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RESEARCH ARTICLE

Plant community responses to alterations in soil abiotic and biotic conditions are decoupled for above- and below-ground traits

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Abstract

1. Plant functional traits are increasingly recognised as being impacted by soil abiotic and biotic factors. Yet, the question to what extent the coupling between community-level above- and below-ground traits is affected by soil conditions remains open.
2. In a field experiment in dune grassland, we quantified the responses of both community-level leaf and root traits to changes in soil abiotic and biotic conditions using soil inoculation by living and sterile soil inocula originated from different dune ecosystems.
3. Altered soil conditions resulted in a strong decoupling in responses of community-level leaf and root traits. Changes in soil abiotic conditions imposed by soil inoculation were more important in determining the decoupling of the leaf vs root relationships than additions of soil biota. Altered soil abiotic factors influenced both leaf and root traits at the community level and caused the entire community-level trait spectrum to shift, while experimental additions of living soil inocula only significantly influenced root traits towards longer and thinner roots.
4. *Synthesis*. Our results bring direct evidence that, at a plant community level, the dynamics of plant above-ground traits are not informative of below-ground traits. Particularly, below-ground abiotic processes are a major driver of commonly observed trait spectra. We suggest that future study is required to test the general pattern of leaf and root correlations across different ecosystems under field conditions.

KEYWORDS
leaf, plant community-weighted mean traits, plant trait coordination, plant–soil interactions, root, soil community, soil inoculation

1 | INTRODUCTION

Plant traits reflect the evolutionary and community assembly processes as influenced by abiotic and biotic factors (Valladares et al., 2007; Westoby & Wright, 2006). Plants adapt to different abiotic conditions by adjusting multiple aspects of carbon and nutrient allocation, architecture, morphology and physiology (Nicotra et al., 2010; Van Kleunen & Fisher, 2001). A growing body of studies indicates that plant functional trait values strongly depend on not only on species identity (phylogeny) (Roscher et al., 2011), but also on soil abiotic properties such as soil moisture, texture and nutrient availability (Bergmann et al., 2016; Freschet et al., 2017; Gross et al., 2008; Maire et al., 2015; Ordoñez et al., 2010). It has also been reported that many phenotypic properties of plants are derived from the interplay between the plant and its soil microbial associates (Friesen et al., 2011; Weigelt et al., 2021). Soil microbes interact with plants, intimately affecting the plant's capacity to acquire nutrients, uptake water and tolerate stresses (Bardgett & van der Putten, 2014; Van der Heijden et al., 2008). The interactions between plant and soil communities thus may affect plant functional trait expression by modifying plant responses to environmental stresses, and resource acquisition (Baxendale et al., 2014; Kulmatiski et al., 2017; Lau & Lennon, 2012; Petipas et al., 2021; Xi et al., 2021).

The impacts of soil biotic and soil abiotic factors commonly interact in regulating plant growth (Bennett & Klironomos, 2019; Kostenko & Bezemer, 2020). Negative plant–soil interactions could play a central role in early communities which are generally characterised by resource-acquisitive traits on nutrient-poor soils during primary succession (Castle et al., 2016), while positive interactions have been shown to affect plant communities at later successional stages generally characterised by resource-conservative plant traits in competitive environments (Carbajo et al., 2011; Cortois et al., 2016; De Deyn et al., 2004; Kardol et al., 2006). Therefore, it is expected that the variations in soil nutrient availability may interact with soil communities in modulating plant growth and plant defence through shaping plant trait values (Bjørnlund et al., 2012; Porazinska et al., 2003). For instance, the effects of beneficial soil microbes including plant growth-promoting bacteria (PGPB), arbuscular mycorrhizal (AM) fungi and rhizobia on the host plant traits depend on the nutrient availability and forms in agricultural crop species (Saia et al., 2020; Wang et al., 2011). Yet, even though soil properties are recognised to be critical mediators of plant functional traits, the nature of the interactions between soil abiotic factors and soil biota on plant functional traits remains poorly studied due to the difficulty to experimentally modify below-ground communities.

Based on the whole-plant economic traits (Poorter et al., 2014; Reich, 2014), it is generally assumed that there are correlations between leaf and root traits to maximise the efficiency of obtaining and utilising limited resources (Kramer-Walter et al., 2016). Indeed, there is a growing body of evidence that at the level of individual plant species significant correlations exist between above- and below-ground traits, such as specific leaf area (SLA) and specific root length (SRL) (Fort et al., 2013; Liu et al., 2010), and tissue density of leaves and roots (Craine et al., 2001; Craine & Lee, 2003; Fort et al., 2013). Nevertheless, recent studies demonstrate that root resource strategies are not fully consistent with leaf resource strategies across grasses, forbs and woody plant species (Bergmann et al., 2016; Comas et al., 2014; Kembel & Cahill, 2011). Root trait complexity might result from the range of below-ground resource uptake strategies that can be employed (Bergmann et al., 2017; Kramer-Walter, 2016; Ma et al., 2018). In contrast to above-ground leaf carbon acquisition by photosynthesis being conducted exclusively by plants, the below-ground parts of many plant species can outsource resource acquisition to associated soil microbes (Bardgett et al., 2014; Bergmann et al., 2020). For example, the symbiosis AM fungi and plants can shape root traits including root cortical area and diameter, to provide intraradical habitats for AM fungi (Bergmann et al., 2020; Brundrett, 2002; Weemstra et al., 2016). This suggests a potential role of soil biota in driving certain aspects of root trait variation that are not mirrored in leaf traits, causing a decoupling of relationships between above- and below-ground traits (Isaac et al., 2017; Laliberté, 2017; Wang et al., 2017; Weemstra et al., 2016). Furthermore, the dynamics of functional traits of individual plant species is not necessary predictive for the dynamics of plant community-level traits. The latter, f.i. community-weighted mean trait values accounts for the variation in traits as well as for the between-species interactions and community composition. Yet, the extent to which entire soil communities modify these above- and below-ground trait correlations is understood poorly.

