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Contrasting latitudinal clines of nematode diversity in *Spartina alterniflora* salt marshes between native and introduced ranges

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Abstract

Aim: Introduced species may display or foster novel latitudinal clines because they are not well adapted to their new habitats. We tested the hypothesis that the latitudinal cline in nematode diversity in salt marshes would differ between the native (United States) and introduced (China) ranges of *Spartina alterniflora*.

Location: East Coasts of the United States (30.32–43.33°N) and China (30.36–39.14°N).

Methods: We extracted nematodes from soil samples collected at 32 sites along the United States East Coast and 41 sites along the Chinese coast. We compared latitudinal patterns in nematode diversity and composition between the native and introduced ranges.

Results: In the native range of *S. alterniflora*, nematode richness at lower latitudes was almost twice as high as that at higher latitudes. In contrast, we found no latitudinal pattern in nematode richness or diversity in the introduced range of *S. alterniflora*. Nematode genus richness at all sites in China was about half that at lower latitudes in the United States. Beta diversity of nematodes increased with geographic distance in the United States, but not China.

Main conclusions: Nematode diversity did not show latitudinal clines in salt marshes dominated by introduced *S. alterniflora* in China. A likely explanation is that the recently introduced populations are still relatively genetically homogenous, whereas in the native range, genetic variation in plant populations across latitude drives different nematode communities. We suggest that future studies of introduced species will gain additional insights by taking an explicitly geographic perspective.

KEYWORDS

latitudinal clines, native range, nematodes diversity, non-parallel pattern, plant invasion, salt marshes, *Spartina alterniflora*

1 | INTRODUCTION

Belowground organisms play important roles in regulating ecosystem functioning in terrestrial ecosystems (Bardgett & van der Putten, 2014; Zhang, Li, Wu, & Hu, 2019), mediating the cycling of carbon and other elements, and affecting aboveground community dynamics (Morriën et al., 2017). Compared with the well-known geographic patterns in the diversity and abundance of aboveground organisms (Hillebrand, 2004; Mannion, Upchurch, Benson, & Goswami, 2014), the geographic patterns of belowground organisms are relatively understudied (but see Decaëns, 2010; Hendershot, Read, Henning, Sanders, & Classen, 2017; Maraun, Schatz, & Scheu, 2007). Because of the important interactions between aboveground and belowground processes, a better understanding of geographic patterns of belowground organisms is needed (Fierer, Strickland, Liptzin, Bradford, & Cleveland, 2009; Lu, He, Ding, & Siemann, 2018; van der Putten, 2012; Wilschut et al., 2019), especially in light of multiple global change factors (Bardgett & Wardle, 2010; Coyle et al., 2017) that may perturb both aboveground and belowground communities.

One of important global change factors is the introduction of species to areas outside their historic geographic ranges (Alba, Fahey, & Flory, 2019; van der Putten, 2012). Species that spread rapidly may not be well adapted to their new geographic ranges or to the species in their new communities (Allen et al., 2017; Zhang, Pennings, Li, & Wu, 2019). One of the consequences may be that the invasive species may not show the same latitudinal clines in traits or species interactions that are often found in native species (Bhattarai et al., 2017; Liu, Strong, Pennings, & Zhang, 2017). For example, Cronin, Bhattarai, Allen, and Meyerson (2015) found that herbivory decreased with latitude for native *Phragmites australis* genotypes in Europe, but in its introduced range, North America, there was no latitudinal gradient in herbivory, suggesting either that the invasive *P. australis* had not yet evolved latitudinal clines in plant defences typical of the native range, or that local herbivores had not yet adapted to utilize the introduced species. Whether a similar non-parallel latitudinal pattern occurs for plant–soil biota interactions needs to be explored.

Species invasions can occur in various habitats, but are particularly consequential in coastal habitats because these habitats are typically dominated by a small number of plant species, making it likely that an invader will dramatically change species composition, the physical environment, or both (Li et al., 2009; Zhang, Pennings, et al., 2019). Examples of widespread invaders in coastal habitats include introduced genotypes of the grass *Phragmites australis* on the Atlantic and Gulf coasts of the United States (McCormick, Kettenring, Baron, & Whigham, 2010), and the grass *Spartina alterniflora* on the West Coast of the United States (Kerr, Hogle, Ort, & Thornton, 2016; Strong & Ayres, 2016) and in China (Li et al., 2009; Liu et al., 2019; Zhang et al., 2017). In China, introduced *S. alterniflora* displays latitudinal clines in plant traits that are not parallel to those of native plants or of *S. alterniflora* in its native range (W. Liu et al., personal communication; Y. Zhang et al., unpublished data). Here, *S. alterniflora*, with its continental-scale invasion, offers us an opportunity to investigate the biogeography of species invasions and interactions.

