1 and PCA2 captured 63.20% and 19.15% of the total variation in nematode trait variances, respectively. Similar to the ordination of the means of community traits, variances of all traits were also highly correlated along PCA1. The second ordination axis (PCA2) separated grazed wet meadow samples, which were characterized by communities of soil nematodes with a greater variance in mass and a lower variance in b-ratio and average number of gonads. Despite the observed covariances in community weighted means and variances of nematode traits, neither topography nor grazing were able to explain the observed patterns of covariance of nematode traits (CWM: RDA global

model: $F_{2,45}=1.51$, $p=0.191$) nor the CWV of traits (CWV: RDA global model: $F_{2,45}=2.24$, $p=0.075$).

A) Community-weighted means



B) Community-weighted variances

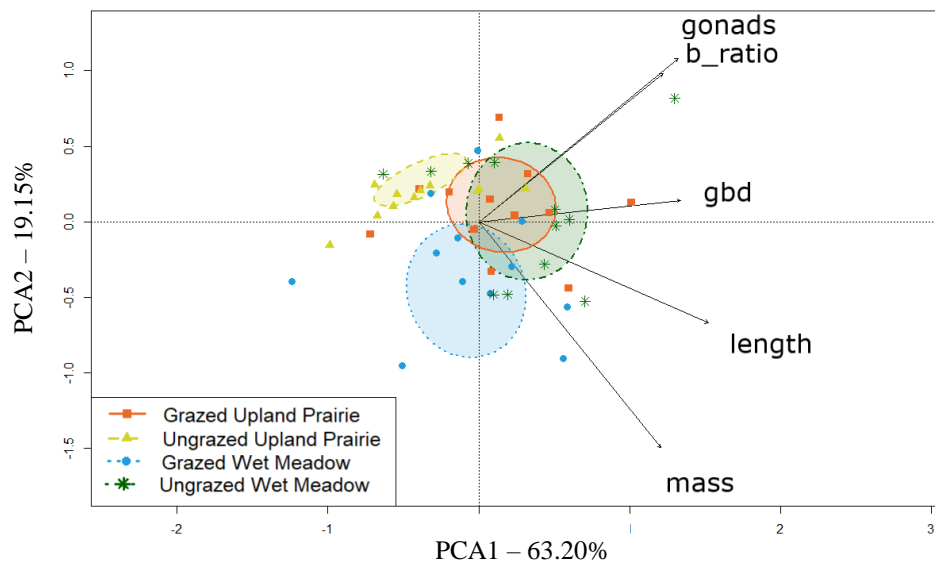


Figure 2.4. Principal component analysis biplot of community-weighted mean traits (A) and variances (B) of dominant nematode genera across a topographic gradient in grazed and ungrazed wet grasslands in Manitoba, Canada. Points represent individual samples (see legend), ellipses represent standard error at 95% confidence, and nematode traits (black vectors) include log-transformed average body length (length, μm), average greatest body diameter (gbd, μm), average mass (mass, μg), average b-ratio (b_ratio, equal to length/anterior length), and average number of gonads (gonads). Trait variables were standardized across traits for consistency.

Discussion

Diversity of nematodes

Although the richness of soil nematode genera in this two-site wet grassland project was high compared to other global (e.g., 0-89 genera, Song et al. 2017) and regional (e.g., 61 genera, Otfinowski and Coffey 2022; 53 genera, Otfinowski et al. 2023) studies, my hypothesis that topography and grazing affect soil nematode diversity was not supported. Since the results presented demonstrate that no significant differences in the diversity of nematode genera exist across the topographic gradient in grazed and ungrazed wet grasslands, it is possible that broad continental features drive soil nematode diversity more than the local parameters of topography and grazing, for example, climate and geography (Liu et al. 2019). In another wet grassland study, alpha diversity of nematode genera decreased towards climatic extremes (Ekschmitt et al. 2001). Wu et al. (2016) found that the diversity of nematode species decreased with increasing latitude in coastal wetlands. Although no global consensus exists in support of the inverse relationship between latitude and nematode diversity (Liu et al. 2019), perhaps due to low sample sizes (Meyer et al. 2018), inadequate sampling depth (Powers et al. 2009), or taxonomic resolution in nematode studies (Brustolin et al. 2018), other studies have supported the trend of decreasing nematode diversity with a shift away from the equator on a generic level (Spedicato et al. 2023) and on a species level (Porazinska et al. 1999, Brustolin et al. 2018).

A common finding in soil ecology is that plants aboveground can predict soil community composition belowground (Zak et al. 2003, Wardle 2004), despite mixed results for different soil biota groups (Fierer 2009). In this study, I was unable to complete vegetation surveys, however, differences in plant communities between upland prairies and wet meadows were documented in inventory reports by Nature Conservancy of Canada staff (Neufeld 2013, Hamel 2015, Becker

and Hamel 2017). For example, in other wet grassland studies, upland prairies are typically more plant-diverse even though wet meadows are generally more plant-productive (Austin et al. 2007, Fayiah et al. 2019). From a grazing perspective, Marty (2005) showed that plant species richness increased with cattle grazing (October-June, 1 AUM/2.4 ha) in ephemeral wetlands and Otfinowski and Coffey (2022) showed that plant diversity is maintained in grazed wet meadows depending on the timing and intensity of grazing (August-September, 1.3 AUM/ha). While aboveground herbivore grazing may increase plant diversity in wet grasslands, the consumption of plant material by grazers reduces aboveground plant biomass (Biró et al. 2019). Therefore, the lack of observed differences in nematode diversity between topographic positions and between grazing treatments suggest that variation in plant diversity and productivity may not cascade belowground to significantly drive soil nematode diversity across wet grasslands (Yeates 1984). This is the case in Kerfahi et al. (2016) where there was no difference in nematode alpha diversity of operational taxonomic units (OTUs) between plant-diverse tropical rainforests and high arctic tundra ecosystems with low plant diversity. Also, Viketoft et al. (2009) found that plant species identity more strongly influenced nematode species richness than did plant diversity in grasslands with a history of barley and potato cultivation. However, high precipitation across all treatments during my sampling year (2022) (Manitoba Agriculture Staff 2022) could have masked possible diversity links between plants and soil nematodes (Nielsen et al. 2014, Franco et al. 2022), which would have been more consistent with other studies (Eisenhauer et al. 2011, Cortois et al. 2017, Dietrich et al. 2021).