This study aimed at elucidating the responses of plant community traits to the alternation in both soil abiotic and biotic conditions, and especially how these responses influence the relationship between community-level leaf and root traits. To address this question, we manipulated the soil conditions by introducing different types of living and sterilised soil inocula originating from distinct dune ecosystems (primary dune, dune grassland and dune forest) in a newly established dune plant community. The additions of soil inocula from distinct dune ecosystems enabled a range of nutrient availabilities and induced shifts in the soil microbial composition in the recipient plots (Tables S1 and S2). In addition, the set-up of soil sterilisation allowed us to explicitly test the effect of changes in both abiotic and biotic soil conditions on the plant community (Middleton & Bever, 2012; Wubs et al., 2016). We have sown a standardised mixture of seeds of plant species in the inoculated soils and after 3 years assessed plant community-level traits in each community to examine their responses to the different soil inoculation treatments.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The experiment was carried out in the Terra–Dunes experiment in 2020 (the field work is collaborated with the owner of the experimental site, Dunea duin & water). The Terra–Dunes experiment was established in Spring 2018 in a bare sandy dune area (Meijendel Nature Reserve, Wassenaar, the Netherlands. GPS: 52°07′50.4″N; 4°20′27.6″E). A detailed outline of the experimental design can be found in (Gao et al., 2022). In short, the Terra–Dunes experiment is a long-term field experiment where the soil abiotic and biotic properties (soil microbial composition, particularly for soil fungi) were manipulated through the addition of soil inocula (Tables S1 and S2). Inoculation with living soil inocula enables alternations of soil biotic and abiotic conditions, with the latter one being altered because donor ecosystem soil is unavoidably added together with living inocula. Inoculation with sterilised soil inocula enables teasing apart the impacts of inoculation on soil abiotic conditions. A graphical illustration of the experimental design is provided in Figure S1. The material used for soil inocula was sieved to remove roots and stones. Soil sterilisation was conducted through applying gamma radiation (>25 KGray gamma radiation, Isotron, Ede, the Netherlands), the soil sterilisation treatment known to impose minimal alterations in soil nutrient availability. Half of the inocula of each origin was sterilised. Accordingly, a half of the inoculated plots was treated with sterile inocula, while the other half was treated with unsterile inocula. Inocula additions constituted a layer of 0.5 cm of living or sterilised inocula, and were supplemented by the addition of layer of 1.5 cm of sterilised soil originated from the same ecosystem as the applied inocula. The latter was done in order to promote establishment of plant community, which would otherwise be extremely slow in the bare soil. Seeds of 30 plants typical for European coastal dune ecosystems were sown into the experimental plots simultaneously with soil inocula additions (Figure S1).

2.2 | Plant functional trait measurements

The absolute percentage cover of each plant species was recorded visually within each plot (2 × 2 m) in July 2020. For each species, above- and below-ground plant traits were measured following standard trait measurement protocols (Cornelissen et al., 2003). Based on this vegetation survey, we selected those plant species that together comprised the top 80% of the total species cover in each plot. For selected species in each plot, we randomly sampled 15–20 matured, undamaged and unshaded leaves from at least five individuals in each plot. The following leaf traits were selected for the assessment: specific leaf area (SLA), leaf thickness (LT), leaf dry-matter content (LDMC), leaf carbon content (LCC), leaf nitrogen content (LNC) and leaf phosphorus content (LPC). These traits are most tightly related to the plant economic spectrum. Fresh leaves were weighed and scanned using a Cannon LiDE 210 scanner. Leaf area was obtained by analysis with software ImagineJ. Leaf thickness was measured at 2 points on the leaf, avoiding midribs, using a high precision calliper (+/− 0.01 mm). Thereafter, the leaf samples were oven-dried at 65°C for 48 h and weighted and then ground to fine powder. Specific leaf area was calculated as leaf area divided by its dry mass. Leaf dry-matter content was obtained as the ratio of leaf dry mass to fresh mass. Leaf C and N contents were analysed using a Flash EA 1112 elemental analyser (Thermo Scientific). Leaf P content was determined using a UV/visible spectrophotometer after acid digestion with a 1:4 mixture of 37% (v/v) HCl and 65% (v/v) HNO_3 (Murphy & Riley, 1962). For each selected plant species, we calculated the mean values of its leaf traits in each plot, and we calculated the relative abundance of each species in each plot as a ratio of plant cover of a given species to the community cover in plot. These relative abundances were used to calculate the community-weighted means (CWM) of the foliar traits for each plot.

