On the controls of abundance for soil-dwelling organisms on the Tibetan Plateau

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Abstract. After decades of research, we are starting to understand more about why the number of species varies from place to place on the planet. However, little is known about spatial variation in abundance, especially for soil-dwelling organisms. In this study, we aimed to disentangle the relative influences of climatic factors, soil properties, and plant diversity on the abundance of soil-dwelling invertebrates (i.e., nematodes and soil arthropods) at 48 alpine grassland sites on the Tibetan Plateau. We found that the abundance of these two groups of soil organisms was negatively correlated with soil pH and temperature seasonality, and was positively correlated with soil organic carbon (SOC), mean annual precipitation, and plant species richness; there was no effect of mean annual temperature or seasonality in precipitation on the abundance of nematodes or soil-dwelling arthropods. When we considered only the nematodes, we found that soil pH, mean annual precipitation, temperature seasonality, and SOC were the best predictors of abundance. However, plant species richness was the best predictor of the abundance of soil-dwelling arthropods. Different orders within the arthropods responded differently to the suite of factors we examined. Taken together, our results suggest that increases in temperature alone might not alter the abundances of soil organisms in these alpine grasslands. Instead, altered precipitation regimes and increases in intra-annual variation in temperature, changes in plant community diversity, and the resulting changes in soil characteristics (e.g., pH and organic carbon) could reshape soil communities in the Tibetan grassland ecosystems, and likely elsewhere on the planet.

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INTRODUCTION

Changing temperature and precipitation regimes are transforming the Earth's ecosystems, but the focus of most research to date has been on the aboveground components of ecosystems (Van der Putten et al. 2010, Bardgett and van der Putten 2014). However, belowground components, especially soil faunal communities, are important in carbon and nutrient cycling through a variety of both direct and indirect pathways (Petersen and Luxton 1982, Wardle et al. 2004,

Wagg et al. 2014). For example, soil-dwelling organisms can affect decomposition processes directly through fragmentation of litter and indirectly through controlling the diversity and composition of microbial communities (Bardgett and Wardle 2010, Kardol et al. 2011). Thus, a better understanding of the factors that influence soil-dwelling organisms will improve our ability to predict the roles of these taxa in maintaining ecosystem structure and function, especially under changing climatic regimes.

Previous work suggests that the diversity (typically the number of species or operational taxonomic units) and composition of soil faunal communities can be influenced by a wide range of biotic and abiotic factors such as soil properties, climatic factors, and plant diversity and productivity (Wardle et al. 2002, Nielsen et al. 2010, Blankinship et al. 2011, Wu et al. 2011, Bardgett and van der Putten 2014). For example, in one set of studies, the abundance and diversity of nematodes increased with soil pH (Wu et al. 2011) and soil moisture (Sylvain et al. 2014), but the abundance and diversity of arthropods tended to be lower at low pH (Wu et al. 2011). Furthermore, climatic conditions, especially temperature and precipitation, can directly and indirectly affect soil-dwelling organisms. For instance, changes in precipitation and temperature can directly affect soil-dwelling organisms by altering their physiology and activity (Cregger et al. 2014, Classen et al. 2015), and indirectly by affecting soil nutrient availability and leaching rates or altering plant diversity or net primary productivity (Wardle et al. 2002, Wardle 2006, Pen-Mouratov et al. 2008, Sylvain et al. 2014). While it is clear that numerous biotic and abiotic factors can directly and indirectly influence soil-dwelling organisms, the relative importance of these factors singly or in combination has rarely been evaluated at regional scales along extensive environmental gradients (Bardgett and van der Putten 2014, Sylvain et al. 2014).

Of course, neither all soil-dwelling organisms nor the soil itself is homogeneous from place to place. For example, nematodes inhabit soils with higher water availability than do mites (Sylvain et al. 2014). Therefore, changes in soil water availability should have greater effects on nematodes than on those soil-dwelling organisms that generally live in an air-filled soil habitat (e.g.,

mites, arthropods) (Wu et al. 2011, Sylvain et al. 2014). Furthermore, climate changes can influence soil community abundance and composition by directly and indirectly altering soil water and resource availability (Kardol et al. 2011). In fact, numerous modeling studies suggest that soil water availability (interactive with temperature) influences the dynamics of nematode populations (Moorhead et al. 1987, Weicht and Moorhead 2004). In contrast, the abundance and diversity of soil arthropods are mostly correlated with the quantity and quality of soil resources (e.g., root biomass, soil carbon content, and carbon-to-nitrogen ratios; Wu et al. 2011) and are sometimes correlated with plant diversity and productivity (Borer et al. 2012). Therefore, nematodes and soil arthropods may respond differentially to changes in soil water and soil nutrient availability, climate, and plant diversity. However, we still have little understanding of whether nematodes and soil arthropods respond differentially to environmental changes in high-alpine environments (Meyer and Thaler 1995), where climates are changing rapidly.

The Tibetan Plateau, therefore, is an ideal field laboratory to study the effects of soil, climate, and plant diversity on soil-dwelling organisms for several reasons. First, previous studies in the system have demonstrated that both climate and soil properties (e.g., soil pH and water availability) influence a number of ecological processes and patterns for both above- and belowground components (Ma et al. 2010, Zhuang et al. 2010, Chen et al. 2013, Jing et al. 2015). Second, the Tibetan Plateau stores a large amount of soil organic carbon (SOC; Yang et al. 2007, 2008, Shi et al. 2012) and is expected to be particularly vulnerable to climate change (Sala et al. 2000, Thompson et al. 2000, Giorgi et al. 2001, Dunne et al. 2003). Finally, despite its role as a carbon sink and its susceptibility to climate change, very little research on the biogeographic distribution of soil organisms in response to environmental changes has been done on the Tibetan Plateau (but see Gai et al. 2009, Jing et al. 2015, Wang et al. 2015, Shi et al. 2016).

