


LETTER

Changes in Plant Biomass Are Driven by Persisting Plant Species, but Species Gains Drive Nematode Carbon Dynamics

Anning Zhang^{1,2} | Shuyan Chen² | Ziyang Liu¹ | Jingwei Chen¹ | Hongxian Song² | Hanwen Cui¹ | Zi Yang² | Sa Xiao¹  | Lizhe An^{2,3} | Mark A. Genung⁴

¹State Key Laboratory of Herbage Improvement and Grassland Agro-Ecosystems, College of Ecology, Lanzhou University, Gansu, China | ²Key Laboratory of Cell Activities and Stress Adaptations Ministry of Education, School of Life Sciences, Lanzhou University, Gansu, China | ³State Key Laboratory of Efficient Production of Forest Resources, Beijing Forestry University, Beijing, China | ⁴Department of Biology, University of Louisiana at Lafayette, Lafayette, Louisiana, USA

Correspondence: Sa Xiao (xiaos@lzu.edu.cn)

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ABSTRACT

Global change drivers, such as shrub encroachment, alter above- and belowground communities, and the consequences of these changes for ecosystem functioning are largely unknown. We used the modified Price equation to quantify how the presence of shrubs alters the richness, composition, and abundance of plant and nematode communities and the resulting effects on ecosystem functioning (i.e., plant biomass and nematode carbon [C] metabolism) on the Qinghai-Tibet Plateau. Plots with shrubs had increased plant biomass (mostly due to persisting plant species producing more biomass) and nematode C metabolism (mostly due to increases in nematode species richness). The strength of the species richness effect on plant biomass was positively associated with the strength of the species richness on nematode C metabolism. Increases in the biomass of persisting species and species gains promote plant biomass and nematode C metabolism, respectively, which may accelerate decomposition and C turnover on the Qinghai-Tibet Plateau.

1 | Introduction

Understanding the relationship between biodiversity and ecosystem function has been a major goal in ecology (Scherer-Lorenzen et al. 2022). Biodiversity loss due to climate change and anthropogenic activities can impact ecosystem functioning (Hogan et al. 2024). However, ecological communities rarely undergo simple declines in richness in response

to pressures at local scales (Blowes et al. 2019; Dornelas et al. 2014). Instead, changes in species composition are common due to local species losses and gains of species through colonisation (Ladouceur et al. 2022; Sandau et al. 2017). Little work has explored the effects of compositional changes on ecosystem processes and functions, which limits our understanding of which mechanisms explain changes in ecosystem functioning (Bannar-Martin et al. 2018). Therefore,

Anning Zhang and Shuyan Chen should be considered joint first author.

understanding how changes in biodiversity, species composition, and ecosystem function are interrelated is important for predicting the impacts of environmental drivers on ecosystems and their functions.

A major driver of biodiversity change is species range expansion from climate change (Collins et al. 2018). One prevalent global change is shrub encroachment, which mainly occurs through large-scale changes, such as changes in precipitation and precipitation, large-scale fire suppression, and overgrazing, causing the conversion of grasslands into shrublands across the globe (Collins et al. 2018; Ratajczak, Nippert, and Collins 2012; Van Auken 2000). Shrub encroachment is often accompanied by large changes in the spatial pattern of soil resources and vegetation, which can strongly impact biodiversity and ecosystem functioning (Eldridge et al. 2011; Maestre et al. 2009). Specifically, shrubs can often form complex microhabitats that can intercept wind- and water-transported detritus and seeds, improve soil nutrients, and change soil moisture and temperature, all of which affect above- and belowground community composition and therefore ecosystem functioning (Collins et al. 2020; Eldridge et al. 2011; Maestre et al. 2009). The few investigations of the relationship between species composition and ecosystem functions focus on aboveground organisms such as plants (Ladouceur et al. 2022; Navarro-Cano, Goberna, and Verdú 2021) and insects (Bloom, Northfield, and Crowder 2019; Genung, Fox, and Winfree 2020), despite decades of biodiversity-ecosystem functioning (BEF) research. To our knowledge, little work has tested the relative importance of species richness and identity (i.e., community composition) for functions provided by belowground communities (De Deyn et al. 2004; Leff et al. 2018).