The root systems of plants are intertwined in soil, and therefore we directly sampled the community-weighted mean traits. We took a composite measure of root traits from the mixed root systems collected from four soil cores ($ø$ = 3.5 cm, h = 10 cm) in each plot. Then roots were carefully washed under tap water to allow the separation of roots by flotation using sieve stacks. Dead roots were separated by visual clues. 0.1 g fine roots were randomly selected and stored in 50% ethanol. AM fungal structures were stained with Trypan blue using a standard protocol (Robertson et al., 1999). Roots were cleared with 5% KOH solution in a 75°C water bath for 30 min. Roots were then acidified in 1% HCl solution for 30 min and subsequently stored in 0.01% Trypan blue for 30 min in a 75°C water bath. Roots were stored in 50% glycerol for microscopic investigation. The percentage of AM fungal root colonisation (AMFC) was estimated according to the grid line interaction method (McGonigle et al., 1990). The remaining fresh roots were weighed and scanned on a Cannon LiDE 210 scanner. Thereafter, the root samples were weighted after oven-drying at 65°C for 48 h and ground to fine powder. Root C and N contents (RCC, RNC) were analysed using an elemental analyser (Thermo Scientific). Root P content (RPC) was determined using a UV/visible spectrophotometer after acid digestion. Total root length, volume and average diameter (AD) were determined using the scanned images with the software of WinRhizo (Regent Instruments). Specific root length (SRL) was calculated as root total length divided by its dry mass. Root tissue density (RTD) was calculated as root volume divided by its dry mass. All trait abbreviations are listed in Table 1.

2.3 | Soil sampling

Soil samples were collected from all plots in September 2018 and sieved (2 mm mesh size) in laboratory. Soil samples were then separated into two parts for the measurement of soil abiotic properties

TABLE 1 List of 13 measured CWM traits (94 samples), as well as their descriptive statistics.

Trait	Abbreviation	Unit	Mean (SD)	Range
Leaf thickness	LT	mm	0.23 (0.04)	0.16–0.43
Specific leaf area	SLA	$cm^2\ g^{-1}$	124.91 (22.30)	70.86–203.25
Leaf dry matter content	LDMC	$mg\ g^{-1}$	173.02 (27.33)	114.88–256.12
Leaf carbon content	LCC	%	33.88 (3.86)	24.82–43.42
Leaf nitrogen content	LNC	%	1.59 (0.26)	1.00–2.16
Leaf phosphorus content	LPC	%	0.19 (0.04)	0.08–0.31
Average diameter	AD	mm	0.35 (0.04)	0.25–0.49
Specific root length	SRL	$m\ g^{-1}$	82.22 (37.64)	12.95–172.03
Root tissue density	RTD	$g\ cm^{-3}$	0.16 (0.08)	0.08–0.42
Root carbon content	RCC	%	50.33 (2.55)	44.27–59.03
Root nitrogen content	RNC	%	2.14 (0.31)	1.18–3.11
Root phosphorus content	RPC	%	0.18 (0.03)	0.12–0.26
Percentage of AMF colonisation	AMFC	%	34.07 (14.82)	4.12–67.47

and molecular analysis for the soil microbial composition following the protocols in supplementary materials. The complete set of results for the soil chemical results is presented in Table S1 and Figure S2. The responses of the soil microbial composition to soil inoculation treatments are presented in Table S2, indicating that soil inoculation treatments were effective and significantly influenced soil microbial composition.

2.4 | Data analysis

To enable the application of a two-factor statistical analysis, all 22 control plots were a-priori randomly assigned as control to either living or sterile soil inocula treatments. Due to the loss of some samples, there were a few missing values. The missing data include: the leaf carbon, nitrogen and phosphorus content of sample from plot 90. The root carbon, nitrogen and phosphorus content of samples from plot 6, 21 and 84. Also the root AMF colonisation rates of plot 84. Prior to analysis, missing data were replaced with the mean of each variable. Pairwise trait relationships were assessed using Pearson's correlation test. We used principal component analysis (PCA) to visualise the axes of main variation in CWM trait values. Permutational multivariate analysis of variance (PERMANOVA) was used to test the effect of the soil inoculation treatments on the variation in CWM traits, for all traits together and for root and leaf traits separately, based on a Bray–Curtis dissimilarity matrix in R using the package 'VEGAN'. In order to further evaluate the effects of soil inoculation treatments on individual CWM traits, two-way ANOVAs were run to test the effects of different types of soil inocula and soil sterilisation treatments on CWM traits. Model assumption of normality and homoscedasticity were checked on the model residuals (Kozak & Piepho, 2018) and variables were transformed when necessary to meet the assumption of model residuals. Effect size of the analyses was calculated using the function 'eta_squared()'. In case the effects of model parameters were significant in an ANOVA, a Tukey's HSD test was performed for post hoc comparisons among different types of soil inocula using the LSMEANS package (Lenth, 2016).

