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Research

Plant genotypic diversity effects on soil nematodes vary with trophic level

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Summary

- At local spatial scales, loss of genetic diversity within species can lead to species loss. Few studies, however, have examined plant genotypic diversity effects across trophic levels.
- We investigated genotypic diversity effects of *Phragmites australis* on belowground biomass and soil nematode communities.
- Our results revealed that belowground plant biomass and nematode abundance responses to plant genotypic diversity were uncoupled. Decreasing plant genotypic diversity decreased the abundance of lower, but not higher trophic level nematodes. Low plant genotypic diversity also decreased the structural footprint and functional indices of nematodes, indicating lowered metabolic functioning of higher trophic level nematodes and decreased soil food web stability.
- Our study suggests that plant genotypic diversity effects differ across trophic levels, taxonomic groups and ecosystem functions and that decreasing plant genotypic diversity could destabilise belowground food webs. This highlights the importance of conserving intraspecific plant diversity.

Introduction

Human impacts are causing the rapid loss of biodiversity at local to global scales (Chapin *et al.*, 2000). Biodiversity loss may have profound ecological consequences because high-diversity communities are usually more productive and stable than low-diversity communities (Tilman, 1996; Tilman *et al.*, 1997; Hector *et al.*, 1999; Lehman & Tilman, 2000). Biodiversity–ecosystem functioning (BEF) studies have generally focussed on how plant diversity influences plant productivity (Duffy *et al.*, 2007; Miki *et al.*, 2010). In recent decades, however, it has been recognised that diversity change at one trophic level can affect other trophic levels (Hooper *et al.*, 2005; Schuldt *et al.*, 2019), that is 'vertical species loss' effects (Duffy *et al.*, 2007). For example, decreasing plant diversity supports fewer herbivores and predatory arthropods (Siemann *et al.*, 1998; Knops *et al.*, 1999; Haddad *et al.*, 2009) and pollinators (Biesmeijer *et al.*, 2006). Taking a multitrophic perspective can elucidate BEF relationships (Bardgett *et al.*, 2008; Miki *et al.*, 2010; Scherber *et al.*, 2010; Crawford & Rudgers, 2013).

The response of consumers to plant diversity may depend on trophic level (Scherber *et al.*, 2010). Lower trophic level animals, such as herbivores and bacterivores, are more responsive to changes in plant species diversity and composition than organisms from higher trophic levels (De Deyn *et al.*, 2004; Scherber *et al.*, 2010). High trophic level consumers may have access to a larger variety of prey than lower trophic level consumers (Scherber *et al.*, 2010), thus the strength of bottom-up control by plant diversity may be weaker at higher trophic levels. Bennett *et al.* (2020) suggested that a lack of differences in predators among plant diversity treatments may be due to diet shifts. Schuldt *et al.* (2019) indicated that plant diversity effects on species richness at higher trophic levels may also be masked by modifications in prey abundances. Weaker effects of plant diversity on higher trophic levels may also reflect time lags (Cortois *et al.*, 2017). The relationships between multitrophic biotic groups and plant diversity need to be studied further (Bennett *et al.*, 2020).

Studies of plant diversity effects are focussed relatively on diversity at the species level and above (e.g. functional diversity), with fewer centred on intraspecific variation, especially its effect on multiple trophic levels. Intraspecific genotypic diversity, however, also influences ecological processes and communities (Wimp *et al.*, 2004; Hughes *et al.*, 2008; Raffard *et al.*, 2019). Within species, plant genotypes can differ in traits. As trait variation underlies the ecological effects of plant species diversity, intraspecific variation may play a similar role in structuring communities and mediating ecosystem functions (Madritch & Hunter, 2002; Whitham *et al.*, 2006; Hughes *et al.*, 2008). While genotypic diversity has generally been assumed to have weaker ecological consequences than species diversity, recent studies have shown that genotypic diversity has similar (Johnson *et al.*, 2006;

Cook-Patton *et al.*, 2011), or even stronger, effects (Crawford & Rudgers, 2013) in structuring consumers. For example, the genetic diversity of *Solidago altissima* positively affected arthropod diversity and equalled the effects of species diversity (Crutsinger *et al.*, 2006). Similarly, greater genetic diversity of *Brassica oleracea* harboured a higher abundance of herbivorous arthropods, due to genetic control of foliar glucosinolates (Bustos-Segura *et al.*, 2017). Other studies have shown that species-specific herbivore traits, such as diet, mobility and larval survival, can lead to different responses of insect herbivores to plant genetic diversity (Abdala-Roberts *et al.*, 2015; Wetzel *et al.*, 2018).

Soil nematodes consist of a wide range of taxa at many trophic levels, including first-order and second-order consumers. Plants provide the major carbon source for soil microbe and nematode communities that in turn help make nutrients available for plants (Wardle & Bardgett, 2004; Geisen *et al.*, 2019). Given their reliance on plants, it is likely that belowground communities respond strongly to plant diversity. Previous work on the response of belowground communities to plant species diversity have found that both plant species diversity and identity influence belowground organisms (Wardle *et al.*, 1999, 2003; De Deyn *et al.*, 2004; Ball *et al.*, 2009; Sherber *et al.*, 2010; Kostenko, 2015). Few studies, however, have tested the hypothesis that intraspecific plant variation influences belowground organisms. Some studies have found that soil microbial communities respond unimodally to plant genetic diversity (Schweitzer *et al.*, 2011), while others have found that plant genotypes accumulate different soil invertebrate communities (Vandegehuchte *et al.*, 2011; Fitzpatrick *et al.*, 2018; Wilschut *et al.*, 2019). Nonetheless, the effects of plant genetic diversity in the soil have yet to be examined across trophic levels (Koricheva & Hayes, 2018).

We investigated the influence of genotypic diversity and identity of *Phragmites australis* across trophic levels in a soil microfood web. Soil nematodes were used to represent soil microfood webs because of their abundance, ubiquitous distribution and broad representation across trophic levels (Yeates, 1981; Yeates *et al.*, 1993; Bongers & Ferris, 1999). Nematodes are an active component of the plant rhizosphere (Hoeksema *et al.*, 2000), important in regulating soil nutrient cycling, closely associated with plant communities, and respond rapidly to changes in microbial communities caused by variation in resources that plants transfer to soils by litter or root inputs (Yeates, 1999). Nematodes also play a role in plant community development (Bardgett & Cook, 1998). Thus, nematodes are a model system for studying soil food web and ecological processes (Bongers & Ferris, 1999). As decreasing nematode abundance and diversity are associated with declining plant species diversity (De Deyn *et al.*, 2004) and plant functional diversity (Chen *et al.*, 2016), we hypothesised that plant genotypic diversity will also influence soil nematode communities.

