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Nematode community diversity and function across an alpine landscape undergoing plant colonization of previously unvegetated soils

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ABSTRACT

Climate warming is a key factor driving species range shifts. While previous work has focused on shifts of aboveground plant communities, changes in climate and vegetation should affect soil communities and hence ecosystem-level nutrient cycling and ecosystem functioning. High alpine ecosystems are particularly sensitive to climate warming because snow is among the main drivers of ecosystem structure and function. Climate-warming snow cover changes at Niwot Ridge in the Colorado Rocky Mountains have resulted in a consistent plant colonization of previously unvegetated soils generating a natural gradient of soil habitats ranging from unvegetated to increasingly vegetated. We used this gradient of plant communities at different successional stages to determine if nematodes respond to climate-driven changes in this high-alpine landscape and if they play a role in changes in soil C and N. We hypothesized that: 1) there would be clear shifts in nematode communities along the gradient as a function of snow cover, plant richness and density, and water holding capacity but that these shifts would be dependent on nematode feeding habits and their positioning in the soil foodweb and 2) the shifts would be associated with accumulating soil C and N. To test these hypotheses, we measured nematodes, plants, and soil microbes, snow cover, pH, soil water holding capacity, and different forms of soil C and N in 98 plots across the plant successional gradient. As predicted, nematode communities exhibited extensive shifts from a few individuals of a single species in unvegetated soils to hundreds of individuals and tens of species within every feeding group under complex plant communities. Representatives of omnivorous and bacterivorous K-strategists preceded plants and plant parasites and root associates depended on plants most. Linear regression models indicated that plants, microbial communities and soil water holding capacity, but not snow cover, were the most predictive factors of nematode diversity and density across all trophic levels and that all nematode groups were positively related to all measures of soil C and N. Structural equation models confirmed these results, but also indicated that effects of climate warming on nematodes were indirect primarily through shifts in plant and microbial communities and changes of soil water holding capacity. Moreover, nematode trophic group densities, but not their diversity, played a potential role in the accumulation of soil N, and to a lesser degree of soil C. Because nematode communities at Niwot Ridge are largely at their early phases of assembly, with continuing climate warming, we predict their increasing abundance and diversity will likely continue, as will their impact on soil C and N processes.

1. Introduction

Climate change is resulting in global-scale biological redistribution of marine, freshwater, and terrestrial species (Pecl et al., 2017; Tomiolo and Ward, 2018). Among the most common strategies of species to cope with climate warming is colonization of habitats in cooler places,

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including higher latitudes and altitudes. Mountain ecosystems are considered to be exceptionally sensitive to climate warming primarily because alpine life is governed by cold conditions (Grabherr et al., 2010; Pauli et al., 2019) and to escape increasing temperatures, alpine species move up to higher elevations and colonize previously inhospitable to them environments.

The patterns of colonization of higher elevation habitats in response to climate warming have been well documented for plant communities (e.g., Callaghan et al., 2011; Pauli et al., 2019, 2012). Because plants and soil biota are inherently linked with each other through primary production, decomposition, and nutrient cycling (Bardgett and W, 2010; Bardgett and Van Der Putten, 2014; Wardle et al., 2004), colonization by plants may result in parallel colonization by soil biota with potentially significant effects on the functioning of alpine ecosystems. Unfortunately, studies examining patterns of concerted plants and soil microbiota colonization of higher elevations as well as the effects on alpine ecosystem functioning are limited.

Nematodes are a major component of soil microbiota (Schratzberger et al., 2019). They are the most abundant (~10^8 individuals/m^2) and diverse (1 million species) metazoans (Hodda et al., 2009). Through their ubiquitous presence in all soils, diversity of feeding habits (e.g., bacterial- and fungal-feeders, plant parasites, omnivores, and predators) (Yeates et al., 1993) and lifestyles (r-K strategies) (Bongers, 1999), and positioning at various trophic levels (e.g., primary decomposers, primary consumers, or predators), nematodes by being directly linked to plants and soil microbes, play important roles in ecosystem functioning (Neher, 2010; Schratzberger et al., 2019). Because nematodes are considerably easier to study and interpret than other components of the soil community (i.e., bacteria, fungi, and protists), studies of patterns of high alpine colonization by nematodes can contribute to a better understanding of the role of climate warming in colonization patterns of other soil microbiota.

Although not even a single study has yet examined the role of climate warming on nematode redistribution and colonization of high alpine, relatively well-known biology and ecology of nematodes can provide for well-informed predictions. In fact, predictions provided by Nielsen and Wall (2013) for Arctic and Antarctic invertebrate communities can be easily extended to communities in the high alpine. The main predictions directly applicable to nematode communities include the role of changes in snowpack, soil moisture, and vegetation all allowing for range expansion and increase of nematode abundance, diversity, and activity as environment becomes less severe. In addition, via greater abundance and diversity, nematodes are predicted to increase their role in nutrient cycling and decomposition processes and together with plant and other soil microbiotic communities, lead to an accumulation of organic matter and likely changes in C and N dynamics (Nielsen and Wall, 2013). Unfortunately, none of these predictions have yet been tested on nematode communities.

An ecosystem that experiences clear effects of climate warming is the high alpine in the Colorado Rocky Mountains. Our study site, Niwot Ridge, spans the higher edge of the alpine tundra and extends 3600 m above sea level (a.s.l.). It is generally accepted that at these elevations the amount of snowfall, the depth of snowpack, and the extent of snowpack cover constrain distributional limits of plant communities (Gottfried et al., 2011), but other factors such as poor soil development, nutrient limitations, and interactions with soil microbes may also be important (Bueno de Mesquita et al., 2020b; Darcy and Schmidt, 2016). Over the last 50 years at Niwot Ridge, warmer climate has been associated with a thinner snowpack that melts earlier (Jepsen et al., 2012; Kittel et al., 2015). These changes in climate and snow cover have resulted in plant colonization of previously unvegetated areas (Bueno de Mesquita et al., 2017, 2018b) creating a mosaic of terrestrial environments ranging from completely unvegetated to increasingly vegetated. We used this long-term natural plant colonization experiment as a space for time substitution where areas with simple plant communities (i.e., low diversity, biomass, and ground cover) represent space most recently colonized in contrast to space with most complex communities colonized long ago. This gradient provided a unique opportunity to examine patterns of nematode colonization and whether they affect soil C and N pools.