In this study, we investigated a suite of biotic and abiotic factors that account for spatial variation in the abundance of nematodes and soil-dwelling arthropods in the alpine grasslands on the Tibetan Plateau. In particular, we examined

the relative importance of soil properties (pH and SOC), climatic factors (mean annual precipitation and temperature, seasonality of both precipitation and temperature), and plant species richness on the abundance of soil nematodes and arthropods. We tested two predictions: (1) Precipitation would be the dominant driver of the abundance of soil nematodes, while (2) SOC and plant species richness would be the dominant drivers of the abundance of soil arthropods.

Methods

Study sites

We originally sampled plant and soil faunal communities at 60 sites during the growing season of 2011 (Jing et al. 2015). We excluded samples from twelve sites because of either >5 days of sample delivery to the laboratory (three sites) or failure of soil faunal extraction in the laboratory (nine sites). Thus, we reported only samples from 48 sites across the Tibetan Plateau (91.7–101.0° E, 31.8–37.5° N) that included three vegetation types: alpine steppe (dominated by cold-xerophytic, short, dense tussock grasses such as *Stipa purpurea* and *Festuca ovina*), alpine meadow (dominated by perennial tussock grasses such as *Kobresia pygmaea* and *Kobresia tibetica*, usually mixed with alpine forbs, including *Polygonum viviparum* and the species of *Gentiana* and *Pedicularis*), and desert steppe (dominated by *Chenopodiaceae* such as *Ceratoides latens*, *Salsola abrotanoides*, and *Halogeton arachnoideus*). The 48

sites were arranged such that there was ~100 km between adjacent sites (Appendix S1: Fig. S1). Along the transect, mean annual temperature ranged from −6.6° to 4.0°C, mean annual precipitation from 112 to 537 mm (Appendix S1: Fig. S2), and elevation from 2918 to 5228 m. pH in the topsoil (0–5 cm) ranged from 6.71 to 9.01, and SOC ranged from 0.6% to 21.0%. Average plant species richness at the sites ranged from 3 to 28 (see Table 1 for more summary information on characteristics of the sites, climate, soils, and plant diversity).

Soil sampling and plant community survey

At each of the 48 sites, we selected five plots along a 100-m transect and took five soil cores (diameter 3.5 cm and depth 15 cm) in each of the plots. One limitation of the soil core approach was that it can underestimate the diversity of arthropods for the obvious reason that we might miss many larger species that are active elsewhere in the plots or are too big to be captured by a soil corer. However, the method provided a robust large-scale comparative analysis of soil faunal diversity and their relationships with environmental factors. For soil physicochemical analyses, we collected 5–7 soil cores (0–5 cm depth) from three of the five plots. All samples were delivered to the laboratory and kept in coolers with ice packs for no more than five days for logistical reasons. For the plant community surveys, we identified all vascular plant species in three 1-m^2 plots in the field. We then quantified plant species

Table 1. Summary of the sites, soil, climate, and plant diversity characteristics with their ranges across the sampling sites ($n = 48$).

Variables	Unit	Mean (1 SEM)	Range
Site			
Latitude	°N	34.83 (0.03)	31.83–37.48
Longitude	°E	96.85 (0.06)	91.67–101.02
Elevation	m	4042 (12)	2918–5228
Soil			
pH	Unitless	7.83 (0.01)	6.71–9.01
Organic carbon	%	4.94 (0.10)	0.63–21.03
Climate			
Mean annual precipitation	mm/yr	355 (2)	112–537
Precipitation seasonality	Unitless	99 (0.19)	82–119
Mean annual temperature	°C	−1.8 (0.05)	−6.6 to 4.0
Temperature seasonality	Unitless	8177 (12)	6833–9693
Plant diversity			
Species richness	Numbers of species/m^2	12 (0.1)	3–28

richness by counting the number of species that occurred at each site in the laboratory.

Sampling processing and measurements

We assessed the abundance of soil organisms by collecting five soil cores from each of the five plots. Soil nematodes were extracted by a modified Baermann's funnel technique (Viglierchio and Schmitt 1983), and soil arthropods were extracted using the Berlese-Tullgren funnel method (dry funnel method; Jeffery et al. 2010). All organisms from each sample were identified to order, counted, and preserved in 75% ethyl alcohol. Note that we focused on only the major groups of soil micro- and meso-fauna that could be consistently extracted—the nematodes and the arthropods. Within the nematodes and arthropods, we further classified the organisms into orders: Aphelenchida, Dorylaimida, Enoplida, Rhabditida, Tylenchida, Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera, and Isopoda. Then, for each site, we tallied the total abundance of nematodes and arthropods, and the abundance of nematodes and arthropods in each order. Abundance is expressed as the number of individuals/m^2 of soil (e.g., Darby et al. 2011, Eisenhauer et al. 2012, Youngsteadt et al. 2016). From these abundances, we also estimated biomass (biomass C/m^2 of soil; Fierer et al. 2009). To convert number of individuals into biomass, we used estimates that based on average dry weights per individual (Edwards 1967, Petersen and Luxton 1982, Hanagarth and Brandle 2001) and carbon content of each organism (see Fierer et al. 2009 for more detailed information). Abundance and biomass were strongly correlated ($r = 0.82$–1.00; Appendix S1: Fig. S3), so we report only abundance.