3 | RESULTS

3.1 | Relationship between root and leaf traits under different soil inoculation treatments

Pairwise relationships between all CWM leaf traits and between most root traits were strong and highly significant (Table 2). All leaf traits were positively related to one another. All relations between root morphological traits were significant. SRL was negatively related to AD ($r = -0.79$; $p < 0.01$) and RTD ($r = -0.81$; $p < 0.01$). The root chemical trait associated with resource acquisition, RNC, was significantly positively related to SRL ($r = 0.43$; $p < 0.01$), RPC ($r = 0.33$; $p < 0.01$) and AMFC ($r = 0.32$; $p < 0.01$), and significantly negatively with AD ($r = -0.32$; $p < 0.01$), RTD ($r = -0.51$; $p < 0.01$) (Table 2). There were almost no significant relationships between leaf traits and roots traits apart from a low correlation between LNC and RNC ($r = -0.24$; $p = 0.02$), LPC and AD ($r = 0.22$; $p = 0.03$), RTD ($r = 0.22$; $p = 0.04$).

The main variation among all 13 CWM traits was visualised by a PCA. The first and second axes accounted for 26.9% and 22.4% of the total variation of plant community-level traits, respectively (Figure 1; Table S3). The first axis of this PCA primarily reflected differences in community-level root traits, whereas the second reflected differences mainly in community-level leaf traits except for RPC (Figure 1). Qualitatively, all the leaf traits covaried along with the leaf economics spectrum, while root traits covaried along an independent trait spectrum (Figure 1). Additional PCA analyses separately for plots with living or sterile soil inocula also showed orthogonal response patterns of leaf and root traits (Figure 2). These results strongly suggest that the leaf traits are orthogonal to root

TABLE 2 Pearson correlation coefficients for pairwise traits with original data (lower-left diagonal, 94 samples). Correlations significant at $^{**}p<0.01$, $^{*}p<0.05$ are presented in bold.

	LT	SLA	LDMC	LCC	LNC	LPC	AD	SRL	RTD	RCC	RNC	RPC	AMFC
LT													
SLA	**0.26***												
LDMC	**0.34****	**0.34****											
LCC	**0.53****	**0.67****	**0.53****										
LNC	**0.34****	**0.63****	**0.30****	**0.76****									
LPC	**0.36****	**0.48****	**0.33****	**0.50****	**0.42****								
AD	−0.02	0.02	0.03	0.03	0.04	**0.22***							
SRL	0.15	0.07	0.03	0.01	−0.09	−0.09	**−0.79***						
RTD	−0.08	0.04	0.06	0.03	0.09	**0.22***	**0.58***	**−0.81****					
RCC	−0.05	0.00	0.02	−0.04	−0.20	−0.10	**−0.21***	**0.29****	−0.03				
RNC	−0.07	−0.07	−0.04	−0.10	**−0.24***	−0.11	**−0.32****	**0.43****	**−0.51****	**0.32****			
RPC	−0.02	0.09	0.00	0.11	0.03	0.07	0.02	0.06	−0.06	−0.01	**0.33****		
AMFC	0.03	−0.13	0.13	0.09	−0.04	−0.10	−0.11	0.09	−0.18	0.08	**0.32****	0.15	

Abbreviations: AD, average diameter; AMFC, percentage of AMF colonisation; LCC, leaf carbon content; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; LT, leaf thickness; RCC, root carbon content; RNC, root nitrogen content; RPC, root phosphorus content; RTD, root tissue density; SLA, specific leaf area; SRL, specific root length.

FIGURE 1 Principal component analyses (PCA) of plant community-weighted mean (CWM) traits under soil inoculation treatments. Arrows on the figure show the projections of the CWM traits within the PCA (green arrows indicate CWM leaf traits, orange arrows indicate CWM root traits). AD, average diameter; AMFC, percentage of AMF colonisation; LCC, leaf carbon content; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; LT, leaf thickness; RCC, root carbon content; RNC, root nitrogen content; RPC, root phosphorus content; RTD, root tissue density; SLA, specific leaf area; SRL, specific root length.

traits in response to alternations in soil conditions, and the orthogonality is driven by the other factors than presence or absence of soil biota.

3.2 | Impacts of soil inoculation treatments on the variation of above-ground vs below-ground CWM traits

The PERMANOVA revealed that the variation in plant CWM trait values was significantly influenced by soil inocula origin (pseudo-F = 2.23, $p<0.05$, 7% explained variation, Table 3) and by the interactive effect of soil inocula origin and soil sterilisation (pseudo-F = 2.02, $p<0.05$, 6% explained variation, Table 3). Interestingly, when the CWM trait values were separated into leaf and root traits, leaf traits composition was only significantly affected by soil inocula origin (pseudo-F = 3.05, $p<0.05$, 9% explained variation, Table 3). By contrast, root traits were significantly affected by the interactive influence of soil inocula origin and soil sterilisation (pseudo-F = 3.33, $p<0.05$, 10% explained variation, Table 3), suggesting that the added soil biota likely to play a more important role in modifying the values of root traits, compared to affecting leaf traits.

