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Higher species diversity improves soil water infiltration capacity by increasing soil organic matter content in semi-arid grasslands

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Running Head: Higher diversity improves water infiltration

Abstract

Understanding the mechanisms mediating biodiversity effects on ecosystem functions and services is considered a core issue in ecological and environmental sciences. We studied the direct and indirect effects of plant diversity on soil organic carbon storage and soil infiltration capacity in semi-arid grasslands. Plant species diversity enhances soil organic carbon and soil infiltration capacity via multiple plant-soil feedback mechanisms in long-term natural restoration grasslands. Plant species diversity increases community productivity, resulting in increasing soil carbon storage, which improves soil infiltration capacity by influencing soil aggregate stability and porosity. The present study indicates that plant species diversity is conducive to increasing atmospheric CO_2 sequestration and reducing the risk of soil erosion. Our study provides a framework for interpreting the relationships among plant species diversity, soil organic carbon and soil infiltration capacity to understand plant-soil feedback mechanisms in semi-arid grasslands.

Keywords: diversity, plant species richness, soil organic carbon, soil infiltration capacity, plant-soil feedback

INTRODUCTION

Understanding how biodiversity affects ecosystem functions and services has been considered as a core issue in the ecological sciences over the past decades (Loreau et al., 2001; Isbell et al., 2011; Cardinal et al., 2012). Significant advances have been made in understanding the effects of species diversity on ecosystem processes and the associated underlying mechanisms for these effects (Loreau et al., 2001). For example, biodiversity enhances ecosystem functions (Cardinal et al., 2002; Chen et al., 2018), maintains ecosystem services (Isbell et al., 2011) and decreases invasion (Fargione & Tilman, 2010). Identification of the influences of biodiversity on ecosystem functions and services requires long-term research in experimental systems (Reich et al., 2012; Lange et al., 2015; Isbell et al., 2018). This idea is especially true for soil carbon storage because of slow material turnover (Liu et al., 2017a), high spatial heterogeneity (Isbell et al., 2018), and complex relevant processes (Schmidt et al., 2011).

Changes in soil carbon storage result from long-term effects of vegetation (Don et al., 2015; Liu et al., 2017a; Chen et al., 2018), climate (Crowther et al., 2016) and human activities (Yang et al., 2010). Moreover, soil carbon sequestration plays an important role in alleviating the increasing global CO_2 concentrations in the atmosphere (Crowther et al., 2016). Soil organic carbon storage (SOCS) is indicative of the balance between carbon inputs (plant litter production) and losses (microbial decomposition) (Chen et al., 2018). Previous studies have reported that biodiversity has the potential to affect SOCS by modifying the input/output balance (Lange et al., 2015; Hooper et al., 2012). Higher plant species diversity (PSD) both enhanced microbial activity (Lange et al., 2015) and SOCS (Wu et al., 2017a) in long-term experimental grasslands. Higher PSD promotes greater soil carbon accumulation by functional plant complementarity (Fornara & Tilman, 2008). Moreover, an increase in SOCS associated with PSD occurs through the decreased decomposition of plant residue inputs (Schmidt et al., 2011) or increased microbial decomposition (Liang et al., 2011). Therefore, whether species diversity positively impacts SOCS in natural grasslands remains unclear. Additional investigations should be carried out to determine the effects of PSD on SOCS. In addition, higher SOCS can promote PSD and productivity by improving soil water-holding capacity and maintaining soil fertility (Chen et al., 2018). This positive feedback plays a momentous role in grassland restoration, especially in semi-arid areas characterized by scarce water and barren soil.

