Multiple abiotic and biotic drivers of soil water storage capacity in temperate forests recovering from disturbances

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Abstract

Background and aims

Soil water storage capacity acts as a vital forest function to intercept rainfall and retain water for plant growth processes. However, whether or how plant functional trait diversity and composition regulate soil water storage capacity remains poorly understood.

Methods

Structural equation modeling (SEM) was used to detect the direct and indirect effects of multiple biotic (i.e., functional trait composition and functional diversity) and abiotic (topography and soil organic carbon) factors on soil water storage capacity, i.e., in terms of soil capillary water storage content (CW), soil non-capillary water storage content (NCW), and soil saturated water storage content (TSW), in temperate forests recovering from different logging disturbance intensity levels.

Results

The community-weighted mean of specific leaf area (CWM_{SLA}) increased CW but decreased NCW directly, whereas improved NCW and TSW indirectly via soil organic carbon. Disturbance influenced soil water storage capacity mainly in indirect ways via promoting CWM_{SLA} and soil organic carbon. Elevation increased NCW and TSW but decreased CW directly, and it also had indirect effects on soil water storage capacity via decreasing CWM_{SLA} and soil organic carbon. Moreover, soil organic carbon influenced NCW and TSW directly or mediated the effects of elevation, disturbance, and CWM_{SLA} on soil water storage capacity.

Conclusions

The quick return on investments trait of CWM_{SLA} shows a positive effect on soil water storage capacity (CW and TSW), supporting the mass ratio mechanism in temperate forests recovering from disturbances. Soil organic carbon also presents additional importance to soil water storage capacity.

1. Introduction

Soil water storage capacity is one of the major soil functions which could potentially affect biogeochemical cycle, and hence, mitigate the influences of global climate change (Lü et al. 2015; Reich et al. 2018; Zhang et al. 2016). For example, soil water storage capacity regulates the water flow to alleviate the negative effect of hydrological variations, which in turn could regulate climate change events (Andreassian 2004; Zhang et al. 2011). In addition, the plant diversity effect usually presented a

significant relation with soil water-related functions, indicating that plant diversity is one of the main biotic factors underlying soil water storage capacity (Kammer et al. 2013; Wen et al. 2019). Although several studies have reported the differences of soil water storage capacity among diverse vegetation types (Fang et al. 2011; Hao and Wang 1998; Jiao et al. 2011; Wang et al. 2013), none of the studies has reported on the complex interactions of biotic (functional trait diversity and community-weighted mean trait composition; CWM) and abiotic (i.e., topography, climate, and edaphic) factors for determining soil water storage capacity in forests recovering from logging disturbances (see Fig. S1 for a conceptual model).

It is generally well explored that the niche complementarity (the diversity effect) and mass ratio (the CWM effect) mechanisms could explain several ecosystems functions in natural assembled communities (van der Plas 2019). For example, in the semi-arid grassland ecosystem of China, plant diversity is positively correlated with soil water content with the increasing community coverage (Wu et al. 2014). In addition, higher species diversity could improve soil water infiltration capacity by changing soil properties as the long-term feed-back between soil and high above- and below-ground biomass (Liu et al. 2019). Indeed, the ecological mechanism behind this positive effect might be associated with the niche complementarity hypothesis i.e., species having different niches can use the available resources or facilitate their coexistence, then could improve ecosystem functions (Lange et al. 2019; Tilman et al. 1997). Besides the diversity effect, the trait of most dominant species (i.e. measured in CWM) could also drive ecosystem functions under the assumption of the mass ratio hypothesis (Grime 1998). For instance, the CWM of specific leaf area (CWM_{SLA}) could explain more variance of water retention capacity than other predictors in semi-arid forest ecosystems (Teixeira et al. 2020). Moreover, tree species functional group, litterfall quality per se, and its decomposing rate rather than the diverse or the amount of litterfall input better explained the variance of soil functions (Dawud et al. 2017). Taken together, these prominent ecological theories could provide the quantitative relationships between diverse plant species, composition and soil water storage capacity, and hence may improve our understanding regarding underlying mechanisms when simultaneously testing their effects on ecosystem functions (Fig. S1) (Ali et al. 2017; Becknell and Powers 2014; Yuan et al. 2019).