Soil samples for chemical analyses were taken from three out of the five plots within the 48 sites. Soil organic carbon and soil inorganic carbon ($CaCO_3$) analyses were air-dried, sieved with a 2-mm mesh, and the fine roots were removed by hand and then ground in a ball mill. The total carbon content was determined with a CHN elemental analyzer (2400 II CHN elemental analyzer; Perkin-Elmer, Boston, Massachusetts, USA). Soil inorganic carbon was analyzed volumetrically using a calcimeter (Eijkelkamp, Giesbeek, The Netherlands). Soil organic carbon was calculated as the difference between total soil carbon and carbon bound in soil $CaCO_3$. Soil samples for the pH assay were packed in polyethylene bags and transported to the laboratory. Soil pH was determined separately for each plot from each site using a fresh soil-to-water ratio of 1:5 with a Thermo Orion-868 pH meter (Thermo Fisher Scientific, Inc., Pittsburgh, Pennsylvania, USA). We only used site average values of SOC and soil pH for statistical analysis.

Climate data

We obtained site-scale climatic data from WorldClim (Hijmans et al. 2005) at 1 km^2 spatial resolution. We compiled mean annual precipitation, precipitation seasonality (coefficient of variation of precipitation), mean annual temperature, and temperature seasonality (the amount of temperature variation over the course of one year; standard deviation × 100) to represent measures of precipitation and temperature in the Tibetan grasslands. We note that the WorldClim (mean annual precipitation and mean annual temperature) data were strongly correlated with long-term weather station data near our sites ($R^2 > 0.76$ in both cases). The long-term weather station data were from the climate database of 59-year average temperature and precipitation records (1951–2010) at 716 weather stations across China (http://data.cma.cn/en). Thus, for comparison to other studies, we used WorldClim data rather than long-term weather data from the region.

Data analyses

All statistical tests were conducted using packages for R (2016, version 3.3.2, R Foundation for Statistical Computing, http://www.r-project.org). The R code together with the data file can be found at https://github.com/XJingPKU/TibetFauna.

We conducted correlation analyses to evaluate the relationships between soil factors (pH and SOC), climatic variables (mean annual precipitation, precipitation seasonality, mean annual temperature, and temperature seasonality), plant species richness, and total abundances and biomass of the soil nematodes and arthropods (Appendix S1: Fig. S3). Biomass was highly correlated with abundance (nematodes: $r = 1.0$, arthropods: $r = 0.93$; Appendix S1: Fig. S3), so we report only abundance here. We also examined abundance and biomass within each order of nematodes and arthropods; these values are reported in Appendix S1: Table S1. In addition, precipitation seasonality and mean

annual temperature were not correlated with the total abundances of soil nematodes or arthropods, so we excluded them from further statistical analyses. Then, we did regression analysis to investigate the bivariate correlations among site-scale soil (soil pH and SOC), climate (mean annual precipitation and temperature seasonality), and plant species richness for the total and separate abundance of soil nematodes and arthropods (Figs. 1, 2). A modified *t* test can be used in the regression analysis to effectively correct for the sample correlation coefficient and the rate of type I error between two spatially correlated variables (Legendre et al. 2002). Thus, we performed the modified *t* test of spatial association (Clifford et al. 1989, Dutilleul et al. 1993) to relate biological response variables (the abundances of soil nematodes and arthropods) to explanatory variables (abiotic and biotic factors; Fig. 1, Table 2). The modified *t* test was implemented in "*SpatialPack*" package (Osorio and Vallejos 2014).

To assess which explanatory variables (abiotic and biotic factors) were the most important drivers of the abundances of soil nematodes and