Alternatively, differences in vegetation communities between topographic positions (Neufeld 2013, Hamel 2015, Becker and Hamel 2017), as well as potential differences in plant diversity as a result of grazing (Gao and Carmel 2020), may still be responsible for driving soil

nematode diversity but their signals were too weak to shift nematode generic diversity overall or on the short timescale of this project (Reich et al. 2012). For instance, Coffey and Otfinowski (2019) demonstrated that soil nematode communities in restored grasslands may experience a “lag” in response to afforestation disturbances and that legacies of plant compositional changes affect nematode communities for >20 years. As a result, it may be important to consider these long-term effects on nematodes in this experiment (Biswal 2022) because changes in topographic positioning may be slight (Ehrlich et al. 1953, Pratt et al. 1961), which results in frequent fluctuations in plant communities as water levels advance and retreat annually that characterize these types of wet grasslands (Cowardin et al. 1979, Warner and Rubec 1997). In Otfinowski et al. (2023) the diversity of nematode genera in wet meadows decreased when grazing intensity was high (8.83 AUM/ha), however, a recent meta-analysis of 28 grassland studies examined the impact of grazing duration (<5, 5-10, >10 years), intensity (low, moderate, high), and livestock type (cattle, sheep, mixed, other) on nematode communities and found that grazing did not affect nematode generic diversity (Zhou et al. 2023). The lack of observed impact of grazing on nematode generic diversity in the above studies, some of which have a higher intensity and a longer duration of grazing than in this experiment, suggests that generic diversity of nematodes may be an inadequate resolution for nematode taxonomic analysis in environmental studies (Yeates 2003, Brustolin et al. 2018) or that grazing does not drive soil nematode diversity. Thus, the results presented in this study emphasize that generic diversity and total abundance of nematodes may not be a sufficiently sensitive indicator of environmental change across topographic gradients in grazed and ungrazed wet grasslands and reinforces the need for trait-based analysis. However, it remains to be tested whether grazing consistently affects other levels of taxonomic diversity in nematodes (e.g., species, molecular) (but see Vink et al. 2020).

Feeding composition

My second hypothesis that topography and grazing affect soil nematode feeding composition was supported. My results illustrate that soils in wet meadows and grazed treatments were characterized by bacterivores whereas upland prairies and ungrazed treatments were dominated by herbivores; however, topography and grazing did not affect mean proportions of predators and omnivores. Potential nutrient loading in wet meadows from rainfall, snowmelt, and surface water runoff (Aandahl 1949, Manning et al. 2001, Florinsky et al. 2002) and nutrient additions from cattle excretions in grazing treatments (Sanderson et al. 2010) may have increased soil nutrient concentrations and therefore could explain the observed changes in the feeding composition of nematodes (Ferris et al. 2001, Sanchez-Moreno et al. 2021). Specifically, nitrogen is found in higher concentrations in wet meadow soils compared to upland soils (Aandahl 1949, Gergans et al. 2011) and phosphorus concentration is also higher in wet meadow soils (Florinsky et al. 2002), especially wet meadows near upland pastures (Dunne et al. 2010). Additionally, low utilization of nitrogen and phosphorus by cattle in some plant communities (Bai et al. 2013) may result in manure with high nutrient concentrations, as well as urine with high levels of urea (Jungnitsch et al. 2011). For soil nematodes, potential increases in mineral substrates may increase soil bacteria populations (Sterner and Elser 2002) that can support a higher abundance of bacterivorous nematodes (Ingham et al. 1985). For example, Chen et al. (2015) demonstrated that nutrient-rich wet soils with high plant productivity were characterized by bacterivorous nematodes whereas dry and nutrient-poor soils with slow-growing plants were dominated by herbivorous nematodes. In my study, high soil moisture during my sampling year (Manitoba Agricultural Staff 2022) may have also increased the abundance of bacterivorous nematodes in wet meadows (Aupic-Samain et al. 2021), and potentially upland prairies

(Andriuzzi et al. 2020), but cannot explain the observed increase of bacterivores in grazed treatments or the observed interaction between grazing and topography.

In upland prairies, the mean proportions of herbivores and fungivores increased as bacterivores decreased in abundance. The negative effects of herbivorous nematodes on individual plants and plant communities are extensively studied in agriculture (van der Putten et al. 2013). For instance, root-feeding nematodes interfere with plant acquisition of carbon and nutrients, thereby decreasing plant abundance, halting the establishment of particular plant species, and shifting successional vegetation dynamics (Brussaard 1998). However, light belowground grazing on plant roots by nematodes can promote soil nutrient transfer and root growth in grasslands (Bardgett et al. 1999). Fungivores may impact plant performance and vegetation dynamics with mixed effects and indicate differences in decomposition pathways (Thakur and Geisen 2019). Fungus-feeding nematodes cycle phosphorus quickly, which may increase rates of mineralization and thus uptake by plants (Ingham et al. 1985, Irshad et al. 2011). Consumption of pathogenic fungus by nematodes leads to increased plant richness in grazed grasslands (Bae and Knudsen 2001, Brussaard et al. 2001) whereas fungal feeding on mycorrhizal hyphae by nematodes may harm (Hussey and Roncadori 1981, Ingham et al. 1985), benefit (Hua et al. 2014), or have no effect on plant growth (Bakhtiar et al. 2001). The observed increase in the abundance of fungivores in potentially low-nutrient upland soils may suggest that arbuscular mycorrhizal fungi (AMF) could be an important member in upland prairie soil communities by facilitating the transfer of resources from nutrient-limited soil to plant roots (Guo et al. 2016). Additionally, this study demonstrates that higher abundances of fungivores in upland prairie soils may indicate a shift towards fungus-dominated decomposition pathways

(Yeates 2003) whereas wet meadow soils and grazed soils may depend more on bacteria for the decomposition of organic matter (Thakur and Geisen 2019).