Many advanced ecological studies have suggested that abiotic factors (e.g., topography) can potentially affect plant diversity, composition and ecosystem functions (Jucker et al. 2018). For example, changes in soil physicochemical properties could be highly attributed to topographical factors (Chapin et al. 2011; Zhang et al. 2019). Fine soil particles, as well as soil organic carbon, tended to accumulate in lower elevational gradients because of the soil erosion processes when rainfall events appeared (Chapin et al. 2011; Zhang et al. 2019). Accordingly, soil water retention ability could be enhanced by fine soil texture, whereas soil water infiltration function could be improved by increased soil organic carbon contents (Chen et al. 2019; Fischer et al. 2015; Zhang et al. 2019). On the other hand, elevation as an important topographical factor can regulate soil water storage capacity indirectly through influencing climatic factors which in turn could impact vegetation structure and composition (Hao et al. 2003). For example, along with the decline of elevational gradients, plant composition presents to be a quick return on

investment species, and this kind of litterfall could be beneficial for the accumulation of soil organic carbon which in turn could influence the soil structure and water storage capacity (Cotrufo et al. 2013; Fischer et al. 2019).

Under global change circumstances, forest ecosystems are impacted by a diversity of human activities, i.e., logging disturbance which is a common disturbance for timber use in forests (Edwards et al. 2014), resulting in changing vegetation structure and functions. The disturbance activities in forests could lead to alteration of forest types, associated above- and below-ground functions (Millar and Stephenson 2015; Yuan et al. 2018) as well as impact biogeochemical processes (de Avila et al. 2018). As such, the time lag effect of soil water storage functions may appear because of the different recovering rate of ecosystem functions and the process of plant-soil feedback (Thom and Seidl 2016; Trumbore et al. 2015). For instance, a decade-long Jena Experiment proved that plant species diversity affecting soil water contents from the shading effect in the early years was shifted to the soil properties in later years (Fischer et al. 2019). Although the effects of different types of disturbance (e.g., logging, fire, cutting, clearing) on different forest functions have been widely reported (Edwards et al. 2014), there is no actual study dealing with soil water storage capacity in the forests recovering from logging disturbances. This knowledge is crucial for understanding forests resilience and recovering from disturbances as increasingly considered vital in the face of climate change and human interventions (Seidl et al. 2016).

This study aims to explore how multiple biotic (i.e., functional trait composition and functional diversity) and abiotic (topography and soil organic carbon) factors drive soil water storage capacity, i.e., in terms of capillary water storage content (CW), soil non-capillary water storage content (NCW), and soil saturated water storage content (TSW), in temperate forests recovering from different logging disturbance intensity levels (Fig. 1). To do so, we used data from eleven permanent forest sites (in total 260 subplots) on Changbai Mountain in the northeast of China where forests underwent through three disturbance intensity levels. Using the conceptual model (Fig. 1), we answered the following main research questions. 1) Which ecological mechanism – the mass ratio or the niche complementarity - explain variation in soil water storage capacity? 2) How do disturbance and topographic factors affect soil water storage capacity directly, and indirectly via functional trait diversity, CWM of trait, and soil organic carbon. 3) How does soil organic carbon mediate the effects of disturbance, elevation, functional trait diversity, and CWM of trait on soil water storage capacity? We hypothesize that multiple abiotic and biotic factors jointly regulate soil water storage capacity in temperate forests recovering from logging disturbances.

2. Materials And Methods

2.1 Study area, sites and forests

Our study area is located in the northeast of China, covering the Liaoning and Jilin Provinces (Fig. 1), which is classified as a temperate continental climate. The mean annual air temperature is 2.8°C, and the coldest and warmest monthly mean are – 13.7°C in January and 19.7°C in July (Hao et al. 2007). The mean annual precipitation is 700 mm which mostly occurs during the growing seasons (from June to

September). Broad-leaved Korean pine (*P. koraiensis*) mixed forest, well-known for their high species diversity, productivity and complex stand structure, was the dominant vegetation type in the study region. The predominant soil type of the studied area is Eutric cambisols according to the FAO soil classification system (Hao et al. 2007). Some areas had been subjected to variable intensities of human disturbances, but there were no severe human disturbances since 1998 when the forest protection policy was strictly implemented (Dai et al. 2004). Thus, forests recovering from disturbances include stands with different successional stages in the study area (Chen et al. 2014).