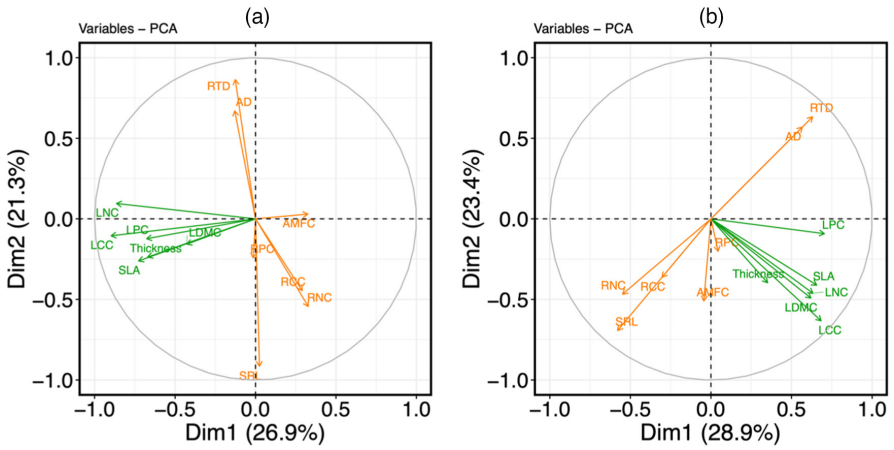

FIGURE 2 (a) Principal component analyses (PCA) of plant community-weighted mean (CWM) traits under (a) living soil inoculation and (b) sterile soil inoculation. Arrows on the figure show the projections of the CWM traits within the PCA (green arrows indicate CWM leaf traits, orange arrows indicate CWM root traits). LT, leaf thickness; SLA, specific leaf area; LDMC, leaf dry matter content; LCC, leaf carbon content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; AD, average diameter; SRL, specific root length; RTD, root tissue density; RCC, root carbon content; RNC, root nitrogen content; RPC, root phosphorus content; AMFC, percentage of AMF colonisation.

CWM traits	Treatments	df1, df2	*F*-value	R^2	*p*-value
All traits	**Inoculum**	**3, 93**	**2.23**	**0.07**	**0.029**
	Sterilisation	1, 93	0.42	<0.01	0.718
	I × S	**3, 93**	**2.02**	**0.06**	**0.048**
Leaf traits	**Inoculum**	**3, 93**	**3.05**	**0.09**	**0.013**
	Sterilisation	1, 93	0.28	<0.01	0.743
	I × S	3, 93	0.43	0.01	0.830
Root traits	Inoculum	3, 93	1.25	0.04	0.283
	Sterilisation	1, 93	0.50	<0.01	0.503
	I × S	**3, 93**	**3.33**	**0.10**	**0.018**

TABLE 3 Summary statistics of a PERMANOVAs testing the effects of different types of soil inocula, soil sterilisation and their interactions on the response patterns of CWM traits (Inoculum, I; Sterilisation, S; permutation = 9999). Control plots (without any inoculation; see Figure S1) were randomly assigned as control to either the living or sterile soil inocula treatments. Presented are degrees of freedom, variance explained (R^2), *F*-values and *p*-values. Significant effects ($p < 0.05$) are presented in bold.

3.3 | Response of individual CWM traits to soil inoculation treatments

Community-weighted mean values of LDMC, LCC and LNC were significantly influenced by the addition of different types of soil inocula with soil sterilisation having no effect (Table 4). This indicates that the effects were caused by the origin of the soil inocula and likely by the small amount of soil nutrients added with inoculation than by soil biota. The addition of soil inocula from later dune ecosystems (grasslands and forests) reduced LDMC (Figure 3c), LCC (Figure 3d) and LNC (Figure 3e) and values of these traits tended to be lower in plots with soil inocula compared to control plots that had no soil inocula. LCC tended to be lower in plots with soil inocula from dune grassland and dune forest (Figure 3d), while there was no difference in the response of LNC (Figure 3e) and LDMC (Figure 3c) to different types of soil inocula. The SLA also showed the same response pattern to the addition of later-successional soil inocula although these responses were non-significant (Figure 3b).

Some CWM root trait values were significantly influenced by the interactive effects of soil inocula origin and sterilisation. For example, the effects of soil inocula on AD and SRL depend on the sterilisation treatment of soil inocula (Table 4). Plant communities had thicker and denser roots when grown in plots with sterile grassland soil inocula than when grown in plots with living inocula (Figure 3g; Figure 3h). Changes in soil abiotic condition through soil inocula had significant influences on RPC and AMFC (Table 4). The addition of later-successional soil inocula had a negative effect on RPC leading to higher RPC values when grown in plots treated with sterile soil inocula (Figure 3l). Plant communities had higher AMFC when grown in plots with dune soil inocula compared with plant communities grown in plots treated with grassland soil inocula (Figure 3m). In addition, there was a marginally significant ($p = 0.07$) impact of soil sterilisation on RNC with plant communities having higher RNC values in plots with living soil inocula (Table 4; Figure 3k).

4 | DISCUSSION

Our study demonstrates that community-level above- and below-ground responses of plant traits to manipulated soil conditions are

TABLE 4 Effects of different types of soil inocula (Inoculum, I), soil sterilisation (Sterilisation, S) and their interaction on the plant CWM traits (*F*, *F*-value; *p*, *p*-value; η^2, eta squared). Control plots (without any inoculation; see Figure S1) were randomly assigned as control to either the living or sterile soil inocula treatments. Significant effects ($p < 0.05$) are presented in bold.