The results presented in this study demonstrate that topography and grazing affect the feeding composition of soil nematodes but the specific drivers of these changes need to be verified in future research. As nutrient levels potentially increase with a shift from upland prairies to wet meadows (Aandahl 1949, Manning et al. 2001, Florinsky et al. 2002), plant roots may simultaneously decrease in quantity and quality, especially in the shallow depth used for sampling nematodes (De Deyn et al. 2004). This suggests that changing plant communities with a shift towards wet meadows (e.g., *Carex* sp, *Juncus balticus*, *Spartina pectinata*, *Calamagrostis stricta*) (Neufeld 2013) and corresponding changes in plant root biomass may also play a key role in nematode feeding composition (DuPont et al. 2014) in tandem with soil nutrient concentrations (Verschoor et al. 2001) across wet grassland topography by regulating food resources of nematodes and soil food webs (Chen et al. 2013). This would help to explain the observed stronger effect of topography on nematode feeding composition compared to effect of grazing. Still, more research needs to be conducted, especially natural field experiments in heterogeneous wet grasslands that include spatial and temporal testing of soil chemical properties (e.g., mineral nitrogen, plant available phosphorus, organic carbon), physical properties (e.g., bulk density, moisture) (Fynn 2012) and vegetation parameters (e.g., root biomass, plant diversity) to determine the specific drivers of change in nematode feeding composition (Hedde et al. 2023). Moreover, the mean proportions of omnivores and predators remained similar across all treatments, which suggests that analysis of feeding group composition may not be a sufficient nematode community analysis tool and that trait-based analysis could provide a more

mechanistic perspective of changing nematode communities along a disturbed environmental gradient (Mulder 2006).

Morphological, metabolic, and reproductive traits

Impacts on soil nematode communities from topography and grazing were evident in the trait-based analysis of dominant genera. Nematodes in wet meadows were on average larger (mass) but more variable in size (mass and length) than nematodes in upland prairies. Also, nematodes in wet meadows had a lower and more variable b-ratio. However, the introduction of grazing removed the effect of topography on these nematode traits. Consequently, the disturbance of grazing alone did not impact CWM traits and only minorly affected the CWV of traits, but the interaction of grazing with topography had significant impacts when traits were analyzed univariately.

Following the observation from other grassland studies that soils in wet meadows may be more nutrient-rich than soils in upland prairies (Aandahl 1949, Manning et al. 2001, Florinsky et al. 2002), these results are consistent with Verschoor et al. (2001) who demonstrated a positive relationship between soil nitrogen and nematode biomass for plant- and fungus-feeding nematodes across a topographic gradient from a dry sandy plateau to a wet meadow stream bank. Although Verschoor et al. (2001) only measured herbivorous and fungivorous nematodes, individuals were identified to the species level, which suggests that the observed increase in nematode biomass was a result of increased nitrogen concentration as opposed to a product of taxonomic resolution (Yeates 2003). In my study, nematodes were identified to the genus level, therefore species variation in nematode traits may explain some of the observed variance (Ghaderi 2020). It is possible that intra-genus variation is greater in bacterivorous nematodes than in herbivorous or fungivorous nematodes since the CWV for length and mass was greater in

wet meadows, where bacterivores are more abundant. However, the observed changes in the CWM of the average number of gonads, values which were standard across each genus, suggest that intra-genus variation cannot explain all of the observed variability and that topography and grazing impact nematode traits and variances.

Alternatively, moisture is another soil property that may have changed across the topographic gradient (Davis et al. 2006, Moeslund et al. 2013) and impacted soil nematode traits (Andriuzzi and Wall 2020). For example, wet meadow soils typically have greater moisture than soils in upland prairies (Florinsky et al. 2002), which Mills and Adl (2011) found to be positively associated with nematode length in grazed temperate pastures. While potentially high soil moisture in wet meadows might explain some of the observed changes in the CWM traits from topography, it cannot explain the observed effect of grazing. In another study, Liu et al. (2015) showed that the CWM of nematode body size increased with fertilizer additions in both wet paddy rice and drier upland wheat fields and that the CWM of body size was positively correlated with organic carbon, total nitrogen, available phosphorus, and available potassium in wet and dry soils. Hou et al. (2023) examined the effects of warming and nitrogen fertilization on the CWM traits of nematodes and found that fertilization increased nematode body size whereas warming, a disturbance that can reduce soil moisture (Castanha et al. 2018), had no effect on any CWM traits in the nematode community.

Contrary to my prediction, communities of soil nematodes had a lower CWM of b-ratio in wet meadows (i.e., bigger esophagus relative to body length). These results may be inconsistent with findings from Hou et al. (2023), who demonstrated that increasing levels of soil nitrogen fertilization was correlated with smaller nematode esophagi. However, research on soil nematode metabolic traits (e.g., mouth, esophagus, and gut traits) and their functional

implications in soil are scarce (Auclerc et al. 2022). Nematode guts lack specialization, making the only known adaptation for nutrient uptake to be increasing the surface area of absorption in the gut (Tita et al. 1999). This can be accomplished in two ways: 1) increasing the length of the gut or 2) increasing the density and length of microvilli in the gut (Lee 2002). Residence time of food in a nematode gut is determined by the pumping rate of the muscular esophagus and the defecation rate at the rectum. Therefore, nematodes that eat low quality food (e.g., bacteria) may benefit from a longer esophagus that can pump food more rapidly through the body and may not require a long gut to absorb a relatively low-nutrient diet. Since intestinal contents are almost entirely emptied within 45 seconds in common soil nematode *Caenorhabditis elegans*, Lee (2002) suggests that digestive enzymes do not have time to play a key role in nematode digestion, instead, there is a nutritional advantage to having a high through-put of digesta. An alternative hypothesis for variation in b-ratio is purely physical: short nematodes may require a longer esophagus in order to maintain a rigid hydrostatic skeleton with their pseudocoelom for locomotion (Malakhov 1994). Considering that nematodes were similar lengths across all treatments, these results suggest a low b-ratio may be an adaptation to processing food quickly when food resources become available rather than to maintain internal pressure for locomotion (Freckman and Baldwin 1990).