arthropods (Fig. 3, Table 3), we conducted random forest analysis for regression (Breiman 2001) by using "*randomForest*" package (Liaw and Wiener 2002). Random forest is a nonparametric machine-learning algorithm (Breiman 2001) that does not assume any data distribution and does not require any predictor selection (Cutler and Stevens 2006, Cutler et al. 2007). The error rates of the random forest for the total abundances of nematodes and arthropods were decreasing when more trees were grown, and the error rates finally reached a stable level (~500 trees; Appendix S1: Fig. S4). Thus, we fitted a forest of 500 multiple decision trees. The significance of the random forest model was tested with 9999 permutations of the abundances of nematodes and arthropods in the "*rfUtilities*" package (Evans and Murphy 2016). The significance of the relative importance for each the explanatory variable on each response variable was determined by assessing the decrease in prediction accuracy (Percentage of increase in mean square error), and a total of 9999 permutations of the abundances of nematodes
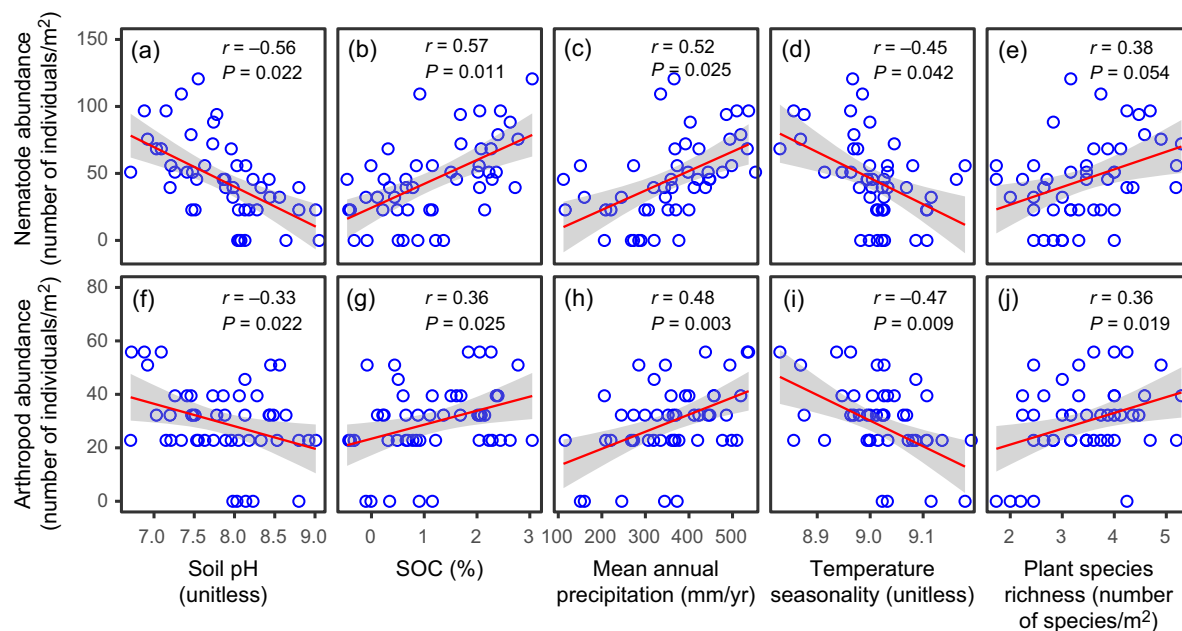

Fig. 1. Bivariate correlations among site-scale biotic and abiotic factors (soil pH, soil organic carbon (SOC), mean annual precipitation, temperature seasonality, and plant species richness) and the total abundance of soil nematodes (a, b, c, d, e) and arthropods (f, g, h, i, j). We used the modified *t* test of spatial association (*r*, sample correlation coefficient; *P*, the *P*-value for the test) to assess the bivariate correlations. The red lines are fitted from a linear regression. Shaded areas show the 95% confidence interval around the fit.
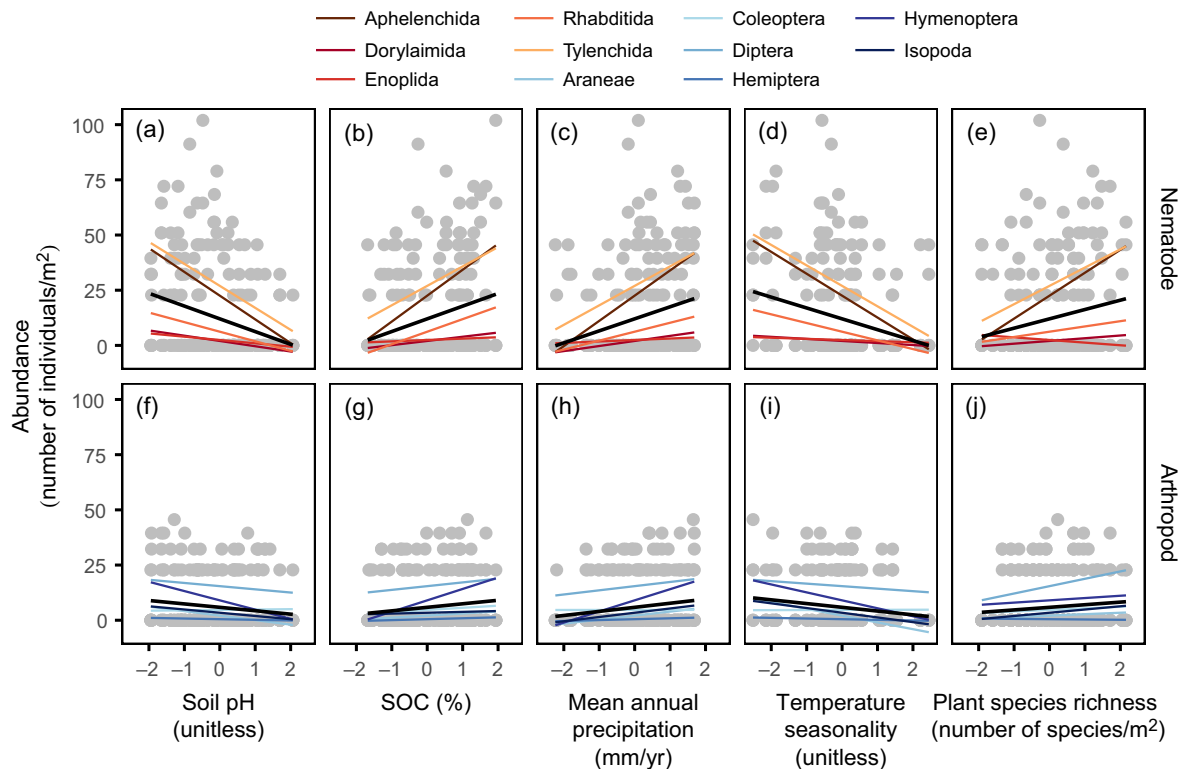
Fig. 2. Bivariate correlations among site-scale biotic and abiotic factors (soil pH, soil organic carbon (SOC), mean annual precipitation, temperature seasonality, and plant species richness) and the separate abundance of two soil faunal taxonomic groups, nematodes (a, b, c, d, e) and arthropods (f, g, h, i, j). Abundances are sqrt-transformed. We scaled and centered (*z*-score transformation) each abiotic and biotic variable for visualization. Lines are fitted from a linear regression. Black lines are the overall fitting of the bivariate correlations. The other lines are the separate fitting of the bivariate correlations for each taxonomic group of nematodes and arthropods.

and arthropods were implemented by using the "*rfPermute*" package (Archer 2013).