Recent biodiversity–ecosystem functioning (BEF) studies have emphasised functional group responses (Semchenko *et al.*, 2017; Ebeling *et al.*, 2018). Species richness and other taxonomy-based measurements of biodiversity have been used to quantify the relationship between producers and other trophic groups (Scherber *et al.*, 2010). However, they cannot detect variation in the functional conditions of communities, which directly relate to the ecosystem functions and services that communities provide (Dias *et al.*, 2013). Explicitly incorporating taxonomic as well as functional measures are needed to understand BEF relationships (Scherber *et al.*, 2010). Thus, we analysed nematode metabolic footprints, representing the amount of carbon and energy entering different functional groups (Ferris, 2010), to reflect the functional condition (e.g. metabolic rates and self-regulation) of the soil microfood web. Nematode metabolic footprints include enrichment, structure and functional components. The enrichment footprint index indicates the quantity and quality of labile organic matter in the soil, the structure footprint index implies the ability of soil communities to tolerate environmental disturbance, while the functional footprint index can suggest the stability of the soil system (Ferris, 2010).

In this study we tested the hypotheses that: (1) belowground trophic groups are differentially influenced by plant genotypic diversity and identity; and (2) plant genotypic diversity impacts taxonomic (abundance and diversity) and functional (metabolic footprint) aspects of the nematode communities.

Materials and Methods

Field site and experiment design

To investigate how plant genotypic diversity and identity affect soil nematode communities, we established a field common-garden experiment in Dongtan, Chongming Island, Shanghai (31°30′N, 121°59′E), China (Supporting Information Fig. S1). *Phragmites australis* is one of the dominant plant species in the high tide zone of the Dongtan wetlands and shows high genetic diversity. Randomly distributed independent clumps of *P. australis* were collected from the low tidal zone of Dongtan, *c.* 100 m from our common-garden site and genotyped using published microsatellite loci (Table S1). Genotyping using microsatellite markers is a common practice in genotype diversity–ecosystem function studies. Six genotypes of *P. australis* were chosen at random and designated A–F. To test the effect of genotype identity and diversity, experimental plots were transplanted with one, two, three or six genotypes of plants drawn from the genotype pool (A–F) using a random partition design (Bell *et al.*, 2009; see Table 1 and Fig. S1 for details). Using this design, each genotype is represented at the same frequency at each genotypic diversity level. Therefore, the random partition design removes the possibility that highly influential genotypes are overrepresented at the highest levels of genotypic diversity (Huston, 1997). In total, there were 48 plots: 12 monoculture plots, 18 plots of two genotypes, 12 plots of three genotypes and six plots of six genotypes. Each plot was 1 m × 1 m. Plots were randomised completely and spaced 5 m apart. We transplanted six individuals of *P. australis* per plot, with each mixture plot consisting of an equal number of individuals of component genotypes. Plots were established in May 2011. Along the edges of each plot, PVC sheets were buried into the soil to a depth of 0.6 m to prevent *P. australis* from growing out of the plot or

colonisation from outside of the plot. The upper part of the sheets was 0.2 m above the ground.

Belowground plant biomass

After two growing seasons (29 October 2013), belowground plant samples were collected by randomly taking five (6 × 30 cm, width × depth) soil cores from each plot (20 cm from plot margins). Soil cores were mixed to form a composite sample for each plot. Belowground plant material was washed immediately, oven dried at 50°C to constant weight and weighed. Belowground plant biomass was expressed as g m^{-2}.

Nematode extraction and identification

We took an additional six soil cores of 20 cm depth and 2 cm diameter from each plot and mixed them to form a composite sample for nematode extraction. A subsample of 20 g of fresh soil was used to determine soil moisture content by drying at 65°C for 2 d and weighing. Nematodes were extracted from a subsample of 200 g fresh soil using the Ludox™ flotation method (Griffiths *et al.*, 1990) and fixed by addition of hot formaldehyde solution (4%). Nematodes were then counted, identified (100 randomly-selected individuals per plot or all individuals if fewer than 100) to genus level using ×1000 magnification and classified into four feeding groups (bacterial feeders, plant feeders, algal feeders and omni-carnivores) following Yeates *et al.* (1993). Bacterial feeders, plant feeders and algal feeders are usually classified as low trophic level nematodes, and omni-carnivores are classified as high trophic level nematodes. Nematode abundance was expressed as individuals per 100 g dry weight (DW) soil, diversity was expressed as the genera richness and Shannon–Wiener Diversity Index at the genus level (H' diversity).

The metabolic nematode footprint was calculated to assess the amount of C and energy entering the soil food web (Ferris, 2010; Ferris *et al.*, 2012). We calculated the metabolic nematode footprint in each plot, using enrichment, structure and functional footprints as indicators. The enrichment footprint (F_e) represents the metabolic footprint of nematodes that respond quickly to resource changes (coloniser–persister groups 1 and 2, to be described later), which are mostly low trophic level nematodes such as bacterial feeders. The structure footprint (F_s) is the metabolic footprint of nematodes that can regulate soil food web functions (coloniser–persister groups 3–5, to be described later), which are mainly higher trophic level carnivorous and omnivorous nematodes. The functional footprint (F_f) integrates the enrichment and functional footprints. Higher functional footprints indicate that the productivity and turnover rate of the prey (enrichment indicators of the low trophic levels) are sufficient to maintain the predators (structure indicators of the high trophic levels), so that the system is in metabolic balance. Nematode footprints were calculated as follows. First, nematode taxa were divided into five coloniser–persister (cp) scale groups, with cp 1 to cp 5 indicating life-history strategies ranging from r-strategist to K-strategist (Bongers, 1990; Ferris *et al.*, 2001). The fresh weight (FW) (μg) of each nematode genera was obtained from the nematode parameter database Nematode Plant Expert Information System (http://nemaplex.ucdavis.edu). The metabolic footprint was calculated using the formula $F = \sum\left(N_t\left(0.1\left(W_t/m_t\right)+0.273\left(W_t^{0.75}\right)\right)\right)$, where N_t, W_t and m_t are the abundance, FW and cp value of genus t, respectively. The functional footprint (F_f) was calculated as $F_f = (F_e \times F_s)/2$.

Table 1 Details of the experimental design.

Plant genotype diversity level	Genotype combinations	Number of replicates for each genotype combination	Total number of plots
1	A, B, C, D, E, F	2	12
2	AF, BE, CD AB, CF, DE AD, BF, CE	2	18
3	ABD, CEF ABE, CDF ABF, CDE	2	12
6	ABCDEF	6	6

Data analysis

To test whether plant genotype identity (using data from only monoculture plots) or diversity (using data from all plots) affected belowground plant biomass, abundance, richness and H' diversity of total nematodes and of each nematode feeding group, and nematode metabolic footprints, we used one-way analysis of variance (ANOVA) followed by Tukey's honest significant difference (HSD) test for pairwise comparisons (IBM SPSS Statistics v.19; IBM Corp., Armonk, NY, USA). Data were log or reciprocal transformed to meet normality before the ANOVA analyses. The R package EFFECTS was used to show confidence interval symmetry of transformed data.