Plant and nematode communities are important components of above and belowground communities, playing crucial roles as producers and consumers, thus providing multiple concurrent ecosystem functions (Ferris 2010; Ladouceur et al. 2022). Firstly, plant biomass is a major resource input to the soil subsystem, supporting soil food webs, energy flow, and C cycles (Wardle et al. 2004). Moreover, nematodes feed on bacteria, fungi, and plant belowground biomass, thereby functioning as key links of the C transfer from producers to higher trophic levels (Franco et al. 2022). Carbon metabolism based on body size and life-history strategies, including nematode biomass, production, and respired C, represents the contribution of these organisms to C cycling and provides more information on the biomass, metabolic activity, and magnitude of C flow in soil food webs (Ferris 2010; Franco et al. 2022). The species composition of, and functions provided by, both plant and nematode communities are closely related to environmental changes such as the presence of shrubs. Therefore, elucidating the patterns of the relationship between species composition and ecosystem functions provided by plant and nematode communities would advance our understanding of above- and belowground interactions and how different facets of biodiversity (e.g., richness and composition) maintain ecosystem functions.

Well-established in ecology, the Price equation was originally developed in evolutionary biology but has been successfully used to examine the biological relationships that underpin the variation among aggregate changes in species richness,

composition, and additive measures of ecosystem functioning (Fox 2006; Ladouceur et al. 2022; Winfree et al. 2015). We used the Community Assembly and the Functioning of Ecosystems (CAFE) approach, based on Fox and Kerr's (2012) modification of the Price equation into five components: species richness (e.g., loss and gain), species identity (e.g., loss and gain), and context-dependent effects (Bannar-Martin et al. 2018; Fox and Kerr 2012). All five components of the Price equation are closely associated with ecological, historical, and evolutionary processes, which can describe complex, nonlinear, and non-additive mechanisms affecting species richness, composition, and species' functional contributions (Bannar-Martin et al. 2018; Fox 2006; Fox and Kerr 2012). Shrubs can cause species loss and gain and can affect the identity of species persisting in communities by changing how the environment filters for certain species with specific functional contributions (Zhang et al. 2023). Environmental changes therefore alter the dynamics of competition and coexistence, changing patterns of community assembly, which results in changes in ecosystem functions (Ladouceur et al. 2022). Understanding how changes in species composition affect ecosystem functions is critical to better determine the consequences of global environmental change for communities and ecosystems.

To quantify how changes in above- and below-ground communities altered ecosystem functioning in the context of shrub encroachment, we investigate the plant and nematode communities and the functions they provide between shrubs and open space from 378 plots at 63 sites on the Qinghai-Tibet Plateau. We hypothesised that shrubs would increase microhabitat quality and resource availability, which would alter community composition and increase functions provided by plants and nematodes (Hortal et al. 2015). However, the relationship between species composition and functions under shrubs varies in direction and strength across climate, biotic, and soil factors (Brooker 2006). Thus, we further hypothesised that climate, biotic, and soil factors may alter how species composition affects ecosystem functions. Finally, we hypothesised that the strength of each price equation term would be correlated across plant and nematode functions (e.g., the strength of SRE.L for plant biomass would be similar to the strength of SRE.L for nematode biomass C).

2 | Materials and Methods

2.1 | Study Design

Dasiphora fruticosa is a widespread dominant shrub on the Qinghai-Tibetan Plateau (Li et al. 2010), which can strongly impact productivity and below-ground communities (Wang et al. 2018, 2023). Therefore, in the growing season of 2019, we selected 63 sites across a 1200 km × 1200 km area with *Dasiphora fruticosa* on the Qinghai-Tibet Plateau (96°21'34" E–103°13'41" E, 31°05'44" N–38°39'51" N, Figure S1). Sites were separated by at least 30 km. At each site, we set up one large plot (50 m × 50 m) and randomly selected three well-developed and similar-sized shrubs. Beneath each shrub, we set up a 30 cm × 30 cm plot. We also haphazardly set up three plots of the same 30 cm × 30 cm size in nearby open space, at least 5 m away from any shrubs. In total there were 378 plots across the 63 sites.

2.2 | Plant and Nematode Sampling

In each plot, all herbaceous plants (i.e., from the soil surface upwards) were harvested and sorted into species. Plant biomass was oven dried at 65°C for 72 h. Subsequently, after removing litter and rocks, we collected soil samples (0–15 cm depth) using a soil auger. All soil samples were divided into two parts and stored at –80°C for DNA extraction and 4°C for nematode extraction and soil properties analysis, respectively.

We extracted nematodes from 50 g of fresh using Baremann funnels. Extracted nematodes were observed under a 100× inverted microscope (Olympus CX43) for genus-level identification. The number of nematodes was expressed as individuals per 100 g of dry soil. We collected the estimates for fresh weight of the nematode genera from Nematode Ecophysiological Parameters in the Nematode Information System (<http://nemaplex.ucdavis.edu>). Nematode biomass C was calculated as 10.4% of fresh weight. Nematode production and respired C were calculated based on nematode biomass, diet, and life history (C-P value) from published dimensions of each species and averaged across genera (Ferris 2010; Franco et al. 2022).