For all analyses, nematodes and arthropods were analyzed with site means because this allowed us to assess the potential correlations and relative importance of variables in explaining variation in soil faunal abundance across sites. Values of soil pH and mean annual precipitation are untransformed, SOC and temperature seasonality are ln-transformed, and plant species richness and abundances of nematodes and arthropods are sqrt-transformed.

RESULTS

Soil faunal abundance in the Tibetan grasslands

The abundance of soil organisms (nematodes and arthropods) ranged from 11 to 1386 individuals/m² of soil per site (Appendix S1: Table S1).

Specifically, Hemiptera had the lowest abundance (11 individuals/m² of soil) and Tylenchida had the highest abundance (1386 individuals/m² of soil). In total, the nematodes were much more abundant than the soil-dwelling arthropods (2945 and 1072 individuals/m² of soil, respectively).

Bivariate correlations among abiotic and biotic factors with soil faunal abundance

Nematodes and soil-dwelling arthropods responded in similar ways to variation in soil, climate, and plant species richness (Fig. 1). In particular, we found that the abundances of both soil nematodes and soil-dwelling arthropods increased as soil pH and temperature seasonality decreased (Fig. 1a, d, g, i) and increased with increases in SOC, mean annual precipitation, and plant species richness (Fig. 1b, c, e, f, h, j). However, the strengths of the bivariate correlations differed

Table 2. Summary of the modified *t* test to assess the bivariate correlations among abiotic and biotic factors and the separate abundance of nematodes and arthropods.

Raw and fine taxonomic levels	Modified *t* test	Soil pH	Soil organic carbon	Mean annual precipitation	Temperature seasonality	Plant species richness
Nematode						
Aphelenchida	*r*	**−0.41**	**0.45**	**0.44**	**−0.38**	**0.40**
	F_{stat}	**4.59**	**7.59**	**7.06**	**5.25**	**6.34**
	P	**0.043**	**0.010**	**0.012**	**0.029**	**0.017**
Dorylaimida	*r*	−0.28	0.22	**0.27**	−0.11	0.14
	F_{stat}	**4.21**	2.92	**4.77**	0.84	1.06
	P	**0.05**	0.093	**0.033**	0.364	0.309
Enoplida	*r*	−0.18	0.07	0.08	−0.06	−0.14
	F_{stat}	1.06	0.19	0.22	0.14	0.85
	P	0.312	0.669	0.639	0.706	0.362
Rhabditida	*r*	**−0.31**	**0.41**	0.29	−0.28	0.17
	F_{stat}	**6.42**	**7.82**	3.14	2.35	1.38
	P	**0.014**	**0.008**	0.085	0.137	0.246
Tylenchida	*r*	−0.38	0.34	0.34	−0.36	0.32
	F_{stat}	3.29	2.73	2.83	3.85	3.32
	P	0.086	0.113	0.107	0.060	0.079
Arthropod						
Araneae	*r*	−0.24	0.11	0.21	**−0.36**	0.08
	F_{stat}	3.53	0.60	2.10	**5.75**	0.28
	P	0.065	0.443	0.154	**0.021**	0.596
Coleoptera	*r*	0.02	0.10	0.00	0.00	0.07
	F_{stat}	0.03	0.61	0.00	0.00	0.26
	P	0.870	0.436	0.995	0.976	0.614
Diptera	*r*	−.10	0.12	0.13	−0.08	0.23
	F_{stat}	0.52	0.64	0.73	0.25	2.38
	P	0.475	0.429	0.397	0.620	0.130
Hemiptera	*r*	−0.09	0.13	0.12	−0.09	−0.04
	F_{stat}	0.36	0.76	0.68	0.37	0.08
	P	0.550	0.389	0.413	0.548	0.783
Hymenoptera	*r*	**−0.33**	**0.41**	**0.40**	−0.28	0.08
	F_{stat}	**4.36**	**6.25**	**5.17**	2.18	0.27
	P	**0.044**	**0.018**	**0.031**	0.153	0.603
Isopoda	*r*	−0.16	0.04	0.21	−0.23	0.16
	F_{stat}	1.00	0.08	1.81	2.07	1.03
	P	0.324	0.783	0.186	0.158	0.317

Notes: r, sample correlation coefficient; F_{stat}, the value of the *F*-statistic; *P*, the *P* value for the test. Values in bold are significant at $P < 0.05$.

between nematodes and soil-dwelling arthropods (Fig. 1). For example, we found that soil pH was strongly correlated with nematode abundance ($r = -0.56$, $P = 0.022$), but the abundance of soil-dwelling arthropods was not as tightly correlated with soil pH ($r = -0.33$, $P = 0.022$). Similarly, SOC was more strongly correlated with nematode abundance ($r = 0.57$, $P = 0.011$) than with the abundance of soil-dwelling arthropods ($r = 0.36$, $P = 0.025$).

