



Identifying Carbon-Degrading Enzyme Activities in Association with Soil Organic Carbon Accumulation Under Land-Use Changes

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ABSTRACT

Land degradation and restoration strongly influence terrestrial soil organic carbon (SOC) dynamics. However, the underlying mechanisms are not well understood. Here, based on a meta-analysis of 803 observations from 138 studies worldwide, our data analyses suggest that C-degrading enzymes play a crucial role in regulating SOC dynamics under land degradation and restoration. Our result showed that decreased cellulase activity but unchanged ligninase activity was associated with land degradation, whereas higher increased cellulase activity compared with ligninase activity was associated with land restoration. Consequently, the ligninase-to-cellulase ratios were higher under land degradation and lower under land restoration. Also, the specific enzyme activity (the amount of enzyme produced per unit microbial biomass) was greater under land degradation but lower under land restoration. By comparison with the short-term (≤ 30) land degradation, the long-term

(> 30 years) land degradation significantly increased the ligninase-to-cellulase ratio. On the contrary, the long-term land restoration exerted a more negative effect on the ligninase-to-cellulase ratio. The increases in the specific enzyme activity and ligninase-to-cellulase ratio were tightly correlated with decreases in SOC content under land degradation. A similar correlation was also found between decreases in specific enzyme activity and ligninase-to-cellulase ratio and increases in SOC content under land restoration. Overall, the decrease of SOC storage under land degradation is not only due to the low plant inputs, but also likely because of the accelerated degradation of recalcitrant C pools. However, the reverse applies for land restoration. The novel insights provided by our results contribute to the understanding of microbial mechanisms underlying the changes in SOC accumulation in response to land-use changes.

Key words: Cellulase; Land-use change; Ligninase; Meta-analysis; Soil organic carbon; Specific enzyme activity.

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INTRODUCTION

Land degradation and restoration strongly influence the accumulation or release of soil organic carbon (SOC) (Zhou and others 2018; Ledo and others 2020; Luo and others 2020; Veldkamp and others 2020; Arias-Ortiz and others 2021). Most of the previous studies have reported that land degradation and restoration alter SOC accumulation by changing the quantity and quality of plant litter input (Li and others 2012; Ledo and others 2020; Mayer and others 2020), soil structure (DeGryze and others 2004; Spohn and Giani 2011; Garcia-Franco and others 2015) and microbial community composition (Nazaries and others 2015; Pressler and others 2020). However, microbial mechanisms in regulating the loss and accumulation of SOC in response to land degradation and restoration, respectively, are still lacking (Malik and others 2018; Yang and others 2020).

The accumulation of SOC is primarily determined by the balance between C inputs from plants and C outputs through microbial decomposition (Cotrufo and others 2015; Jackson and others 2017; Malik and others 2020). However, the decomposition and transformation of SOC are mediated by microbially produced extracellular enzymes (Sinsabaugh 2010; Burns and others 2013; Zhang and others 2019b), especially the two types of C-degrading enzymes: cellulase and ligninase (Chen and others 2018a, 2020; Margida and others 2020). Typically, cellulases, such as β -1,4-glucosidase (BG), β -1,4-xylosidase (BX) and β -D-cellobiohydrolase (CBH), are associated with decomposition of labile C substrates (that is, polysaccharide), while ligninases, such as peroxidase (PER) and polyphenol oxidase (POX), are related to decomposition of relatively recalcitrant C substrates (that is, lignin and polyphenols) (Sinsabaugh 2010). Land degradation, which usually occurs when natural forest is converted to plantation forest or cropland, usually resulted in a rapid loss of labile SOC (Moreno and others 2019; Wang and others 2020a), which could inhibit the activity of cellulase (Könönen and others 2018; Xu and others 2020; Vázquez and others 2020). However, the activity of ligninase rarely showed significant response to land degradation (Jin and others 2019; Wang and others 2020b), or the ligninase activities could increase under land degradation (Moreno and others 2019; Maslov and Maslova 2020). The changing microbial C use strategy toward recalcitrant SOC substrates under land degradation could have profound influences on SOC dynamics (Liang

and others 2017; Sauvadet and others 2018; Chen and others 2020). For instance, metabolic investments heavily in ligninase production for resource acquisition can reduce the efficiency of cellular growth and microbial growth yield (Malik and others 2019; Malik and others 2020; Ramin and Allison 2019) and consequently contribute more to decomposition and C loss.