Additionally, general linear mixed models were used to examine the effects of genotype identity (i), genotypic diversity (D) and partition genotype pools (Q) on plant belowground biomass and all ecological indices of nematodes (R v.3.1.1; R Development Core Team, Vienna, Austria). Genotypic combination (M) was used as a random term. This general linear mixed model partitioned the effects of plant genotypic diversity and genotype identity on measured responses. In combination with the random partition experimental design, it assessed diversity effects when the contribution of individual genotypes on belowground plant biomass and soil nematode parameters in the mixtures are unknown. Our model followed Bell *et al.* (2009):

$$y = \beta_0 + \beta_D x_D + \sum_i^S \beta_i x_i + \beta_Q x_Q + \beta_M x_M + e$$

where β_0 and e are the intercept and residual, β_D, β_i, β_Q and β_M are coefficients of genotypic diversity – x_D for genotype identity, x_i for genotype identity, x_Q for partition genotype pools and x_M for composition, respectively, and S is the total number of genotypes. We used the R package NLME for the analysis. We tested all

factors, then removed nonsignificant factors to obtain the simplest model. Only the significant items retained are shown in the results table.

One-way analysis of similarities (ANOSIM) was used to test the difference of nematode community structure between different plant genotypic diversity treatments. Bray–Curtis similarity was used to calculate pairwise similarity and data was $\log(x + 1)$ transformed before analyses. When the ANOSIM result was significant, we then used SIMPER to identify which nematode genus contributed most to the significant difference of nematode community structures. Both ANOSIM and SIMPER analyses were done in PRIMER (v.5.2; Prime-E, Plymouth, UK).

Two mechanisms for BEF relationships have been proposed: (1) the selection effect, in which multispecies communities have a higher probability of containing a species/genotype that supports greater functions; and (2) the complementarity effect, in which species/genotypes facilitate each other or have complementary resource use (Aarssen, 1997; Loreau & Hector, 2001). In this study, we calculated net effects and transgressive overyielding of genotypic diversity on total belowground plant biomass of *Phragmites australis*, abundance and richness of total nematodes and of each nematode feeding group, and nematode metabolic footprints. Within each measured response, the net effect combined the selection effect and the complementarity effect (Loreau & Hector, 2001). The net effect indicates the mean effect of diversity, that is whether there is a significant difference between the mean response in the highest level of genotypic diversity and the average monoculture yield value of the component genotypes (Cardinale *et al.*, 2006). Transgressive overyielding is indicative of complementarity effects (Cardinale *et al.*, 2006; Schmid *et al.*, 2008) and tests whether the highest level of genotypic diversity performed better than the best-performing monoculture. Net effects (LRnet) and transgressive overyielding (LRtrans) were calculated in accordance with Cardinale *et al.* (2006):

$$\mathrm{LRnet} = \log_e\left(\frac{P_{\mathrm{pi}}}{P_{\mathrm{mi}}}\right)$$

$$\mathrm{LRtrans} = \log_e\left(\frac{P_{\mathrm{pi}}}{P_{\mathrm{maxi}}}\right)$$

where P_{pi} refers to the parameters of the highest genotypic diversity plot, P_{mi} refers to the average parameter value of all single genotypes within the highest genotypic diversity plot and the P_{maxi} is tested parameters of the best-performing monoculture plot. Generally speaking, LRnet > 0 represents a positive effect of diversity, that is, the diverse mixtures performed better than the average monoculture. LRtrans > 0 indicates that mixtures performed better than the best-performing monoculture.

Data availability

The data supporting this article can be found in electronic supplementary material and Dryad Digital Repository (Dryad dataset: https://doi.org/10.5061/dryad.1g1jwstsv).

Results

The mean belowground plant biomass of all the monoculture plots was 1455.60 ± 547.05 g m^{-2} (mean ± SD). Genotype identity had significant effects on total belowground plant biomass ($F_{1,5} = 4.925$, $P < 0.05$) of *Phragmites australis* (Table 2). Monocultures of genotype C and genotype D yielded the highest plant belowground biomass (Figs 1, S2). By contrast, plant genotypic diversity had no significant effect on belowground plant biomass ($F_{1,3} = 0.377$, $P > 0.05$) (Table 2). Mixed linear model analyses indicated that belowground plant biomass was mainly influenced by genotypes C, D and A (Table 3).

One-way ANOVA showed that the genus richness of total nematodes was significantly affected by plant genotype identity ($F_{1,5} = 5.246$, $P < 0.05$) (Table 2). Nematode genus richness was highest in monocultures with *P. australis* genotype E and lowest with genotype A (Figs 2, S2). Nematode genus richness within each feeding group was not significantly affected by plant genotype identity. In terms of H' diversity, only omni-carnivores responded significantly to plant genotype identity ($F_{1,5} = 5.194$, $P < 0.05$) (Table 2). Plant genotypic diversity showed no significant influences on both genus richness and H' diversity of total nematodes or each feeding group (Table 2).

Table 2 One-way analysis of variance (ANOVA) results showing the effects of plant genotype identity (using monoculture plots only) and diversity (using all plots) of *Phragmites australis* on belowground plant biomass and all measured nematode parameters of abundance, richness, diversity and metabolic footprints.

	Plant genotype identity			Plant genotypic diversity		
	F	df	*P*	*F*	df	*P*
Belowground plant biomass	**4.925**	**11**	**0.039**	0.377	47	0.770
Nematode abundance						
Total nematodes	0.635	11	0.683	**4.137**	**47**	**0.011**
Algal feeders	0.151	11	0.972	1.801	47	0.161
Plant feeders	1.130	11	0.435	1.607	47	0.201
Bacterial feeders	0.914	11	0.529	**3.722**	**47**	**0.018**
Omni-carnivores	2.351	11	0.164	1.238	47	0.307
Nematode genus richness						
Total nematodes	**5.246**	**11**	**0.034**	0.010	47	0.999
Algal feeders	0.800	11	0.588	1.366	47	0.265
Plant feeders	1.200	11	0.409	0.174	47	0.913
Bacterial feeders	1.189	11	0.413	0.073	47	0.974
Omni-carnivores	3.867	11	0.065	0.439	47	0.726
Nematode H' diversity						
Total nematodes	3.759	11	0.069	0.203	47	0.894
Algal feeders	1.754	11	0.256	0.504	47	0.681
Plant feeders	2.369	11	0.162	0.136	47	0.938
Bacterial feeders	2.991	11	0.107	0.346	47	0.793
Omni-carnivores	**5.194**	**11**	**0.035**	0.907	47	0.425
Nematode metabolic footprint						
Enrichment footprint	1.100	11	0.447	1.658	47	0.190
Structure footprint	0.519	11	0.756	**3.985**	**47**	**0.014**
Functional footprint	0.760	11	0.609	**3.517**	**47**	**0.023**

Bold indicates significant values ($P < 0.05$).