Specifically, we hypothesized that: 1) there would be clear differences in nematode richness and community composition along the plant colonization gradient, driven by snow cover, plant diversity and density, and availability of water, and 2) shifts in nematode community complexity would directly positively relate to levels of soil C and N pools. We predicted that shifts in nematodes richness and community complexity would be a function of overall increasing foodweb complexity and hence nematode responses would be reflective of feeding habits and positioning in the soil foodweb. For example, because unvegetated soils at Niwot Ridge contain relatively abundant and diverse bacterial and fungal communities, we predicted that bacterivores and fungivores would colonize sites early on where plants were either absent or at early stages of their colonization (e.g., sparse vegetation, deep snow, and low soil ability to retain water). In contrast, plant parasitic, root-associated, and omnivorous/predatory taxa would colonize sites much later where plant communities were well established (e.g., high plant diversity and biomass), and overall foodwebs were more complex. Moreover, we predicted that positive associations between nematodes and soil C and N pools would result from increased direct interactions of nematodes with plants and microbes (e.g., root exudation and cell sloughing due to feeding on plant roots by plant parasites or excretion of organic and inorganic N due to grazing on bacteria by bacterial-feeding nematodes) (Bonkowski et al., 2009; Trap et al., 2016). To test these hypotheses, we examined relationships of nematode communities with plant richness and density, soil microbial communities, microbial C, microbial N, and abiotic factors (snow, pH, soil water holding capacity, total C, total N) in 98 plots across the plant successional gradient.

2. Materials and methods

2.1. Study site and sampling

The study site is located within the Green Lakes Valley adjacent to the Niwot Ridge Long Term Ecological Research site in the Front Range of the Rocky Mountains, Colorado, USA where it expands above the higher limit of alpine tundra (3600 m.a.s.l. up to 4000 m.a.s.l.). The area consists primarily of fellfields and unvegetated to sparsely vegetated gravely soils. The unvegetated sites mostly occur in snow bed areas where snow lingers long enough each year to prevent plant establishment, but not long enough to prevent the establishment of microbial communities actively accumulating soil carbon for several months each year (Freeman et al., 2009; Mladenov et al., 2013). Annual precipitation is 1200 mm/year with 94 % falling as snow (Kittel et al., 2015). Mean annual temperature is below freezing (3.8 C) but during the warmest months it can reach 12.4 C (McGuire et al., 2012). Over the last 50 years, the site has been experiencing changes in at least three categories. First, the climate has been warming as reflected by higher average summer and annual temperatures (Bueno de Mesquita et al., 2018b, 2020; McGuire et al., 2012) and higher number of positive degree-days and growing degree days (Bueno de Mesquita et al., 2020c; Caine, 2010). Second, climate warming has been associated with changes in snow cover that typically lasts from October to late June, but long-term records indicate that snow cover has become thinner and melts earlier (Jepsen et al., 2012; Preston et al., 2016). And third, changes in climate and snow cover have resulted in progressive migration of plants (5 %/decade) into the originally vegetation free landscape creating a gradient of terrestrial environments ranging from plant-free to increasingly vegetated (Bueno de Mesquita et al., 2018b). We used this natural gradient of plant communities at their different stages of successional development to examine patterns of nematode communities as well as factors that could drive these patterns. We included sites without vegetation to examine the extent of nematode colonization prior to plant colonization. Along a 2 km distance, we sampled the site using a spatially explicit grid of 98 circular 1 m radius plots spaced at 50 m intervals with three clusters of plots spaced 5 m apart (Porazinska et al., 2018). Each plot was characterized for plants (species richness, density, and surface cover), soil microbiota (richness and abundance of bacteria, fungi, nematodes, and other non-fungal non-nematode eukaryotes (dominated by SAR and followed by microinvertebrate Opisthokonta, algal Archaeplastida, Amoebozoa, and Excavata)), soil biogeochemical characteristics (soil moisture, water holding capacity, pH, total C, total N, microbial C, microbial N, inorganic forms of N, dissolved organic C and N), and other abiotic factors (snow cover and elevation). Procedural details of sample collection and processing are provided elsewhere (Porazinska et al., 2018) but a synopsis is provided in SI Table 1. To ensure sufficient amount of soil for nematode community analyses, nematodes were extracted from ~20 g soil subsamples (as opposed to 0.3 g for bacteria, fungi, and other non-fungal non-nematode eukaryotes) using Whitehead trays for 24 h, captured on a 38 m mesh sieve (Porazinska et al., 2014), and then processed for 18S sequencing (for more details see SI Table 1). Prior to DNA extraction, live nematodes were counted under an inverted microscope to trophic groups (Yeates et al., 1993) to quantify their density (number of individuals per 20 g dry soil). Likewise, direct microscopy counts and measurements of width and length were used to estimate total biomass of bacteria and fungi (fluorescein isothiocyanate staining and epifluorescent microcopy for bacteria and differential interference contrast microscopy for fungal hyphae) (Babiuk and Paul, 1970; Ingham and Klein, 1984). Values were converted to biomass using the established conversion rates (Van Veen and Paul, 1979).

2.2. *Statistical analyses*

All statistical analyses were performed in R (R Core Team, 2019). Out of 98 sampled plots, we used only those that were characterized by the presence of data points for all variables (no missing data) for a total of 80 plots (N 80). To determine the presence of compositional changes of nematode communities along successional gradient in plant communities, we performed a constrained distance-based redundancy analysis (dbRDA) in 'vegan package to ordinate a Bray-Curtis dissimilarity matrix of nematode communities along the plant richness gradient. Significance of the ordination was evaluated with a PERMAOVA permutation test (999 permutations).

To determine which biotic (e.g., richness and density of plant and soil microbiotic variables) and abiotic factors (e.g., biochemical and snow cover variables) were most important to nematode community composition, we constructed linear models with the *lm* function in 'bestglm package (Mcleod and Xu, 2017) using species richness and density of nematodes within each trophic group (i.e., richness and density of bacterial feeders, fungal feeders, omnivores, plant parasites, and root associates) as response variables of nematode communities. Because biotic and abiotic factors can act together, we extended single-to multiple-factor models by a stepwise (forward) addition of variables in the order of their R^2 values with nematode richness and density (SI Table 2). The nature (positive or negative) of the association was deduced from the signs ( ) of the coefficients in the models. Models were considered significant at P 0.05 and the best models were selected by using the Akaike information criterion (AIC, Akaike, 1974) using 'AICcmodavg package (Mazerolle, 2019). To avoid potential collinearity among variables in any multiple regression model, we assessed variance information factors using the *vif* function in the 'Car package (Firth et al., 2009). With no values exceeding 4, all selected models with their variables were retained. The variables selected for the best forward models were additionally confirmed with the *dredge* function in the 'MuMIn package (Barton, 2018). Because nematodes can affect soil C and N dynamics via multiple ways (e.g., grazing on plants by plant-parasitic nematodes stimulates rhizodeposition and feeding on microbes by bacterial-feeding nematodes can alter microbial turnover and/or microbial biomass) (Bonkowski et al., 2009; Trap et al., 2016), we wanted to determine whether nematode colonization and hence richness and density of each trophic group played a role in changes of soil C and N. We used single factor linear models as described above with C and N variables as response variables.