In addition, we found that the strength of the bivariate correlations differed within orders of soil nematodes and soil-dwelling arthropods

(Fig. 2, Table 2). Within the nematodes, different orders responded differently to the biotic and abiotic correlates (Fig. 2, Table 2). In contrast, most of the taxa within orders of arthropods were not significantly correlated with any of the biotic and abiotic variables (Table 2), except for Araneae and Hymenoptera (Table 2).

Relative importance of abiotic and biotic factors on soil faunal abundance

Soil pH, mean annual precipitation, temperature seasonality, and SOC were the best predictors of variation in the abundance of nematodes.
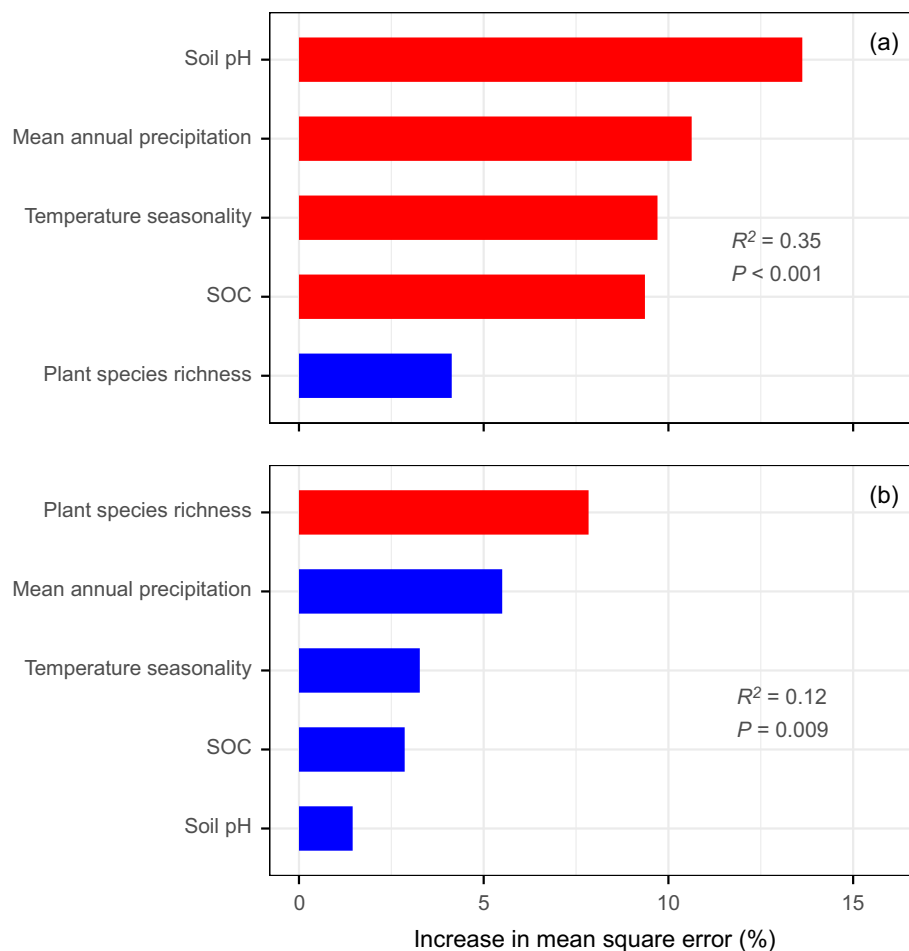
Fig. 3. Relative importance (Percentage of increase in mean square error) of abiotic and biotic factors on the total abundance of soil nematodes (a) and arthropods (b). The relative importance measures are estimated (by random forest statistic) for each tree and averaged over a forest (500 trees). Significance of the random forest models and each variable is assessed by permuting the response variable for 9999 times. Red bars represent significance levels at $P < 0.05$, and blue bars represent significance levels at $P \geq 0.05$. SOC, soil organic carbon.

In contrast, plant species richness was the best predictor of the abundance of soil-dwelling arthropods (Fig. 3). For orders within the nematodes and soil-dwelling arthropods, the best predictors of abundance varied considerably (Table 3). We found that if we did not consider soil pH, the error rates of predicting the abundance of Tylenchida were significantly increased; the same was true for the effects of SOC on Aphelenchida and Hymenoptera, mean annual precipitation on Diptera, temperature seasonality on Tylenchida, and plant species richness on Diptera and Hemiptera, but not for all the groups of soil fauna (Table 3).

DISCUSSION

A growing body of research has begun to explore biogeographic patterns of soil diversity and its underlying causes (Bardgett and van der Putten 2014, Hendershot et al. 2017). Across an extensive environmental gradient in grasslands of the Tibetan Plateau, we found that neither precipitation seasonality nor mean annual temperature was ever an important predictor of the abundance of nematodes or soil-dwelling arthropods. Our findings did not support our original hypothesis that soil nematodes and soil-dwelling arthropods would differentially respond to

Table 3. Relative importance of the abiotic and biotic factors on the separate abundance of nematodes and arthropods