Nematodes dominate most soil communities and are the most abundant metazoan known on Earth (Bardgett & van der Putten, 2014; van der Hoogen et al., 2019). They occupy all major trophic levels of the soil food web (Boag & Yeates, 1998; Yeates, 1979), affect the physical and chemical properties of soil, and regulate nutrient cycling (Hunt & Wall, 2002; Neher, 2010; Neher, Wu, Barbercheck, & Anas, 2005). Many previous studies have focused on the relationship between nematode diversity and environmental parameters including climatic and edaphic variables (Nielsen et al., 2014; Song et al., 2017; Wu, Chen, & Zhang, 2016). For example, in a meta-analysis, Song et al. (2017) found that the diversity of nematodes was positively correlated with annual mean temperature. Likewise, Wu et al. (2016) found that climatic variables including annual temperature range and edaphic variables like pH were very important in influencing nematode community structure in coastal wetlands dominated by native plants. Because soil nematodes may respond to fine-scale changes in soil resources, pH and moisture, they interact with environmental parameters at fine spatial scales, and these interactions and processes may be important in determining diversity patterns (Neher, 2010). Also, because plants are one of the major factors affecting nematode communities, introduced species may alter natural patterns of nematode diversity and distribution. In China, the nematode communities associated with native *P. australis* show a geographic pattern of decreasing genus-level diversity with increasing latitude; however, the nematode communities associated with introduced *S. alterniflora* do not show similar patterns, which may be related to the edaphic parameters and plant traits (Zhang, Pennings, et al., 2019). This finding suggests that the introduced *S. alterniflora* has homogenized the native nematode community across latitude; however, results were not compared with the native range of *S. alterniflora*.

Here, we compared latitudinal clines in nematode diversity in stands of *S. alterniflora* between the native and invaded ranges to better assess the ecological impact of the invader on soil communities. We sampled nematodes in stands of *S. alterniflora* from 32 sites in the native range in the United States and 41 sites in the invaded range in China. We tested three hypotheses: (a) nematode diversity in the native range of *S. alterniflora* will decrease with increasing latitude, this pattern should be similar to that which was found in the native range of *P. australis* in China; (b) the cline of nematode diversity in the introduced range of *S. alterniflora* will differ from that in the native range; and (c) different climatic and edaphic variables will explain the latitudinal patterns of nematode diversity in the native range of *S. alterniflora* versus the introduced range. Because nematodes occupy a variety of trophic positions and vary considerably in life history, we examined geographic patterns both from the perspective of taxonomic diversity, by looking at species and genus richness, and also from the perspective of functional diversity, by looking at geographic variation in different feeding groups and different life-history groups.

2 | METHODS

We sampled soil in June and July 2018 at 32 sites along the East Coast of the United States, from Florida to Maine, which spans a latitudinal range of 30–43°N (Figure 1, Appendix S1: Table S1). These data were compared with those from 41 sites along the East Coast of China that spanned a latitudinal range of 30–39°N (Appendix S1: Table S1). Samples from China were collected in June 2015 ($n = 24$) and June 2017 ($n = 17$). The 2015 data were previously published (Zhang, Pennings, et al., 2019). In both countries, individual sites were at least 1 km apart. We chose 35°N to divide the sites into similar numbers of higher- and lower-latitude sites for comparison. All study sites fall into the temperate region, however, and this distinction was otherwise arbitrary. Climate data from the station closest to each site (mean annual temperature, MAT, and mean annual precipitation, MAP) were obtained from http://data.cma.cn/ and https://www.wunderground.com/.