Water shortage is a key limiting factor for the sustainability of ecological restoration in arid and semi-arid areas (Wu et al., 2017b). Maximizing precipitation infiltration and reducing run-off are critical factors for vegetation restoration and soil and water conservation in semi-arid areas. Vegetation type and community composition also impact soil water dynamics (Fischer et al., 2018; Liu et al., 2018), soil properties (Sibylle et al., 2008; Don et al., 2015), and soil hydraulic characteristics (Wu et al., 2017b; Huang et al., 2017). PSD also influences soil hydraulic properties. A decade-long experiment revealed that PSD increased soil infiltration capacity (SIC) and soil water content by altering soil properties (Fischer et al., 2015; 2018). SIC is increased by water flow via macropores that are formed by soil fauna or root systems, as well as cracks and fissures in grassland (Wu et al., 2017b). The increase in PSD can enhance soil organic carbon and belowground biomass, thus increasing soil porosity and soil aggregate stability (Six et al., 2004); therefore, an increase in PSD has the potential to increase the SIC. The effects of PSD on SIC are mainly the result of complex interrelations between species diversity and soil properties, except for soil texture (Fischer et al., 2015). Many studies have reported the effects of PSD on community productivity (Fornara & Tilman, 2008; Liu et al., 2017b; Chen et al., 2018). Changes in plant productivity affect earthworm activities, which produce many macropores through burrowing activity and thus increase the SIC (Fischer et al., 2015). Earthworm performance is closely related to PSD; as the PSD increases, the number of macropores formed by earthworms increases and the soil structure is improved (Dimitrakopoulos & Schmid, 2004; Eisenhauer et al., 2009). However, earthworms and PSD influence SIC through different pathways in long-term experimental grasslands (Fischer et al., 2015).

Previous studies have focused on the interaction between PSD, SIC, and SOCS in artificially controlled experimental grasslands, while little attention has been given to the effects of PSD on SOCS (Chen et al., 2018) and SIC in natural grasslands. The PSD of natural grasslands is influenced by complex interactions between environmental factors and human disturbance (Cardinale et al., 2002; Tilman et al., 2012). In turn, the change in habitat also results in the different plant characteristics, which determine the competitive patterns among community species and may ultimately influence biodiversity patterns (De Deyn et al., 2003). Thus, the effects of PSD on SOCS and SIC should be better understood in natural grasslands. Additional studies on this effect are expected to play a crucial role in the conservation of water and nutrients, which are two limiting factors for vegetation restoration in semi-arid areas.

In this study, we examined the influences of PSD on SOCS and SIC in a semi-arid grassland in China. To understand the effect of restoration time on the variables of interest, we investigated four natural grasslands at different succession stages (0 yr, 10 yr, 20 yr, and 30 yr). To facilitate our analysis, we explored the effects of diversity on SOCS and SIC by analyzing both species diversity and richness indices. Specifically, the objectives of this study were to (a) explore how PSD affects SOCS and SIC, and (b) identify the direct and indirect processes of plant-soil interactions in semi-arid grassland.

MATERIALS AND METHODS

Study site

The study site was located in typical steppe grassland of the Loess Plateau at the Yunwu Mountain Natural Reserve (36°13′-36°19′ N, 106°24′-106°28′ E), Guyuan city, Ningxia Hui Autonomous Region, China. The Yunwu Mountain Natural Reserve has remained the largest steppe grassland natural reserve (total area is 7150 hm^2) on the Loess Plateau since 1982. The climate of the study area is moderate semi-arid, with a mean annual temperature of 6.7 °C. The annual average precipitation is 400-455 mm, of which more than 60%-75% occurs from July to September. The average annual evaporation is 1330-1640 mm. The soil types are mainly loessial soil and Heilu soil (Zhao et al., 2013). The dominant species in study area are *Stipa capillata*, *Stipa grandis*, *Agropyron cristatum*, *Thymus mongolicus*, *Artemisia frigida*, *Artemisia sacrorum*, and *Potentilla acaulis*.