My results from principal component analysis illustrate that the community-weighted means of nematode morphological, metabolic, and reproductive traits covary across the topographic gradient in grazed and ungrazed wet grasslands. However, there was little separation in grazed samples for CWM trait values, which indicates that traits were similar across grazed treatments regardless of topographic positioning. This homogenization may be explained by cattle transporting nematodes during feeding, pugging, and congregating at pasture (Ptatscheck

and Traunspurger 2020). Specifically, cattle may aid nematode dispersal through hitchhiking across grasslands, which could result in the passive transportation of nematodes with similar traits across a long distance. Since nematodes typically move at an annual rate of 10-100 cm through the soil matrix (van den Hoogen et al. 2019), dispersal over long distances requires assistance from other transporters (Moyle and Kaya 1981). The passive transportation of nematodes is enhanced by their small bodies (generally between 0.1 and 2.5 mm in length) (Lee 2002), greater activity in the top ten centimeters of mineral soil (Moyle and Kaya 1981), and due to the development of numerous survival strategies that enhance their ability to tolerate adverse travel conditions (Liu et al. 2019); for example anhydrobiosis (Treonis and Wall 2005), anaerobiosis (Crowe and Cooper 1971), and hypobiosis (entry into a Dauer larvae state) (Lee 2002). Potential dispersal mechanisms of soil nematodes via cattle are not well documented but studies have shown that insects, birds, wild boards, and turtles transport soil containing nematodes (Ptatscheck and Traunspurger 2020). Furthermore, grazing consistently increased the CWV of nematode traits in upland prairies but inconsistently affected the CWV of traits in wet meadows. This inconsistency could be explained by heterogeneous grazing of cattle across wet meadows due to vegetation preferences or physical barriers preventing congregation of cattle (e.g., large puddles, muddy terrain) (Burke et al. 1998, Putfarken et al. 2008, Leff et al. 2015, Liu et al. 2019). Lastly, when community-weighted means and variances were tested in a multivariate dimension with redundancy analysis, I found that topography and grazing alone could not predictably explain the covariance of nematode traits observed in the PCA biplots. Therefore, finer resolution studies that consider other environmental variables mentioned previously (e.g., soil organic carbon, mineral nitrogen, plant available phosphorus, plant root biomass) must address this gap in knowledge.

Potential effects of soil nematodes on the function of grassland ecosystems

Bacterivores non-discriminately filter feed bacteria in soil pores and excrete excess nutrients, mainly nitrogen and phosphorus (Ingham et al. 1985), in mineralizable or readily mineralizable forms (Ferris and Venette 1998). Because the carbon:nitrogen ratio in bacterivores is high compared to other nematode feeding groups (up to 10:1 in bacterivores) (Anderson et al. 1981), wet meadows and grazed soils may have an increased rate of nitrogen turnover (Bardgett and van der Putten 2014). As a potential result of increased access to nitrogen, plant growth may be improved through increased plant biomass production (Gebremikael et al. 2016). Furthermore, the dominance of bacterivores in soil promotes bacterial diversity and biomass (Xiao et al. 2014, Jiang et al. 2017) which is generally positive for plant performance (Bjørnlund et al. 2012). Therefore, these results help to explain high plant productivity in wet meadows compared to more plant-diverse upland prairies (Austin et al. 2007, Fayiah et al. 2019).

Large-massed nematodes may increase carbon sequestration in wet meadows and grazed upland prairies while also increasing ecosystem exergy (the amount of work a system at equilibrium can perform) (Ray et al. 2001). Some of the assimilated carbon by nematodes is used to increase biomass, which can be made available to plants during decomposition or as food sources for predators in the soil food web, including other nematodes (Gebremikael et al. 2016). Given the prevalence of bacterivores in wet meadows and grazed upland prairies, larger body masses in these soils may amplify the positive functional effects of bacterivores in ecosystem function. Although some nematodes utilize food more efficiently than others, even within the same feeding group (Lee 2002), a lower b-ratio may increase the rate that food is pumped through a nematode and consequently, may increase carbon and nutrient turnover in wet meadow

soils (Freckman and Baldwin 1990). These are important functional considerations for rangelands managers.

Conclusion

To conclude, findings from this research indicate that topography and grazing have belowground impacts in wet grasslands and that changes in soil function may be reflected by changes in nematode communities. Topography was a stronger driver of change in nematode communities overall but the interaction with grazing presents important considerations for rangeland management. These results reinforce the important role of soil nematodes as valuable bioindicators of soil health that may reflect changes in carbon sequestration, nutrient cycling, and decomposition of organic matter. Specifically, these results support the use of trait-based analysis as a more sensitive approach to nematode community analysis than taxonomic diversity based on nematode genera and analysis of feeding groups (Brondani et al. 2022, Hou et al. 2023). While this work provides important baseline information for understanding soil nematode communities and their implications in soil health, ongoing work testing how changes in soil chemical properties (e.g., mineral nitrogen, plant available phosphorus, organic carbon), soil physical properties (e.g., bulk density, moisture), and plant composition (e.g., root biomass, plant diversity) as a result of grazing across wet grassland topography will provide additional data for understanding the specific drivers of the observed changes in soil nematode communities. This research expands current efforts to incorporate soil faunal communities into the evaluation of grazing impacts on wet grasslands by providing a belowground perspective of ecosystem function. As climate change continues to alter grazing regimes regionally (Haigh et al. 2021) and globally (Asner et al. 2004, Godde et al. 2018), incorporating soil faunal communities in land-

management decisions puts forward an important conceptual basis to predict and evaluate the outcomes of land-use changes and to maintain soil function of impacted grasslands.

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CHAPTER 3: GENERAL CONCLUSION

Incorporating components of belowground community analysis in the evaluation of wet grassland ecosystems can elucidate our understanding of the consequences of disturbance across topographic gradients (Bardgett and Wardle 2003, Andriuzzi and Wall 2017). By examining soil nematode diversity, feeding composition, and traits in my evaluation of the effects of grazing across topography, I provided a baseline perspective for the inclusion of soil community analysis in wet grassland conservation and for the development of sustainable grazing practices.

Developing grazing practices that improve ecosystem function is relevant because livestock grazing is a globally extensive agricultural activity that covers more than half of all land on this planet (Follet and Reed 2010) and is expected to expand and intensify in order to meet increasing forage demands in a changing climate (Asner et al. 2004, Godde et al. 2018, Haigh et al. 2021).

The results of this study show that topography and grazing did not affect the total abundance of nematodes nor the uniqueness of nematode genera within samples and between samples across wet grasslands. The feeding composition of nematodes, specifically bacterivores, fungivores, and herbivores changed as topography shifted from upland prairie to wet meadow but only bacterivores were impacted by the interaction between topography and grazing. However, changes in the traits of dominant nematode genera were evident across wet grassland topography and significantly interacted with grazing to alter the structure of the nematode community. Therefore, my research demonstrates that traditional measures of alpha and beta diversity of nematode genera provide a valuable glimpse into soil nematode community assembly by revealing key members of the soil community but are not sufficiently sensitive to capture changes in nematode communities that may reflect changes in soil function, which is consistent with other findings (Sechi et al. 2017, Green et al. 2022). For instance, selection

pressures imposed by environmental change can act rapidly on the existing variation in nematode traits to select the optimal size and shape of nematodes without significantly impacting generic turnover (Hou et al. 2023). Consequently, diversity indices are relatively stable during short-term environmental change and require many generations to reflect sustained impacts from long-term alterations in nematode communities. While this study did not directly compare the sensitivity of faunal indices (Du Preez et al. 2022) to trait-based approaches, the results presented indicate that community-weighted means and variances of nematode traits of dominant genera respond to environmental change and may provide a mechanistic understanding of soil function.