To better understand the direct and indirect way by which abiotic and biotic variables influenced nematode functional group abundance, richness, and their effects on ecosystem functioning, we used structural equation modelling (SEM) implemented with the *sem* function in the 'lavaan package (Rosseel, 2012). We built our meta model (SI Fig. 1) by selecting variables based on the multiple regression models. From abiotic variables, we included snow cover as the main variable that underlies the structure and function of the entire landscape and water holding capacity as the variable most consistently important to all nematodes. From biotic variables, the model included both plant diversity and density, but inclusion of variables representing bacterial and fungal diversity and biomass was dependent on the nature of each nematode trophic group. For example, for bacterial-feeding nematodes, fungal variables were excluded, for fungal-feeding nematodes, bacterial variables were excluded, and for plant-parasites neither bacterial nor fungal variables were included. Because omnivores can feed on bacteria and microbial eukaryotes and root associates on plants and fungi, the models tested both types of feeding options. To examine the potential impact of nematode colonization of the high alpine landscape on soil C and N, we also included into each SEM total and microbial C and N. The most non-significant pathways were iteratively removed from the starting model until Akaike (AIC) reduction was 2. Final model fit was evaluated by a non-significant (P 0.05) chi-square test, a low standardized root mean squared residual (SRMR 0.04), and a high comparative fit index (CFI 0.99) (Hu and Bentler, 1999).

3. Results

3.1. *Relationships of nematodes with plants, soil microbiota, and abiotic factors*

Plant richness varied from 0 to 27 species per plot and was significantly positively correlated with plant density (R^2 0.61) (Porazinska et al., 2018). Out of the 80 plots suitable for complete analysis involving all variables, nematodes were present in all but a single plot with their densities ranging from 5 to 4367 individuals per 20 g dry soil. Out of the total 126 nematode species identified, nematode richness varied from 1 in plots without vegetation to 39 in plots with the most complex plant communities. Both measures of plant communities were positively associated with richness and density of all nematode trophic groups (Fig. 1, SI Table 2). Although this positive relationship was observed for all trophic groups, the amount of variation explained by plant richness and density varied among groups and ranged from 8 % for omnivores to 46 % for fungivores (Fig. 1, SI Table 2).

In addition to plant variables, there were many other factors potentially affecting the richness and density of nematode communities (SI Table 2). With the exception of elevation and snow cover, all relationships between these factors and the richness/density of nematodes in their respective trophic groups were significantly positively correlated. Particularly strong relationships were present with the richness of bacteria and microbial non-fungal eukaryotes (SI Table 2A). In contrast, fungal richness was generally minimally correlated with all nematode trophic groups. From the abiotic soil factors, variables associated with soil water, especially water holding capacity, were the most important. Omnivores were consistently the least explained by any of these variables.

Overall, models that included a combination of the plant (richness and density), soil biotic (richness of bacteria and microbial non-fungal eukaryotes), and abiotic factors (water holding capacity) significantly improved the prediction of the richness and density of nematodes in all

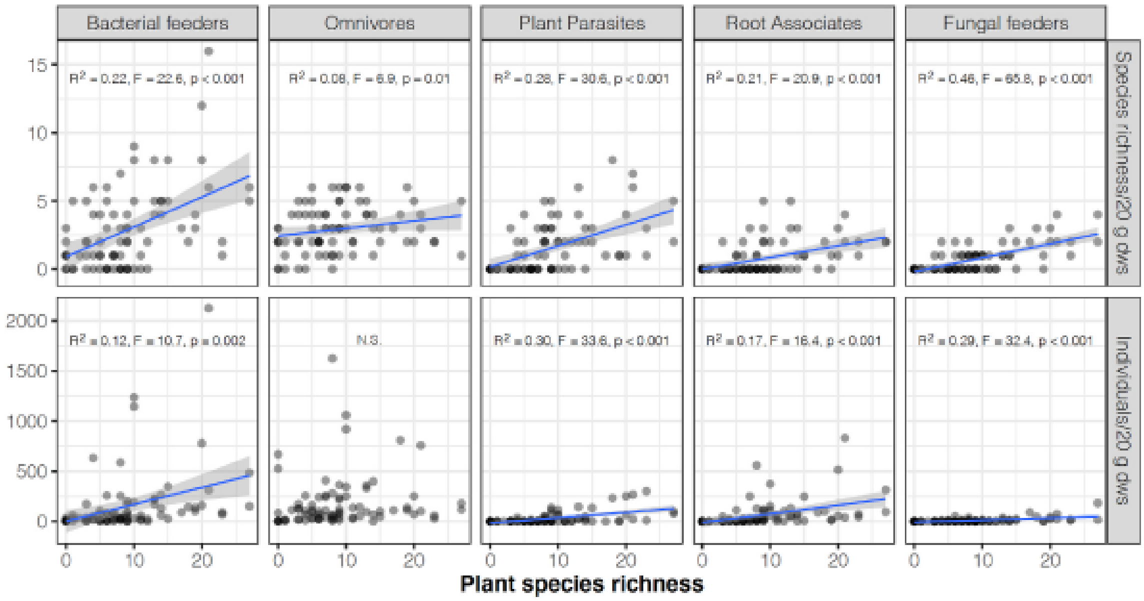

Fig. 1. Relationship between plant species richness (x-axis) and Top pannel Richness (number of nematode species) and Bottom pannel Density (number of nematode individuals) (y-axis) within trophic groups of bacterial feeders, omnivores, plant parasites, root associates, and fungal feeders. dws = dry weight of soil.

trophic groups (Table 1). Interestingly, in contrast to strong positive relationships between soil microbiota richness and both richness and density of nematodes in all trophic groups, the relationships with biomass of soil bacteria and fungi were either non-significant or very weak (SI Table 2). The exception from this pattern was observed for the density of fungal-feeding nematodes where fungal biomass was their best predicting variable (Table 1, SI Table 2B).