	Source of variance									
	Inoculum			Sterilisation			I × S			
Response	*F*	*p*	η^2	*F*	*p*	η^2	*F*	*p*	η^2	Transformation
LT	1.90	0.137	0.059	3.50	0.065	0.036	0.41	0.746	0.013	log()
SLA	2.20	0.094	0.069	0.13	0.722	0.001	0.97	0.412	0.030	—
LDMC	**3.08**	**0.032**	**0.095**	0.45	0.502	0.005	0.51	0.677	0.016	—
LCC	**10.41**	**<0.01**	**0.261**	0.32	0.574	0.003	1.11	0.351	0.028	—
LNC	**4.86**	**<0.01**	**0.140**	0.01	0.992	0.001	1.60	0.196	0.046	—
LPC	0.57	0.636	0.019	0.04	0.841	0.001	0.65	0.583	0.022	—
AD	0.63	0.600	0.020	1.08	0.302	0.011	**2.80**	**0.045**	**0.087**	log()
SRL	1.03	0.384	0.031	0.12	0.727	0.001	**3.63**	**0.016**	**0.110**	—
RTD	1.71	0.172	0.052	0.40	0.530	0.004	2.39	0.074	0.073	log()
RCC	0.22	0.882	0.008	0.01	0.997	0.001	1.39	0.252	0.047	log()
RNC	0.88	0.457	0.029	3.29	0.073	0.036	0.95	0.421	0.031	—
RPC	**4.03**	**0.010**	**0.126**	0.64	0.427	0.007	0.39	0.758	0.012	—
AMFC	**2.96**	**0.037**	**0.093**	0.45	0.504	0.005	0.544	0.654	0.017	—

independent from each other. We further found that community-level leaf traits only depend on soil abiotic conditions, while root traits show variable responses to changed soil abiotic and biotic conditions. The differences in drivers of root and leaf traits may explain the observed orthogonality of these two trait groups. Our data suggest that experimental treatments did not only affect the individual traits, but soil inoculation also affected plant species composition (Table S4). In combination, these changes likely explain the observed orthogonality.

Our study is unique in experimenting with the impacts of sterilised versus living soil inocula on plant trait relations under field conditions. On the one hand, this allows explicitly accounting for the role of added ecologically realistic suits of soil organisms. On the other hand, it is important to realise that the absence of a response to added soil biota (i.e. impact of the sterilisation treatment and interactions therewith), does not necessary imply the absence of impact of soil biota per se. Plots treated with sterilised as well as nonsterilised inocula most certainly have been colonised by locally available soil organisms. Thus, trait responses to soil abiotic conditions, in combination with the absence of a response to soil biota additions, suggest a response to the activity of these local biota as mediated by the addition of sterilised inoculum. Collectively, in the follow-up discussion, we explicitly articulate the effects of *experimentally added* soil inocula versus possible impacts of soil inocula in general, on for instance root functioning.

4.1 | Community-level leaf and root traits orthogonality

There was no significant correlation between community-level leaf and root traits, which strongly suggests that the response patterns of above- and below-ground community-level traits to alternations in soil abiotic and biotic conditions were not coordinated. These results contrast the paradigm of coordinated leaf and root economic spectra at plant species level and are consistent with outcomes of some recent studies on the lack of coordination between root economic spectra and leaf spectra across individual species (Isaac et al., 2017; Wang et al., 2017). One explanation for the decoupled relationship of root and leaf traits lays in the large variety of root functions and resulting complex relationships to soil biotic and abiotic conditions, as proposed in the 'multidimensional root trait framework' (Kramer-Walter et al., 2016; Weemstra et al., 2016). Compared with leaf traits which are mainly directly driven by the main function of light and CO_2 capture (Hendrik et al., 2009), the variation in root traits is driven by a more complex suit of abiotic and biotic selective pressures (Bardgett et al., 2014; Laliberté, 2017; Weemstra et al., 2016). Such constraints to root traits do not directly operate in leaves, resulting in a larger variety of below-ground resource acquisition mechanisms and trade-offs (Bardgett et al., 2014; Freschet et al., 2018). Therefore, roots have more freedom to construct a variety of different trait combinations and may improve plant fitness under different conditions (Laughlin, 2014).

Second, outsourcing the nutrient acquisition task to beneficial soil microbes, such as mycorrhizal fungi, could also reduce the necessity of developing a profound system of acquisitive roots. Thus, multiple aspects of soil biotic and abiotic conditions, for which there are no analogues may control root traits (Bergmann et al., 2020; Ma et al., 2018). In agreement with this supposition, our results show that manipulation of the soil community influenced only the root traits but not leaf traits (Table 3). The main variation in leaf and root traits was explained by orthogonal axes of PCA, for which the great fraction of variation in leaf traits was explained by axes 1, while the main variation in root traits