In contrast, land restoration is generally accompanied with an increased amount of labile C input (Zhang and others 2019a, 2019b; Raiesi and Salek-Gilani 2020) and, as a result, could enhance the activity of cellulase (Carreira and others 2008; Singh and others 2012; de Oliveira Silva and others 2019; Zhang and others 2019a; Zhang and others 2019b). The production of cellulase generally has lower microbial energy cost compared with the production of ligninase (Moorhead and others 2013; Jian and others 2016; Chen and others 2020), which could lead to a higher microbial C use efficiency (CUE, the ratio of C allocated for growth versus respiration) (Bahri and others 2008; Dijkstra and others 2011). Higher CUE can contribute to more formation of stable SOC by microbial products associated with soil mineral particulate (Cotrufo and others 2013; Kallenbach and others 2015; Malik and others 2018; Poeplau and others 2019). Meanwhile, the ratio of ligninase to cellulase has been widely used to quantify microbial preference in using various substrates of soil organic matter (SOM) (Yang and others 2019; Chen and others 2020), and the shifts of microbial C use strategy by adjusting the relative proportion of ligninase and cellulase are also tightly linked to CUE (Takriti and others 2018). The differential responses of cellulase and ligninase activities to land-use change and their critical roles in mediating SOC decomposition indicate that land degradation and restoration could affect SOC dynamics through changing the activities of cellulase and ligninase. Although several studies have revealed global change (that is, warming and nitrogen deposition) affect SOC storage through altering the activities of C-degrading enzymes (Chen and others 2018b, 2020), the direct evidence is still lacking on how land degradation and restoration alter the activities of C-degrading enzymes and then influence SOC accumulation.

In the present study, we conducted a meta-analysis of 803 observations from 138 individual studies to identify the general patterns of the effects of short- and long-term (≤ 30 and > 30 years, respectively) land degradation and restoration on C-degrading enzymes activities and SOC dynamics. We specifically explored the linkages between SOC

dynamics and ligninase-to-cellulase ratio and specific enzyme activity (the amount of enzyme produced per unit microbial biomass) under land degradation and restoration. Given that cellulase is mainly targeting the decomposition of relatively labile C substrates, while ligninase is associated with decomposition of relatively recalcitrant C substrates (Margida and others 2020; Chen and others 2020), and also because the labile C pools lost more quickly than recalcitrant C pools under land degradation (Solomon and others 2007; Dieckow and others 2009), we hypothesized that the decreased cellulase activity and non-significantly changed ligninase activity would be associated with land degradation. In contrast, higher increased cellulase activity compared with ligninase activity would be associated with land restoration (H1). We then hypothesized that compared with control, land degradation would be associated with the higher ratio of ligninase to cellulase, and land restoration would be associated with lower ratio of ligninase to cellulase (H2). As microbial CUE was negatively correlated with ligninase-to-cellulase ratio (Takriti and others 2018), and also because microbial invest in enzyme production was at the expense of microbial growth yield or efficiency (Malik and others 2019, 2020; Ramin and Allison 2019), we hypothesized that land degradation and restoration could exert effect on SOC dynamics through changing the ratio of ligninase to cellulase and specific enzyme activity (H3).

MATERIALS AND METHODS

Data Compilation

To investigate the effect of land degradation and restoration on C-degrading enzyme and its association with SOC, we collected data from peer-reviewed studies until September 1, 2020, through the Institute for Scientific Information (ISI) Web of Science and China National Knowledge Infrastructure (CNKI) databases. The search terms included ("land use" OR "land cover" OR deforestation OR degradation OR afforestation OR restoration OR revegetation) AND (glucosidase OR xylosidase OR cellobiohydrolase OR peroxidase OR polyphenol oxidase). We used the following criteria to select appropriate studies: (1) the studies should be carried out in paired plot design using the 'space-for-time' approach (Han and Zhu 2020), which means that the climatic parameters and soil conditions should be similar for the land-use types before and after land-use change; (2) if one study

reported land-use change from one type to several others, every corresponding change was treated as independent observation; (3) if one study contained different chronosequence of land degradation or restoration (for example, different afforestation chronosequence), each year was viewed as independent observation; (4) data from the same experiment site reported in different studies were collected only from the latest study; (5) the standard deviation (SD) about the data had to be reported or could be calculated from the information provided. Finally, these criteria yielded a total of 803 observations from 138 publications for further analysis.