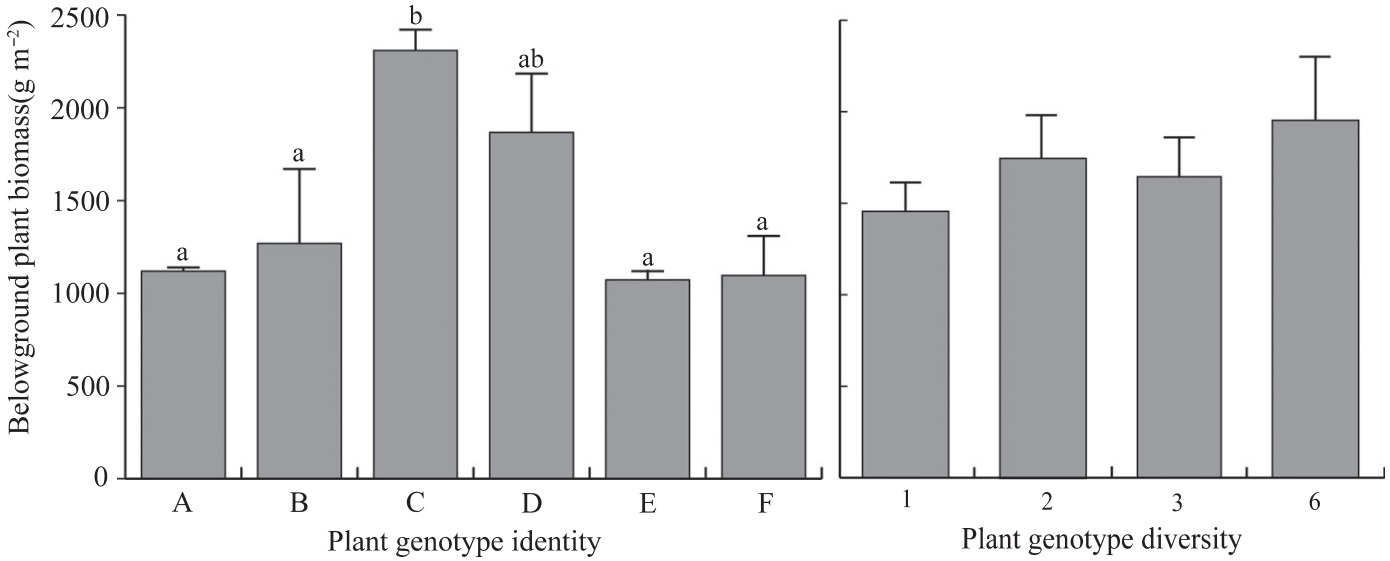

Fig. 1 Belowground plant biomass of *Phragmites australis* (mean with 1SE). Different letters indicate significant differences ($P < 0.05$) between different plant genotypes.

Table 3 Effect of plant genotype identity (genotypes A–F) and diversity (GD) of *Phragmites australis* on its belowground plant biomass and all measured nematode parameters of abundance, richness and metabolic footprints based on mixed linear model results.

	Fixed items	*F*	df	*P*
Belowground plant biomass	Genotype C	12.665	1, 19	0.002
	Genotype D	5.708	1, 25	0.025
	Genotype A	5.796	1, 19	0.026
Total nematode abundance	GD	17.026	1, 20	< 0.001
Bacterial-feeder abundance	GD	12.919	1, 20	0.002
Enrichment footprint	GD	5.189	1, 20	0.034
	Genotype E	5.003	1, 25	0.035
Structure footprint	GD	11.904	1, 20	0.003
Functional footprint	GD	10.362	1, 20	0.004
	Genotype E	5.374	1, 25	0.029

F, *F*-value; df, nominator and denominator degrees of freedom for *F*-value; *P*, error probability. Only significant items are shown in the table.

In the one-way ANOVAs, nematode abundance was not significantly affected by genotype identity, irrespective of the feeding group (Table 2). However, there was a significant effect of plant genotypic diversity on abundance of total nematodes ($F_{1,3} = 4.137$, $P < 0.05$) and bacterial-feeding nematodes ($F_{1,3} = 3.722$, $P < 0.05$) (Table 2). Nematode total abundance was much higher in the six-genotype treatment (1323 ± 139 individuals/100 g dry soil) than in the best-performing monoculture (genotype C, 853 ± 2 individuals/100 g dry soil). Both the net effect and transgressive overyielding effect were positive for total nematode abundance and bacterial-feeder abundance (LRnet > 0, LRtrans > 0) (Fig. 3). Among all of the mixed linear models, genotypic diversity was the best-performing model and significantly influenced total nematode abundance and bacterial-feeder abundance (Table 3).

In the one-way ANOVAs, plant genotypic diversity had a significantly positive effect on nematode structure and functional footprints (Table 2). The structure footprint ($F_{1,3} = 3.985$, $P < 0.05$) and functional footprint ($F_{1,3} = 3.517$, $P < 0.05$) significantly increased with increasing plant genotypic diversity (Table 2; Figs 2, S2). Both the net effect and transgressive overyielding effect were positive for these two nematode metabolic footprints (LRnet > 0, LRtrans > 0) (Fig. 3). The mixed linear model showed that the nematode enrichment footprint and functional footprint were both significantly influenced by plant genotypic diversity and genotype E, and structure footprint was significantly influenced by plant genotypic diversity (Table 3).

ANOSIM analyses showed that there was significant difference in nematode community structures between monocultures and six-genotype treatment ($R = 0.224$, $P = 0.045$) (Table S2). SIMPER analyses showed that the first three contributing genera to this difference were *Haliplectus* (bacterial feeders, contribution = 12.49%), *Terschellingia* (bacterial feeders, contribution = 9.78%) and *Diplolaimella* (bacterial feeders, contribution = 7.64%) (Table S2). The abundance of all these three genera increased from monocultures to six-genotype plant treatment.

Discussion

Plants are the major carbon and energy source fuelling belowground biota in soil food webs (Wardle & Bardgett, 2004). Greater plant inputs are likely to support more soil organisms. Our study found that greater genotypic diversity of *P. australis* did not increase belowground plant biomass but did increased soil nematode abundance. This suggests that, due to plant genotypic diversity, belowground producer and consumer biomass responses were uncoupled.