In addition to general increases in richness and density of nematodes with increased complexity of plant communities, there were significant ($P < 0.001$) shifts in the overall nematode community composition and structure (Fig. 2). Omnivorous and to a lesser extent bacterial-feeding nematodes were the only components of nematode communities in plots where plants were absent (SI Fig. 2 AB). While the relative contribution of omnivorous taxa to the overall community generally decreased along the gradient of plant richness/density, the relative contribution of bacterial feeders increased. Neither plant-parasites, root-associates, nor fungal-feeders were observed in plots without any vegetation (SI Fig. 2 CDE). In fact, their presence was not observed until plants were well-established (>25 plants/plot representing 3–4 plant species). Similar to bacterial-feeding nematodes, their contribution to the community increased as plant communities became more diverse and complex. Although nematode representatives of all trophic groups were observed in plots with <80 individuals of 5 different plant species, the first time they all occurred together was observed in a plot with 110 individual plants of 10 different plant species. However, higher plant richness and/or density did not guarantee that all trophic groups remained present. In fact, there were many plots at the higher plant richness/density spectrum with missing nematode trophic groups, specifically plant-parasites, root associates, and fungal-feeders (SI Fig. 2CDE). Omnivores were the only nematodes present throughout the entire plant richness/density gradient (SI Fig. 2B).

In addition to the increasing complexity of nematode communities at the trophic level, species richness within every nematode trophic groups increased as well. There was a general trend of new taxa being added to every trophic level along the plant richness/density gradient. *Paractinolaimus*, *Pungentus*, and *Aporcelaimellus* species represented the earliest omnivorous colonizers and *Teratocephalus*, *Plectus*, and *Prismatolaimus* the earliest bacterivorous colonizers. In contrast, *Mesodorylaimus* and *Wilsonema* (an omnivore and a bacterivore, respectively) represented species present only at the later stages of the nematode community development. It is also worth noting that not all species within the same genera presented equally early colonizing abilities. For example, while two species of *Paractinolaimus* were observed in plots without vegetation, two other species were only observed in plots where plant communities were already very well-established (>13 plant species, >150 plant individuals). Rhabditid species (e.g., genus *Rhabditis* or *Mesorhabditis*) traditionally considered as classic bacterivorous colonizers based on their life traits characteristics (or r-strategists) (Bongers and Bongers, 1998) were not detected in our soils. The 'classical' predators from the order of Mononchida representing persisters (or K-strategists) were not detected either.

Patterns of early and late successional species were also observed among plant-parasites and fungal-feeders. For example, plant-parasitic *Pratylenchus*, *Anguina*, and *Nagelus* and fungal-feeding *Aphelenchoides*, were noted in plots early on with 3–5 plant species (SI Fig. 2CE). In contrast, species of *Ogma* (plant parasite) and *Aphelenchus* (fungal feeder) were only present where plant richness and density exceeded 13 plant species and 90 individuals.

Regardless of the feeding habit or life strategy, the majority of observed species were either unknown or undescribed. Using 18S DNA, less than 10 % of species produced 100 % matches to a registered reference sequence.

3.2. Relationships between nematodes and C and N pools

In general, both richness and density of nematodes within all trophic groups showed significant positive relations with all measures of C and N (Table 2). Nematode richness, however, was less predictive than nematode density (average $R^2 = 0.20$ and 0.30, respectively). Overall, the strongest relationships with C and N measures were observed for bacterial feeders ($R^2 = 0.41$ and 0.37 for C and N, respectively), plant parasites ($R^2 = 0.34$ and 0.34), and root-associates ($R^2 = 0.28$ and 0.29) and the weakest for omnivores ($R^2 = 0.09$ and 0.06). From all C and N measures, microbial C ($R^2 = 0.32$) and N ($R^2 = 0.36$) was predicted better by nematodes than other C and N measures ($R^2 = 0.20$ for %C, 0.28 for DOC, 0.20 for % N, and 0.21 for TDN).

3.3. Pathways of interactions inferred from SEMs

Our SEMs indicated that water holding capacity was the most

Table 1
Forward-selection linear models predicting nematode "species" richness (number of OTUs equivalent to species) and abundance (number of individual specimens) within respective trophic groups by selecting best predictors from plant only variables, microbial only variables, physico-chemical only variables, and their combinations.

	R^2	F	DF	P
RICHNESS				
Bacterivores				
+PR, +PD	0.27	13.97	1, 78	6.68E-06
+BacR	0.32	35.80	1, 78	6.25E-08
+WHC	0.30	33.64	1, 78	1.35E-07
+WHC, +BacR	0.43	28.97	2, 77	4.17E-10
Fungivores				
+PR, +PD	0.50	37.82	2, 77	3.61E-12
+EukR	0.44	62.88	1, 77	1.29E-11
+WHC	0.39	49.98	1, 77	5.81E-10
+WHC, +PR, +PD, +EukR, +BacR	0.62	24.43	5, 74	1.94E-14
Omnivores/predators				
+PD	0.08	6.94	1, 78	0.01
+BacR	0.14	12.4	1, 78	0.001
+moisture	0.09	7.90	1, 78	0.006
+BacR, +moisture	0.17	7.84	2, 77	0.002
Plant-parasites				
+PR, +PD	0.33	19.27	1, 78	1.64E-07
+EukR	0.30	33.71	1, 78	1.32E-07
+WHC	0.29	31.97	1, 78	2.47E-07
+WHC, +PR, +PD, +EukR	0.43	14.06	4, 75	1.32E-08
Root-associates				
+PR	0.21	20.88	1, 78	1.81E-05
+EukR	0.17	16.19	1, 78	0.00001
+WHC	0.24	24.70	1, 78	3.78E-06
+WHC, +PR	0.29	15.38	2, 77	2.40E-06
Total				
+PR, +PD	0.46	32.24	2, 77	3.34E-10
+BacR	0.48	71.6	1, 78	1.19E-12
+WHC	0.41	54.08	1, 78	1.66E-10
+WHC, +PR, +PD, +EukR, +BacR	0.66	28.33	5, 74	6.30E-16
DENSITY				
Bacterivores				
+PD	0.14	12.99	1, 78	0.0006
+BacR	0.24	24.31	1, 78	4.53E-06
+moisture	0.46	66.94	1, 78	4.18E-12
+moisture, +BacR	0.53	42.81	2, 77	3.16E-13
Fungivores				
+PR	0.29	32.44	1.78	2.08E-07
+FunBiom	0.46	18.01	1, 78	6.00E-05
+WHC	0.31	34.92	1, 78	8.54E-08
+FunBiom, +PR	0.54	45.70	2, 77	8.23E-14
Omnivores/predators				
+BacR	0.07	5.89	1, 78	0.02
+WHC	0.41	54.08	1, 78	1.66E-10
Plant-parasites				
+PD	0.40	52.41	1, 78	2.75E-10
+EukR	0.32	36.73	1, 78	4.52E-08
+WHC	0.47	69.48	1, 78	2.11E-12
+WHC, +PD, +EukR	0.57	33.79	1, 76	5.54E-14
Root-associates				
+PD	0.23	23.72	1, 78	5.72E-06
+BacR	0.17	16.16	1, 78	0.0001
+WHC	0.28	30.96	1, 78	3.57E-07
+WHC, +PD	0.32	18.30	2, 77	3.14E-07
Total				
+PD	0.20	19.03	1, 78	3.89E-05
+BacR	0.25	25.43	1, 78	2.91E-06
+moisture	0.48	70.49	1, 78	1.61E-12
+moisture, +BacR	0.54	45.58	2, 77	8.70E-14

