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Effects of Experimental Warming and Canada Goldenrod Invasion on the Diversity and Function of the Soil Nematode Community

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Abstract: Both global warming and alien plant invasion can affect the biotic communities in the soil. Most studies are focused on the soil microbial community, but little is known about how global warming, along with alien plant invasion, affects the diversity and function of the soil nematode community. In this study, the individual and interactive effects of experimental warming and Canada goldenrod (*Solidago canadensis* L.) invasion on soil nematode communities were measured. Experimental air warming, in combination with different levels of *S. canadensis* invasion, were applied. The results showed that *S. canadensis* invasion significantly increased chao1, maturity, and structure indexes of the nematode community by 31.44%, 25.57%, and 329.3%, respectively, and decreased the basal index by 48.70% (all $p < 0.05$). Only the Simpson index was affected by the interaction between warming and *S. canadensis* invasion. Warming enhanced the *S. canadensis* invasion effect on the soil nematode community. The changes in nematode community were correlated with shifts in nutrient availability and resource stoichiometry, as well as microbes in the soil. These findings demonstrated that global warming and *S. canadensis* invasion may, directly and indirectly, alter the soil nematode community, which may considerably affect the functioning of underground food webs.

Keywords: global warming; alien plant invasion; soil nematode; soil nutrient availability and stoichiometry; *Solidago canadensis* L.

1. Introduction

It is well known that many soil ecosystem functions are mediated by biodiversity in natural ecosystem [1]. Interactions between plants and soil animals are drivers of soil ecological processes and the backbone of soil biodiversity [2]. The plant–animal interactions can be complex, since the changes in vegetation community can cause shifts in simultaneous interactions with soil animals and a mutualistic–antagonistic gradient [3]. Hence, understanding the complexities of the plant–animal interactions and the ecosystem consequences of disrupting their diversity in the advent of climate change have become important research topics.

Soil nematodes are one of the important parts of soil biodiversity and are the animals with the richest biodiversity and the most diverse functions in the soil [4]. Soil nematodes can participate in soil ecological processes and have a significant effect on soil organic matter decomposition, nutrient transformation, and energy transfer [5–8]. Numerous studies have demonstrated that global warming can directly or indirectly affect the soil nematode community [5]. For example, it was reported that global warming altered the soil nematode community structure and reduced the nematode community abundance and composition in the agricultural and grass ecosystems [9,10]. However, in the desert ecosystem, the warming effect was not observed [11]. In addition, other studies have shown that the response of soil nematodes to warming is not related to the warming amplitude, but is negatively correlated with the duration of warming, mainly because warming reduces the available water content in the soil and restricts the growth and reproduction of organisms [12,13]. These findings suggested that the response of the soil nematode community to warming may be influenced by the ecosystem type and local climatic conditions. Thus, understanding the mechanistic framework by which the global warming impact soil nematode community is crucial for predicting and maintaining natural ecosystem functionality and biodiversity in the warming world.

One of the profound consequences of alien plant invasion is a negative effect on the biotic community in the soil. Similar to the alien plant invasive effect on soil microbial communities, alien plant invasion can affect the richness, diversity, and characteristic trophic groups of soil nematode community via varied mechanism [14,15]. Zhang et al. (2019) found that *Spartina alterniflora* invasion can homogenize nematode communities in wetland soil, because *Spartina alterniflora* invasion induced the extraordinary homogenization of soil microbial communities [16]. Lazzaro found that *Robinia pseudoacacia* invasion altered nematode communities by changing the soil microenvironment via substrate input into the soil. (i.e., soil moisture, pH, nutrient) [17]. However, most of the studies described the alterations in the nematode community induced by alien plant invasion from the perspective of the soil microbial community, or the perspective of the soil microenvironment, but did not explain the effect of the soil microenvironmental and microbial indicators on the changes in the nematode community [18,19]. Furthermore, compared to the soil microbial community, the soil nematode response to alien plant invasion is poorly understood. The limited knowledge of soil nematode responses to alien plant invasion may pose challenges to the accurate prediction of the underlying negative effect on the processes and functions of soil ecosystem, such as the carbon cycle, and mitigation of its contribution to global warming.