To quantify the effects of abiotic factors, disturbance intensity, plant trait diversity and composition on soil water storage capacity, we established 11 permanent forest sites during 2012 ~ 2013 (Table 1), and then re-investigated those forest plots at an interval of five years using the standard field approaches (Yuan et al. 2018). Within each site, all trees with a diameter at breast height (DBH) > 1 cm were marked, measured, recognized to species level, and positioned in contiguous 20×20 subplots (Hao et al. 2007). In this way, our data covered 22,766 stems in total belonging to 81 species, 46 genera, and 26 families across 260 subplots (Yuan et al. 2018). In addition, the topography of each subplot was measured by assessing the elevation of four corners of each subplot using Electronic Distance Measuring Device (Hao et al. 2007), and then the mean elevation, convexity and slope were calculated for each subplot (Harms et al. 2001). Elevation of the studied plots ranged from 640.4 to 1023.1 m.

Table 1. The descriptive summary of the studied sites and plots.

Site	Site size (ha) (dimension, m)	No. of subplots	Latitude longitude	Elevation (m) ^a	Species richness	DBH (cm) ^a
Plots of low-disturbance level						
L1	1 (100*100)	25	127.98N; 42.35E	877.5 (875.1; 879.7)	25	8.68 (1.0, 115.2)
L2	1 (100*100)	25	126.23N; 43.18 E	727.5 (724.2; 731.1)	35	8.98 (1.0, 152)
L3	1 (100*100)	25	127.88N; 42.25E	998.8 (995.6; 1002.1)	38	7.56 (1.0, 110.0)
L4	1 (100*100)	25	127.91N; 42.21E	1107.2 (1105.6; 1108.3)	21	8.64 (1.0, 96)
Plots of medium-disturbance level						
M1	1 (100*100)	25	127.86N; 42.48E	1010.9 (1016.3; 1023.1)	34	7.83 (1.0, 96.5)
M2	1 (100*100)	25	127.94N; 44.01E	721.6 (698.4; 743.7)	41	8.98 (1.0, 75.0)
M3	0.8 (80*100)	20	124.79N; 40.91E	834.1 (817.0; 851.0)	40	7.22 (1.0, 60.9)
Plots of high-disturbance level						
H1	1 (100*100)	25	126.48N; 42.36E	758.6 (749.6; 764.8)	47	3.4 (1.0, 75.0)
H2	1 (100*100)	25	128.17N; 42.19E	652.9 (640.4; 666.2)	45	6.35 (1.0, 68.5)
H3	1 (100*100)	25	130.16N; 43.39E	717.7 (705.6; 726.2)	34	6.3 (1.0, 70.0)
H4	0.6 (60*100)	15	124.90N; 41.33E	892.2 (873.1; 909.4)	43	7.15 (1.0, 53.8)

^a Mean value and range (min, max) of each 20*20m subplots. DBH, diameter at breast height.

2.2 Assessment of disturbance intensities

The 11 permanent sites are located in Broad-leaved Korean pine mixed forest fragments which underwent three levels of logging disturbance, and the sites provide a good platform for the research of biodiversity and ecosystem functions under disturbance (Dai et al. 2004; Song et al. 2014; Yuan et al. 2018). The disturbance intensity of each plot was assessed by counting the number of removed tree stumps, and the disturbance was mostly happened in 1990s (Kahl and Bauhus 2014). Besides, the official records of the Local Forestry Bureau in Jilin and Liaoning Provinces were checked to collect the relevant selective logging data. Collectively, plots were primarily classified into three disturbance intensity levels according to the partial harvesting (e.g., thinning, selective harvesting): relatively low (< 10%), medium (10–20%), and high (20 ~ 30%) disturbance. Plots with medium and high disturbance levels were primarily located around the residential area, whereas plots with low disturbance level were located in the main region of

the Changbai Mountain Nature Reserve (Fig. 1), which was established in 1960 and is part of the World Biosphere Reserve Network under the Man and the Biosphere Project in 1980 (Shao et al. 1994).