The dataset included the following variables: (1) the activities of C-degrading enzymes ($\text{nmol g}^{-1} \text{h}^{-1}$). If one paper reported two or three kinds of cellulase or all those two kinds of ligninase, their sum values were considered as the overall cellulase and ligninase activities; (2) SOC content (g kg^{-1} soil); (3) environmental variables, including latitude, mean annual temperature (MAT) and mean annual precipitation (MAP); (4) soil and microbial properties, including pH, carbon-to-nitrogen ratio (C/N), dissolved organic carbon (DOC, mg kg^{-1}), microbial biomass carbon (MBC, mg kg^{-1}) and microbial metabolic quotient ($q\text{CO}_2$); (5) the time since land-use change (year). The substrates used for the measurement of C-degrading enzymes are mainly MUB and *p*NP. The different substrates used in different publications may result in some differences. However, the substrate used for the measurement of C-degrading enzymes of different land-use types in each individual publication is consistent. Thus, there may have little effects of different methods used in different publications on the response ratios of C-degrading enzymes to land degradation and restoration. If a study did not provide all the variables mentioned above, we searched extensively for matching the missing information from the relevant studies. These data were retrieved directly from tables and data sets provided by the publications, or from graphs using GetData Graph Digitizer (version 2.24, <http://getdata-graph-digitizer.com>, Russian Federation).

The types of land-use change were classified into two categories for land degradation and restoration following our previous study (Wu and others 2020). Land degradation refers to conversion from natural ecosystem to disturbed ecosystem, and it is generally accompanied with decreasing primary productivity and SOC content, whereas land restoration means ecosystem recovers from degraded ecosystem induced by natural factors or human activities, with the primary productivity

and SOC content usually being increased with restoration time. In brief, land degradation included: (a) the conversion of natural forest to plantation forest; (b) the conversion of natural forest to grassland; (c) the conversion of nature forest to cropland; (d) the conversion of grassland to cropland; (e) other types of land degradation (that is, desertification, grassland degradation resulted from over grazing). Land restoration included: (a) the conversion of artificial grassland to plantation; (b) the conversion of cropland to plantation; (c) the conversion of cropland to grassland; (d) the conversion of barren land to grassland or plantation (that is, natural regeneration).

Data Analysis

We conducted the meta-analysis to evaluate the response of C-degrading enzyme and SOC content to land degradation and restoration by using the natural log-transformed response ratio (RR) (Hedges and others 1999; Zhou and others 2020):

$$RR = \ln\left(\frac{\bar{X}_t}{\bar{X}_c}\right) = \ln(\bar{X}_t) - \ln(\bar{X}_c) \quad (1)$$

where \bar{X}_t and \bar{X}_c are the mean values of each variable for land-use types after (treatment) and before (control) land-use change, respectively. Its variance (v) is calculated as:

$$v = \frac{S_t^2}{n_t \bar{X}_t^2} + \frac{S_c^2}{n_c \bar{X}_c^2} \quad (2)$$

where S_t and S_c are the standard deviations for the treatment and control groups, respectively. n_t and n_c are the sample sizes of the concerned variable for the treatment and control, respectively.

A nonparametric weighting function was used to weight individual studies (Hedges and others 1999; Bai and others 2013; Zhou and others 2017). The weighting factor ω was calculated as the inverse of the pooled variance ($1/v$). When more than one observation was extracted from the same study, we adjusted the weights by the total number of observations (n) per study. The final weight (ω') used in the analyses was:

$$\omega' = \omega/n \quad (3)$$

The weighted response ratio RR' was calculated as:

$$RR' = \omega' \times RR \quad (4)$$

The overall weighted response ratio $\overline{RR'}$ for all observation was calculated as:

$$\overline{RR'} = \frac{\sum_i RR'_i}{\sum_i \omega'_i} \quad (5)$$

where RR'_i and ω'_i are weighted response ratio and adjusted weighting factor of the i th observation, respectively.