Raw and fine taxonomic levels	Variable importance	Soil pH	Soil organic carbon	Mean annual precipitation	Temperature seasonality	Plant species richness
Nematodes						
Aphelenchida	%IncMSE	7.47	**8.52**	6.44	5.54	3.74
	P	0.050	**0.028**	0.093	0.128	0.204
Dorylaimida	%IncMSE	−1.73	−0.59	−1.87	2.64	−3.12
	P	0.940	0.882	0.981	0.551	0.966
Enoplida	%IncMSE	3.09	0.44	5.42	−0.05	5.13
	P	0.586	0.862	0.402	0.877	0.196
Rhabditida	%IncMSE	3.78	5.86	5.02	3.96	3.39
	P	0.400	0.201	0.339	0.357	0.313
Tylenchida	%IncMSE	**12.09**	1.28	4.92	**9.26**	7.12
	P	**0.002**	0.535	0.199	**0.016**	0.053
Arthropods						
Araneae	%IncMSE	−4.03	−1.29	−1.07	2.82	−0.89
	P	0.995	0.933	0.974	0.579	0.842
Coleoptera	%IncMSE	3.29	5.42	6.86	2.21	0.20
	P	0.406	0.221	0.133	0.519	0.616
Diptera	%IncMSE	2.53	2.80	**8.83**	−0.36	**9.41**
	P	0.300	0.272	**0.023**	0.595	**0.014**
Hemiptera	%IncMSE	6.24	4.69	5.68	4.83	**8.75**
	P	0.148	0.297	0.245	0.269	**0.011**
Hymenoptera	%IncMSE	6.38	**8.45**	3.70	0.59	−3.07
	P	0.074	**0.027**	0.255	0.516	0.844
Isopoda	%IncMSE	0.15	−2.26	8.91	0.11	−3.45
	P	0.843	0.971	0.043	0.834	0.968

Notes: %IncMSE, Percentage of increase in mean square error. P = P values estimated by 9999 times of permutations. Values in bold are significant at $P < 0.05$.

environmental changes in the alpine grasslands. However, we found that soil pH, mean annual precipitation, temperature seasonality, and SOC were the most important predictors of the abundance of nematodes. In contrast, we observed that only plant species richness predicted the abundance of soil-dwelling arthropods. Together, these results highlight the importance of contemporary climate, soil characteristics, and plant diversity on the abundances of soil-dwelling organisms. Moreover, they indicate that altered precipitation regimes, soil acidification, and nitrogen deposition have the potential to rapidly alter belowground communities on the Tibetan Plateau.

In recent years, soils in natural grasslands and croplands have experienced significant acidification (mostly due to nitrogen deposition and fertilization) in China. For example, Yang et al. (2012) observed an overall decrease in soil pH of 0.63 from the 1980s to 2000s in both alpine grasslands on the Tibetan Plateau and temperate grasslands on the Inner Mongolian Plateau. Guo et al. (2010) also reported that soil pH declined significantly during the same period in the major Chinese crop-production areas. Here, we observed that soil pH was strongly and negatively correlated with the abundance of both nematodes and soil-dwelling arthropods across the Tibetan Plateau (Fig. 1). The negative correlations may be caused by the relatively high soil pH among our sites (the lowest soil pH was >6.70; Table 1). For example, Fierer and Jackson (2006) observed a negative correlation between soil pH and soil microbial richness and diversity when the value of pH is >7 (suboptimal pH for most soil organisms). This likely arises because soil pH may directly impose stress or indirectly interact with the other biotic and abiotic variables on soil organisms (Fierer and Jackson 2006). In addition, our findings were partially consistent with those from Wu et al. (2011), where they found that nematodes are more common in soils with high pH, while soil-dwelling arthropods are more abundant in soils with low pH. Similarly, Mulder et al. (2005) also observed a negative correlation between soil pH and the abundance of arthropods along a pH gradient.

Given that arthropods account for more than 80% of all known living animal species (Ødegaard 2000), it will be an interesting and fruitful avenue for future research to examine whether and why soil-dwelling arthropods are affected by changes in soil pH.

In the Tibetan grasslands, the most abundant soil organisms were nematodes (including Tylenchida, Aphelenchida, Rhabditida, Enoplida, and Dorylaimida) and soil-dwelling arthropods. Changes in these groups may influence the composition of the rest of the soil-dwelling community. Perhaps not surprisingly, different groups within the arthropods responded differently to the suite of biotic and abiotic factors we examined (Fig. 2). For example, the abundances, within orders, of soil-dwelling arthropods were not significantly correlated with any of the biotic and abiotic variables (except for Araneae and Hymenoptera). Furthermore, we found that the two arthropod classes were the two lowest abundance arthropod groups (Appendix S1: Table S1). In fact, the rare species (low abundance) can be functioning as a seed bank and may become active in response to changes in the environment (Epstein 2009, Shade et al. 2012).

Numerous studies have shown that changes in precipitation can alter soil faunal communities and associated ecosystem processes (Powers et al. 2009, Kardol et al. 2010, 2011, Blankinship et al. 2011, Sylvain et al. 2014). Similarly, we found that precipitation matters: Mean annual precipitation, but not precipitation seasonality, had a strong and consistent influence on the abundances of nematodes and soil-dwelling arthropods (Fig. 1). This suggests that soil organisms might show a strong response to climate change, especially changes in precipitation (Nielsen et al. 2010, Kardol et al. 2011). Why do soil organisms track precipitation on the Tibetan Plateau? First, precipitation obviously influences soil water availability (Sylvain et al. 2014), which directly changes the soil habitat for the soil organisms. This is especially important for aquatic-living organisms such as nematodes. For instance, we found that mean annual precipitation was the second most important variable to influence the abundance of soil nematodes (Fig. 3). Furthermore, although precipitation was not the most important influence on soil-dwelling arthropods, we found that the effects of precipitation on the soil fauna were positive among different orders within the nematodes and arthropods; there were no exceptions within any of the groups of nematodes or arthropods (Fig. 2, Table 2). Finally, Sylvain et al. (2014) found that the abundances of nearly all taxa (nematodes and arthropods) in their study increased with increasing soil moisture, but only when soil moisture was below a threshold between 10% and 15%. This further supports our observations that mean annual precipitation, but not precipitation seasonality, had a strong and consistent influence on the abundance of soil organisms in the Tibetan grasslands. Note that in our study region, the alpine grassland soils are frequently exposed to freeze-thaw cycles, and thus, soil water might often freeze. Such cycles may influence the activity and distribution of numerous soil organisms.