Variables were added to models based on best pairwise R^2 values SI Table 1. PR = plant richness, PD = plant density, BacR = bacterial richness (Chao 1), EukR = non-fungal non-nematode eukaryotic richness (dominated by SAR and followed by microinvertebrate Opisthokonta, algal Archaeplastida, Amoebozoa, and Excavata) (Chao 1), FungBiom = fungal biomass, WHC = water holding capacity, moisture = soil water content, +/− = positive/negative relationship inferred from the signs of coefficients.

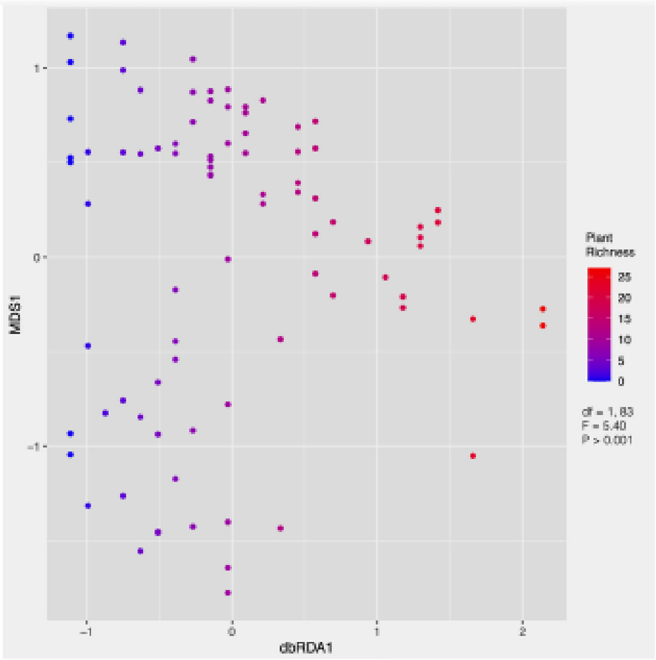

Fig. 2. Constrained redundancy analysis ordinating Bray-Curtis dissimilarity distance matrix of nematode communities to illustrate compositional shifts along the gradient of plant richness.

Table 2
Linear models predicting the influence of nematode trophic groups (diversity and abundance) on soil C and N pools. All numbers are significant R^2 values at $P < 0.05$ and df = 1, 78. ns = nonsignificant.

Nematode	Carbon Pools			Nitrogen Pools		
	%C	MicC	DOC	%N	MicN	TDN
RICHNESS						
BF (+)	0.24	0.20	0.36	0.23	0.26	0.27
OM (+)	ns	ns	ns	ns	ns	ns
PP (+)	0.22	0.26	0.09	0.23	0.29	ns
RA (+)	0.10	0.14	0.10	0.11	0.15	0.06
FF (+)	0.27	0.36	0.13	0.27	0.38	0.11
DENSITY						
BF (+)	0.36	0.36	0.50	0.35	0.35	0.42
OM (+)	0.10	0.08	0.08	0.10	0.08	ns
PP (+)	0.36	0.43	0.24	0.36	0.49	0.17
RA (+)	0.16	0.25	0.43	0.16	0.36	0.34
FF (+)	ns	0.50	0.13	ns	0.50	0.13

BF = bacterial feeders, OM = omnivores/predators, PP = plant parasites, RA = root associates, FF = fungal feeders. Carbon pools: %C = percent of total carbon, MicC = microbial carbon, DOC = dissolved organic carbon. Nitrogen pools: %N = percent of total nitrogen, MicN = microbial nitrogen, TDN = total dissolved nitrogen, + = positive relationship inferred from the signs of coefficients.

important and most consistent factor directly positively influencing both richness and density of nematodes in all trophic groups (Fig. 3, SI Figs. 3, 4, 5). The path coefficients for nematode richness ranged from |0| for omnivores to |0.36| for bacterial feeders and for nematode density ranged from |0.23| for omnivores to |0.52| for fungal feeders. Generally, snow cover had no direct effect on nematodes, except for its negative effect on the richness of plant-parasitic nematodes |0.29| (SI Figs. 3C and 5C). The direct effects of measures associated with plants were nematode trophic group specific. For instance, neither plant richness nor density directly influenced the richness of bacterial-feeding nematodes (SI Figs. 3A and 5A). While plant richness directly positively influenced the richness of fungal-feeding |0.36| and root-associated nematodes |0.26|, there was no such effect on richness of omnivorous and plant-parasitic groups. Likewise, while plant density directly positively