2.3 | Climate, Biotic, and Soil Factors

Our climatic variables were mean annual temperature (MAT) and mean annual precipitation (MAP), which we obtained from the global Worldclim version 2.1 dataset (<http://www.worldclim.org>).

Our biotic variables were soil, bacterial, and fungal DNA. Soil DNA was extracted from 0.5 g of fresh soil using PowerSoil DNA Isolation Kits (Mo Bio Laboratories Inc., Carlsbad, CA, USA). Bacterial and fungal DNA were amplified using primers 515F/806R (GTGYCAGCMGCCGCGGTAA/GGACTA CNVGGGTWCTAAT) and ITS1f/ITS2 (CTTGGTCATTTAG AGGAAGTAA/GCTGCGTTCTTCATCGATGC), respectively. PCR amplification and sequencing were made by NOVOGENE.

Our soil variables were soil moisture, total nitrogen, organic matter, pH, and electrical conductivity. Soil moisture (SM) was determined by drying 30 g of soil at 105°C for 72 h. Soil total nitrogen (TN) was measured using an automatic chemical analyser. Soil pH and electrical conductivity (EC) were measured using a pH electrode and a conductivity meter in 1:5 soil-water ratios, respectively.

2.4 | Price Equation

We used the CAFE approach (Bannar-Martin et al. 2018), which aims to place a framework around the five-term ecological Price equation developed by Fox and Kerr (2012). The CAFE approach allows us to explore how plots with shrubs varied in (1) plant biomass and (2) nematode biomass, production, and respired C, compared with plots without shrubs. In our ecological price equation approach, any change in ecosystem function between sites with and without shrubs must happen through changes in species richness, species identity, or the context-dependent effect, as explained below. The ecological Price equation approach

we use here uses a pairwise method, with differences in function from a baseline to a comparison community partitioned into five terms (Figure 1). Species richness loss (SRE.L) and gain (SRE.G) effects are the effects of species loss/gain on function under the condition that species loss and gain happen randomly with respect to species' contributions to function. Species identity effects, both loss (SIE.L) and gain (SIE.G), are effects of non-random species loss, i.e., the functional difference between actual lost/gained species and the “random” loss expectation established by the SRE terms. The context-dependent (CDE) effect is the change in function by species that persists in the community, and is driven by changes in persisting species' abundances and/or per-capita function between sites. To better quantify and test the relative importance of species richness and composition for functions, we partitioned them into three additive terms: species richness effects (SRE, total of SRE.L and SRE.G), species identity effects (SIE, total of SIE.L and SIE.G), and CDE (Genung, Fox, and Winfree 2020). This reflects ecologists' more frequent interest in the net effect of species richness and identity changes, rather than focusing solely on lost and gained species.

At each site, we designated “open” (i.e., no shrubs) communities as baseline communities, and “shrub” communities as the comparison. We then conducted all possible pairwise comparisons between baseline and comparison communities (Figure S2). We then standardised across three terms for each pairwise combination by scaling the values for each component by dividing it by the absolute value of the most extreme value (Bloom, Northfield, and Crowder 2019). Standardisation made each term's relative strength comparable between shrubs and open spaces with different plant and nematode functions (Bloom, Northfield, and Crowder 2019).

2.5 | Statistical Analyses

To assess how the presence of shrubs affected both the compositional change of plant and nematode communities and the alteration of ecosystem function as a result of these changes, we used generalised linear mixed models (GLMM) and linear mixed models (LME) to explore the shrub effects on the richness and functions of plant and nematode communities, respectively, with presence of shrubs as the fixed variable and site as the random variable (Table S1). We used type III ANOVA tests to assess significant differences. We used nonmetric multidimensional scaling ordination (NMDS) and nonparametric multivariate analysis of variance (NPMANOVA) with 999 permutations based on the Bray–Curtis dissimilarity to explore the shrub effects on plant and nematode community composition.