Canada goldenrod (*Solidago canadensis* L.), introduction from North America in 1935, has become one of the profound consequences of invasive alien plants in China [20,21]. Numerous studies have revealed that *S. canadensis* invasion seriously threatens the biodiversity and ecological functions of the invaded ecosystems. Thus, the objective of the present study was to investigate the patterns and its drivers of the soil nematode community following the combined effect of global warming and *S. canadensis* invasion. To test this, an artificial warming simulation and *S. canadensis* invasion experiment was conducted. Here, the study was predicated upon the following hypothesis: warming and *S. canadensis* invasion and their interaction will alter the diversity and function of the soil nematode community via inducing changes in both soil microenvironment and microbes. The response patterns of the soil nematode community to global warming, along with *S. canadensis* invasion, revealed in the present study will improve the understanding of the alterations in biota communities during alien plant invasion processes under global warming.

2. Materials and Methods

2.1. Study Design

The study was conducted in a greenhouse on the Jiangsu University campus (32° 12′ N, 119° 30′ E) in Zhenjiang City, China. To avoid the influence of *S. canadensis* invasion on soil's physical, chemical, and biological characteristics, the experimental soil was obtained from a green space without *S. canadensis* invasion from the Jiangsu University campus in April 2020. The collected soil samples were sieved and placed in plastic pots (17 cm top diameter, 15 cm bottom diameter, and 18 cm height). *S. canadensis* and the native plant *Solidago decurrens* L. were cultivated in the soil in April 2020. After two months of cultivation, S. *canadensis* and *S. decurrens* seedlings of similar sizes were transplanted into pots.

Briefly, the experiment was established on 15 June 2020, and ended on 13 January 2021. The experiment consisted of two levels of air warming treatment: warmed air temperature by 3 °C (W) and natural air temperature unwarmed as the control (U). It was crossed with three levels of *S. canadensis* invasion treatment: non-invasion (NI), middle invasion (MI), and complete invasion (CI). Thus, there were a total of six treatments that were performed in triplicate. Warming treatments were applied with the thermostat and heaters. *S. canadensis* invasion treatments were set up by simulating the natural *S. canadensis* invasion process by planting different ratios of *S. canadensis* to *S. decurrens* seedlings in a pot (a total of two seedlings planted in each pot), based on the substitution of space for time method: NI treatment with two *S. decurrens* seedlings, MI treatment with one *S. decurrens* seedling and one *S. canadensis* seedling, and CI treatment with two *S. canadensis* seedlings [22]. All pots were placed in the greenhouse and watered every 2–3 days.

2.2. Soil Sample Collection and Preparation

The topsoil (0–10 cm) was collected using a soil corer (2.0 cm diameter) on 13 January 2021 and divided into three parts after mixing. One part was to extract the soil nematode within 48 h after sampling, one part was temporarily stored in a 4 °C refrigerator for analysis of soil microbial properties, and the last portion was air-dried at room temperature for analysis of physical and chemical properties of the soil.

2.3. Soil Property Measurements

The soil moisture content (SM) was measured by machine drying, and the mass loss was calculated after 72 h of drying at 105 °C. The pH value was measured by a pH meter in a 5:1 ratio of deionized water to air-dried soil. The contents of soil dissolved organic carbon (DOC) and nitrogen (DON) were measured by the methods in Li et al. (2020) [23]. Determination of soil available phosphorus (SAP) was conducted by molybdate colorimetry [24,25]. Soil inorganic nitrogen is the sum of nitrate nitrogen and ammonium nitrogen, and were measured by Miranda et al. and Mulvaney's method, respectively [26,27]. Determination of soil microbial biomass carbon (MBC) and nitrogen (MBN) was by chloroform fumigation [28,29]. Determination of soil microbial biomass phosphorus (MBP) was by chloroform fumigation extraction and molybdate colorimetry [24,25,28,29].