At each site, we worked in the salt marsh habitats within areas dominated by monospecific stands of the grass *Spartina alterniflora*. We worked in the middle of the *S. alterniflora* zone, avoiding Creekbank locations. Within each site, we haphazardly located at 8 m transect and collected nine sediment cores at 1 m intervals along the transect, using a modified O'Connor split corer (3.2 cm diameter) to 10 cm depth. We mixed the nine sediment samples to create a single composite sample, fixed a 150 g subsample in 4% hot formalin for nematode analysis, split the remaining sediment into a number of subsamples and measured several edaphic parameters to identify potential correlates of nematode community structure (detailed methods in Appendix S1).

We extracted nematodes from the soil samples by flotation in Ludox TM, examined each sample under a dissecting microscope and identified the first 100 nematodes to genus level that we encountered from each sample on glass slides. Thus, we calculated the Shannon–Wiener diversity index (H′) at the genus level for each sample, but not the density of nematodes in each sample. We quantified the beta diversity of nematode communities among samples as Bray–Curtis dissimilarity (Bray & Curtis, 1957), using the "vegan" package in R (Oksanen et al., 2016).

Each genus was assigned to one of six feeding types (plant-feeders, bacterial-feeders, fungal-feeders, algal-feeders, carnivores and omnivores) based on the literature (Yeates, Bongers, De Goede, Freckman, & Georgieva, 1993). Each genus was also assigned a colonizer–persister (*c–p*) value ranging from 1 to 5 based on the literature (Bongers, 1990). The nematodes with higher *c–p* values have longer generation times, larger body sizes, lower reproductive capacities, and are more sensitive to disturbance than those with lower *c–p* values. We collapsed these five categories into three based on the literature (De Goede, Bongers, & Ettema, 1993): enrichment opportunists (*c–p* 1), general opportunists (*c–p* 2) and persisters (*c–p* 3–5). We calculated the proportion of individuals and the proportion of genera in each category.

We compared nematode genus richness and H' diversity indices across latitude and between the two countries using general linear mixed models, with site as a random effect, and latitude and country as fixed effects, using the *nlme* package in R version 3.4.3 (R Development Core Team, 2014). Within each country, we related nematode feeding types and colonizer–persister (*c–p*) groups to latitude using linear regression in SPSS (version 19.0).

To further examine latitudinal patterns in nematode community structure, we divided the sites into high (>35°N) and low (<35°N) latitude, and produced ordination plots for each country using non-metric multidimensional scaling (NMDS) using a ranked similarity matrix based on Bray–Curtis similarity measures of nematode communities. We used one-way ANOSIM to determine the significant difference between groups, using permutation/randomization methods with 999 times on the similarity matrix. Both analyses were done using PRIMER version 5.2 (Primer-E Ltd.). The proportional data were $\log(x + 1)$ transformed before analysis. We also pooled samples from *S. alterniflora* in China and the United States to run a single principle components analysis (PCA) in CANOCO 5.0 (ter Braak & Smilauer, 2012) and tested for a country × latitude interaction on nematode community structure using PERMANOVA in R 2.15.1 (R Development Core Team, 2014).

Redundancy analysis (RDA) is a powerful multivariate analysis technique with wide ecological applications (Borcard, Legendre, & Drapeau, 1992). In RDA, variables are chosen to maximize the extent of their correlation with a set of predictor variables (Borcard et al., 1992). We used redundancy analysis (RDA) to evaluate how the nematode diversity (genus richness and the Shannon–Wiener diversity index H′) was related to the climate and edaphic variables using CANOCO 5.0 (ter Braak & Smilauer, 2012). To exclude the variables that were highly correlated with each other in this analysis, we calculated Spearman rank-order correlations between all variables using the cor.test function in the *stats* library of R. Based on this analysis, we selected MAT, MAP, pH, salinity, soil organic matter, C:N ratio, soil moisture, porosity, proportion of clay and proportion of silt to explain nematode richness and diversity patterns through RDA.