Vegetation and soil survey

A typical grassland with flat terrain and a consistent soil type was selected in the study area 2016. According to the chronosequence of community succession, the grasslands were classified as 0 yr, 10 yr, 20 yr and 30 yr grasslands. In each grassland study site, five 10 m × 10 m plots were established, and five 1 m × 1 m quadrats were established along a diagonal line in each plot. The coverage of each plant species and the total vegetation coverage in each quadrat were estimated. Plant abundance and the total number of herbaceous species (plant species richness) in each quadrat were recorded. The above-ground plant parts were harvested and separated by species, and the litter in each quadrat was collected in envelopes. The samples were taken to laboratory to measure above-ground biomass (AGB). The below-ground biomass (BGB) was collected from 0~50 cm soil layers at 10 cm intervals from three sites along the diagonal line in each quadrat with a 9 cm diameter root auger. The root samples were sifted with a 2 mm sieve to separate the plant matter from the soil. All samples were oven-dried at 65 °C to a constant weight, and the dry mass was calculated.

Three soil samples were collected from the remaining soil after sieving the roots. The samples were labelled and air-dried and the soil organic matter content (SOC) was analyzed via the dichromate oxidation method. Soil aggregate tests were conducted with a fast-wetting treatment and indicated by mean weight diameter (MWD, mm). Soil moisture (SM, %) content was determined using a 38 mm diameter soil auger and was measured by oven-dried at 105 ℃ to a constant weight. SM was calculated as the ratio of soil moisture to dry soil mass. Soil bulk density (BD) was measured by a cutting ring with a volume of 100 cm^3, and then the soil was oven-dried to a constant weight. Five samples per quadrat were collected to measure SM and BD.

PSD was calculated as follows:

Plant species richness (PSR): *R*=*S*

Shannon–Wiener diversity index (H):

$$H = \sum_{i=1}^{s} (Pi \;\; lnPi)$$

where *S* is the total number of plant species in the sample quadrat, *Pi* is the relative abundance of species *i*, and $Pi=n_i / N$, where n_i is the individual number of species *i*, and *N* is the total number of all individual species in the quadrat.

SOCS (Mg hm^{-2}) was calculated as follows:

$$SOCS = \sum_{i=1}^{n} (D_i \times B_i \times SOC_i)$$

where *n* is the number of soil layers, *Di* is the depth of layer *i* (cm), and *Bi* is BD of layer *i*.

Soil total porosity (TP, %) was calculated as follows:

$$TP = \frac{DS - BD}{DS} \times 100$$

where, *DS* is the particle density (2.65 g cm^{-3}), and *BD* is the soil bulk density (g cm^{-3}).

Infiltration measurement

A SIC automatic measurement system was used for situ infiltration measurements. The device measured the whole infiltration process without disturbance to soil structure. The system was mainly composed of a computer, a camera and a peristaltic pump. The peristaltic pump ensured that the water supply was constant during the infiltration process. The camera captured the wetted area of the soil every 3 minutes. The computer mainly estimated the infiltration capacity of the soil by calculating the wetted area over time (Wu et al., 2017b). This method considered the complete infiltration process and included a high infiltration rate in the initial infiltration stage and a decrease of infiltration rate as it approached a steady state. The steady infiltration rate represented the SIC for further analyses in the study. Analysis of the SIC was conducted on flat ground next to each quadrat.

Statistical analyses

The influences of PSR on SOCS and SIC were estimated using analysis of variance (ANOVA) and linear mixed-effects models. Pearson correlations were used to determine the variables significantly correlated with PSR, SOCS, and SIC ($p < 0.05$). Regression analysis was performed to evaluate the relationships between PSR, PSD, SOCS, and SIC. Path analyses (maximum likelihood) were used to test the effects (direct and indirect) of soil properties (SM, SOC, MWD, and TP), and plant community properties (PSR, PSD, AGB, BGB, and litter) on SOCS and SIC. All variables were naturally logarithmically transformed before the path analysis. The reliability of the relationships was measured using chi^2-tests (χ^2) and root mean square error of approximation (RMSEA) tests.

RESULTS

Variation in PSD and SOCS with succession stages

With the increase in succession years, SOCS and species richness first increased and then decreased. The SOCS peak occurred in the 10^{th} year of succession (21.83 ± 7.20 Mg hm^{-2}), and the SOCS rate was significantly higher (P<0.05) than those in the other succession years (Fig. 1). Maximum species richness (16.33 ± 0.85) was observed in the 30^{th} year and minimum species richness (13.04 ± 0.91) was observed in the 20^{th} year. At the whole-grassland-community level, a significant positive linear relationship (P<0.01) between PSD and the diversity index was found. In view of this relationship, we studied the influences of PSD on soil properties. The results of the linear mixed-effects model showed that restoration time had a significant random effect on the relationships between PSD and SOCS as well as PSD and SIC (Table 1).