2.4. Soil Nematode Extraction, Classification, and Analyses

Soil nematodes were extracted from 80 g of soil from each subsample using the Baermann funnel method [30]. Nematode community composition classification was conducted using molecular tools on all the extracted soil nematodes. Nematode DNA in the soil was extracted using the PowerLyzer Power-Soil®DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. To generate amplicons, primers NF1 and 18Sr2b were used in a pre-amplification step followed by amplification in a semi-nested procedure. NF1 and 18Sr2b were tag-encoded using the forward primer GGTGGTGCATGGCCGTTCTTAGTT and the reverse primer TACAAAGGGCAGGGACGTAAT. The obtained sequences were further grouped into operational taxonomic units. Taxonomic classification of each operational taxonomic unit was obtained by classifying alignments against the SILVA Release 123 database.

2.5. Statistical Analyses

In the present study, we calculated seven ecological function indexes to evaluate the changes in the taxon diversity, richness, and function of soil nematode communities induced by the treatments. In detail, the taxon diversity and richness of soil nematode communities was calculated by using the Simpson and chao1 indexes. The maturity index was calculated according the vital parameters and ecological requirements of nematodes [31].

The enrichment, structure, and channel indexes were calculated based on Ferris et al. (2001) [32], which indicates the abundance and activity of primary detrital consumers, the complexity and stability of the food web, and the predominant decomposition pathways of the food web, respectively [33].

Principal component analysis (PCA) was performed to identify differences in soil properties among different soil samples. Generalized linear model (GLM) and Fisher's least significance difference test ($p < 0.05$) were performed to evaluate the differences in the effects of warming and *S. canadensis* invasion on the ecological function indices of the soil nematode community. Redundancy analysis (RDA) and a permutational multivariate ANOVA (PERMANOVA) were used to analyze differences in the ecological function indices of the soil nematode community in relation to soil environmental variables. Furthermore, RDA results were used for variance partitioning analysis (VPA) to further evaluate the relative importance of soil environmental variables in the changes of the nematode community. The partial least squares path model (PLS-PM) was used to establish the possible paths of warming and *S. canadensis* invasion on the diversity and function of the nematode community in the soil. All analyses were performed using R software version 4.1.1 [34].

3. Results

3.1. Soil Properties

Principal component analysis (PCA) showed that the two-dimensional PCA of the soil properties could explain 66% of the total variance for all samples. Moreover, PCA showed a clear shift for soil properties along the first axis of PCA induced by warming treatment (Figure 1). Soil pH ($p < 0.01$), dissolved organic carbon (DOC; $p < 0.05$), dissolved organic nitrogen (DON; $p < 0.05$), and inorganic nitrogen (SIN; $p < 0.05$) were significantly affected by warming. Compared with unwarmed treatment pots, the pH changed by 6.66%, 1.87%, and –1.74%, in non-invasion (NI), middle invasion (MI), and complete invasion (CI) treatment pots, respectively. In addition, warming altered soil DOC and DON by 24.50% and –10.81%, 14.01% and 66.39%, and 41.07% and 64.70%, while warming decreased SIN by –60.96%, –18.64%, and –44.57% in the NI, MI, and CI treatment pots under unwarmed treatment, respectively (Figure S1 in Supplementary Materials).

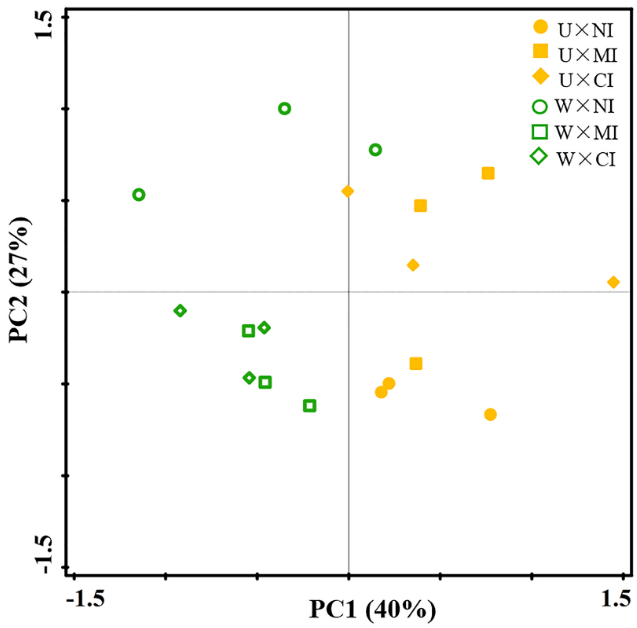

Figure 1. Principal component analysis (PCA) based on soil properties. W × NI = warming and non-invasion treatment; W × MI = warming and middle invasion treatment; W × CI = warming and complete invasion treatment; U × NI = unwarmed and non-invasion treatment; U × MI = unwarmed and middle invasion treatment; U × CI = unwarmed and complete invasion treatment.