3 | RESULTS

We identified 64 nematode genera from 24 families and six orders from the 32 sites in the United States, and 63 genera from 32 families and seven orders from the 41 sites in China (Appendix S1: Table S2). Geographic patterns of nematode genus richness (ANCOVA: Latitude: $p = .03$; Country: $p < .001$; Latitude × Country: $p < .001$) and Shannon–Wiener diversity (ANCOVA: Latitude: $p = .03$; Country: $p = .23$; Latitude × Country: $p = .006$) differed strikingly between the two countries (Figure 2). In the United States, richness and Shannon–Wiener diversity decreased with increasing latitude, with the richness at low latitudes being almost twice that at high latitudes; however, there was no relationship between richness or diversity and latitude in China (Figure 2). Because the composition of the nematode community might change over time, we conducted separate analyses for the samples collected in China in 2015 and 2017, and obtained similar results for the

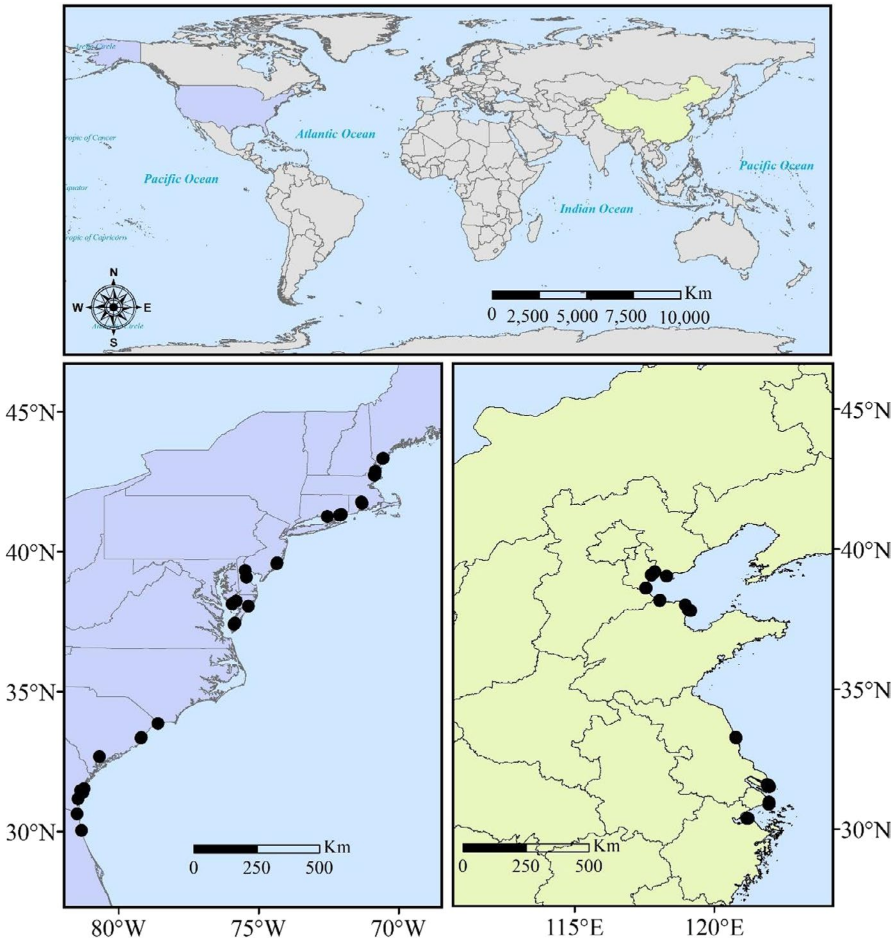

FIGURE 1 Sampling sites for soil nematodes from salt marshes dominated by *Spartina alterniflora* on the coast of the United States (left) and China (right). Detailed information about each site is provided in Appendix S1 (Table S1)

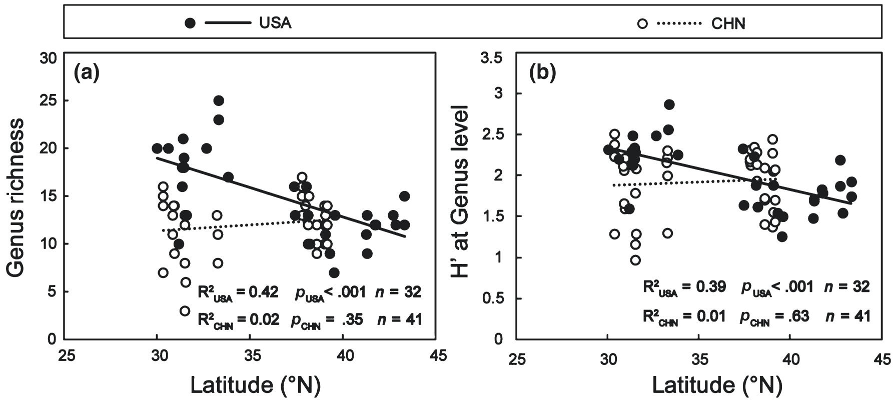

FIGURE 2 Relationship between soil nematode (a) genus richness and (b) Shannon–Wiener diversity index (H′) and latitude for salt marshes dominated by *Spartina alterniflora* in the United States and China. Sample sizes (*n*) for each regression are shown in the figures