Influence of PSD on SOCS

There was a significant positive correlation between SOCS and PSR (Fig. 2c). As PSD increased, AGB, litter, and SM increased significantly (Table 2, Fig. 2b). Because of the complex impacts of the various related variables on SOCS, a path analysis was applied to identify the direct effects, indirect effects and interaction effects. The path analysis revealed that PSD had direct positive influences on AGB, litter, and SM, all of which exhibited consistently positive effects on SOCS (Fig. 2a). There was no direct relationship between species diversity and SOCS. SOCS was mainly associated with AGB and litter. Species diversity indirectly explained 53% of the variation in SOCS by AGB, litter and SM and the path analysis model explained 84% of the variation in SOCS.

Influence of PSD on SIC

With increasing PSR, soil properties changed obviously. BGB, MWD and TP showed an increasing trend with increasing PSR (Fig.3b, c, d). The correlation analysis results showed that species diversity, SIC, SOC, BGB, NWD, and TP were all positively correlated (Table 3). SIC was significantly positively correlated with PSR (Fig. 3e). The path analysis model indicated that PSD had direct positive influences on BGB and SOC, both of which had positive impacts on soil properties (NWD and TP), and NWD and TP were directly positively related to SIC (Fig. 3a). Species diversity indirectly explained 26% of the variation in SIC, and the path analysis model explained 53% of the variation in SIC.

DISCUSSION

Effects of PSD on SOCS and underlying mechanisms

Our results supported the general theoretical prediction that PSD enhances SOCS in natural grasslands. During grassland restoration, PSD promotes AGB, alters the community structure and composition of litter, and increases SOC inputs. PSD mainly affects SOCS through plant communities. The results were consistent with the study by Cong et al. (2015), that suggested that PSD promotes SOCS through increased plant community productivity, and in turn, increasing SOCS provide positive feedback to plant communities through enhanced soil fertility. That is, the positive effects of PSD on SOCS are likely strengthened by the positive effect of high SOCS on PSD (Chen et al., 2018). Previous long-term and broad-scale experiments also showed that the responses of SOC to PDS play crucial roles in influencing the relationship between diversity and carbon cycles in natural grasslands (Tilman et al., 2012; Chen et al., 2018). Moreover, the positive relationship between PSD and AGB in grasslands may reinforce the positive effect of PSD on SOC because the carbon composition rate is relatively low in semi-arid areas (Yang et al., 2010).

Our findings also indicate that increased PSD results in increased AGB and litter, which increase carbon inputs, thereby increasing SOCS. Positive relationships between PSD and productivity have been well reported in many large-scale experiments in grasslands (Grace et al., 2016). PSD enhances SOCS by increasing the amount of plant litter, mainly due to the priming effect of plant litter on SOC mineralization and litter decomposition rates (Rasse et al., 2005). Although previous studies have reported that the rhizodeposition of root exudates can impact the decomposition rate of SOC, SOCS is increased more by shoot and litter compounds than by root compounds (Rasse et al., 2005). This theory is corroborated by the slight influence of roots on SOCS in the current study (path coefficient close to 0). Moreover, higher PSD enhances rhizosphere carbon inputs in the soil causing increased microbial activity and reduced carbon losses from microbial decomposition, thereby enhancing SOCS (Fornara & Tilman, 2008; Lange et al., 2015). The positive effect of PSD on microbial communities is primarily the result of improved microclimatic conditions (Lange et al., 2014). Carbon inputs and favourable microclimatic conditions from high-PSD communities lead to more active and more diverse soil microbial communities (Lange et al., 2015). Additionally, high PSD plant communities increase the canopy density of plant stands, reduce the evaporation of SM and increase soil temperature, which all in turn improve soil microbial activity and growth. Litter decomposition and nutrient inputs, such as soil carbon and nitrogen and microbial and nematode communities, mediate litter carbon and nitrogen losses and play a dominant role in decomposition (García-Palacios et al., 2016). Therefore, litter plays an important role in the interactions between PSD, soil conditions and microbial communities.