3.2. Soil Nematode Diversity and Functional Indices

S. canadensis invasion significantly increased the chao1 index ($p < 0.05$), maturity index ($p < 0.05$), and structure index ($p < 0.01$) of nematode communities, which were 31.44%, 25.57%, and 329.3%, respectively, and significantly decreased the basal index by 48.70% ($p < 0.05$). Moreover, the Simpson index and structure index were also affected by the interaction between warming and *S. canadensis* invasion (all $p < 0.05$). Compared with NI soil, the Simpson index and basal index in CI soil decreased by 60.68 and 69.84% under warming treatment, while they decreased by 58.80% and 18.28% under unwarmed treatment. In addition, the chao1 index, maturity index, structure index, and enrichment index in CI soil were 41.57% and 20.94%, 38.11% and 13.98%, 287.1% and 88.99%, and 161.9% and 24.67% higher than those in NI soil under warming and unwarmed treatment, respectively. The channel index in the warming treatment pots were higher than in the unwarmed treatment pots (Table 1).

Table 1. The ecological function indexes of the soil nematode community for each treatment, presented as the mean ± standard error ($n = 3$).

	Unwarmed			Warming			Main Effects and Interactions
	NI	MI	CI	NI	MI	CI	
Simpson	4.11 ± 0.09abc	2.50 ± 0.29c	6.53 ± 1.06c	6.00 ± 0.50ab	3.93 ± 1.49bc	2.36 ± 0.63c	W × I **
Chao1	10.67 ± 1.67bc	9.33 ± 1.20bc	12.90 ± 0.92ab	11.07 ± 1.55bc	8.83 ± 1.09c	15.67 ± 0.83a	I **
Maturity Index	2.16 ± 0.07bc	2.62 ± 0.16a	2.46 ± 0.23ab	1.99 ± 0.02c	2.14 ± 0.05bc	2.75 ± 0.21a	I *
Basal Index	57.53 ± 6.12ab	31.92 ± 7.26b	47.01 ± 21.23b	82.78 ± 5.57a	53.36 ± 9.28ab	24.97 ± 6.90b	I *
Enrichment Index	25.94 ± 10.07a	33.55 ± 6.62a	32.34 ± 15.02a	15.35 ± 6.41a	28.83 ± 15.23a	40.20 ± 1.38a	ns
Structure Index	24.68 ± 9.112cd	61.67 ± 9.70ab	46.65 ± 19.46abc	2.33 ± 1.25d	30.24 ± 0.61bcd	69.33 ± 9.78a	I **
Channel Index	100.00 ± 0.00a	100.00 ± 0.00a	100.00 ± 0.00a	99.38 ± 0.62a	85.48 ± 14.52a	79.63 ± 14.99a	ns

NI = non-invasion treatment; MI = middle invasion treatment; CI = complete invasion treatment, W = warming treatment; I = invasion treatment. Values followed by a different letter are significantly different to each other ($p < 0.05$). ns= significant at the level of $p > 0.05$, * = significant at the level of $p < 0.05$, and ** = significant at the level of $p < 0.01$.

3.3. Relationship among Soil Properties and Ecological Function Indexes of Soil Nematode Community

The redundancy analysis (RDA) results showed that ecological function indexes of the soil nematode community could explain 46.11% of the total variance in different warming and *S. canadensis* invasion for all samples (Figure 2). According to RDA results, pH and microbial biomass nitrogen (MBN) had a positive effect on BI and CI, the ratio of microbial biomass carbon (MBC) to MBN had a negative effect on SI, and DOC, DON, and the ratio of DON to soil available phosphorus (SAP) had the greatest influence on EI (Figure 3). At the same time, variance partitioning analysis (VPA) revealed that the soil's physical and chemical properties, nutrient properties, and microbial properties explained 28%, 33%, and 46% of the changes in the soil nematode community ecological function indexes, respectively (Figure 3).