2.3 Quantification of plant functional trait diversity and composition indices

For quantifying the multiple facets of plant diversity, six functional traits were measured which were closely associated with forest growth, recruitment and death (Yuan et al. 2019), including maximum height (MH), leaf area (LA), specific leaf area (SLA), leaf carbon content (LCC), leaf nitrogen content (LNC), and leaf phosphorus content (LPC). The detailed measurement approaches for these six functional traits are described in Yuan et al. (2016). Using the data of six functional traits, we measured three multidimensional functional trait diversity indices, namely, functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis). FRic represents the multivariate traits space that species in the community occupied, FEve indicates the regularity of community traits distribution, and FDis is the mean distance of the species trait to the centroid of all species weighted by basal area (Laliberté and Legendre 2010; Villeger et al. 2008). Besides, we also calculated the community-weighted mean of each trait (CWM_{MH} , CWM_{LNC} , CWM_{LCC} , CWM_{LPC} , CWM_{LA} , and CWM_{SLA}) within each plot, weighted by the species' relative basal area, to represent the plant functional trait composition (Ali et al. 2017; Yuan et al. 2019). The CWM and FD indices were calculated by *FD* package in R 3.5.3 (Laliberté and Legendre 2010).

2.4 Quantification of soil water storage capacity and soil organic carbon

In 2018, we randomly selected three soil sampling sites in the midpoints between the central point and four corners in each 20 m×20 m subplot. In each sampling site, two soil corers using stainless cylinders of 100 cm³ in volume were selected for the bulk soil density and capillary water storage contents measurement after removing large debris. The corers containing large roots were abandoned for the precise analyses of data. Subsequently, five soil cores (3.8 cm in diameter, 10 cm deep) at each sampling point were collected, pooled, and transferred to the laboratory with plastic zipper bags for further chemical analyses. Each soil sample was further divided into two parts, i.e., one for soil organic carbon analysis using the dichromate oxidation method (Lu 1999), and another one for soil moisture measurement after 12 hr dried at 105°C.

Soil water storage capacity was measured through soil porosity, and this could be divided into capillary porosity, non-capillary porosity and total porosity corresponding to soil capillary storage (CW), soil non-capillary storage (NCW), and soil saturated water storage (TSW) (Chen et al. 2019; Xia et al. 2017). The CW represents the soil water content in the soil water retention curve when the pressure is -33 kPa whereas the NCW reflects the water contents difference between 0 ~ -33 kPa (Ahuja et al. 1993; Liu et al. 2009). Moreover, these two parts also indicate soil water retention and infiltration capacity (Mo et al. 2011; Rabot et al. 2018). TSW, CW, and NCW were calculated using Eq. (1), Eq. (2) and Eq. (3) (Chen et al. 2019; Wu et al. 2016; Zhang et al. 2010):

$$TSW = 10000 \times TP \times h \quad (1)$$

$$CW = 10000 \times CP \times h \quad (2)$$

$$NCW = 10000 \times NCP \times h \quad (3)$$

Where TP is the total soil porosity (%) measured as $TP = (1 - BD/ds) \times 100$, BD is the soil bulk density ($g\ cm^{-3}$), ds is the soil particle density ($2.65\ g\ cm^{-3}$); CP is the soil capillary porosity (%) measured as $CP = (W_c/V) \times 100$, W_c is the soil capillary water contents ($g\ cm^{-3}$) (Liu et al. 2009), V is the volume of the soil core (cm^3); NCP is the soil non-capillary porosity (%) measured as $NCP = (TP - CP) \times 100$; h is the height of soil top layer (0.2 m), TSW is the total soil water storage content ($t\ hm^{-2}$), NCW is the non-capillary storage content ($t\ hm^{-2}$), and CW is the capillary storage content ($t\ hm^{-2}$).