The contributions of PSD to SOC, whether through root systems or plant litter inputs, are mediated by the soil microbial community. The contributions become more important over time through increased positive PSD effects on AGB (Reich et al., 2012) and an increased contribution of soil microbial activity to SOCS (Eisenhauer et al., 2010). Both mechanisms may be responsible for the contributions of PSD to SOC (Lange et al., 2015). The current study shows that PSD enhances SOCS in natural grasslands in semi-arid areas.

Effects of PSD on SIC and underlying mechanisms

Our study found that PSD impacts SIC by influencing SOC, soil aggregates and roots. PSD can improve soil water stable aggregates, soil structure, soil TP and SIC by influencing SOC and the distribution of roots, which is an effective way to supplement soil reservoirs. The findings indicate that PSD may have significant impacts on soil hydraulic properties, and thus potentially influence surface run-off and soil erosion. The results represent a significant expansion of previous studies because they demonstrate the impacts of PSD on SIC and suggest an underlying mechanism. The contribution of PSD to SOC has been well demonstrated. Many previous studies have shown that increasing SOC and roots can improve soil TP and soil aggregate stability (Six et al., 2004), which can increase SIC (Huang et al., 2017; Wu et al., 2017b). These findings were also confirmed in the current study. Moreover, our study showed that PSD influenced SIC by improving BGB, SOC, TP and soil aggregates; the findings is the first time have been confirmed in natural grasslands.

SOC plays a crucial role in the relationship between PSD affecting SIC. First, an increase in SOC can reduce BD and increase soil porosity; the correlations have been well demonstrated (Fischer et al., 2015). Soil porosity is considered to be the primary driver of SIC (Fischer et al., 2015). Second, soil aggregates can influence the development and distribution of soil porosity through their particle size distribution and stability characteristics, which affect SIC (Duiker et al., 2001). The formation of soil water-stable aggregates depends on SOC, and the soil microbial community is an important biological factor forming soil aggregates. Some microbes can bind soil particles to one another and form soil aggregates through their own activities, while others form aggregates by cementing soil particles together with their secretions and other organic matter. Third, SOC improves soil structural and soil hydraulic properties, thereby increasing SIC (Dekker et al., 2007).

PSD increases the AGB and BGB of plant communities (Roscher et al., 2010; Tilman et al., 2012), while an increase in roots affects SIC by realigning soil particles and forming well-connected macropores or root channels (Wu et al., 2017b). PSD also affects the presence of earthworms, which influence SIC through the formation of macropores by burrowing (Fischer et al., 2015). Increasing the SIC results in an increase in the amount of precipitation retained in the soil, which is crucial for reducing run-off and soil erosion in arid and semi-arid areas. Moreover, an increase in the SIC means reduced soil nutrition loss (Zhao et al., 2013), which plays a crucial role in promoting vegetation growth and maintaining soil quality in arid and semi-arid areas.

CONCLUSIONS

PSD seems to enhance on soil organic carbon and SIC via multiple plant-soil feedback mechanisms in semi-arid grasslands. Our research shows that PSD increases community productivity resulting in increasing SOCS, which improves SIC by influencing soil aggregate stability and porosity. The present study indicates that PSD is significantly conducive to increasing the sequestration of atmospheric CO_2 and to reducing the risk of run-off and soil erosion in semi-arid grasslands.

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Table 1 ANOVA for the effect of PSR on SOCS and SIC using linear mixed-effects models. The effects of restoration time as a random factor.

Dependent variable	Num DF	Den DF	*F* value	*P* value
SOCS	1	16.03	8.44	0.010
SIC	1	17.00	5.14	0.037

Note: Num DF indicates the nominator degree of freedom and Den DF indicates denominator degree of freedom.