The PLS-PM model was established for path analysis of the soil nematode community, and it was found that warming and *S. canadensis* invasion significantly affected the soil nematode community (Figure 4a). On the one hand, warming affected soil physicochemical properties (e.g., moisture content and pH), soil nutrient properties, and soil microbial properties and significantly influenced the nematode community. On the other hand, *S. canadensis* invasion significantly influenced the nematode community, and the capacity of warming and *S. canadensis* invasion on the influence of soil nematode community functional indexes were 0.196 and 0.594, respectively (Figure 4b).

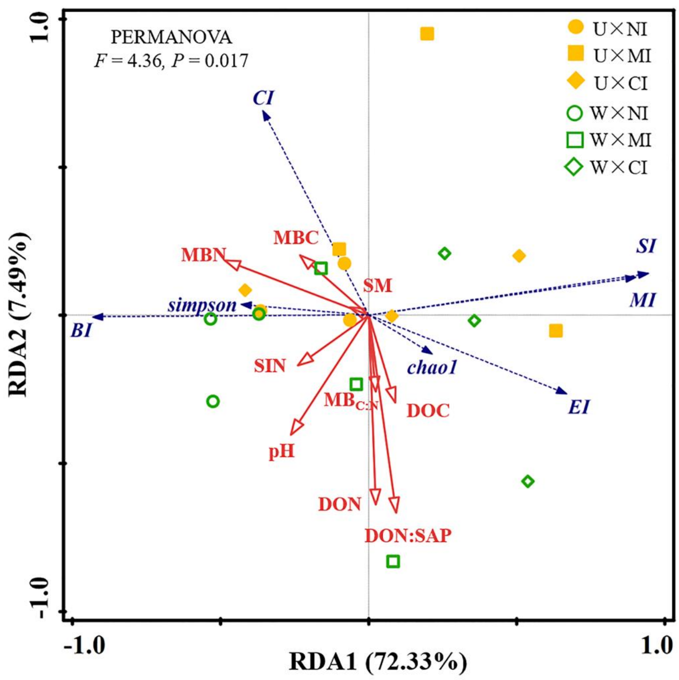

Figure 2. Result of redundancy analysis (RDA) and permutational multivariate analysis of variance (PERMANOVA) based on soil nematode community ecological function indexes and soil properties. W × NI = warming and non-invasion treatment; W × MI = warming and middle invasion treatment; W × CI = warming and complete invasion treatment; U × NI = unwarmed and non-invasion treatment; U × MI = unwarmed and middle invasion treatment; U × CI = unwarmed and complete invasion treatment. MI = maturity index; EI = enrichment index; BI = basal index; SI = structure index; CI = channel index; SM = soil moisture; DOC = soil dissolved organic carbon; DON = dissolved organic nitrogen; DON: SAP = the ratio of dissolved organic nitrogen to available phosphorus; SIN = inorganic nitrogen; MBC = microbial biomass carbon; MBN = microbial biomass nitrogen.