Total soil porosity (TP) was measured based on the measured soil bulk density while assuming that soil particle density is $2.65\ g\ cm^{-3}$, W_c was additional water weight after placing the stainless cylinders soil core in a tray with a 5-mm level of water until filter paper at the top of each core became moist (Liu et al. 2009), whereas non-capillary was the difference between TP and CP (Eq. (3)) (Wu et al. 2016).

2.5 Statistical analyses

We assessed the effects of disturbance on soil water storage capacity (i.e. TSW, NCW and CW) using a two-way ANOVA with Tukey's test as a *post hoc* analysis to assess the significant differences among disturbance levels. As such, we also tested the differences for associated variables, which may influence soil water storage capacity (i.e. above-ground and below-ground variables), among disturbance intensity levels.

Before testing the conceptual model in Fig. S1, we assessed the spatial autocorrelation in the response variables (TSW, NCW and CW) among subplots using the generalized least-square models (GLS) with and without spherical autocorrelation. Our GLS analysis indicated that the models without spherical autocorrelation structures usually showed the lower Akaike Information Criterion (AIC) values compared to spherical autocorrelation models (Table S2, S3 and S4), suggesting that there was no strong spatial autocorrelation among subplots.

Based on Pearson's correlation (Table S5), the best combination of variables (Tables S6 and S7), and the conceptual model (Fig. S1), we identified elevation, CWM of traits, functional trait diversity, and soil organic carbon as the best factors influencing soil water storage capacity (i.e. CW, NCW, and TSW). To test the conceptual model in Fig. S1, we used structural equation modeling (SEM) because it allows us to test the multiple theories, direct and indirect effects. To critically evaluate the best-fitted SEM (Hoyle 2012), we used the highest Bentler's Comparative Fit Index ($CFI > 0.90$), the root mean square error of

approximation ($RMSEA \leq 0.05$), chi-square (χ^2) test ($P\text{-value} > 0.05$), standardized root mean square residual ($SRMR \leq 0.05$) and lowest AIC value. To compare the mass ratio hypothesis and niche complementarity effects on soil water storage capacity, we selected CWM_{SLA} and FEve as the representative of plant functional trait composition and diversity, respectively, in SEMs. The direct, indirect, and total effects of predictors on response variables were calculated. The relative importance of each predictor was calculated as the percent of the given predictor standardized coefficient to the sum of standardized coefficients of all predictors (Yuan et al. 2019).

To complement the results from SEMs, we also conducted partial regressions and simple bivariate regressions (Grace et al. 2016). The SEM analysis was conducted using the “lavaan” package (Rosseel 2012). All analyses were conducted in R. 4.0.2 (Team RDC, 2019). All predictors in our research were standardized to a mean of 0 and standard deviation of 1, and the response factors (i.e. CW, NCW and TSW) were natural-log transformed before further analyses. Summary of variables used in the analysis is provided in Table S1.

3. Results

3.1. ANOVA: differences for soil water storage capacity and associated variables among disturbance intensity levels

The ANOVA results showed that CW and TSW significantly increased with increasing disturbance intensity, but no significant differences were found for NCW (Fig. 2). The average values for CW, NCW, and TSW of the top 20 cm soil layer were respectively 1118.2 t hm^{-2} , 468.2 t hm^{-2} , and 1604.7 t hm^{-2} while showing general variations across eleven forest plots and disturbance intensity levels (Fig. S2). Meanwhile, above-ground biomass and soil bulk density decreased whereas plant species diversity indices and soil organic carbon increased with increasing disturbance intensity levels (Fig. S3). Furthermore, disturbance also severely influenced most of the community trait composition; for example, CWM_{LA} , CWM_{SLA} , CWM_{LNC} , and CWM_{LPC} increased whereas CWM_{MH} and CWM_{LCC} decreased with increasing disturbance intensity levels (Fig. S3).