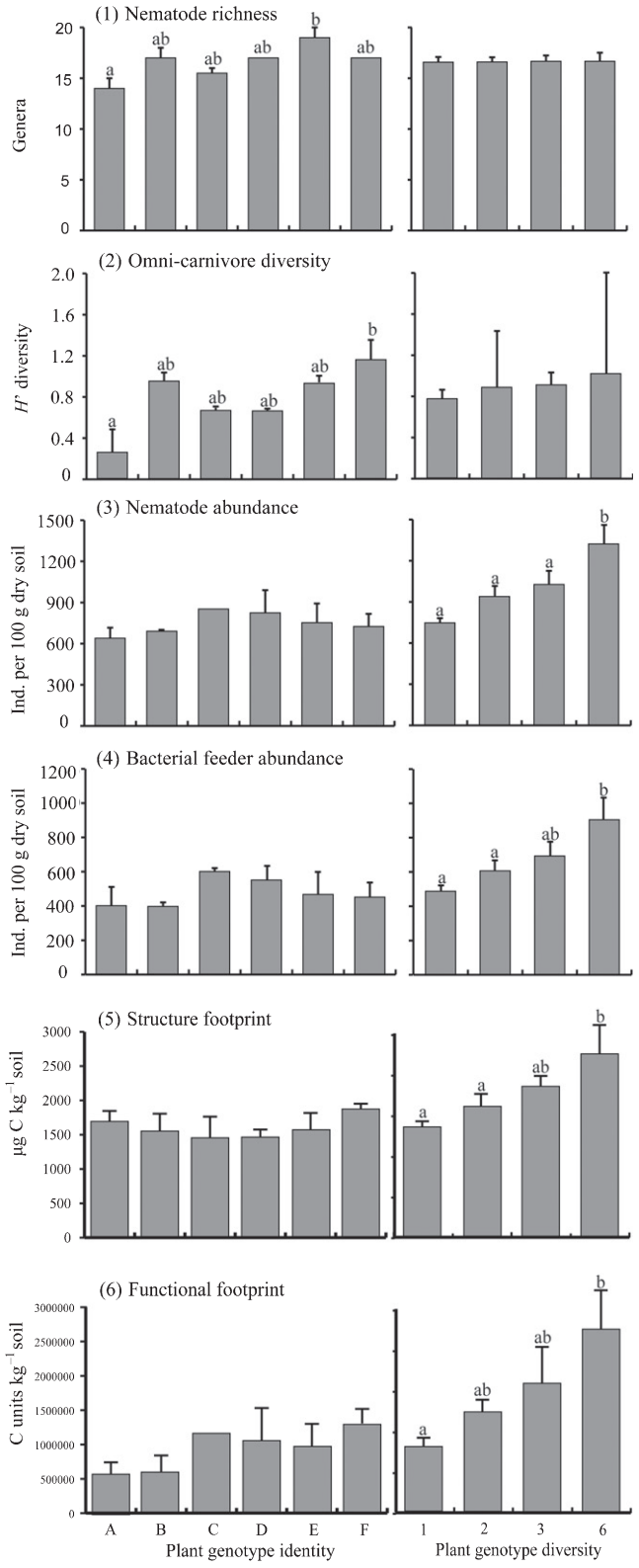

Fig. 2 (1) Total nematode genus richness, (2) omni-carnivore diversity, (3) total nematode abundance, (4) bacterial feeder abundance, (5) nematode structure footprint and (6) functional footprint (mean with 1SE). Different letters indicate significant differences ($P < 0.05$) between different plant genotypes or between different plant genotype levels.

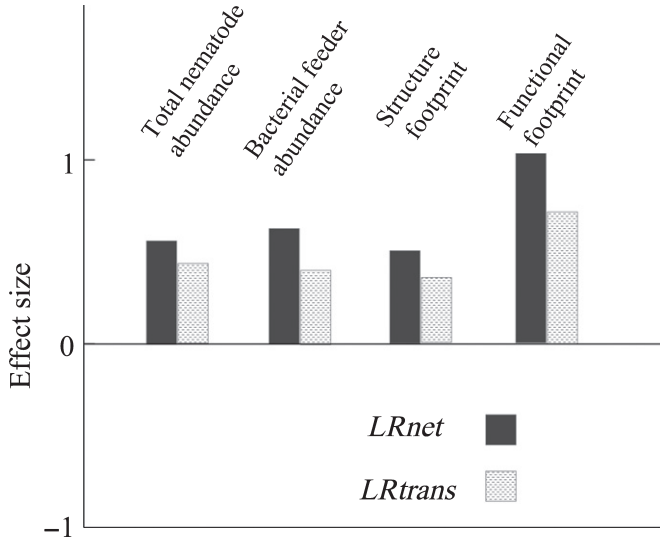

Fig. 3 Net effect (LRnet) and transgressive overyielding (LRtrans) of genotypic diversity of *Phragmites australis* on total nematode abundance, bacteria feeder abundance, nematode structure footprint and functional footprint.

More diverse systems are expected to be more productive (Cardinale *et al.*, 2007; Tilman *et al.*, 2014). A previous genotypic diversity experiment found that the aboveground net primary productivity of *Solidago altissima* was one-third greater than that in single-genotype plots (Crutsinger *et al.*, 2006). Niche complementarity and positive selection led to this relationship (Crutsinger *et al.*, 2006). Our experiment did not show the same phenomenon. Plant genotypic diversity in populations of *P. australis* did not influence plant belowground biomass (Table 3). If genotypes with large effects on ecosystem properties (in this case, belowground biomass) performed more poorly in mixtures than in monocultures (a negative selection effect), this could produce a significantly negative transgressive overyielding index (Jiang, 2007; Drummond & Vellend, 2012). Belowground biomass of *P. australis* in the six-genotype mixture was not significantly greater than that of the best-performing single-genotype plot (Fig. 1), and the transgressive overyielding index was negative (LRtrans: −0.1677). Thus, a negative selection effect probably caused the lack of relationship between plant belowground biomass and genotypic diversity. In other words, the high-productivity genotype performed poorly in mixtures, possibly due to space limitation or resource constraints, thus leading to a negative selection effect.

Before our experiment, little information was known about how intraspecific plant diversity influences nematode abundance. In Mongolian grasslands nematode abundance increased with increasing plant functional diversity by up to 60% (Chen *et al.*, 2016). Our study found that nematode abundance was significantly increased by plant genetic diversity, with total nematode abundance in the six-genotype mixtures almost double that in the monocultures (Fig. 2). This suggests that plant diversity above and below the species level can affect nematode abundance and that their effects may be almost equal. We found evidence of

transgressive overperformance for nematode abundance, suggesting that complementarity effects play a critical role in enhancing nematode abundance (Loreau & Hector, 2001). Thus, the inconsistent responses of plant belowground biomass and soil nematode abundance to plant genotypic diversity may be caused by different mechanisms with negative selection effects acting on plant biomass and complementarity effects on nematode abundance.