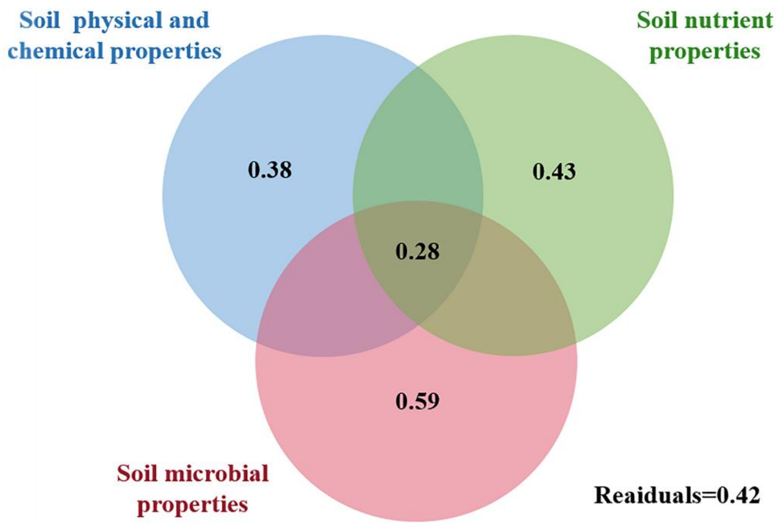

Figure 3. Results of variation partitioning analysis (VPA) showing the effects of the soil's physical and chemical properties, soil nutrient properties, and soil microbial properties on soil nematode community ecological function indexes. Soil's physical and chemical properties include soil moisture and pH; soil nutrient properties include soil dissolved organic carbon, dissolved organic nitrogen, the ratio of dissolved organic carbon to available phosphorus, and inorganic nitrogen; Soil microbial properties include microbial biomass carbon, microbial biomass nitrogen, and the ratio of microbial biomass carbon to microbial biomass nitrogen.

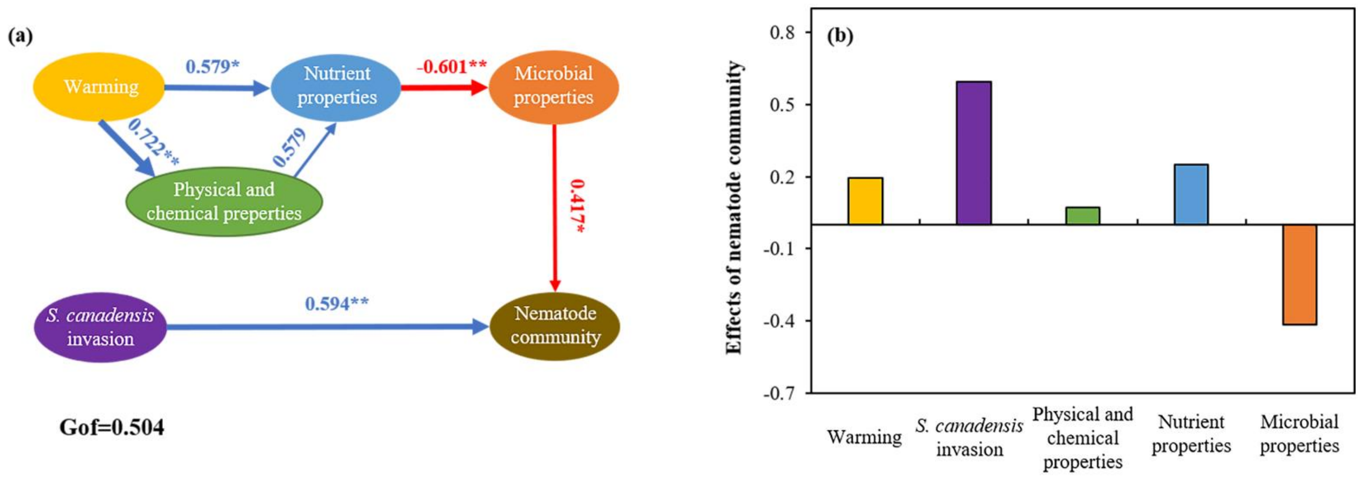

Figure 4. (**a**) Cascading relationships of the soil nematode community with soil properties among treatments and (**b**) each unit has a total effect on soil nematode community. Partial least squares path modeling (PLS-PM) disentangling major pathways of the influences of soil properties and treatments on the soil nematode community. Red and blue arrows indicate positive and negative flows of causality. * = significant at the level of $p < 0.05$, and ** = significant at the level of $p < 0.01$.