3.2. SEMs: what determines soil water storage capacity

The tested best-fitted SEMs showed that FEve did not significantly influence soil water storage capacity (i.e. CW, NCW, and TSW) whereas CWM_{SLA} influenced them either directly and/ or indirectly via soil organic carbon (Fig. 3; Tables S8, S9 and S10). More specifically, CWM_{SLA} had significantly increased CW but decreased NCW directly. However, CWM_{SLA} improved NCW and TSW indirectly via soil organic carbon (Fig. 3; Tables S8 and S9). Although disturbance did not influence soil water storage capacity directly, it had indirect variable (positive or negative) effects on soil water storage capacity via promoting CWM_{SLA} and soil organic carbon, respectively (Fig. 3; Tables S8, S9 and S10). Likewise, elevation showed indirect effects on soil water storage capacity via decreasing CWM_{SLA} and soil organic carbon, but it directly increased NCW and TSW, and decreased CW (Fig. 3; Tables S8, S9 and S10). In SEMs, soil organic carbon

demonstrated the significant importance of mediating the effects of elevation, disturbance and CWM_{SLA} on soil water storage capacity, as it had crucial improvement influence on NCW and TSW directly (Fig. 3; Tables S8, S9 and S10).

The relative contribution analysis (Fig. 4a) showed that elevation was the most important influencing factor for CW but not for TSW, whereas elevation, soil organic carbon and disturbance contributed much to the explained variation in NCW. Disturbance and soil organic carbon seemed to be the most important influencing factors for TSW. However, FEve and CWM_{SLA} seemed to be of additional importance for explaining variation in CW, NCW and TSW, and were almost equally important across CW, NCW and TSW (Fig. 4a). In addition, the comparison of direct and indirect effects showed that the direct effects of disturbance, elevation, soil organic carbon, FEve and CWM_{SLA} were much higher than indirect effects on CW (Fig. 4b). However, the indirect effects of disturbance mattered for explaining variation in NCW, whereas the indirect effects of disturbance, elevation, CWM_{SLA} and FEve mattered much for explaining variation in TSW (Fig. 4b).

3.3. Supporting analyses: partial regressions and simple bivariate regressions

The SEMs results showed that soil organic carbon was the important variable which influenced soil water storage capacity directly as well as mediated the effects of disturbance, elevation and CWM_{SLA} (Fig. 3). We, therefore, further conducted the simple regression and partial regression analyses between soil organic carbon and soil water storage capacity (Fig. S4) to clarify the importance of soil organic carbon to soil water storage capacity. The partial regression analysis showed that soil organic carbon was significantly positively related with NCW and TSW but not related with CW when other factors (disturbance, elevation, CWM_{SLA} , and FE_{VE}) were kept constant (Fig. S4a). This was a contrast with the simple regression analysis (Fig. S4b), which showed that soil organic carbon was significantly related with CW but not related with NCW, whereas soil organic carbon showed a significant constant relationship with TSW in both simple and partial regression analyses (Fig. S4). The partial regression results were in line with SEMs results, indicated that soil organic carbon was controlled by elevation, disturbance and CWM_{SLA} , which in turn influence NCW and TSW but not CW (Fig. 3 and Fig. S4a).

All bivariate relationships for hypothesized paths in SEMs are provided in Fig S4, S5 and S6. More specifically, we found that there was a significant positive bivariate relationship between CWM traits and soil water storage capacity (Figs S5, S6 and S7). Typically, high CWM_{LA} , CWM_{SLA} , CWM_{LNC} , and CWM_{LPC} values but low CWM_{LCC} and CWM_{MH} values were beneficial for CW and TSW, whereas we found the opposite results for NCW. However, there was no consistent and robust relationship between diversity indices and soil water storage capacity (Figs S5, S6 and S7).

4. Discussion

In this study, we tease apart the direct and indirect effects of abiotic (elevation and soil organic carbon) and biotic (functional trait diversity and composition) on soil water storage capacity in temperate forests recovering from logging disturbances. Our results can be discussed in the following points: 1) CWM of a trait (functional composition) was a much more important direct factor to soil water storage capacity than functional trait diversity as well as providing an important role for mediating the effects of elevation and disturbances on soil water storage capacity; 2) disturbance influenced soil water storage capacity indirectly via soil organic carbon and CWM of trait but not directly; 3) soil organic carbon was also the key factor influencing soil water storage capacity directly as well provided an important role for mediating the effects of elevation, disturbances and CWM of trait on soil water storage capacity; and 4) elevation regulated soil water storage capacity directly and indirectly via soil organic carbon and CWM of a trait.