As an essential part of the hydrothermal conditions, temperature should have influenced soil faunal abundances in the Tibetan grasslands. However, we found that mean annual temperature was surprisingly weak as a predictor (Appendix S1: Fig. S3). This result may arise partly because the diurnal variation in temperature is usually dramatic, approximating the seasonal variation on the Tibetan Plateau, and perhaps the soil organisms are pre-adapting to such relatively wide variation in seasonal temperature. In contrast to the apparent lack of an effect of mean annual temperature, we found that temperature seasonality was negatively correlated with soil faunal abundances (Fig. 1); that is, where temperature is more consistent within the year, abundance is higher. Apparently temperature seasonality is another measure for soil faunal abundances in the Tibetan grasslands, which suggests that climate extremes may impact the structure and functioning of belowground communities in natural ecosystem (Easterling et al. 2000, Sylvain et al. 2014). Our findings are consistent with Bhusal et al. (2015), in which they found that temperature variation accounts for most of the variation in nematode metabolic footprints. The exact mechanistic explanation linking patterns of belowground communities and the relative importance of climate means and variability is still unclear (Easterling et al. 2000). These uncertainties emphasize the need to consider building climatic variability into next generations of climate change experiments and models (Thompson et al. 2013).

In this study, we found that changes in SOC were positively correlated with soil faunal abundance (Fig. 1). Soil organic carbon is a direct measure of resource quantity, such that low SOC might select for efficient use of food resources by the soil organisms, leading to low abundance. As a predictor that directly influenced soil faunal abundance, SOC was also a factor that partially mediated the effects of precipitation, soil pH, and plant diversity on soil faunal abundance. Specifically, changes in precipitation (negatively correlated with temperature seasonality; see Appendix S1: Fig. S3) can indirectly influence the soil faunal abundance by altering soil properties, especially SOC and nutrient availability (Kardol et al. 2010, Wu et al. 2011) and soil moisture (Sylvain et al. 2014). This may be because precipitation influences plant diversity and productivity (Bakkenes et al. 2002, Kardol et al. 2010, Ma et al. 2010), litter quality, and decomposition rates (Aerts 1997). Interestingly, we found that plant diversity was one of the strongest influences on the abundance of soil-dwelling arthropods (Fig. 3). Although plant diversity may not directly control arthropod abundance, changes in plant productivity (Borer et al. 2012) and habitat heterogeneity (Tews et al. 2004) can be a more parsimonious explanation for why plant diversity predicts the abundance of soil-dwelling arthropods. Collectively these changes in climatic factors and aboveground plant communities directly and indirectly lead to changes in the soil carbon-to-nitrogen ratio, a factor known to influence soil communities (Wardle 2006, Blankinship et al. 2011). However, soil pH may cause differences in the carbon-to-nitrogen ratio of soils through changes in the microbial community (Fierer and Jackson 2006, Feng et al. 2014), both of which eventually alter soil faunal communities.

Limitations

To our knowledge, our study is the first to address the effects of soil, plant, and climate on the biogeography of soil-dwelling organisms in the Tibetan grasslands. However, our study has limitations that should be addressed by future research. For example, we used morphological traits to identify taxa to the ordinal level. Although we used abundance measurement of soil organisms, diversity estimates are widely used (Garcia-Palacios et al. 2015, Youngsteadt

et al. 2016) and multiple-site comparisons (Sylvain et al. 2014). We could estimate diversity in our study, though the taxonomic resolution in our study would not be directly related to diversity measured at the species level in other studies. Thus, it would be interesting to examine soil faunal diversity at the species level by using molecular approach (e.g., Wu et al. 2011). Such a study might detect any relationships between several taxa or categories of soil organisms and environmental and biotic factors (e.g., temperature, precipitation, soil pH, plant diversity). It would also allow the determination of the relative importance of the biotic and abiotic factors to soil faunal community at finer levels of taxonomic resolution.

Conclusions

Our results have important implications for predicting the effects of climate change on soil organisms, and perhaps ecosystem functions, on the Tibetan Plateau. We found that the abundance of soil-dwelling organisms was associated with soil properties and with plant and climatic factors. However, most of the variation in abundance was explained by mean annual precipitation, soil characteristics, and plant diversity, rather than the direct effects of mean annual temperature. In the foreseeable future, the sensitive ecosystems of the Tibetan Plateau are projected to experience dramatic changes in climate, which are likely to alter precipitation and soil pH, perhaps resulting in extensive changes in soil communities and their associated functioning of carbon and nutrient cycling. Understanding the patterns and drivers of soil communities under the extreme environments of the Tibetan Plateau will undoubtedly improve our ability to predict ecosystem responses to climate change, both on the Tibetan Plateau and elsewhere.

Acknowledgments

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