4. Discussion

Studies have demonstrated that climate change (e.g., global warming, altered precipitation patterns) can, directly and indirectly, alter the biodiversity of the aboveground vegetation community [35,36]. The changes in vegetation community would further induce shifts in belowground soil biota (e.g., animals, microbes) and biodiversity via various mechanisms [37,38]. Besides this, plant invasion also has detrimental effects on the biodiversity of soil biota by changing the substrate (e.g., litter, root exudates) input into soil [39]. In addition, Song et al. (2020) found that warming could enhance the plant invasion effect on soil microbial communities [40]. The soil nematode, as an important component of soil biota, can affect the soil ecosystem functions and processes. However, the knowledge of climate change and plant invasion effects, as well as their interaction, on soil nematode was limitation.

Previous studies showed that soil temperature and aboveground vegetation community could affect the growth, reproduction, and community composition of soil nematodes. Thus, we originally hypothesized that warming and *S. canadensis* invasion and their interaction will alter the soil nematode community via induced changes in both soil microenvironment and microbial biomass. In contrast to this prediction, warming was shown to indirectly affect the soil nematode community (Table 1, Figure 4a). This finding was inconsistent with some previous studies that showed warming can directly affect the growth, reproduction, and community composition of soil nematodes, as well as the soil microbial community [9,41,42]. In the present study, warming affected soil environmental conditions (moisture, pH, nutrient) and microbial biomass (Figure 1), thereby indirectly altering the diversity and function of the soil nematode community (Figure 4a), which confirmed that soil status is significantly correlated with the nematode community [43,44].

Some studies have indicated that alien invasive plants have a certain inhibitory effect on soil nematode communities. For example, Ren and Bal et al. (2005) compared the differences in soil nematode communities between invasive and non-invasive sites of *Heracleum Sosnowskyi* and found that *Heracleum Sosnowskyi* invasion led to a decrease in nematode abundance and species diversity [15]. Similarly, Lazzaro et al. (2018) found that soil nematode community richness was reduced in invaded region [17]. The alien plant invasive effects may be related to the invasion-induced alterations in the soil microbial community and vegetational community in the invaded region, since some of nematode feed on the microbes and plants [45]. In the previous studies, we found that *S. canadensis* invasion can alter the metabolism and structure of the microbial community as well as vegetational community [21,46]. Thus, the observed inhibitory effect of *S. canadensis* invasion on soil nematode communities may be due to the *S. canadensis* invasion-induced alterations in soil microbes and vegetational community.

Interestingly, less interaction effects of warming and *S. canadensis* invasion on the soil nematode community were observed (Table 1). However, we found that warming enhanced the destruction effects of *S. canadensis* invasion on the soil nematode community (Table 1). Since the channel index indicates the decomposition path of the food web, the decrease in the channel index indicates the decomposition path of the food web gradually changed from fungal decomposition to bacterial decomposition [47]. In the present study, the inhibition effects of *S. canadensis* invasion on channel index under warming treatments were more drastic than under unwarmed treatments. These findings revealed that warming increased the inhibition of *S. canadensis* invasion on the fungal community, which was in line with Anthony et al. (2020) who found that warming enhanced the inhibitory effect of invasive plants on soil fungal communities [48]. Moreover, the lowest value of basal index and the highest value of Simpson, maturity, enrichment and structure indexes were founded at the warming and complete invasion treatment among all the treatments (Figure 2). These results indicate that warming leads to decreased diversity of soil nematode communities and makes soil nematode favor a K-selection strategy, indicating that warming would greatly strengthen the destruction of the nematode communities by invasive plants. Combining the present results with others, it was found that warming can enhance the negative effects of plant invasion on the soil biota community.

5. Conclusions

By an artificial warming simulation and *S. canadensis* invasion experiment, we studied the response mechanism of the soil nematode community to *S. canadensis* invasion under global warming. On the one hand, the nematode community can be directly damaged by *S. canadensis* invasion, which reduces the basic components of the nematode community and damages the soil food web. On the other hand, warming can also affect the nematode community by affecting soil nutrients and microbial biomass. In this study, we also found that warming enhances the destruction of nematode communities by *S. canadensis* invasion. However, this study was only conducted over seven months and experienced a growing season of invasive plants. It is not clear whether the structural changes in the nematode community affect the survival of invasive plants under the condition of continuous plant invasion, which needs to be further studied.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/su132313145/s1, Figure S1: The influence of warming and Canada goldenrod invasion on soil properties.

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