First, we found that plant community trait composition rather than functional trait diversity was the key factor influencing soil water storage capacity (Finegan et al. 2015; Loreau and Hector 2001; Xu et al. 2020). Our finding was in contrary with the importance of functional trait diversity on hydrological ecosystem service and soil water content (Fischer et al. 2015; Wen et al. 2021), but was consistent with other ecosystem functions, such as aboveground and soil carbon stocks, fine root biomass and necromass (Lin et al. 2016; Xu et al. 2020). This result confirms the mass ratio effect instead of the niche complementarity effect for the explaining variation in soil water storage capacity in temperate forests. More specifically, we found that quick return on investment traits (i.e. high CWM_{LA} , CWM_{SLA} , CWM_{LNC} , and CWM_{LPC} values; but low CWM_{LCC} and CWM_{MH}) directly increased CW, and slow return on investment traits improved NCW (Fig. 3, S5, and S6). This result might be due to the reason that quick return on investment leaf traits is usually linked with fast decomposing litterfalls, which could be beneficial to the formation of mineral-stabilized soil organic carbon (Cotrufo et al. 2013; Zhou et al. 2019) and soil macroaggregates (Blanco-Canqui and Lal 2007; Wang and Wang 2005), which in turn related to fine soil textures, thereby increasing CW. Slow return on investment leaf traits has usually more recalcitrant litterfalls which may facilitate the formation of coarse particulate organic matter (Cotrufo et al. 2015) and large soil porosities while improving NCW as well as soil infiltration capacity (Liu et al. 2019). We found that that CWM_{SLA} also improved NCW and TSW indirectly via increasing soil organic carbon, which was consistent with the notion that vegetation improves soil organic carbon contents, thereby enhancing soil water contents (Fischer et al. 2019; Liu et al. 2019). However, the total effect of CWM_{SLA} on NCW was negative which was dominated by the direct pathway.

Second, we observed that logging disturbance significantly changed community trait composition (Fig. S3), and then changed soil water storage capacity in studied forests (Fig. 3). With the intensity of disturbance level, community weighted traits tended to be higher CWM_{LA} , CWM_{SLA} , CWM_{LNC} and CWM_{LPC} values but lower CWM_{LCC} and CWM_{MH} values (i.e. indicating the quick return on investment traits). This phenomenon followed the fact that past logging activities have decreased the number of large trees which in turn creating a forest gap, and hence, more light-demanding species are doing well in less disturbed forests (Yuan et al. 2018). Along with the transformation of the plant community, soil organic carbon content increased because of the large amount of easily decomposed litterfalls (Cotrufo et al.

2013). As such, disturbance mainly affected soil water storage capacity indirectly via CWM_{SLA} and soil organic carbon, whereas there was no significant direct influence of disturbance on soil water storage capacity. The lack of direct effect of disturbance on soil water storage capacity might be due to the reason that the response of changes in soil properties to disturbances are usually slower than aboveground attributes following the plant-feedback processes (Trumbore et al. 2015). Hence, our study suggests that soil water storage capacity reacted slowly to disturbances, and careful consideration is required when studying or quantifying the consequences of disturbances on diverse ecosystem functions.

Third, we argue that soil organic carbon is the key factor of soil water characteristics responding to the plant transformation after disturbance. For example, soil organic carbon was an important response factor to the species richness which could change the soil water infiltration capacity in semiarid grasslands (Liu et al. 2019). In a recovering grassland, the soil water contents changed as a result of the accumulation of soil organic carbon as well as the improved soil aggregation (Fischer et al. 2019). In an alpine grassland, SOC dominated the soil water retention capacity in five different matric potentials (from 0 to -1500 kPa) because of the large amount of SOC accumulated in the soil (Yang et al. 2014), and as such Rawls et al. (2003) reported that soil organic carbon has different effects on soil water retention capacity due to the change of soil textures. Our results demonstrated that soil organic carbon was as an important regulating factor for soil water storage capacity as disturbance happened, and hence, it controlled TSW in temperate forests. However, the influence of soil organic carbon on NCW and CW declined, which may be related to soil texture because of the great influence of elevation on CW and NCW (Liu et al. 2009; Wösten et al. 2001; Zhang et al. 2019).