We calculated how environmental factors (climate, biotic, and soil) changed across the baseline and comparison communities. Because these environmental factors may covary, we checked the multicollinearity among the seven environmental factors and found that it was less than three. We applied the Box-Cox transformations to the linear mixed models to approach normality. We used multiple regression models and linear mixed models together to explore the effects of climate, biotic, and soil factors on the three terms of the Price equation and relationships between the three terms and both plant biomass and nematode C metabolism. We calculated the marginal and conditional R^2

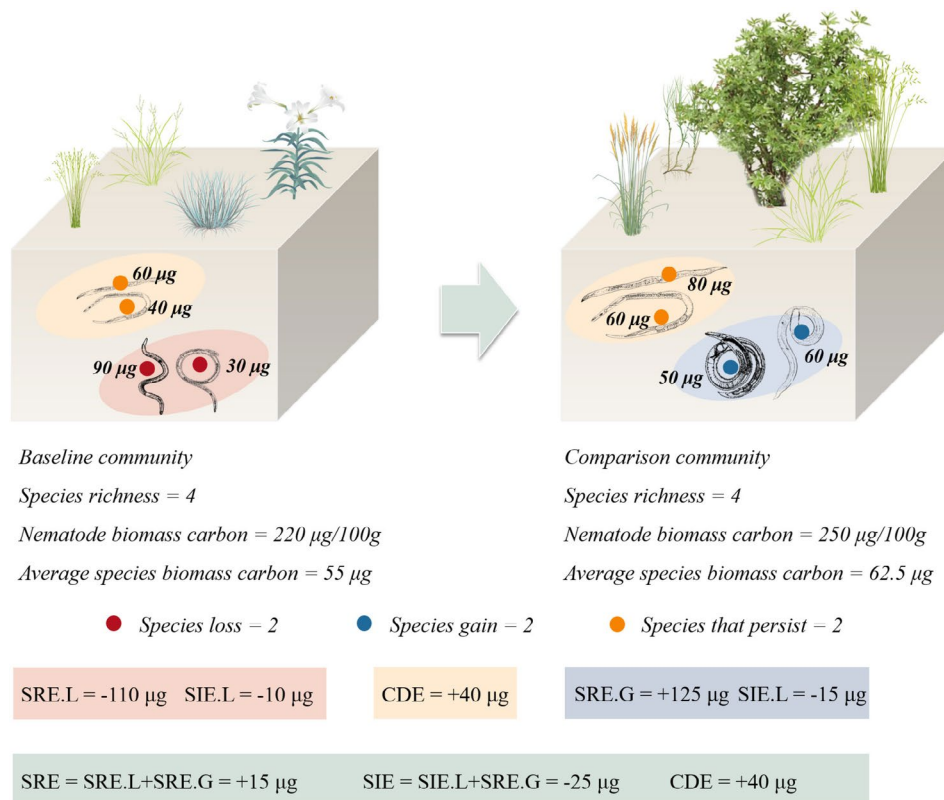


FIGURE 1 | Schematic illustration of compositional change and the contribution to altered nematode biomass carbon based on the modified Price equation partition suggested by Bannar-Martin et al. (2018), with soil nematode community as an example. The numbers in the boxes indicate the biomass carbon per nematode. species losses (red), species gains (blue), and change in persistent species (orange) are additive components of the relationship between composition and nematode biomass carbon. SRE.L, species richness effect of loss; SRE.G, species richness effect of gain; SIE.L, Species identity effect of loss; SIE.G, Species identity effect of gain; CDE, context-dependent effect; SRE, species richness effect; SIE, species identity effect.

for each multiple regression model using the ‘r.squaredGLMM’ function in the ‘MuMIn’ package.

All analyses were performed in R 4.1.3 with package ‘price-Tools’ version numbers: 0.0.0.9000 (Bannar-Martin et al. 2018), ‘lme4’ version numbers: 1.1–28 (Bates et al. 2015), ‘glmmTMB’ version numbers: 1.1.3 (Brooks et al. 2017), ‘vegan’ version numbers: 2.5–7 (Oksanen et al. 2018), ‘MuMIn’ version numbers: 1.46.0 (Barton 2018), and ‘lmerTest’ version numbers: 3.1–3 (Kuznetsova, Brockhoff, and Christensen 2017).

3 | Results

Over the 378 plots on the Qinghai-Tibet Plateau, 185 plant species were recorded, with plant biomass ranging from 0.77 to 38.75g. Plots with shrubs had significantly altered plant community composition ($F=16.083$, $p<0.001$), and significantly increased plant biomass (+18.4%, 18.3g, $p<0.001$, Figure S3). However, plant richness did not vary between plots with and without shrubs ($p=0.649$). Similarly, 45 nematode genera were recorded, with nematode biomass, production, and respired C ranging from 0.60 to 273.43g, 0.21 to 75.69g, and 1.31 to 180.81g, respectively. Plots with shrubs had significantly altered nematode community composition ($F=4.330$, $p<0.001$) and also had increased nematode richness (+19.0%, 2.2, $p<0.001$),

biomass (+43.1%, 15.2µg, $p<0.001$) production (+41.5%, 4.9µg, $p<0.001$), and respired C (+35.4%, 11.7µg, $p<0.001$, Figure S4).