The overall weighted response ratio ($\overline{RR'}$) was calculated with a categorical random effects model by using MetaWin 2.1 software (Rosenberg and others 2000). Confidence intervals (95%; CIs) were generated by the bootstrapping (999 iterations). The overall weighted response ratio was significantly positive or negative if the 95% confidence interval did not overlap with zero at the $\alpha = 0.05$ level. The percentage changes in C-degrading activities and SOC content caused by land degradation and restoration was measured by:

$$\text{Change (\%)} = \left[\exp\left(\overline{RR'}\right) - 1 \right] \times 100\%$$

In addition, to assess temporal variation in the effects of land degradation and restoration, we made a separation between short- (≤ 30) and long-term (> 30) observations. The heterogeneity of the weighted response ratio of variables between short- and long-term land-use changes was obtained through between-group Q statistical test and expressed as Q_M value. $P < 0.05$ indicates the weighted response ratios differed between short- and long-term land-use changes. We also performed linear regression to analyze the relationships between the response ratios of SOC content and the response ratios of ligninase to cellulase and specific enzyme activity under land degradation and restoration. ANCOVA was performed to estimate the slopes of these linear regressions and compare the differences between land degradation and restoration. Structural equation modeling (SEM) was applied to investigate how possible direct and indirect effects of environmental variables and ligninase-to-cellulase ratio on the response of SOC content to land degradation and restoration. Since not all of the selected publications and their related studies provided all the variables that were used for SEM analysis simultaneously, we found 55 and 59 observations which contained all the variables for land degradation and restoration to perform SEM analysis. Given that the MAT and MAP were strongly correlated, we conducted principal component analysis (PCA) to create a multivariate functional index named 'climate' before SEM construction. The first component (PC1), which explained 84.4% and 82.0% of the total variance for this group under land degradation and restoration, respectively, was then introduced as a

new variable into the subsequent analysis. Owing to the conversion of natural forest and grassland to cropland usually associated with more intense human activities than other types of land degradation, we created a categorical exogenous variable as “intensity” with 2 for the conversion of natural forest and grassland to cropland and 1 for other types of land degradation. The maximum-likelihood estimation method was applied to fit the model. Here, we used the commonly used metrics to evaluate the goodness of fit of SEM: the Chi-square test (χ^2 ; the model has a good fit when $0 \leq \chi^2/df \leq 2$, and $0.05 < P \leq 1$) (Schermelleh-Engel and others 2003). The final model was improved by removing the relationships between variables from prior models based on these indices. SEM analyses were conducted by using AMOS 24.0 (Amos Development Co., Greene, Maine, USA).

RESULTS

Effects of Land Degradation and Restoration on the C-Degrading Enzyme Activities

Across all studies, the data indicated that land degradation significantly decreased the pooled cellulase activity by 27.1% and the individual cellulase BG by 25.7%, respectively (Figure 1a; Figure S1a). In contrast, neither ligninase nor any of the individual ligninase enzymes PER and POX

showed significant response to the land degradation (Figure 1a; Figure S1b). Without exception, both cellulase and ligninase activities showed significant positive response to the land restoration (Figure 1b). The meta-analysis suggested that land restoration significantly increased activities of cellulase by 65.5%, BG by 63.3%, CBH by 58.3% and BX by 94.1%, respectively. For ligninase, land restoration significantly increased the activities of pooled ligninase by 27.2%, PER by 42.1% and POX by 22.2% (Figure 1b). It was worth noting that the enhancing effect of land restoration on the activities of ligninase was weaker ($Q_M = 17.35$, $P < 0.001$) compared to that on the activities of cellulase (Figure 1b). Additionally, the analysis also indicated that land degradation significantly increased the activities of specific total C-degrading enzyme, cellulase and ligninase by 45.4%, 29.4% and 55.0%, respectively (Figure 2a), but land restoration significantly decreased them by 23.4%, 26.5% and 19.1%, respectively (Figure 2b).