While resource quantity (plant belowground biomass) cannot explain the increased nematode abundance, other pathways may result in the decoupling of plant belowground biomass and soil nematode abundance to plant genotypic diversity, such as changes in resource quality (Cortois *et al.*, 2017) or rhizosphere morphological structure (Van der Putten, 2003). The plant root systems of different genotypes may differ in their vertical distributions in the soil profile. In a gradient study of plant species diversity, belowground plant biomass of mixture plots was more concentrated in deep soil layers than in monocultures (Mueller *et al.*, 2013). Our study revealed differences among genotypes in belowground plant biomass within the top 30 cm of soil (Fig. 1). Thus, plant roots may be concentrated in different soil layers in mixture plots and thereby affect soil fauna by altering microhabitats (Cortois *et al.*, 2017; Schuldt *et al.*, 2019). Furthermore, although not measured, plant quality or plant chemical defensive substances in the rhizosphere could contribute to the effects of genotypic diversity (Van der Putten, 2003; Semchenko *et al.*, 2017).

Although total nematode genera richness was not affected by plant genotypic diversity of *P. australis*, it was significantly influenced by plant genotype identity (Table 2). The nematode H' diversity also showed a similar response that omni-carnivorous nematode diversity only significantly changed with plant genotypic identity rather than with plant genotypic diversity (Table 2). This is consistent with findings at the plant species level. De Deyn *et al.* (2004) observed greater variation in nematode diversity among plant monocultures than between different levels of plant diversity. By contrast, studies of responses to aboveground invertebrate diversity have found strong effects of genotypic diversity. Srivastava & Lawton (1998) and Crutsinger *et al.* (2006) reported that species richness of arthropods was enhanced with increasing genotypic diversity and attributed their results to the increased diversity of food resources at higher levels of genotypic diversity. This suggests that belowground and aboveground invertebrates may respond differently to changes in plant diversity. While the mechanism driving the response of nematode diversity to genotype identity in our study is unknown, it is unlikely that it is related to plant belowground biomass. Both plant belowground biomass, total nematode richness and omni-carnivorous nematode diversity responded to plant genotype identity, but genotype monocultures with the greatest belowground plant biomass did not support the greatest nematode richness. This suggests that greater root biomass does not necessarily lead to an increase in resource diversity – such as root exudate diversity – so it does not lead to an increase in soil fauna taxonomic diversity (Steinauer *et al.*, 2016).

Plant genotypic diversity significantly affected the abundance of lower trophic level nematodes (bacterial-feeding nematodes), but had no significant influence on the abundance of higher trophic level nematodes (omni-carnivorous nematodes). The abundance of bacterial-feeding nematodes increased by 27%, 45% and 89% in two-, three- and six-genotype mixtures compared with those of the monocultures. It has been reported that plant genotypic diversity could affect primary decomposers such as bacteria or fungi (Schweitzer *et al.*, 2011; Latta *et al.*, 2011). Our study suggested that plant genotypic diversity would affect nematodes that feed on primary decomposers via upwards trophic cascading. Previous studies have also observed that plant diversity had a stronger impact on lower trophic levels than higher trophic levels (Viketoft *et al.*, 2009; Scherber *et al.*, 2010). For example, increasing plant species diversity increased the abundance of lower trophic level nematodes, but had only a small effect on higher trophic level nematodes (Kostenko *et al.*, 2015). Another study found that plant species diversity had a greater influence on herbivores than carnivorous and omnivorous consumers, both aboveground and belowground (Scherber *et al.*, 2010). These results, including our own, are consistent with the hypothesis that the effects of plant diversity on soil fauna weaken with increasing trophic levels (Balvanera *et al.*, 2006). Thus, the greater the number of trophic links between plants and consumers, the less likely that plant diversity effects will be detected (Viketoft *et al.*, 2009).

While plant genotypic diversity did not significantly affect nematode taxonomic richness or the abundance of omni-carnivorous nematodes, it did significantly influence the nematode structure footprint, which is indicative of the metabolic function of higher trophic levels (Table 2). Significant transgressive overperformance suggests that complementarity effects play a role in influencing nematode metabolic footprints (Fig. 3). Additionally, genotype E also significantly influenced the nematode metabolic footprint, as indicated by the mixed linear model analysis (Table 3). These findings suggested that both the complementarity effect and selection effect (disproportionate effect of genotype E) functioned simultaneously on nematode metabolic footprints. Previous studies on the relationship between biodiversity and soil nematodes mostly examined nematode abundance or taxonomic richness as indicators of soil nematode community responses (De Deyn *et al.*, 2004). However, these studies usually quantify taxonomy-based measures of biodiversity, such as species richness, which do not necessarily reflect the functioning of these communities (Ebeling *et al.*, 2018). Our results indicated that individual species or groups of species also respond significantly to plant genotypic diversity, but may be overlooked if studies only focus on indicators such as richness or abundance. Importantly, responsive groups may play important roles in mediating ecosystem functions, as in our study. This indication is consistent with the finding of a recent meta-analyses that the ecological effects of intraspecific variation are stronger when they are measured at the ecosystem level than at the community level (Raffard *et al.*, 2019). Conversely, even slight changes in taxonomic measures may cause pronounced changes in the functions of ecological communities (Flynn *et al.*, 2009). Therefore, incorporating a wider range of metrics, including both taxonomic and functional aspects, would help to develop a more comprehensive

understanding of the functional consequences of biodiversity losses (Ebeling *et al.*, 2018; Wang *et al.*, 2019).

Under prevailing global changes – such as plant invasions, human disturbances, global warming – losses of genotypic diversity within species are more likely to occur than losses of diversity at or above the species level. Although previously understudied, the relatively subtle diversity loss within species is increasingly recognised as an important facet of biodiversity that can affect all biological levels (Raffard *et al.*, 2019). A higher nematode structure footprint index can imply a greater ability of soil communities to tolerate environmental disturbance, while a higher functional footprint index indicates greater metabolic balance within the community, which can increase the stability of the soil system (Ferris, 2010). Low plant genotypic diversity has been found to affect ecosystem functioning by decreasing resistance to enemies (Barton *et al.*, 2015; Semchenko *et al.*, 2017). Our study suggests that decreased genotypic diversity within a dominant plant species resulted in a less stable belowground food web and ecosystem processes, which was reflected by the significantly decreased structure and functional footprints of nematodes. More research is needed to address the functional changes of belowground ecosystems under the influence of plant intraspecific diversity losses.