3.1 | Price Equation Analysis

Averaging across all pairwise comparisons, the species richness effect was positive for plant biomass (+7.7g, 95% CI: 2.8 to 12.6g) and explained 42% of the changes in plant biomass (Figure 2a,b, Figure S5a). However, the species identity effect (−1.6g, 95% CI: −3.7 to 0.4g) was negative, such that the identity effect partially cancelled the richness effect, and these terms combined explained only 33% of the changes in plant biomass. These results indicate that the species that were gained (and lost, although species losses were less common) had contributions to function that were slightly below average. Finally, the context-dependent effect was positive (+12.3g, 95% CI: 8.6–16.1g) for plant biomass and explained twice as much variation (67%) in plant biomass, compared with the sum of species richness and identity effects. Thus, increased plant biomass in plots with shrubs resulted mostly from the context-dependent effect (Figure 2b, Figure S5a).

For functions provided by nematodes, and again averaging across all pairwise comparisons, species richness effects were strongly positive. Species richness effects increased nematode biomass (+10.1µg, 95% CI: 7.9–12.4µg), production (+3.2µg, 95%

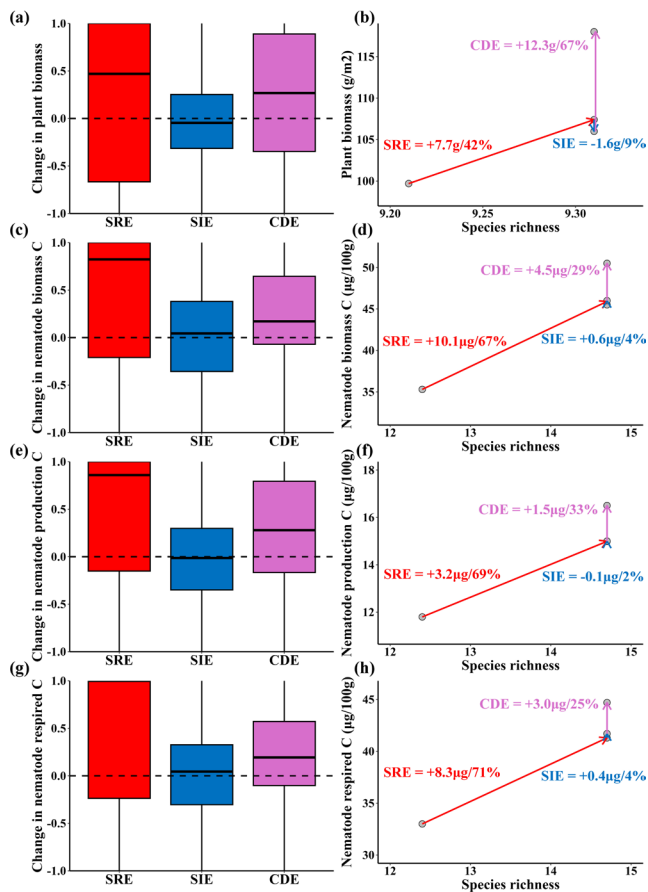


FIGURE 2 | Functional response of plant and nematode communities to the presence of shrubs. The left side boxplot panels depict the responses of plant biomass (a), nematode biomass C (c), nematode production C (e), and nematode respired C (g) to the presence of shrubs. On the boxplots, the horizontal line is the median, the upper and lower hinges correspond to the first and third quartiles, and the whiskers extend to the highest and lowest values. The right side panels (b, d, f, h) depict corresponding vector figures. SRE, species richness effect; SIE, species identity effect; CDE, context-dependent effect.

CI: 2.5–3.9 μg), and respired C (+8.3 μg , 95% CI: 6.6–10.0 μg), explaining 67%–71% of the changes in nematode C metabolism (Figure 2c–h, Figure S5b–d). In contrast with plant biomass, species identity had little effect on nematode functions (biomass C: +0.6 μg , 95% CI: –0.9 to 2.1 μg ; production C: –0.1 μg , 95% CI: –0.4 to 0.3 μg ; respired C: +0.4 μg , 95% CI: –0.4 to 1.3 μg), meaning that species gains and losses were random with respect to function. The context-dependent effect was positive for nematode C metabolism (biomass C: +4.5 μg , 95% CI: 2.2–6.8 μg ; production C: +1.5 μg , 95% CI: 0.8–2.2 μg ; respired C: +3.0 μg , 95% CI: 1.6–4.4 μg). However, in contrast with plant biomass, the context-dependent effect was less than half (ranging from 25% to 33%) as large as the sum of species richness and identity effects. Thus, increased nematode C metabolism in plots with shrubs resulted mostly from the species richness effect (Figure 2c–h, Figure S5b–d).