two years (Appendix S1: Figure S1). Because the samples from the United States extended to higher latitudes than the samples from China, we repeated these analyses with the 10 highest-latitude sites from the United States omitted and obtained similar results as nematode genus richness (Latitude: p = .040; Country: p < .001; Latitude × Country: p < .001) and Shannon–Wiener diversity (Latitude: p = .144; Country: p = .148; Latitude × Country: p = .006) (Appendix S1: Figure S2).

Non-metric multidimensional scaling analyses of nematode community composition similarly indicated stronger latitudinal structuring in the United States than in China. For the United States, the high- and low-latitude samples were almost completely segregated in the NMDS plot (Figure 3a, Appendix S1: Table S4). In contrast, samples from high and low latitudes in China were moderately interspersed (Figure 3b), although still statistically different (Appendix S1: Table S4). Community dissimilarity increased with geographic distance in the United States (Figure 4a), but no pattern was seen in China (Figure 4b). If all the samples were combined in a single PCA analysis, there was a significant country and latitude interaction, confirming that the nematode communities associated

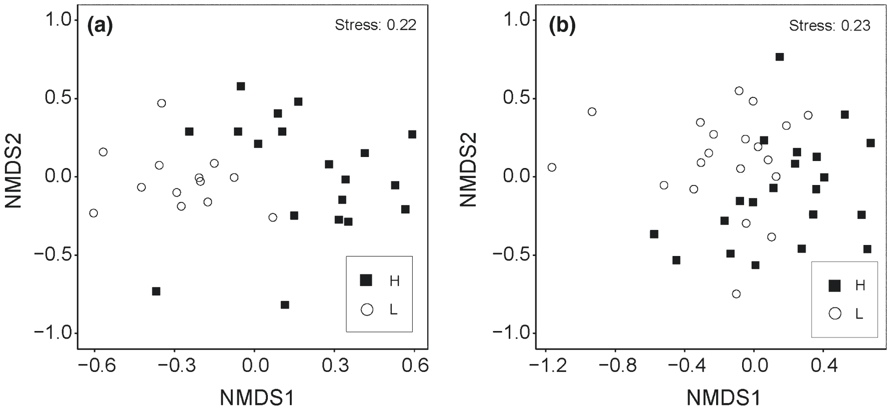

FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination of soil nematode communities from salt marshes dominated by *Spartina alterniflora* in (a) the United States and (b) China. Squares represent sites located at higher latitudes (H, 37.45–43.33°N); circles represent sites located at lower latitudes (L, 30.02–33.85°N)