Specifically, trait-based analysis captures phenotypic variation in nematode communities that may be linked to ecosystem function (Verschoor et al. 2001, George and Lindo 2015). In another study, Brondani et al. (2022) found that nematode traits explained 77% of plant nitrogen and phosphorus amounts whereas faunal analysis and taxonomic identity only explained 33% and 45% respectively. My thesis contributes to the growing recognition of trait-based analysis of soil nematode communities (Mulder 2006) and reinforces the ability of nematode communities to serve as valuable bioindicators of soil function across a disturbed landscape (Bongers and Ferris 1999, Lazarova et al. 2021).

My research is not without limitations. My approach of inferring soil function from the diversity, feeding composition, and traits of nematodes provides important and novel information on soil nematode communities in grazed and ungrazed wet grasslands, which is an approach that has been tested in other disturbed habitats (Sánchez-Moreno et al. 2010, Liu et al. 2015, Hou et al. 2023); however, these methods are indirect. For example, I used feeding groups and weighted trait values to deduce metabolic activity and fertility of nematodes to make conclusions about carbon sequestration and nutrient mineralization in soil (Ingham et al. 1985) that may affect

bacterial populations (Xiao et al. 2014, Jiang et al. 2017) and plant communities (Gebremikael et al. 2016). This approach differs from other studies that calculated carbon and nitrogen flows directly (Chen et al. 2019, Wang et al. 2020) and that measured energetics and metabolic rates of nematodes by calculating biomass and analyzing carbon and nutrient storage or release (e.g., nutrient excretion or gas exchange) (Ferris and Venette 1998, Ferris 2010, Wan et al. 2022). Furthermore, I only used adult females for trait measurements. Although males occur in much lower abundances than females (Nicholas 1984, Freckman and Baldwin 1990), they are still present in soil, as are nematodes at various stages of development. Both males and juveniles are typically smaller than adult females (Nicholas 1984, Lee 2002) and therefore should be considered in future work to determine precise functional contributions of nematode communities in soil (Sohlenius 1980). Consequently, the results presented may not fully represent changes in the structure and function of soil nematode communities and their implications for soil health.

I emphasize that the intensity of grazing in this experiment was light (<1.1 AUM/ac or <2.75 AUM/ha) and acknowledge that grazing is not a homogenous application of a treatment (Putfarken et al. 2008, Thorpe 2014). Therefore, I stress the need for future studies to explore variation in grazing intensity, timing, and duration across rangeland habitats to better understand how different aspects of livestock disturbance affect nematode communities as grazing expands and intensifies regionally (Haigh et al. 2021) and globally (Asner et al. 2004, Godde et al. 2018). Such research may help to clarify how different grazing regimes can be used to restore rangeland habitat using soil nematode communities as bioindicators of soil health (Wardle et al. 2004, Fuhlendorf et al. 2012). Furthermore, grassland complexes are characteristically heterogeneous, which leads to variation in soil chemical (e.g., soil organic carbon, mineral nitrogen, available

phosphorus) and physical (bulk density, moisture) properties and therefore may complicate soil sampling procedures (Burke et al. 1998). For example, sampling soil at different points of the growing season may provide very different soil analysis results for concentrations of nitrogen, phosphorus, potassium, and calcium (Fynn 2012). Thus, nematode communities may respond to surges in soil nutrients or other chemical alterations on a different timescale than soil sampling could occur. For instance, a fecal deposition from a cow or a heavy rain event may drive changes in the following generation of soil nematodes weeks or months later. These questions must be addressed in future work, perhaps by using a repeated measures design; specifically, testing how changes in soil nitrogen (mineral nitrogen) and phosphorus (plant available phosphorus) change alongside plant root biomass and nematode traits (Fynn 2012, Hedde et al. 2023) across the topographic gradient. I am especially interested in these soil and plant variables because they indirectly or directly control food resources for soil nematode communities (Ingham et al. 1985, DuPont et al. 2014).

Despite the above limitations, I have been able to show that wet meadow soils are characterized by large and metabolically active nematodes that may sequester carbon and cycle nutrients at greater rates than the small and herbivorous nematodes that dominate upland prairie soils. However, the addition of grazing removed the effect of topography and homogenized trait profiles of nematodes. My results illustrate that grazing alone may not significantly impact nematode traits but the interaction of grazing and topography may have functional consequences in soil. In addition, my results may point towards potential nutrient additions in wet meadows and grazed treatments (e.g., nitrogen, phosphorus) as likely drivers of the observed changes in the feeding composition and trait profiles of nematodes (Briar et al. 2011, Andriuzzi and Wall 2018, Hou et al. 2023) but spatial distribution of cattle may still play a key role in mediating the

effects of nutrient enrichment (Moyle and Kaya 1981, Ptatscheck and Traunspurger 2020); these drivers must be validated in future work.

Overall, my work provides a deeper understanding of the potential effects of changing climates on grasslands and the interactions between grazing and topography on the function of grassland soils by incorporating a belowground perspective of ecosystem function. My research helps to establish a link between grazing, the health of rangeland habitats, and the function of their soils by using nematodes as bioindicators. In particular, I have shown that trait-based analysis of nematodes reflects changes in soil health more sensitively than traditional diversity and abundance approaches of nematode genera. I recommend that faunal analysis of nematodes should be accompanied with trait-based analysis to monitor the effects of topography and grazing on soil health and to predict how soil function may change as climate changes (Ekschmitt et al. 2001). Findings from my research will help rangeland managers, producers, and conservation biologists to develop sustainable grazing prescriptions that improve the ecological integrity of rangeland habitats while meeting the growing need for forage demands as food demands increase worldwide (Guyader et al. 2016, Godde et al. 2018). Specifically, my findings suggest that light grazing (<1.1 AUM/ac or <2.75 AUM/ha) may provide a beneficial disturbance to wet grassland habitat and improve soil function. Lastly and equally important, my research adds to the inventory of soil nematode communities in native grasslands in Canada, which is an almost untouched area of ecological research. While this research aims to understand the cascading effects of topography and grazing on soil communities in wet grasslands, this methodology can be applied to a number of disturbances across ecosystems rooted in soil function.