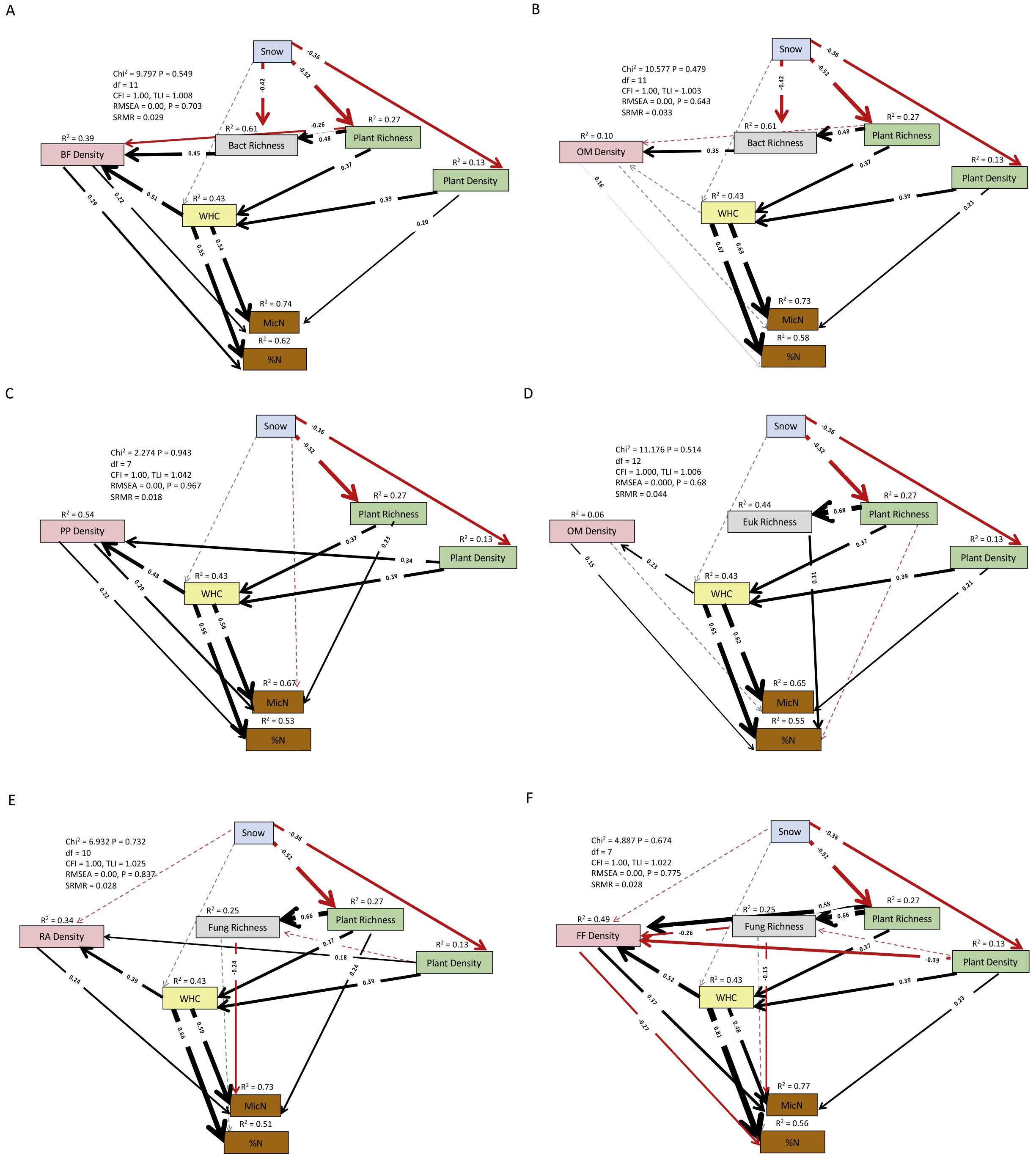

Fig. 3. Structural equation models illustrating how the most effective factors collectively influence densities of nematode trophic groups and their potential role in N dynamics. A. BF bacterial feeders. BD. OM omnivores, C. PP plant parasites E. RA root associates, FF fungal feeders. Bac bacterial, Euk non-fungal microbial eukaryotes (dominated by SAR and followed by microinvertebrate Opisthokonta, algal Archaeplastida, Amoebozoa, and Excavata), Fung fungal, WHC water holding capacity, MicN microbial nitrogen, %N total nitrogen. Black and red arrows indicate significant positive and negative pathways and their path coefficients (positive/negative). Thickness of lines reflect the values of path coefficients. Dashed arrows indicate nonsignificant pathways, however necessary to be retained in the model. R^2 indicates the amount of explained variation associated with specific variables. Final model fit statistic was evaluated by a non-significant (*P* 0.05) chi-square test, a low standardized root mean squared residual (SRMR 0.04), a high comparative fit index (CFI 0.99). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

influenced the richness of omnivorous |0.32| and plant-parasitic nematodes |0.24|, there was no such effect on richness of fungal-feeding and root-associated nematodes. These relationships between plants and densities of nematodes (Fig. 3, SI Fig. 4) were also trophic group specific. Although direct effects of snow cover and plants on nematode trophic groups were limited or trophic group specific, their importance to all nematodes was evident indirectly via negative effects of snow cover on plants and positive effects of plants on water holding capacity and richness of soil microbiota (Fig. 3, SI Figs. 3, 4, 5). In particular, the richness of bacteria had a strong direct effect on richness and density of omnivores |0.44 and 0.45, respectively| and bacterial feeders |0.40 and 0.45|, respectively.

Additionally, we found that densities of most nematode trophic groups (but not their richness) contributed positively to both total and microbial soil C and N pools; for fungal feeders these relationships were negative. In contrast to nematodes, a direct positive impact of plants was observed for C and N in microbial pools only.

4. Discussion

Because plant communities provide the clearest expression of species shifts in response to climate warming in high altitude ecosystems, we examined nematode communities along a plant successional gradient to determine how snow, plants, and other factors associated with climate warming influence nematode colonization and consequently pools of soil C and N. While we did not test direct effects of warming on nematode communities, we show that climate warming, via changes in snow depth, could potentially play an important role in shifts of nematode communities indirectly via effects on plant and microbial communities and the soil environment. Moreover, the shifts in nematode diversity, density, and community composition could possibly contribute to overall changes in soil C and N.

4.1. Nematode communities

The landscape in the subnival zone of Niwot Ridge is dominated by unvegetated soils. Although these soils are unvegetated, it does not imply they are younger (recently deglaciated) than vegetated soils. Instead, each year they have been free of snow for too short time to allow plant colonization but long enough to support development of complex soil communities. In fact, due to their activity, especially photosynthesis by cyanobacteria (Freeman et al., 2009), soil and snow algae (Naff et al., 2013), and aeolian deposition of organic matter such as pollen (Mladenov et al., 2012), these soils now contain noticeable levels of total soil organic carbon (~2 %, King et al., 2008; Porazinska et al., 2018). Despite the presence of relatively complex and active microbial communities, the unvegetated soils supported extremely simple nematode communities composed of a single nematode species. In contrast, the most diverse and most complex nematode communities were recovered from soils under established for a longtime diverse and complex plant communities and even more complex microbial communities (Porazinska et al., 2018). The first nematode colonizers were predominantly omnivores but also bacterivores indicating their unique abilities to colonize soils ahead of plants but also suggesting that soil conditions without plants and more complex and productive microbial communities are largely too inhospitable to support more extensive nematode colonization. As expected, plant parasites and root-associates were directly dependent on plants. More surprisingly, fungal-feeders were also dependent on plants; this could be due to the dependence of the fungi on plants (Porazinska et al., 2018).