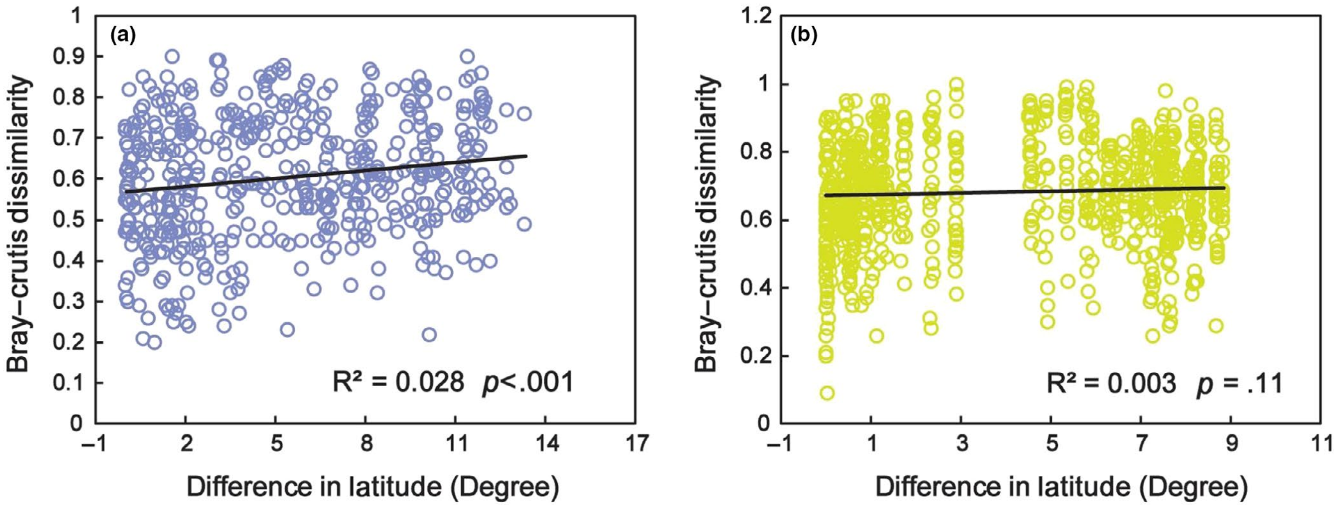

FIGURE 4 Relationship between soil nematode community dissimilarity (Bray–Curtis dissimilarity index) and geographic distance, expressed as differences in latitude, for salt marshes dominated by *Spartina alterniflora* in (a) the United States and (b) China. Summary statistics in each figure are from linear regression

with the two countries varied in different ways across latitude ($p = .05$) (Appendix S1: Table S5, Figure S3).

Despite strong latitudinal patterns of richness, diversity and community structure in the United States, none of the feeding groups or life-history groups were correlated with latitude (Appendix S1: Table S3). Similarly, none of the feeding groups or life-history groups were correlated with latitude in the Chinese samples (Appendix S1: Table S3).

Bivariate regressions between different environmental variables and nematode richness indicated that nematode richness in the USA was positively related to mean annual temperature ($R^2 = .399$, $p < .001$) and soil C:N ($R^2 = .169$, $p = .020$), and negatively related to mean annual precipitation ($R^2 = .179$, $p = .016$) (Appendix S1: Figure S4), whereas the nematode richness in China was negatively related to soil moisture ($R^2 = .206$, $p = .003$), organic matter ($R^2 = .196$, $p = .004$), total C ($R^2 = .227$, $p = .002$) and total *N* ($R^2 = .264$, $p = .001$) (Appendix S1: Figure S4). Bivariate regressions between different environmental variables and nematode Shannon–Wiener diversity indicated that nematode diversity in the USA was positively related to mean annual temperature ($R^2 = .390$, $p < .001$) and negatively related to mean annual precipitation ($R^2 = .202$, $p = .010$) (Appendix S1: Figure S5), whereas nematode diversity in China was negatively related to soil moisture ($R^2 = .282$, $p < .001$), organic matter ($R^2 = .255$, $p = .001$), total C ($R^2 = .305$, $p < .001$) and total *N* ($R^2 = .358$, $p < .001$) (Appendix S1: Figure S5). In the multivariate RDA analysis, nematode richness and diversity in the United States were again highly associated with mean annual temperature (contribution% = 72.6%, $p = .002$), mean annual precipitation (contribution% = 32.6%, $p = .014$) and soil C:N (contribution% = 30.5%, $p = .026$) (Appendix S1: Figure S6a), and nematode richness and diversity in China were again highly associated with soil moisture (contribution% = 34.0%, $p = .006$) and organic matter (contribution% = 32.3%, $p = .006$) (Appendix S1: Figure S6b).

4 | DISCUSSION

In the native range of the salt marsh grass *Spartina alterniflora* in the United States, soil nematode genus richness and diversity decreased with increasing latitude, with genus richness at lower latitudes being almost twice that at higher latitudes. This pattern is consistent with most previous studies of nematode diversity, which typically show higher diversity at low latitudes than at high latitudes (Lee & Riveros, 2012; Nielsen et al., 2014; Song et al., 2017). This pattern is also consistent with the general trend of decreased diversity of species overall, and of richness within most taxa, at higher latitudes (Gaston, 2000; Hillebrand, 2004; Mannion et al., 2014). Previous work along the East Coast of China found that soil nematode richness and diversity decreased with increasing latitude within wetland habitats dominated by the native grass *Phragmites australis*, with nematode richness about twice as high at low (22°) versus high (39°) latitudes (Zhang, Pennings, et al., 2019). Thus, this pattern of decreasing nematode diversity with increasing latitude appears to be consistent for nematode in native plants dominating coastal wetlands as well as for nematodes in terrestrial habitats (Nielsen et al., 2014; Song et al., 2017; Wu et al., 2016).