3.2 | Environmental Drivers

Plant biomass and nematode C metabolism differed substantially in how their price equation terms responded to environmental

variables. Biotic factors were more important than soil factors in predicting changes in plant biomass, whereas soil factors tended to have stronger effects than biotic factors on changes in nematode C metabolism (Figure 3, Table S2–S8). Specifically, bacterial richness ($p=0.010$) amplified the effect of species richness on plant biomass (Figure 3j, Tables S3 and S5). Soil moisture amplified ($p<0.05$ for both variables) the effects of species richness and context-dependence, while soil electrical conductivity mitigated ($p<0.05$ for both variables) the effects of species richness and identity on nematode C metabolism (Figure 3a–i, Tables S4 and S6–S8). However, climatic variables had little effect on the three Price equation terms for plant and nematode functions (Table S2).

3.3 | Functional Linkage Between Plant and Nematode Community

Species richness effects on plant functions and nematode functions were positively associated. The strength of the species richness effect on plant biomass was positively associated with the strength of the species richness effect on nematode biomass, production, and respired C ($p<0.05$ for all variables) (Figure 4b, Table S9).

4 | Discussion

Turnover in community composition is a dominant form of biodiversity change (Hillebrand et al. 2018), though how turnover leads to changes in ecosystem functions and/or services remains elusive (Winfrey et al. 2018). By quantifying how species richness, species identity, and changes in the abundance and per-capita function of persisting species affect plant biomass and nematode C metabolism, we provide new insight into the relationship between compositional changes and ecosystem functions. Further, these results advance our understanding of global climate change's effects on biodiversity-function relationships, both above and below ground.

4.1 | Plant and Nematode Community Responses

Plant communities play crucial roles on the Qinghai-Tibet Plateau because the energy transfer for which they are responsible modulates resource availability to soil communities and food webs (DeCock et al. 2021; Wardle et al. 2004). Our results align with our first hypothesis that the plots with shrubs had increased understory plant biomass, meaning that the understory plant communities can provide more resources to support soil food webs and higher trophic levels. Using a modified version of the Price equation, we found that increases in plant function (biomass) in plots with shrubs were mostly due to context-dependent effects, which were roughly twice as large as the species richness and identity terms added together (Figure 2). Species identity effects had different signs and were lower in magnitude than their richness effects. These results mean that lost and gained species tended to have functional contributions that were lower than the average species. The presence of shrubs can intensify resource competition and reshuffle understory plant communities by favouring species that are better resource competitors, therefore increasing plant biomass (Costa et al. 2017; Hortal et al. 2015; Losapio et al. 2018). This is visible in a strong, positive effect