Table 2 Pearson correlation coefficients between plant species diversity (H), Aboveground biomass (AGB), Litter, soil moisture (SM) and soil organic carbon storage (SOCS).

	H	AGB	Litter	SM	SOCS
H	1.00				
AGB	0.47*	1.00			
Litter	0.46*	0.46*	1.00		
SM	0.53*	0.65**	0.64**	1.00	
SOCS	0.49*	0.82**	0.72**	0.77**	1.00

Note: * represents correlation is significant at $P < 0.05$, ** represents correlation is significant at $P < 0.01$.

Table 3 Pearson correlation coefficients between plant species diversity (H), steady infiltration rate (SIC), soil organic carbon content (SOC), belowground biomass (BGB), soil mean weight diameter (MWD) and total porosity (TP).

	H	SIC	SOC	BGB	MWD	TP
H	1.00					
SIC	0.46*	1.00				
SOC	0.52*	0.56*	1.00			
BGB	0.47*	0.48*	0.48*	1.00		
MWD	0.56*	0.70**	0.47*	0.24	1.00	
TP	0.50*	0.55*	0.45	0.55*	0.44	1.00

Note: * represents correlation is significant at $P < 0.05$, ** represents correlation is significant at $P < 0.01$.

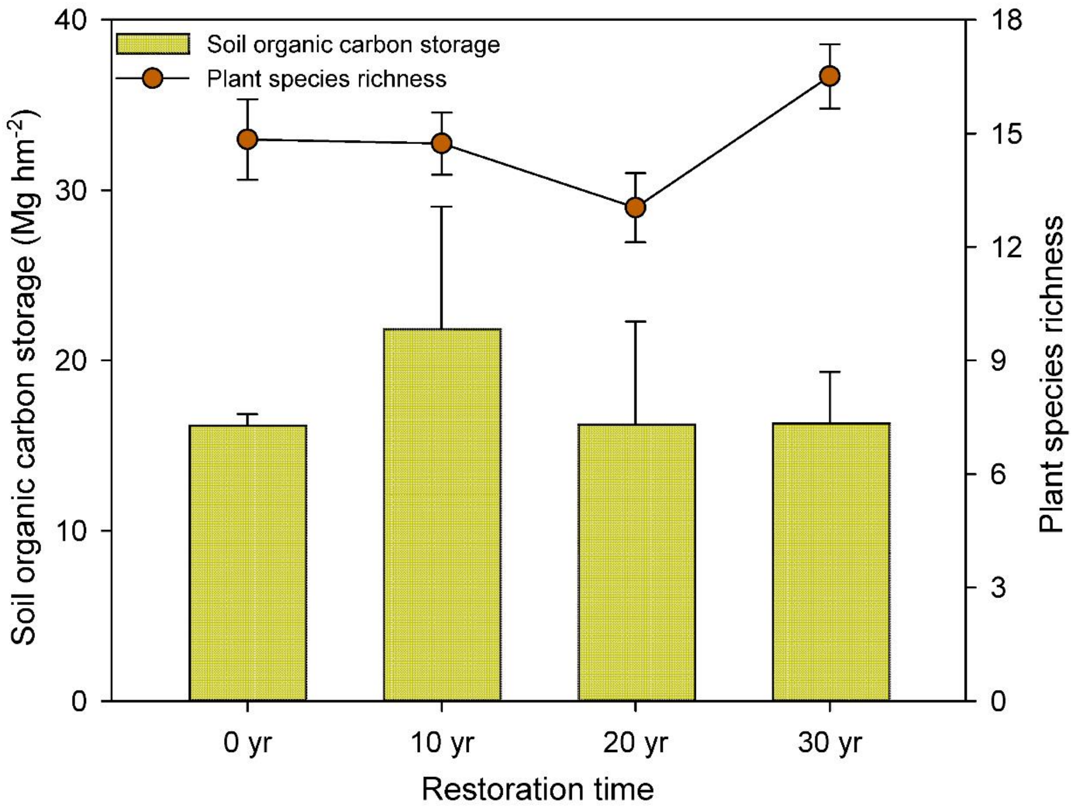

Figure 1 Changes of plant species richness and soil organic carbon storage with restoration time.