In striking contrast, this study, together with our previous work in China (Zhang, Pennings, et al., 2019), found no latitudinal pattern in richness or diversity for nematodes sampled from the salt marshes in China that were dominated by introduced *S. alterniflora*. As a result, beta diversity increased with geographic distance (latitude) in the United States, but not in China. Moreover, the number of nematode genera found at low-latitude sites in the United States was almost twice the number found in China (Figure 2).

In this study in native *S. alterniflora* marshes in the USA and in previous work in native *P. australis* marshes in China, the richness and diversity of soil nematodes were correlated with mean annual temperature and mean annual precipitation along latitudinal gradients (Zhang, Pennings, et al., 2019). This finding is consistent with previous studies focusing on the relationships between nematode distribution patterns and environmental parameters (Nielsen et al., 2014; Song et al., 2017). One of the classic ecological explanations for this geographical diversity pattern is the species–energy hypothesis—that latitudinal variability in hydrothermal conditions (temperature, precipitation, etc.) drives diversity patterns of a broad range of taxa (Mittelbach et al., 2007; Schluter & Pennell, 2017). In addition to climatic parameters, however, other studies have emphasized the importance of edaphic parameters and plant traits in driving patterns of soil nematode richness and diversity (Fonseca & Netto, 2015; Sauvadet, Chauvat, Fanin, Coulibaly, & Bertrand, 2016; Wu et al., 2016). In this study, edaphic parameters were not related to soil nematode richness and diversity in the native range of *S. alterniflora* (Appendix S1: Figures S4–S6). In the introduced range of exotic *S. alterniflora* in China, however, soil nematode richness and diversity were most closely related to edaphic variables. In neither case did we measure relevant plant traits to assess their possible importance.

Why would the results from the two native plants be so different from those obtained from the exotic plant? One possible reason is the short history of *Spartina alterniflora* in China. *Spartina alterniflora* was introduced to China in 1979 from three low-latitude sites (Florida, Georgia, North Carolina) in the United States and propagated in a common garden (Guo et al., 2015; Liu et al., 2019). The following generations of *S. alterniflora* that were distributed across the Chinese coastline likely had little genetic variability and no genetic structure by distance, because the source populations cross-fertilized each other and the same offspring were distributed everywhere (An et al., 2007; Bernik, Li, & Blum, 2016; Guo et al., 2015). The available evidence suggests that *S. alterniflora* in China has little genetic differentiation (Shang et al., 2019) and has not undergone rapid selection for most traits over the following four decades, and thus, the populations remain genetically similar across latitude (Liu, Maung-Douglass, Strong, Pennings, & Zhang, 2016; Liu et al., 2017; Zheng, Shao, & Sun, 2018). Because plant traits are one of the major factors driving nematode community structure, along with soil characteristics and climate (Nielsen et al., 2014; van der Hoogen et al., 2019; Wu et al., 2016), the relatively genetic homogeneity of introduced *S. alterniflora* populations in China may explain the lack of a strong latitudinal trend in associated nematodes. This hypothesis, however, remains to be tested with a common garden experiment and by measuring plant traits that are most relevant to nematodes, such as root structure and plant exudates. Moreover, because *S. alterniflora* is recently introduced to China, the lower nematode genus richness at lower latitudes in China may reflect a lack of time for local nematodes to adapt to the novel soil conditions and food webs associated with this exotic plant. We are unaware of any studies examining species accumulation curves over time for soil communities associated with exotic species, but similar studies of aboveground herbivores suggest that it takes up to 100 years or more before an introduced plant species accumulates as many herbivores in its exotic range as it has in its native range (Bezemer, Harvey, & Cronin, 2013; Brändle, Kühn, Klotz, Belle, & Brandl, 2008; Gruntman, Segev, Glauser, & Tielbörger, 2017).