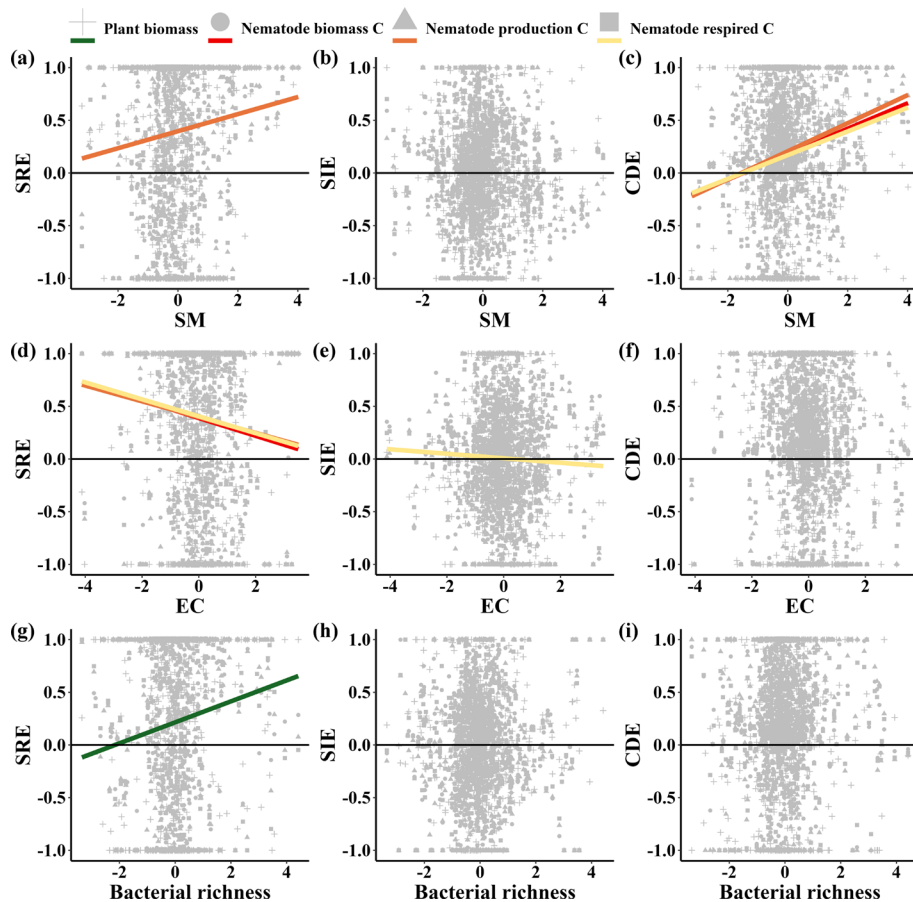


FIGURE 3 | The effects of environmental factors on three Price equation terms for both plant and nematode functions. (a–c) for SM, soil moisture; (d–f) for EC, soil electrical conductivity; (g–i) for bacterial richness; SRE, species richness effect; SIE, species identity effect; CDE, context-dependent effect.

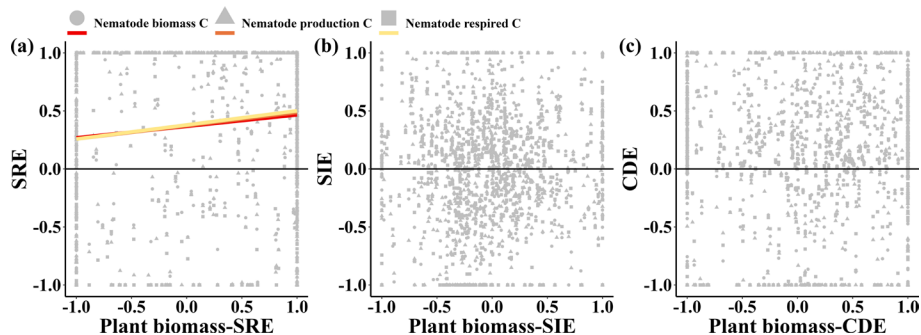


FIGURE 4 | Correlation of the three price equation terms between plant and nematode functions. (a) for SRE, species richness effect; (b) for SIE, species identity effect; (c) for CDE, context-dependent effect.

of species richness, even after accounting for the fact that species turnover comprised species with lower overall importance to functions, as described above. However, changes in plant biomass in plots with shrubs were more driven (67%) by persisting species increasing their functional contributions (i.e., positive context-dependent effect), either because these species become more abundant or because they produce more biomass per individual. This makes ecological sense, as the presence of shrubs often ameliorates microhabitat conditions and increases the accrual of organic matter and nutrients,

which can promote the success of plants (either through increased abundance or increased per-capita function, either of which could drive the CDE term) that persist in the community (Brooker 2006; Michalet et al. 2014; Weber-Grullon et al. 2022). These results, specifically the partial cancelling of richness effects by identity effects and the outsized role of the context-dependent effect, align with previous ecological applications of the Price equation to observational data (Winfree et al. 2015; Genung, Fox, and Winfree 2020; Hogan et al. 2024).

Nematode communities are essential to global soil C cycles because they regulate the decomposition of organic matter, nutrient mineralisation, and soil microorganisms (Bongers and Bongers 1998; Ferris 2010). Plots with shrubs had higher values for all aspects of nematode C metabolism (respiration, production, and biomass C), indicating a fast turnover of the organic matter, possibly resulting in high rates of decomposition and C mineralization. The increase in nematode functions in plots with shrubs was driven mainly (67%–74%) by random species gains (and, to a lesser extent, losses; Figure 2d,f,h). This novel result contrasts with our plant biomass analysis (Figure 2b) and other functions of aboveground communities, such as crop pollination by bees (Winfree et al. 2015) and the biomass of dung beetles (Hogan et al. 2024), which were mostly driven by the context-dependent effect. A possible explanation was that most nematode species provided a similar level of functioning, limiting the potential magnitude of species identity effects. However, we found that plant and nematode species were similarly variable in their contributions to function (Figures S6 and S7). Thus, the limited species identity effects in nematode communities reflect that losses and gains of nematode species happened randomly with respect to function. This contrasts with previous Price equation analyses that have found the mostly rare species lost and gained between sites, leading to identity effects that partially or mostly cancel their corresponding richness effect (Winfree et al. 2015; Genung, Fox, and Winfree 2020; Hogan et al. 2024). Notably, plots with shrubs were more favourable for persisting nematodes, as seen in the positive context dependence effect. Shrubs can increase resource availability and provide milder microhabitats, which may explain the moderate increase in nematode richness in plots with shrubs, from around 12 to 14 nematode genera on average (Figures S4a and S6b–d). These species gains were a key driver that enhanced the nematode community's role in accelerating C turnover in plots with shrubs (Biederman and Boutton 2009; Franco et al. 2019).