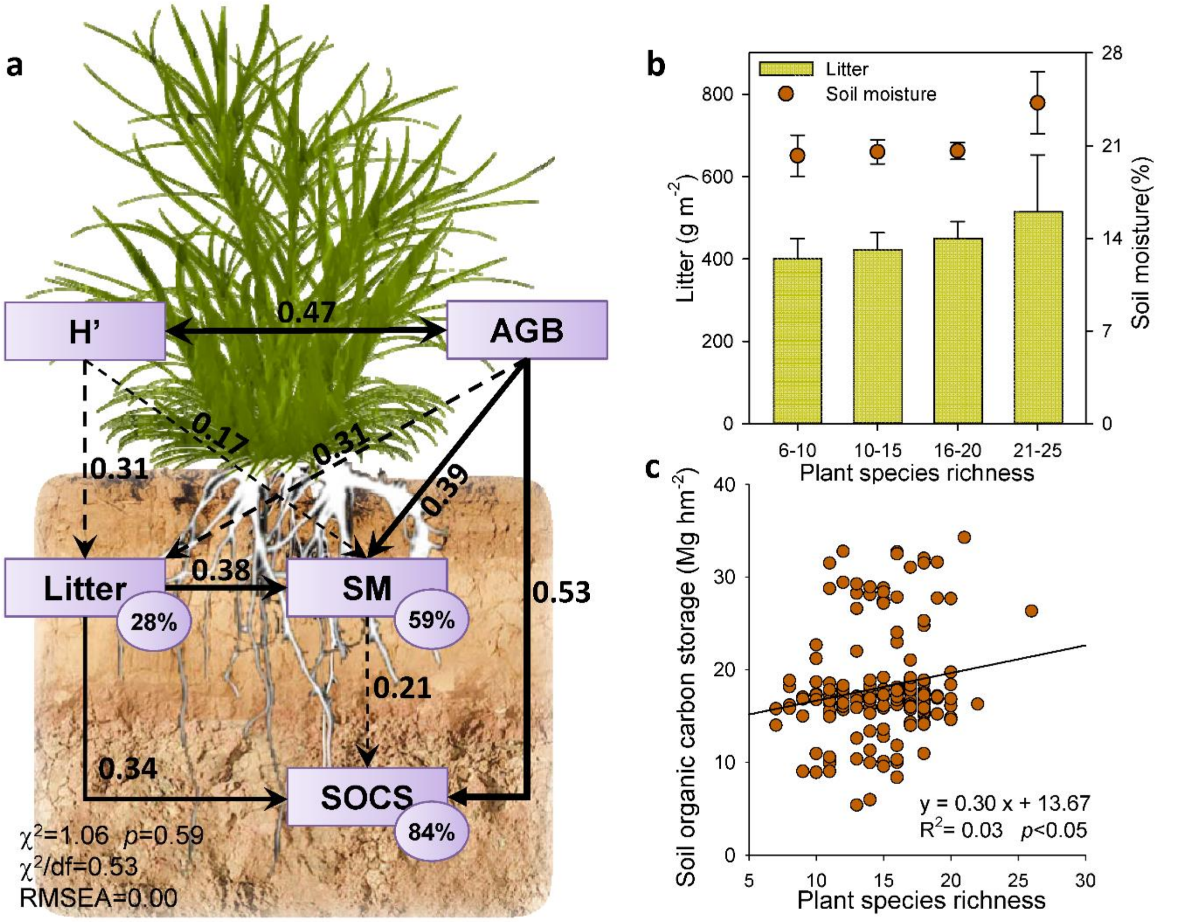

Figure 2 Mechanisms of species diversity increase soil organic carbon storage. (a) Path analysis showing the relationship between species diversity (H'), aboveground biomass (AGB), Litter, and soil moisture (SM at 0-50 cm soil depth), on the soil organic carbon storage (SOCS). Numbers on the path arrows are standardized path coefficients. The thickness of the arrow line shows the strength of the causal influence. Numbers in circles indicate the proportion of variance explained by the model (R^2). Solid arrows represent significant standardized path coefficients ($p \leq 0.05$), and dashed arrows represent nonsignificant standardized path coefficients ($p > 0.05$). (b) Impact of plant species richness on litter and soil moisture. (c) Relationship of plant species richness with soil organic carbon storage at 0-50 cm soil depth.