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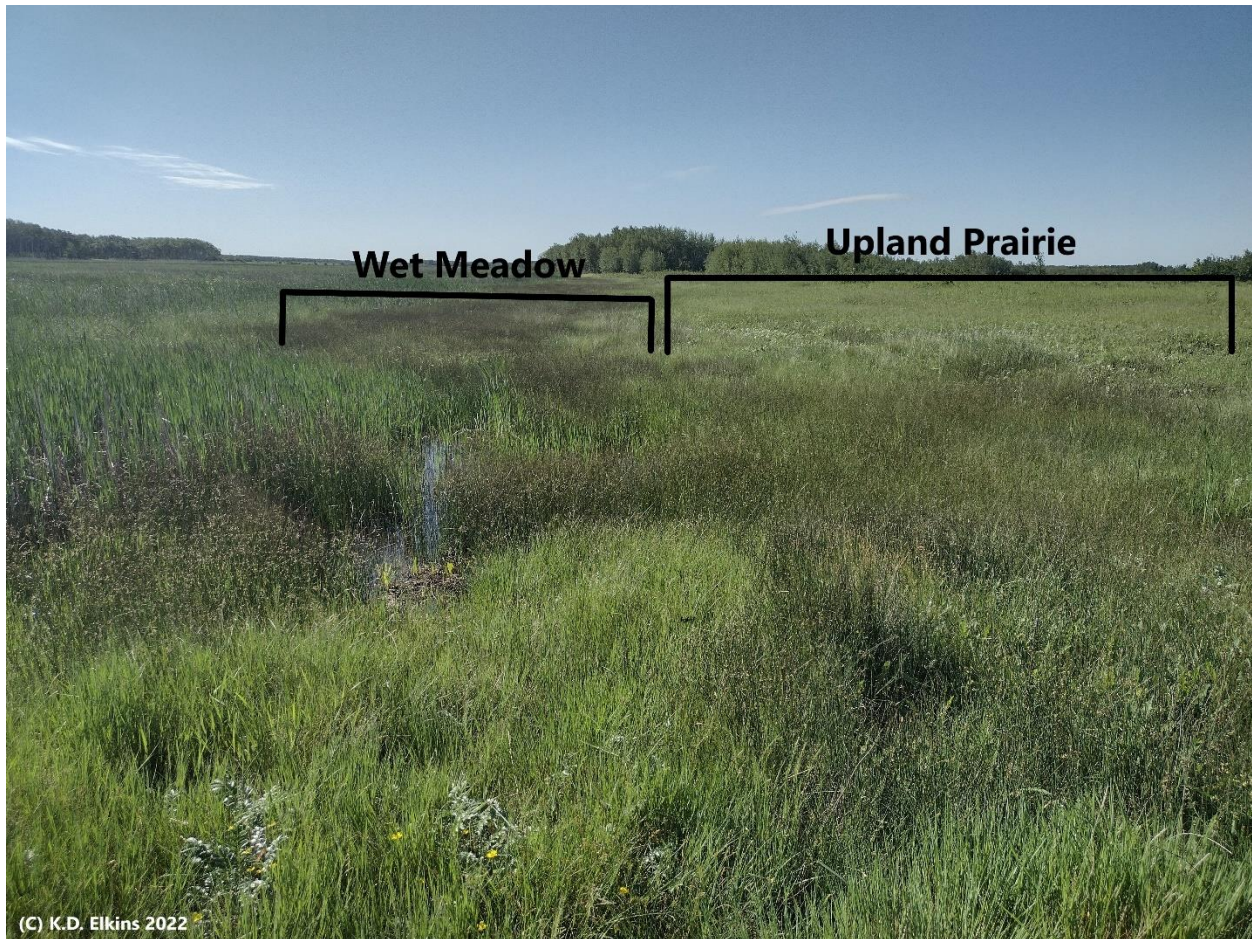
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Appendix

Appendix A. Description of climate, precipitation, soil, and grazing history at Tall Grass Prairie Preserve (Piney Station, 49°02' N, -96°00' W) and East Shoal Lake Property (Delta Marsh Station, 50°11' N, 98°23' W). Climate data were retrieved from Environment Canada (2011) and reported averages are from 1981-2010. Soil descriptions were retrieved from Reports of Reconnaissance Soil Surveys and the Canada – Manitoba Soil Survey (Ehrlich et al. 1953, Pratt et al. 1961). Thorpe (2014) recommends a stocking rate of 1.1 AUM/ac (2.75 AUM/ha) for wet meadows in Manitoba; therefore, all sites are considered lightly grazed.