Salt marshes dominated by exotic *S. alterniflora* in China lack a “normal” nematode community (as defined by the representation of different nematode genera in soils from native *S. alterniflora* in the United States or native *P. australis* in China). This suggests that the belowground food web in Chinese salt marshes dominated by *S. alterniflora* may not be functioning normally. Changes to nematode community composition may alter the microbial community structure, carbon cycling, decomposition, and the abundance of species that compete with or feed on nematodes (Alkemade, Wielemaker, Herman, & Hemminga, 1994; Bastow, 2011; Kreuzinger-Janik, Brüchner- Hüttemann, & Traunspurger, 2019). Given the vast extent of the *S. alterniflora* invasion in China, these potential consequences of the altered nematode communities could have important implications for coastal ecosystem structure and functions, and hence deserve further attention.

Our study was explicitly geographic and examined nematode composition and diversity across a broad range of latitude. If we had limited our research to a few sites from low latitudes, or a few sites from high latitudes, we would have reached opposite conclusions about how nematode diversity differed between the United States and China. Thus, one important lesson from our work and others that have taken a broad geographic perspective (Liu et al., 2016; Nie et al., 2010) is that studies assessing the ecological and evolutionary consequences of exotic species can gain important insights from studying populations from as much of the native and introduced ranges as possible.

One of the possible mechanisms for plant invasion is enemy release: invasive plants may be more productive in their new geographic range because they have escaped consumption by natural enemies (Keane & Crawley, 2002). Compared to the long evolutionary history of the native plant with the biota, there are known examples of rapid host shifts in response to introduced plants, including one example of an herbivore feeding on *S. alterniflora* in China (Zhang, Ju, Pan, Pan, & Wu, 2019); however, most evidence suggests that it takes a century or more for root-associated nematodes (Lu et al., 2018; Wilschut et al., 2019) or an entire community to adapt to a novel host species (Bezemer et al., 2013; Brändle et al., 2008; Gruntman et al., 2017). In this study, we found the opposite result: in the native range of *S. alterniflora*, almost no nematodes were plant-feeders, whereas up to 17 per cent were plant-feeders in the introduced range in China in (Appendix S1: Figure S7). Although this difference was not statistically significant, it was in the opposite direction as predicted by the enemy release hypothesis, and so we ruled out this possibility based on our study. However, one caveat of our study is that we did not sample root endoparasitic nematodes because they live inside the roots of their hosts (Castagnone-Sereno, 2006) and therefore are not sampled well using the Ludox solution method. Little is known about root endoparasitic nematodes in *S. alterniflora*, or whether any such species were introduced from the United States to China along with the introduction of *S. alterniflora*. Future studies could explore latitudinal patterns in root-feeding nematodes in both the native and geographic ranges of *S. alterniflora*.

Grasses in the genus *Spartina* have been aggressive invaders of coastal habitats worldwide (Strong & Ayres, 2013). In these new habitats, *S. alterniflora* typically transforms intertidal mudflats into high-intertidal salt marshes, with profound consequences for aboveground plant communities (Biswas et al., 2018; Li et al., 2009), migratory shorebirds (Ma, Gan, Choi, & Li, 2014), macroinvertebrate communities (Neira, Levin, Grosholz, & Mendoza, 2007), hydrologic and edaphic parameters (Adams et al., 2012), and soil biochemistry (Wang et al., 2019). Our work has shown that the geographic structure of nematode communities is also affected (Zhang, Pennings, et al., 2019; this paper), emphasizing both the importance of examining the soil food web and the importance of taking a geographic approach to studying species invasions.

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DATA AVAILABILITY STATEMENT

The data supporting this article can be found in electronic supplementary material and Dryad Digital Repository (Dryad, Dataset, https://doi.org/10.5061/dryad.djh9w0vwj) once the paper is accepted.

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BIOSKETCH

Our group studies soil animal biodiversity, with emphases on nematode taxonomy and ecology. Our recent work examined aboveground and belowground interactions under various types of human disturbance and global changes.

Author contributions: Y.Z., S.P. and J.W. designed the study; Y.Z. and S.P. collected soil samples from the Chinese and American coast; Y.Z. processed the soil and nematode samples and analysed the data; all authors wrote the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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