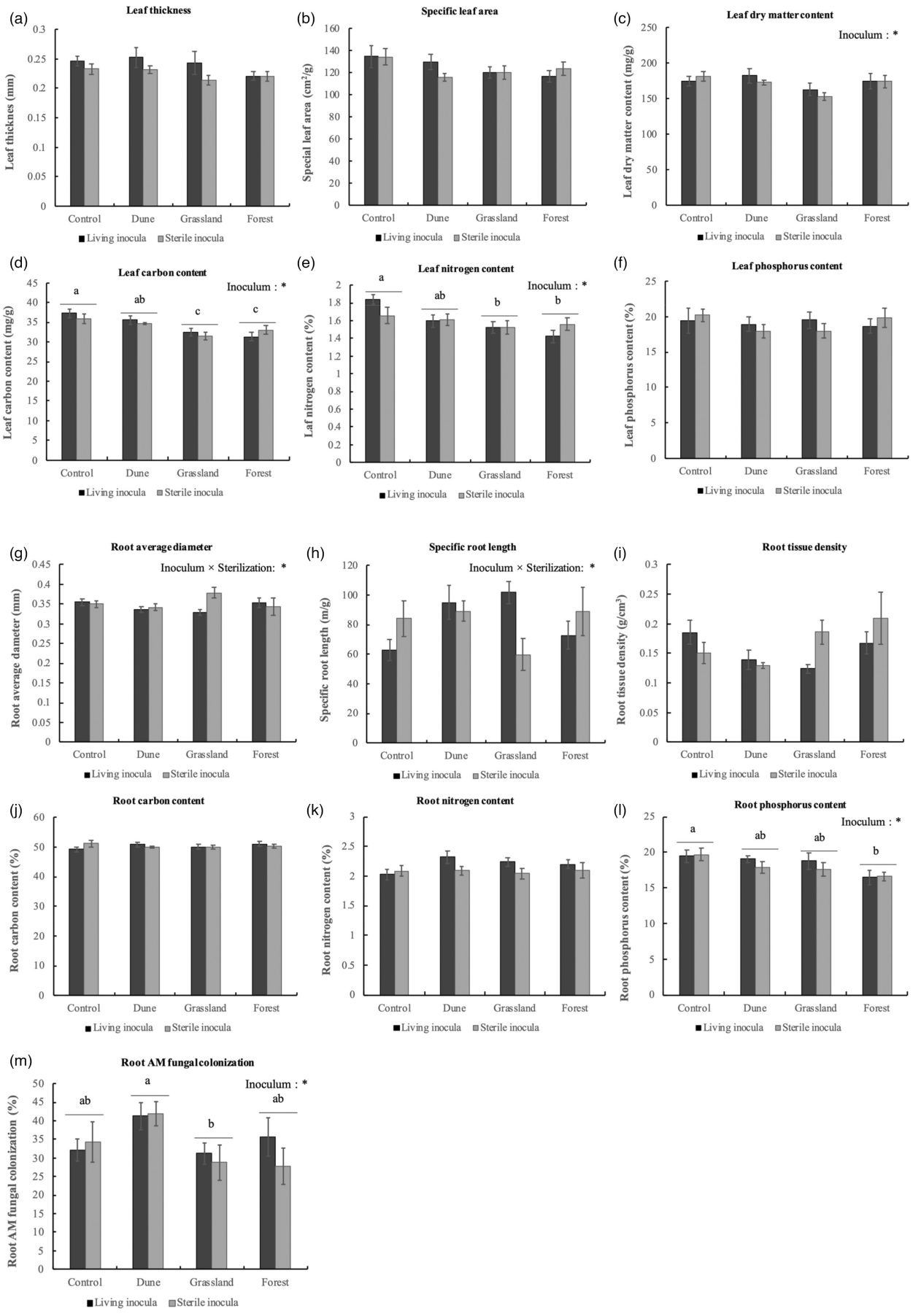

FIGURE 3 Effects of soil inoculation on community level mean weighted trait values: (a) LT; (b) SLA; (c) LDMC; (d) LCC; (e) LNC; (f) LPC; (j) RCC; (h) RNC; (i) RPC; (j) SRL; (k) AD; (l) RTD; (m) AMFC. *$p < 0.05$, Data are means ± SE. The black bar indicate plots with living soil inocula, and the grey bar indicate plots with sterile soil inocula. Text with a star (*) indicated a factor revealed to be significant by the two-way ANOVAs. Control plots (without any inoculation; see Figure S1) were randomly assigned as control to either the living or sterile soil inocula treatments. In case of the inocula origin being significant factor, letters above the bars indicate the outcomes of post-hoc analysis conducted to compare the impacts of distinct inocula origins.

was explained by axes 2 and 3 (Table S3). The only exception to this rule was a weak correlation between root and leaf nitrogen concentrations (Table 2). This indicates that the general nutrient allocation rules governing the partitioning of nitrogen above- and below-ground are still partly valid across plant communities while other aspects of root functional trait variation weaken such correlations.

Remarkably, the orthogonality between above- and below-ground traits was preserved in plots with both sterilised and nonsterilised soil inocula (Figure 2), despite the significant response of individual below-ground traits to additions of living soil biota (Table 3). This indicates that the observed independence of community-level above- and below-ground responses is not driven by the experimental additions of soil biota, but is a principal feature of plant community behaviour across gradients of nutrient availability and soil biota types. Together, this suggests a complementarity in variation of leaf and root functions in response to altered soil conditions. The extent to which such above- below-ground trait orthogonality is a characteristic of an early successional dune plant community, as in our experiment, or is a general feature of plant community ecology, needs further investigation.