In sum, we found that changes in plant (biomass) and nematode (C metabolism) functions varied in whether they were driven mostly by changes in the abundance and per-capita function of persisting species (plant biomass) or random species gain (nematode C metabolism). The former is an unsurprising result, based on what we have learnt from previous analyses of aboveground functions with the ecological Price equation. However, the latter result is novel and highlights how a changed environment (plots with shrubs vs. plots without shrubs) in aboveground plant communities can increase belowground functions by making conditions more favourable for, and increasing the species richness of, belowground communities. More broadly, the functions of above- and belowground communities can increase with shrub encroachment, which can accelerate decomposition and C turnover and enhance the ecosystem functioning and stability on the Qinghai-Tibet Plateau.

4.2 | Drivers of Plant Nematode Function

Consistent with the second hypothesis, the three Price equation terms for plant and nematode functions were related to environmental factors, although the relative importance of biotic and

soil variables shifted between plant and nematode functions. Biotic variables were important in predicting the three Price equation terms for plant function, whereas soil variables tended to have strong effects on the three Price equation terms for nematode functions.

For plant communities, soil bacterial richness amplified the species richness effect on plant biomass. Many studies have shown that bacterial diversity can promote germination and stimulate plant growth by enhancing resistance to pathogens and environmental stresses and by promoting higher enzyme activity (Weidner et al. 2015). For nematode communities, soil moisture amplified species richness and context-dependent effects on C metabolism. Nematodes dwell in soil-water films and are sensitive to soil condition changes (Zhang et al. 2023). Soil moisture can provide more habitable space and resources, which attracts more nematode colonisation and promotes the abundance and body size of nematodes that persist in communities (Andriuzzi et al. 2020; Franco et al. 2019). Moreover, soil electrical conductivity can affect species osmotic pressure and limit the colonisation and survival of nematodes, therefore mitigating the species richness and identity effects on C metabolism.

Moreover, the fixed effects (environmental factors) in the multiple regression models explained 1%–5.8% of the variance in the three Price equation terms for functions; however, the conditional variance (random plus fixed effect) explained 30.6%–65.3% of the variance in the three Price equation terms for functions, aligned with the changes in the five Price equation terms for mammals (Hogan et al. 2024). This suggests that variation among sites is playing a stronger role in plant and nematode functions than environmental factors. Therefore, we speculated that other environmental factors may have an important impact on plant and nematode functions (Jaillard et al. 2014). Future studies should also attempt to examine the effects of other environmental factors on the relationship between biodiversity and ecosystem functioning.

4.3 | The Linkage Between Plant and Nematode Function

Our results align with our third hypothesis that the changes in plant and nematode functions are related. We emphasise that the positive relationship occurred only for species richness effects, which indicated that the gain of plant species had facilitated the gain of nematode species and increased the functions provided by the nematode community in plots with shrubs. Increased plant diversity decreased niche overlap and competition for resource quantity and quality, leading to increased nematode diversity and more complete resource use (Bloom, Northfield, and Crowder 2019; Hodson et al. 2014; Winfree et al. 2015). These results suggest that plant diversity not only resulted in an increase in plant biomass but also promoted nematode C metabolism, which may accelerate decomposition and C turnover on the Qinghai-Tibet Plateau. Therefore, future biodiversity conservation and maintenance of ecosystem functions should focus on increasing plant diversity to promote the diversity and functions of belowground communities.

Author Contributions

S.C. and L.A. designed the study; Z.L., J.C., H.S., H.C., and Z.Y. performed the field and laboratory measurements; A.Z. and S.X. performed statistical analysis and made the figures; A.Z. and M.A.G. drafted the manuscript. All authors contributed substantially to revisions.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available on Figshare at <https://doi.org/10.6084/m9.figshare.28136399.v2>.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70070>.

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Supporting Information

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