Previous studies have indicated that plant genotypic diversity affected arthropod community structure (Johnson *et al.*, 2006). Our results also revealed that changes in plant genotypic diversity can alter the structure of soil nematode communities. ANOSIM test showed that although the nematode community structures of two- and three-genotype mixtures did not strikingly differ from those of monocultures, the highest genotypic level (six-genotype mixtures) exhibited a significant difference (Table S2). The top three nematode genera contributing most to this difference were *Haliplectus*, *Terschellingia* and *Diploaimella*, which are all bacterial feeders (Table S2). This finding proved that, in our experiment, bacterial-feeding nematodes was the feeding group that had the strongest responses to plant genotypic diversity in terms of their individual number.

Conclusion

Intraspecific diversity within populations of *P. australis* affected belowground responses at different trophic levels through different mechanisms. Plant genotypic diversity was generally more important than plant genotype identity in influencing nematode communities. This finding suggests that plant genotypes may express different phenotypes when grown in mixtures relative to genotypic monocultures, and such plasticity may have consequences for belowground biota and processes. We found that nematode taxonomic responses to genotypic diversity were not as strong as nematode functional responses at higher trophic levels, suggesting that losses of plant diversity can cause changes in belowground ecosystem function even when changes in the abundance or richness of soil organisms are not detectable. Given that the influence of plant intraspecific diversity on the soil food web may be as strong as the effect of plant interspecific diversity, conservation of both plant species and intraspecific genetic diversity is needed to maintain belowground community structure and ecosystem function.

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Author contributions

JW and XC conceived and designed the experiment. JY performed the experiment and analysed the data. YZ helped with data analysis. SY performed *Phragmites australis* genotyping and common-garden maintenance. KMC helped with writing the paper and revision. All authors wrote the manuscript.

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References

Aarssen LW. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* **80**: 183–184.

Abdala-Roberts L, Berny-Miery Terán JC, Moreira X, Durán-Yáñez A, Tut-Pech F. 2015. Effects of pepper (*Capsicum chinense*) genotypic diversity on insect herbivores. *Agricultural and Forest Entomology* **17**: 433–438.

Ball BA, Bradford MA, Coleman DC, Hunter MD. 2009. Linkages between below and aboveground communities: decomposer responses to simulated tree species loss are largely additive. *Soil Biology and Biochemistry* **41**: 1155–1163.

Balvanera P, Pfisterer AB, Buchmann N, He JS, Nakashizuka T, Raffaelli D, Schmid B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* **9**: 1146–1156.

Bardgett RD, Cook R. 1998. Functional aspects of soil animal diversity in agricultural grasslands. *Applied Soil Ecology* **10**: 263–276.

Bardgett RD, Freeman C, Ostle NJ. 2008. Microbial contributions to climate change through carbon cycle feedbacks. *ISME Journal* **2**: 805–814.

Barton KE, Valkama E, Vehviläinen H, Ruohomäki K, Knight TM, Koricheva J. 2015. Additive and non-additive effects of birch genotypic diversity on arthropod herbivory in a long-term field experiment. *Oikos* **124**: 697–706.

Bell T, Lilley AK, Hector A, Schmid B, King L, Newman JA. 2009. A linear model method for biodiversity-ecosystem functioning experiments. *American Naturalist* **174**: 836–849.

Bennett JA, Koch AM, Forsythe J, Johnson NC, Tilman D, Klironomos J. 2020. Resistance of soil biota and plant growth to disturbance increases with plant diversity. *Ecology Letters* **23**: 119–128.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD *et al.* 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**: 351–354.

Bongers T. 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* **83**: 14–19.

Bongers T, Ferris H. 1999. Nematode community structure as a bioindicator in environmental monitoring. *Trends in Ecology and Evolution* **14**: 224–228.

Bustos-Segura C, Poelman EH, Reichelt M, Gershenzon J, Gols R. 2017. Intraspecific chemical diversity among neighbouring plants correlates positively with plant size and herbivore load but negatively with herbivore damage. *Ecology Letters* **20**: 87–97.

Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**: 989–992.

Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences, USA* **104**: 18123–18128.

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE *et al.* 2000. Consequences of changing biodiversity. *Nature* **405**: 234–242.

Chen D, Pan Q, Bai Y, Hu S, Huang J, Wang Q, Naeem S, Elser JJ, Wu J, Han X. 2016. Effects of plant functional group loss on soil biota and net ecosystem exchange: a plant removal experiment in the Mongolian grassland. *Journal of Ecology* **104**: 734–743.

Cook-Patton SC, Mcart SH, Parachnowitsch AL, Thaler JS, Agrawal AA. 2011. A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology* **92**: 915–923.

Cortois R, Veen GF, Duyts H, Abbas M, Strecker T, Kostenko O, Eisenhauer N, Scheu S, Gleixner G, De Deyn GB *et al.* 2017. Possible mechanisms underlying abundance and diversity responses of nematode communities to plant diversity. *Ecosphere* **8**: e01719.

Crawford KM, Rudgers JA. 2013. Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology* **94**: 1025–1035.

Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **313**: 966–968.

De Deyn GB, Raaijmakers CE, Van Ruijven J, Berendse F, Van Der Putten WH. 2004. Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. *Oikos* **106**: 576–586.

Dias ATC, Berg MP, de Bello F, Van Oosten AR, Bílá K, Moretti M. 2013. An experimental framework to identify community functional components driving ecosystem processes and services delivery. *Journal of Ecology* **101**: 29–37.

Drummond EBM, Vellend M. 2012. Genotypic diversity effects on the performance of *Taraxacum officinale* populations increase with time and environmental favorability. *PLoS ONE* **7**: e30314.

Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* **10**: 522–538.

Ebeling A, Rzanny M, Lange M, Eisenhauer N, Hertzog LR, Meyer ST, Weisser WW. 2018. Plant diversity induces shifts in the functional structure and diversity across trophic levels. *Oikos* **127**: 208–219.

Ferris H. 2010. Form and function: metabolic footprints of nematodes in the soil food web. *European Journal of Soil Biology* **46**: 97–104.

Ferris H, Bongers T, De Goede RGM. 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Applied Soil Ecology* **18**: 13–29.

Ferris H, Sánchez-Moreno S, Brennan EB. 2012. Structure, functions and interguild relationships of the soil nematode assemblage in organic vegetable production. *Applied Soil Ecology* **61**: 16–25.

Fitzpatrick CR, Mikhailitchenko AV, Anstett DN, Johnson MTJ. 2018. The influence of range-wide plant genetic variation on soil invertebrate communities. *Ecography* **41**: 1135–1146.

Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* **12**: 22–33.

Geisen S, Wall DH, van der Putten WH. 2019. Challenges and opportunities for soil biodiversity in the anthropocene. *Current Biology* **29**: R1036–R1044.

Griffiths B, Boag B, Neilson R, Palmer L. 1990. The use of colloidal silica to extract nematodes from small samples of soil or sediment. *Nematologica* **36**: 465–473.