4.2 | Responses of community-level traits to manipulation in soil biotic and abiotic conditions

We found that the responses of certain individual CWM leaf traits (e.g. LDMC, LCC, LNC and LPC) only depend on the origins of soil inocula, while soil sterilisation, and therewith added soil biota, did not cause any effects. This finding is inconsistent with earlier proposals that there is a close link between above-ground traits and soil community at an individual plant species or functional group level (Lau & Lennon, 2011; Orwin et al., 2010). Thus, the relationships between plant above-ground traits and soil communities measured at individual species or in monocultures are not necessarily representative for natural communities. This could be due to differential species responses to soil treatments (Table S5) and different correlation patterns among traits of individual species (Table S6). For example, in later successional ecosystems, annuals and early-successional plant species are stronger negatively affected by plant–soil interactions due to the build-up of host-specific plant pathogens (Kardol et al., 2006; Kulmatiski et al., 2008). By contrast, the effects of plant–soil interactions on later-successional plant species appear to be more positive (Kardol et al., 2006) allowing for instance stronger plant benefit of AM fungi (Koziol et al., 2015).

Root traits showed more variable responses to changes in soil conditions compared with leaf traits, which responded to the origin of soil inocula only. Root morphological traits were determined by both biotic and abiotic factors of added soil inocula. We speculate that in our system, the presence of added soil biota supported nutrient acquisition by influencing the root morphological traits (higher SRL, lower AD and RTD). These results highlight that manipulations of soil biota alter the root architecture of plant community. This is consistent with recent studies which have shown that biotic interactions of roots with soil biota influence the architectural, morphological root traits across plant species (Bergmann et al., 2020; Grover et al., 2021; Vacheron et al., 2013). Moreover, we found that the presence of added soil biota may promote a 'fast-growing' plant community characterised by a resource-exploitative strategy (construction of long, narrow-diameter roots with minimal biomass investment but high metabolic rates) (Ostonen et al., 2007; Reich, 2014; Ryser & Eek, 2000). This may be explained by the positive effects of accumulated beneficial soil community from later-successional donor ecosystems, such as plant growth-promoting bacteria and rhizobia. These beneficial communities can increase root length and result in increased plant growth and development (Grover et al., 2021; Vacheron et al., 2013).

Plant communities had a lower root AM fungal colonisation when grown with later-successional soil inocula, suggesting that the plant community invests less in its association with AM fungi when grown in better nutrient conditions. Alternatively, these results may be explained by the fact that our experiment was conducted in an early development stage in which most dominant species were early-successional plants (Table S7) which may depend less on AM fungal symbiosis for nutrient uptake (Koziol et al., 2015; Middleton & Bever, 2012).

Unlike other root traits, RPC was lower in plant communities grown in plots with late-successional soil inocula, in comparison with other inoculation treatments. This may have been caused by the extremely low values of soil P in our system (Van der Heijden, 2010). In such situation, uptake of P from fertile soil inocula may become the dominant P uptake pathway. The addition of soil nutrients from later-successional systems may then reduce the immobilisation of P in soil and consequently influence the plant community P uptake efficiency (Van der Heijden, 2010).

5 | CONCLUSIONS

Our results provide valuable evidence that the variation in plant community-level leaf traits across soil conditions are not correlated with the variation in community-level root traits. Community-level leaf traits (LDMC, LCC and LNC) were mainly determined by the changes in the soil abiotic conditions. On the contrary, root traits

showed higher variation along shifts in both soil abiotic and biotic conditions. The plant communities tended to have more nutrient-acquisitive root traits (high SRL, low AD and RTD) in the presence of added soil biota. We conclude that soil inoculations with soil communities affect ecosystem functioning through the modification of below-ground, but not above-ground, community-weighted mean values of plant traits. Our study sets a benchmark in explicit and evidence-based understanding of the role of soil biotic and abiotic conditions in ecosystem functioning. As a next step, we encourage further efforts to test the general pattern of leaf and root correlations across different ecosystems under field conditions.

AUTHOR CONTRIBUTIONS

Chenguang Gao, Nadejda A. Soudzilovskaia and Peter M. van Bodegom design the research. Nadejda A. Soudzilovskaia, T. Martijn Bezemer, Riccardo Mancinelli and Harrie van der Hagen established the experiment of TERRA Dunes. Chenguang Gao, Xiangyu Liu and Riccardo Mancinelli collected samples. Chenguang Gao, Richard van Logtestijn, Meng Zhou processed the samples in lab. Chenguang Gao analysed the data with helpful input from Nadejda A. Soudzilovskaia, Peter M. van Bodegom, T. Martijn Bezemer, Hans C. Cornelissen and Xiangyu Liu. Chenguang Gao wrote the first draft, and all authors contributed to editing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository https://doi.org/10.6084/m9.figshare.21865116.v1 (Gao et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supplementary Methods.

Data S2: Supplementary Tables and Figures.

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