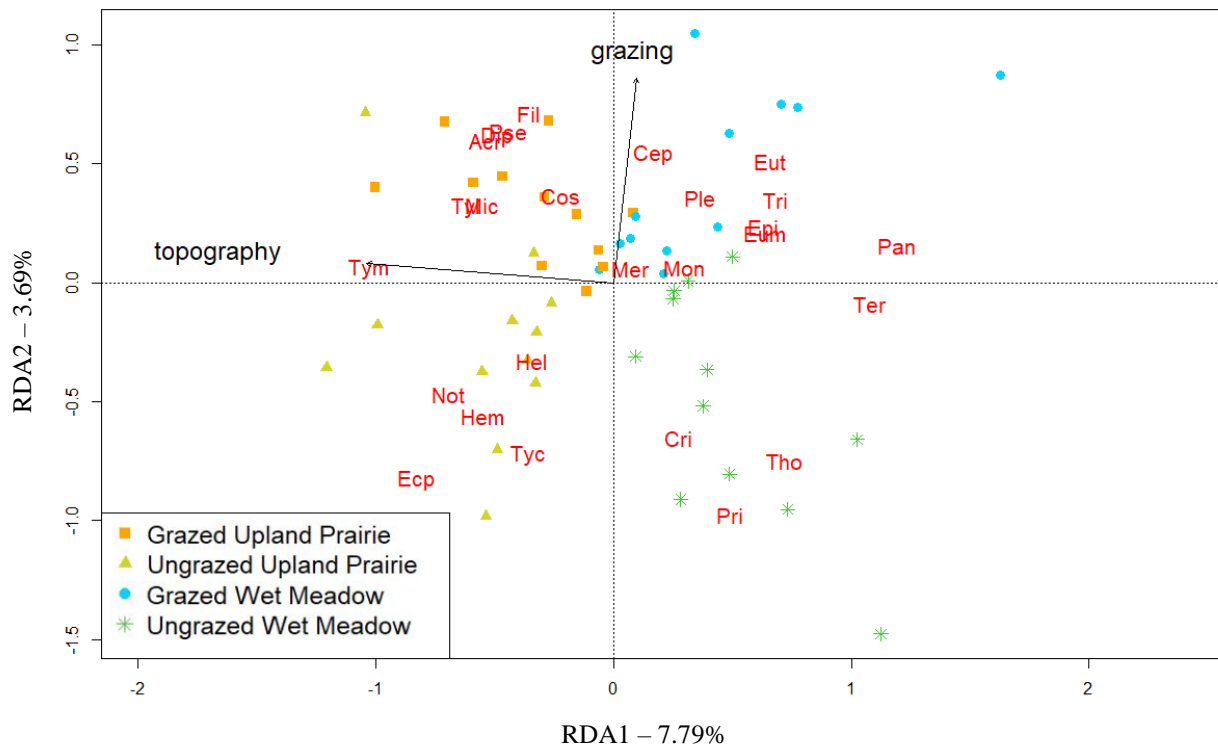
	TALL GRASS PRAIRIE PRESERVE		EAST SHOAL LAKE PROPERTY	
Mean Temperature January (°C)	-15.8		-16.2	
Mean Temperature July (°C)	19.1		19.3	
Average Annual Precipitation (mm.)	605.6		525.8	
SOILS				
	Upland Prairie	Wet Meadow	Upland Prairie	Wet Meadow
Soil Type	Gray Luvisol	Gray Luvisol	Black Chernozem, Gleysol	Gleysol
Parent Material	Thin sandy mantle on gravel or cobble lens over calcareous boulder till	Very thin sandy mantle on stony lens over calcareous boulder till	Very thin loamy or lacustrine sediments over stony, extremely calcareous till	Thin lacustrine clay or mucky loam deposits over extremely calcareous till or clay
Slope	Very gently sloping, meadow	Irregular, very gently sloping, peaty depressions	Irregular to depressional, very gently sloping	Level to depressional
Natural Drainage	Well	Poor	Moderate	Very poor
AGRICULTURE				
Grazing Prescription (AUM/ac)	< 1.1		< 1.1	
Grazing Months	August - October		August - October	
Historic Recommendations	Non-arable (too wet and too stony)		Non-arable (too wet)	



Appendix B. Image of an ungrazed topographic gradient in the grasslands of East Shoal Lake Property (Class II Wetland) (50°17' N, 97°30' W) (Ducks Unlimited Canada 2020). A shallow marsh meadow (Class III Wetland) is pictured directly left of the wet meadow and is unlabeled. Image taken June 22, 2022.

Appendix C. Description of the morphological, metabolic, and reproductive traits measured from the first ten adult female soil nematodes of dominant genera from grasslands across a grazed and ungrazed topographic gradient in Manitoba, Canada. Traits were measured using calibrated high-resolution images (8 MB) in Volocity software version 6.3 (Brown et al. 2016).

Trait	Description
<i>Morphometric Measurements</i>	
Body length	Length of the body measured between the minor diameter of the anterior frustum and the minor diameter of the posterior frustum (μm).
Major diameter of the anterior frustum	The major diameter of the anterior frustum (head region) (μm).
Minor diameter of the anterior frustum	The minor diameter of the posterior frustum (head region) (μm).
Anterior frustum length	The measured distance between the minor and major diameters of the anterior frustum (μm).
Major diameter of the posterior frustum	The major diameter of posterior frustum (tail region) (μm).
Minor diameter of the posterior frustum	The minor diameter of posterior frustum (tail region) (μm).
Posterior frustum length	The measured distance between the minor and major diameters of the posterior frustum (μm).
Anterior frustum modifications	Notes on any modifications to the anterior frustum (head region) (e.g., lip ornaments).
Posterior frustum modifications	Notes on any modifications to the posterior frustum (tail region) (e.g., caudal papillae).
Greatest body diameter	The diameter of the body at the nematode's widest point (μm).
Mass	Mass (ng) of the nematode using an assumed specific gravity of 1.084.
Volume	Volumetric sum of the anterior frustum, core, and posterior frustum (pL) using equation $v = \frac{\pi h}{3} (r_1^2 + r_1 r_2 + r_2^2)$.
Mean body length	The average length of the body for a specified genus (μm).
Mean mass	The average mass of a nematode for a specified genus (ng).
Mean volume	The average total volume of a nematode for a specified genus (pL).
<i>Metabolic Measurements</i>	
Anterior length	The measured distance between the minor diameter of the anterior frustum and the esophageal-intestinal valve (μm).
b-ratio	The ratio of body length to anterior length.
Mean b-ratio	The mean b-ratio of a specified genus (body length/anterior length).
<i>Reproductive Measurements</i>	
Number of gonads	Numerical count of the number of gonads according to literature.
Mean number of gonads	The mean number of gonads for a specified genus.



Appendix D. Redundancy analysis of dominant nematode genera (red), treatments (black), and individual samples (see legend) along a grazed and ungrazed topographic gradient in Manitoba, Canada. Treatment “topography” indicates an upland prairie landscape and treatment “grazing” indicates a grazing application. Acr=*Acrobeles*, Cep=*Cephalobus*, Cos=*Coslenchus*, Cri=*Criconemella*, Dip=*Diplogasteritus*, Ecp=*Ecphyadophora*, Epi=*Epidorylaimus*, Eum=*Eumonhystera*, Eut=*Euteratocephalus*, Fil=*Filenchus*, Hel=*Helicotylenchus*, Hem=*Hemicycliophora*, Mer=*Merlinius*, Mic=*Microdorylaimus*, Mon=*Monhystera*, Not=*Nothotylenchus*, Pan=*Panagrobelus*, Ple=*Plectus*, Pri=*Prismatolaimus*, Pse=*Pseudhalenchus*, Ter=*Teratocephalus*, Tho=*Thornenema*, Tri=*Tripyla*, Tym=*Tylencholaimellus*, Tyc=*Tylenchorhynchus*, Tyl=*Tylenchus* (RDA1: $F_{1,45}=3.6$, $p=0.001$; RDA2: $F_{1,45}=1.87$, $p=0.006$).