Although the patten of increasing nematode diversity from a single species in a single trophic group to numerous species (maximum of 39) in every trophic group, the total numbers of accumulated species varied among groups and ranged from 33 bacterial-feeding species to 16 plant parasites to 5 fungal-feeding species. It is possible that differences reflected relative shifts in diversity of their food resources. For example, relationships between richness of plants and bacteria vs. fungi (Porazinska et al., 2018) were remarkably similar to relationships between richness of plants and bacterial- vs. fungal-feeding nematodes. The strong response from bacterivores could signify a rapidly increasing availability of diverse and easily mineralizable plant-derived organic substrates that facilitated more complex bacterial communities (King et al., 2010; Porazinska et al., 2018) suggesting that plant-microbe interactions may be more important drivers of bacterivorous nematode shifts in this landscape than nematodes from other trophic groups. Moreover, the occurrence of early and late colonizers within each trophic group also points to a likely presence of feeding preferences. For example, bacterial food resources of early colonizers such as *Teratocephalus*, *Plectus*, and *Prismatolaimus* could include the pioneering non-nitrogen fixing Cyanobacteria such as *Microcoleus,* whereas the food of later colonizers such as *Acrobeloides*, *Acrobeles*, and *Wilsonema* could include Spartobacteria and Rhizobiales that were more dominant in soils with more plants (Porazinska et al., 2018). Since richness of fungal-feeding species appeared to be tied more to plants than fungi, potential food resources included fungi symbiotic with plants (e.g., mycorrhizal and dark-septate fungi (Bueno de Mesquita et al., 2018; Porazinska et al., 2018). Interestingly, unvegetated soils did not support a single fungal-feeding nematode species perhaps due to insufficient specific fungal food sources. Unfortunately, beyond laboratory evidence for food selectivity of a handful of nematode species (Liu et al., 2017; Salinas et al., 2007; Venette and Ferris, 1998; Yu et al., 2015), very little is known about nematode food choices in their natural environments, particularly in soils (Quist et al., 2019). Nevertheless, our results were generally in agreement with our first hypothesis that nematode richness, density, and composition would be strongly influenced by the successional gradient of plants, but also that the responses of nematodes would reflect specificities of their trophic and taxonomic identities.

Overall, nematodes identities at the genus/family level in our study were remarkably similar to those observed in other high-latitude and high-elevation environments. In particular, dominant bacterivorous nematodes in unvegetated and/or sparsely vegetated soils in Svalbard and high alpine soils (e.g., debris-covered glaciers, alpine tundra, and summits) in the Alps and Tatra Mountains (Azzoni et al., 2015; Hanel, 2017; Hoschitz and Kaufmann, 2004; Kerfahi et al, 2016, 2017) also included *Plectus, Teratocephalus,* and *Prismatolaimus* confirming their unique ability to thrive under cold and limited resource conditions (Artois et al., 2011; Loof, 1971). Because of their preference for such conditions, with continuing climate warming these microscopic worms may eventually experience climate-driven habitat loss similar to that of aboveground organisms (e.g., cryophilic plants and animals) that are adapted to cold and oligotrophy (Friggens et al., 2018; Pauli et al., 2019).

Terrestrial nematode communities, including those from alpine environments, have been generally dominated by bacterial feeders (Azzoni et al., 2015; Hanel, 2017; Hoschitz and Kaufmann, 2004; van den Hoogen et al., 2019). However, the communities at Niwot Ridge were different from these other sites (e.g., Mont Blanc and Tatra Mountains) probably due to the much higher elevation of our study (3600 m.a.s.l. vs. 3000 m.a.s.l.) likely imposing more extreme temperatures, more restricted availability of water, and more limited food resources including plants. First, nematode communities were dominated by omnivores (i.e., *Paractinolaimus*, *Pungentus,* and *Aporcelaimellus*), particularly where soils were unvegetated or sparsely vegetated. This is noteworthy because communities sustained by sparse resources would be expected to be colonized first by basal opportunists grazing on primary decomposers (bacteria and fungi) rather than by members of higher trophic levels. However, these plant-free soils have been shown to contain relatively diverse algal and cyanobacterial communities (Freeman et al., 2009) that perhaps provide more amenable food sources for omnivores than bacterial-feeders. Alternatively, they are just better adapted to surviving on less specialized diet.

Based on characteristics of life strategies (e.g., body size, generation time, fecundity, and sensitivity to disturbance), nematode families have been ranked on a 1 5 cp colonizer-persister scale (similar to the r-K continuum) (Bongers, 1999; Bongers and Bongers, 1998) where bacterivores and fungivores represent cp 1 3 categories and omnivores/predators cp 4 5 categories. The first colonization and dominance of omnivorous nematode species in our system suggests that members of the cp-4-5 category may have a surprising flexibility to perform as colonizers and persisters (McSorley, 2012) and that ecological inferences based on nematode community ecology at the family level might need to be revisited. In our system, the colonizing ability of *Paractinolaimus*, *Pungentus,* and *Aporcelaimellus* likely reflected their flexibility to feed on algae and perhaps rotifers in unvegetated soils and extend that diet to unicellular eukaryotes, nematodes, and other microinvertebrates in vegetated soils. Again, food preferences of most nematodes are unknown, but as differences in diets could affect nematodes role in soil communities, detailed studies of nematode feeding habits would be welcomed.

Second, bacterivorous species from the suborder of Rhabditina known as the classic cp 1 colonizers (particularly Rhabditidae and Diplogateridae) (Bongers, 1999) were completely missing at Niwot Ridge. Likewise, predatory species from the order Mononchida known as the strict cp 5 persisters were also absent suggesting that both rhabditid and mononchid nematodes representing the extremes of the c-p scale might represent low colonizing abilities in oligotrophic high elevation soils and consequently suggest that their expansion to these environments due to climate warming might be limited. The low colonizing ability of mononchid species was unsurprising and could be explained by their general very low abundance even under most favorable soil conditions. However, the absence of rhabditid nematodes was somewhat unexpected largely because the group comprises a great diversity of bacterial-feeding species that are well-adapted to living under varying environmental conditions including transient or fluctuating in food resources soils (Kiontke and Fitch, 2005, 2010; Susoy et al., 2015). For example, when food is insufficient, the 3rd stage juveniles can enter an arrested non-feeding dauer stage and live off stored intestinal reserves until food availability improves (Kiontke and Fitch, 2005; Sudhaus, 2011). Limited bacterial resource availability was an unlikely explanation as evidenced by populations of other bacterial-feeding nematode species along the entire plant gradient, although rhabditids might require much more enriched conditions (Howard, 2010). Potential explanatory factors could include a limited access to phoretic insects typically involved in transporting members of Rhabditina to new habitats, their inability to cope with cold once there, or their potential absence from the species pool in lower elevation alpine tundra that serves as a seeding source for high alpine soils. Much of the basic biology and ecology of these nematodes still needs to be discovered.