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* **12**: 1029–1039.

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J *et al.* 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123–1127.

Hoeksema JD, Lussenhop J, Teeri JA. 2000. Soil nematodes indicate food web responses to elevated atmospheric CO_2. *Pedobiologia* **44**: 725–735.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**: 3–35.

Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. 2008. Ecological consequences of genetic diversity. *Ecology Letters* **11**: 609–623.

Huston MA. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**: 449–460.

Jiang L. 2007. Negative selection effects suppress relationships between bacterial diversity and ecosystem functioning. *Ecology* **88**: 1075–1085.

Johnson MTJ, Lajeunesse MJ, Agrawal AA. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* **9**: 24–34.

Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E *et al.* 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**: 286–293.

Koricheva J, Hayes D. 2018. The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. *Functional Ecology* **32**: 1704–1717.

Kostenko O, Duyts H, Grootemaat S, De Deyn GB, Bezemer TM. 2015. Plant diversity and identity effects on predatory nematodes and their prey. *Ecology and Evolution* **5**: 836–847.

Latta LC, Baker M, Crowl T, Parnell JJ, Weimer B, DeWald DB, Pfreder ME. 2011. Species and genotype diversity drive community and ecosystem properties in experimental microcosms. *Evolutionary Ecology* **25**: 1107–1125.

Lehman CL, Tilman D. 2000. Biodiversity, stability, and productivity in competitive communities. *American Naturalist* **156**: 534–552.

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity biodiversity experiments. *Nature* **412**: 72–76.

Madritch MD, Hunter MD. 2002. Phenotypic diversity influences ecosystem functioning in an oak sandhills community. *Ecology* **83**: 2084–2090.

Miki T, Ushio M, Fukui S, Kondoh M. 2010. Functional diversity of microbial decomposers facilitates plant coexistence in a plant-microbe-soil feedback model. *Proceedings of the National Academy of Sciences, USA* **107**: 14251–14256.

Mueller KE, Tilman D, Fornara DA, Hobbie SE. 2013. Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. *Ecology* **94**: 787–793.

Raffard A, Santoul F, Cucherousset J, Blanchet S. 2019. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. *Biological Reviews* **94**: 648–661.

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze ED, Roscher C, Weigelt A, Allan E *et al.* 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**: 553–556.

Schmid B, Hector A, Saha P, Loreau M. 2008. Biodiversity effects and transgressive overyielding. *Journal of Plant Ecology* **1**: 95–102.

Schuldt A, Ebeling A, Kunz M, Staab M, Guimarães-Steinicke C, Bachmann D, Buchmann N, Durka W, Fichtner A, Fornoff F *et al.* 2019. Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications* **10**: 1460.

Schweitzer JA, Fischer DG, Rehill BJ, Wooley SC, Woolbright SA, Lindroth RL, Whitham TG, Zak DR, Hart SC. 2011. Forest gene diversity is correlated with the composition and function of soil microbial communities. *Population Ecology* **53**: 35–46.

Semchenko M, Saar S, Lepik A. 2017. Intraspecific genetic diversity modulates plant-soil feedback and nutrient cycling. *New Phytologist* **216**: 90–98.

Siemann E, Tilman D, Haarstad J, Ritchie M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist* **152**: 738–750.

Srivastava DS, Lawton JH. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *American Naturalist* **152**: 510–529.

Steinauer K, Chatzinotas A, Eisenhauer N. 2016. Root exudate cocktails: the link between plant diversity and soil microorganisms? *Ecology and Evolution* **6**: 7387–7396.

Tilman D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**: 350–363.

Tilman D, Isbell F, Cowles JM. 2014. Biodiversity and ecosystem functioning in soil. *Annual Review of Ecology Evolution and Systematics* **45**: 471–493.

Tilman D, Lehman CL, Thomson KT. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences, USA* **94**: 1857–1861.

Van der Putten WH. 2003. Plant defense belowground and spatiotemporal processes in natural vegetation. *Ecology* **84**: 2269–2280.

Vandegehuchte ML, De La Peña E, Bonte D. 2011. Contrasting covariation of above and belowground invertebrate species across plant genotypes. *Journal of Animal Ecology* **80**: 148–158.

Viketoft M, Bengtsson J, Sohlenius B, Berg MP, Petchey O, Palmborg C, Huss-Danell K. 2009. Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. *Ecology* **90**: 90–99.

Wang MQ, Li Y, Chesters D, Anttonen P, Bruelheide H, Chen JT, Durka W, Guo PF, Härdtle W, Ma K *et al.* 2019. Multiple components of plant diversity loss determine herbivore phylogenetic diversity in a subtropical forest experiment. *Journal of Ecology* **107**: 2697–2712.

Wardle DA, Bardgett RD. 2004. Human-induced changes in large herbivorous mammal density: the consequences for decomposers. *Frontiers in Ecology and the Environment* **2**: 145–153.

Wardle DA, Bonner KI, Barker GM, Yeates GW, Nicholson KS, Bardgett RD, Watson RN, Ghani A. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs* **69**: 535–568.

Wardle DA, Yeates GW, Williamson W, Bonner KI. 2003. The response of a three trophic level soil food web to the identity and diversity of plant species and functional groups. *Oikos* **102**: 45–56.

Wetzel WC, Aflitto NC, Thaler JS. 2018. Plant genotypic diversity interacts with predation risk to influence an insect herbivore across its ontogeny. *Ecology* **99**: 2338–2347.

Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, Leroy CJ, Lonsdorf EV, Allan GJ, DiFazio SP, Potts BM *et al.* 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* **7**: 510–523.

Wilschut RA, van der Putten WH, Garbeva P, Harkes P, Konings W, Kulkarni P, Martens H, Geisen S. 2019. Root traits and belowground herbivores relate to plant–soil feedback variation among congeners. *Nature Communications* **10**: 1564.

Wimp GM, Young WP, Woolbright SA, Martinsen GD, Keim P, Whitham TG. 2004. Conserving plant genetic diversity for dependent animal communities. *Ecology Letters* **7**: 776–780.

Yeates GW. 1981. Nematode population in relation to soil environmental factors: a review. *Pedobiologia* **5**: 312–338.

Yeates GW. 1999. Effects of plants on nematode community structure. *Annual Review of Phytopathology* **37**: 127–49.

Yeates GW, Bongers T, De Goede RGM, Freckman DW, Georgieva SS. 1993. Feeding habits in soil nematode families and genera-an outline for soil ecologists. *Journal of Nematology* **25**: 315–331.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Location of the experimental blocks and plots.

Fig. S2 Effect size and confidence intervals derived from the mixed linear model.

Table S1 Genetic information on the six genotypes.

Table S2 Results of one-way ANOSIM tests and SIMPER analysis.

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