Appendix E. Sample size (*n*), mean, standard deviation (S.D.), and coefficient of variance (C.V.) of traits of the dominant genera that comprise 70% abundance in the nematode community. Sample size outside of brackets indicates the total number of individuals measured and inside the brackets indicates sample size at Tall Grass Prairie Preserve followed by East Shoal Lake Property. Traits described in the summary table include length (μm), GBD (μm), volume (pL), mass (ng), and b-ratio. Number of gonads is not included because there is no intra-genus variation.

Genus	<i>n</i>	Length (μm)			GBD ¹ (μm)			Volume (pL)			Mass (ng)			b-ratio ¹		
		Mean	S.D.	C.V.	Mean	S.D.	C.V.	Mean	S.D.	C.V.	Mean	S.D.	C.V.	Mean	S.D.	C.V.
<i>Acrobeles</i>	10(5,5)	369.63	83.06	0.22	26.35	5.10	0.19	110.18	56.51	0.51	119.44	61.25	0.51	3.13	0.26	0.08
<i>Cephalobus</i>	10(5,5)	537.85	91.29	0.17	24.53	3.87	0.16	153.39	66.49	0.43	166.27	72.07	0.43	3.73	0.64	0.17
<i>Coslenchus</i>	10(5,5)	494.45	82.32	0.17	18.31	2.52	0.14	62.90	20.98	0.33	68.18	22.74	0.33	4.98	0.37	0.07
<i>Criconemella</i>	10(9,1)	443.00	102.25	0.23	39.18	7.24	0.18	401.05	223.54	0.56	434.74	242.32	0.56	3.53	0.60	0.17
<i>Diplogasteritus</i>	6(1,5)	453.31	101.57	0.22	19.97	1.67	0.08	85.80	28.74	0.33	93.01	31.16	0.33	4.41	0.78	0.18
<i>Ecphyadophora</i>	10(3,7)	670.69	61.85	0.09	7.49	0.63	0.08	17.79	5.03	0.28	19.28	5.45	0.28	4.76	0.72	0.15
<i>Epidorylaimus</i>	10(5,5)	1,237.59	478.44	0.39	39.72	13.85	0.35	1,239.75	1,191.73	0.96	1343.89	1291.84	0.96	3.96	0.52	0.13
<i>Eumonhystera</i>	10(5,5)	400.16	106.91	0.27	13.27	3.15	0.24	32.31	22.79	0.71	35.03	24.70	0.71	3.95	0.88	0.22
<i>Euteratocephalus</i>	10(9,1)	546.70	127.64	0.23	17.91	3.25	0.18	85.64	45.32	0.53	92.83	49.13	0.53	3.82	0.29	0.07
<i>Filenchus</i>	10(5,5)	463.92	74.69	0.16	14.51	1.53	0.11	37.20	13.56	0.36	40.32	14.70	0.36	5.21	0.59	0.11
<i>Helicotylenchus</i>	10(5,5)	685.33	222.20	0.32	30.74	7.27	0.24	223.80	143.69	0.64	242.59	155.76	0.64	4.89	1.43	0.29
<i>Hemicycliophora</i>	10(10,0)	284.66	46.31	0.16	15.05	2.58	0.17	31.28	18.34	0.59	33.91	19.88	0.59	2.54	0.38	0.15
<i>Merlinius</i>	10(5,5)	888.18	85.83	0.10	33.43	3.38	0.10	354.69	79.75	0.22	384.49	86.45	0.22	5.16	0.44	0.08
<i>Microdorylaimus</i>	10(5,5)	521.34	73.14	0.14	26.79	4.34	0.16	168.36	64.12	0.38	182.50	69.51	0.38	3.24	0.53	0.16
<i>Monhystera</i>	10(5,5)	394.51	60.07	0.15	12.87	2.36	0.18	29.75	16.80	0.56	32.25	18.21	0.56	3.82	0.58	0.15
<i>Nothotylenchus</i>	10(5,5)	703.38	221.02	0.31	22.47	5.05	0.22	162.35	120.60	0.74	175.98	130.73	0.74	5.88	0.96	0.16
<i>Panagrobelus</i>	10(5,5)	366.34	56.20	0.15	25.19	3.67	0.15	109.53	47.42	0.43	118.73	51.40	0.43	3.18	0.37	0.12
<i>Plectus</i>	10(5,5)	720.29	253.26	0.35	27.83	16.92	0.61	421.49	590.31	1.40	456.90	639.90	1.40	3.94	0.53	0.13
<i>Prismatolaimus</i>	10(5,5)	604.89	102.36	0.17	16.55	2.91	0.18	72.48	35.17	0.49	78.57	38.12	0.49	3.43	0.37	0.11
<i>Pseudhalenchus</i>	10(5,5)	575.18	128.11	0.22	20.22	4.71	0.23	92.48	41.80	0.45	100.25	45.31	0.45	6.00	2.15	0.36
<i>Teratocephalus</i>	10(5,5)	440.81	45.99	0.10	16.01	2.14	0.13	38.71	10.23	0.26	41.97	11.08	0.26	4.12	0.35	0.09
<i>Thornenema</i>	10(1,9)	610.60	187.74	0.31	21.85	4.15	0.19	148.89	132.90	0.89	161.40	144.06	0.89	3.90	0.82	0.21
<i>Tripyla</i>	3(3,0)	1719.49	519.57	0.30	43.16	11.07	0.26	1,628.76	1,035.23	0.64	1765.57	1122.19	0.64	4.61	0.67	0.15
<i>Tylencholaimellus</i>	10(5,5)	533.28	105.98	0.20	22.83	4.42	0.19	150.06	77.58	0.52	162.67	84.10	0.52	3.33	0.91	0.27
<i>Tylenchorhynchus</i>	10(5,5)	754.50	110.16	0.15	27.24	2.98	0.11	198.31	64.30	0.32	214.97	69.70	0.32	4.89	0.60	0.12
<i>Tylenchus</i>	10(5,5)	466.75	81.72	0.18	15.88	4.11	0.26	44.70	27.15	0.61	48.45	29.43	0.61	5.11	0.60	0.12

¹GBD = greatest body diameter, b-ratio = body length: anterior length.