Fourth, elevation showed significant influences on CWM of trait and soil organic carbon, as well as the important significant direct effect on soil water storage capacity. This result can be explained based on two main reasons. One reason could be linked with the changing in CWM of trait along the elevation which in turn changed in soil water storage capacity (Hao et al. 2007). Another reason could be due to the different soil erosion levels along elevation when rainfall happened, and hence fine soil components (i.e. higher clay and soil organic carbon contents) accumulated in low elevation areas (Chapin et al. 2011; Zhang et al. 2019). Moreover, the influences of elevation on soil texture could explain the significant differences in the relation of soil organic carbon with CW and NCW when bivariate and partial-regression analyses were conducted (Fig. S4). Elevation influenced soil fine particles and soil organic carbon together which confused the relationship between soil organic carbon and soil water storage capacity in bivariate analyses. However, SEMs disentangled these relations and presented us with the underlying possible reasons. So, this result highlights the necessity of an integral understanding of biotic and abiotic attributes influencing ecosystem functions (Grace et al. 2016).

5. Conclusions

Logging disturbances and elevation modulate the effects of CWM of traits on soil water storage capacity, and the quick return on investments of CWM of specific leaf area shows a positive effect on soil water

storage capacity (CW and TSW). Hence, CWM of specific leaf area is a key biotic predictor for explaining variation in soil water storage capacity compared to functional trait diversity, supporting the mass ratio mechanism in temperate forests recovering from disturbances. As such, soil organic carbon was of additional importance to soil water storage capacity by affecting it directly or providing mediator role to link the responses of soil water storage capacity to elevation, disturbances, and CWM of specific leaf area. We argue that testing the effects of multiple abiotic and biotic factors on soil water storage capacity could advance our understandings into the influential ecological mechanisms underlying soil water storage capacity in forests under the context of human influences.

Declarations

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Authors' contributions

Shufang Liu, Zuoqiang Yuan, and Zhanqing Hao conceived the ideas and designed methodology; Fang Ding, Di Zheng, Shuai Fang, Zhaojie Jia, Zhao Tao, Fei Lin, Ji Ye collected the data; Shufang Liu analysed the data; Shufang Liu led the writing of the manuscript. Zuoqiang Yuan, Arshad Ali, Anvar Sanaei, Xugao Wang contributed critically to the drafts and gave final approval for publication.

Conflict of interest

The authors declare no conflicts of interest.

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Figures

Figure 1

Map of China showing the study area and distribution of 11 permanent forest sites. Color represents disturbance level at each site. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Boxplots showing the differences for soil water storage capacity among disturbance intensity levels. Boxes having different letters are showing significant differences at $P < 0.05$ (Tukey's test). Factors are soil capillary water storage content (CW), soil non-capillary water storage content (NCW), soil saturated water storage content (TSW).

Figure 3

Best-fitted structural equation models for linking disturbance, elevation, functional trait composition, functional trait diversity, SOC and soil water storage capacity, i.e. (a) CW, (b) NCW, and (c) TSW. Solid and dashed arrows represent significant ($p \leq 0.05$) and non-significant effects. For all paths, standardized regression coefficients are given. Model fit statistics: a) CFI = 1.00, SRMR = 0.01, Chi-square = 1.61 ($P = 0.2$), and AIC = 2537.03; b) CFI = 1.00, SRMR = 0.01, Chi-square = 1.61 ($P = 0.2$), and AIC = 2944.87; c) CFI = 1.00, SRMR = 0.01, Chi-square = 1.61 ($P = 0.2$), and AIC = 1910.41.

Figure 4

Relative contribution of each predictors (a), and its direct and indirect effects (b) on soil water storage capacity based on best-fitted SEMs. The solid color filled bar plots (b) shows direct effect whereas the pattern color filled bar shows indirect effect.

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