Third, the great majority of the colonizing species were in the cp 2 5 category. Among the most dominant bacterivores, similar genera/families were also found in the alpine meadows of the Tatra Mountains and summits in the Austrian Alps (Hanel, 2017; Hoschitz and Kaufmann, 2004) and included species in 5 main families: Plectidae, Teratocephalidae, Prismatolamidae, Cephalobidae, and Monhysteridae. Their colonizing ability likely reflects an adaptation to cope with freezing in an anhydrobiotic state (McSorley, 2003). Likewise, the most common plant parasite in our soils, *Pratylenchus*, can also survive in anhydrobiosis. As *Pratylenchus* has been previously observed in high elevation soils in association with a wide range of plant hosts (Kergunteuil et al., 2016), it might be particularly well-suited to climate-driven expansion across the high-alpine landscape.

Given the evidence of expanding nematode community abundance and diversity in parallel to plants, we hypothesize that continuous and established alpine tundra located below the subnival zone likely provides the most immediate pool of species for the developing nematode communities in the high alpine. Alpine tundra has been already recognized as the species pool for plants migrating to high alpine (Grabherr et al., 2010; Pauli et al, 2012, 2019). Preliminary data from another study taking place in the alpine tundra have indicated that while structurally the nematode communities from the two habitats were different (e.g., alpine tundra was characterized by typical high abundance and dominance of bacterivores and plant-parasites), compositionally many species were common (Porazinska, 2019), supporting the idea of source populations in the alpine tundra. More work is needed to formally confirm this hypothesis.

4.1.1. *Factors driving nematode community shifts*

We hypothesized that the main factors driving nematode community shifts would include snow cover, plant richness and density, and soil water holding capacity and generally our results supported this hypothesis. Analyses of linear models indicated that neither diversity nor density of nematodes, regardless of their trophic category, was directly affected by changes in snowpack. This is likely because these soils are too oligotrophic to support complex nematode communities (Bueno de Mesquita et al., 2020a) and a mere reduction of snow cover would be insufficient to improve the soil conditions. However, high elevation soils with reduced snowpack and thus reduced thermal buffering capacity may experience more extreme temperature and soil moisture fluctuations (Ge and Gong, 2010) and thus may provide a harsher environment for nematodes to live in. Because nematodes from all trophic groups showed strong positive relationships with plants (both richness and density) and soil water holding capacity, we propose that the effects of snow cover on nematode communities were indirect via plants facilitating an increased capacity of soil to retain water (Bueno de Mesquita et al., 2020; Porazinska et al., 2018). In general, plants and soil water were the two most consistent and predictive variables of the shifting diversity and density of nematodes in all trophic groups and the best predictive models included both types of variables. However, in agreement with our hypothesis, the predictive power of the models varied among trophic groups. For instance, omnivores were least affected by plants and water while plant parasites and fungivores displayed the opposite pattern. In addition to plants and water, soil microbial communities were also important, but just like plants, the effects on the diversity and density of nematodes were trophic group specific. For example, bacterial richness but not biomass was predictive of the richness and density of bacterivorous nematodes, while fungal biomass but not diversity was predictive of the density of fungivorous nematodes.

Although the results of linear models and SEMs were generally congruent, new insights about the roles of factors on nematode community shifts emerged by using both techniques. First, snowpack was confirmed to affect nematodes predominantly indirectly through its effects on plants (both diversity and density) and richness of soil bacteria (but not fungi or microbial eukaryotes). Plant-parasitic nematodes were an exception from this pattern indicating their higher sensitivity to the snowpack most likely because plants constitute their only food source. Second, the direct effect of plants on nematodes was minimal and reserved predominantly to only nematode groups able to directly feed of plants (i.e., plant-parasites and root-associates). Third, although the direct effect of plant richness was minimal, the indirect effect via positive effects on richness of soil microbial communities was significant. Fourth, soil water holding capacity was the most consistent variable directly affecting both diversity and density of all nematodes. It is important to note that both plant richness and plant density were the sole drivers of water holding capacity likely through the presence of ground cover minimizing soil evaporation and presence of roots providing for more structured soils preventing water runoff. The direct significance of water holding capacity in this environment likely reflects natural nematode life biology. Although many nematodes can survive in water deficient environments primarily in an anhydrobiotic state, all are essentially aquatic and require at least a thin film of water to remain active (Decraemer, 2013; Neher, 2010). Because much of the ground at our sites is unvegetated and exposed to high solar radiation, a frequent restricted access to soil water, especially later in the growing season after snow has melted, must be common and hence the indirect effect of plants on nematodes by improving soil water conditions is very important. Finally, despite these general patterns with respect to snow, plants, water, and microbes, the nature of the relationships was nuanced and dependent on specific species indicating that a thorough understanding of colonization and expansion processes will likely require studies at fine levels of taxonomic resolution.

4.2. Consequences of nematode community shifts on C and N dynamics

Although linear models suggested positive roles of both richness and density of all nematode groups in accumulation of soil C and N, SEMs were more conservative indicating that nematode richness was less important. In contrast, nematode densities appeared stronger contributors to C and N storage and together with plants and water holding capacity explained up to 84 % of the total and microbial C and N variability. This was particularly evident for N dynamics where nematode densities across all trophic groups were associated with higher N pools both microbial and total. The dominant role of water holding capacity points to water s significance in this environment in facilitating all biotic interactions and activities. The potential contribution of free-living nematodes (i.e., bacterivores, fungivores, and omnivores) to higher N pools could be due to differential C:N ratios between nematodes and their prey. When nematodes ingest their prey, typically of lower C:N ratio (4 5) than their own (7 8), the excess of ingested N can be excreted to the soil environment as mineralized ammonia or organic waste and hence be readily available for microbial and plant uptake (Gebremikael et al., 2016; Howard, 2010; Trap et al., 2016). In our oligotrophic soils that experience strong C and P co-limitation (Bueno de Mesquita et al., 2020a), much of this available N can be rapidly immobilized back into microbial biomass especially since competition with plants, due to scarce ground cover, is likely low in this landscape (Porazinska et al., 2018). In addition, a moderate grazing on plant roots by plant-parasitic and root-associated nematodes has been shown to enhance root exudation in laboratory experiments (Bardgett et al., 1999). This increased rhizodeposition can stimulate microbial and microfaunal communities and positively feedback to soil N availability (Bardgett and Wardle, 2003), in agreement with our results. Although other factors besides those studied here could play a role in overall soil C and N storage, the supporting evidence for potential nematode contribution to soil nutrient dynamics is very exciting. Nevertheless, because nematode communities at Niwot Ridge are largely at their initial phases of assembly with persisting climate warming, their expansion in abundance and diversity will likely continue, as will their role in moderating soil nutrients. Experimental and temporal work as well as comparisons to nematode communities in lower elevations are in progress to affirm these interpretations.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108380.

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