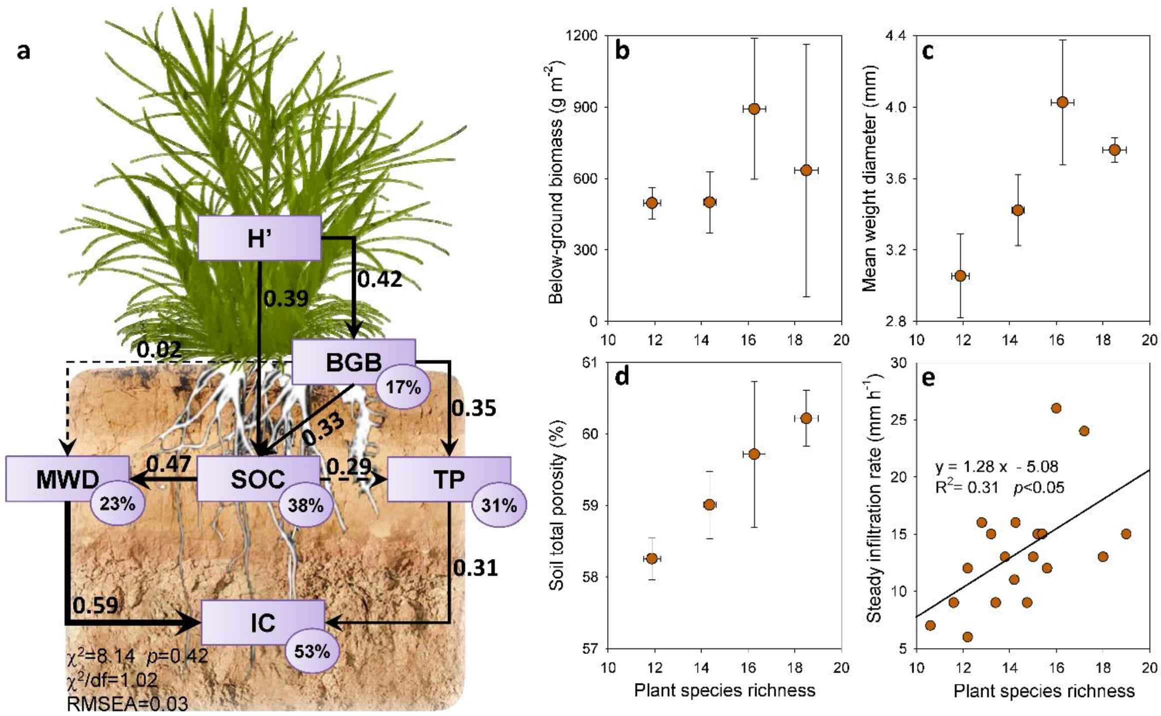

Figure 3 Mechanisms of species diversity increase infiltration capacity. (a) Path analysis showing the relationship between species diversity (H'), belowground biomass (BGB), soil organic carbon content (SOC), soil mean weight diameter (MWD), and soil total porosity (TP), on the soil infiltration capacity (IC). Numbers on the path arrows are standardized path coefficients. The thickness of the arrow line shows the strength of the causal influence. Numbers in circles indicate the proportion of variance explained by the model (R^2). Solid arrows represent significant standardized path coefficients ($p \leq 0.05$), and dashed arrows represent nonsignificant standardized path coefficients ($p > 0.05$). (b), (c) and (d) Impact of plant species richness on belowground biomass, mean weight diameter and soil porosity. (e) Relationship of plant species richness with steady infiltration rate.