There were significant inconsistencies in the responses of cellulase and ligninase to the short- and long-term land degradation and restoration, respectively (Table S1). Our analysis suggested that although the short- and long-term land degradation significantly decreased cellulase activity, the reduction effect (20.8%) of short-term land degradation was significantly lower ($Q_M = 17.95$, $P < 0.001$) than that of the long-term land degradation (41.3%) (Figure 3a). For ligninase,

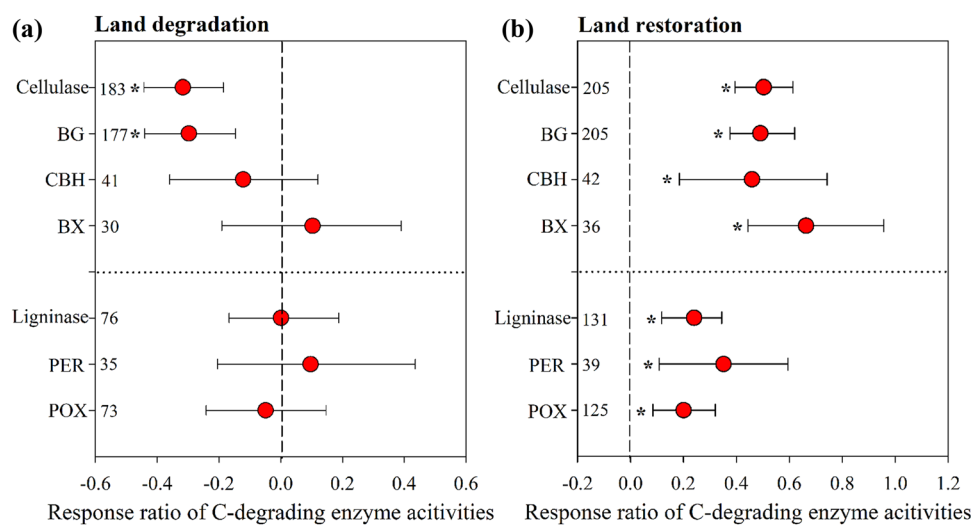


Figure 1. The response ratios of cellulase and ligninase activities to **a** land degradation and **b** restoration. The error bars represent 95% confidence interval (CI). If the CI did not overlap with zero, a response was considered to be significant. The numbers next to the CI bars are sample sizes, and the asterisks indicate significant response. Abbreviations: BG, β -1,4-glucosidase; CBH, β -D-cellobiohydrolase; BX, β -1,4-xylosidase; PER, peroxidase; polyphenol oxidase, POX.

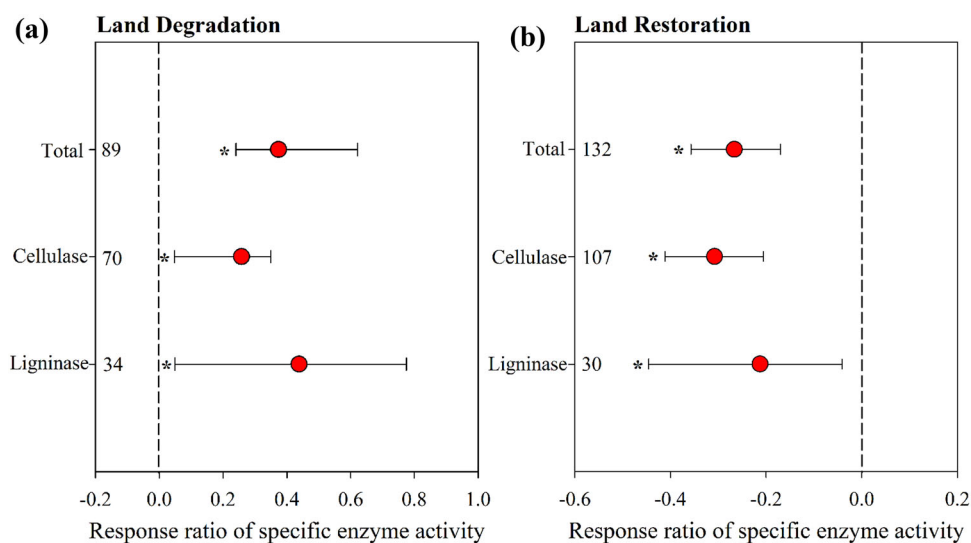


Figure 2. The response ratios of specific enzyme activity to **a** land degradation and **b** restoration. The error bars represent 95% confidence interval (CI). If the CI did not overlap with zero, a response was considered to be significant. The numbers next to the CI bars are sample sizes, and the asterisks indicate significant response.

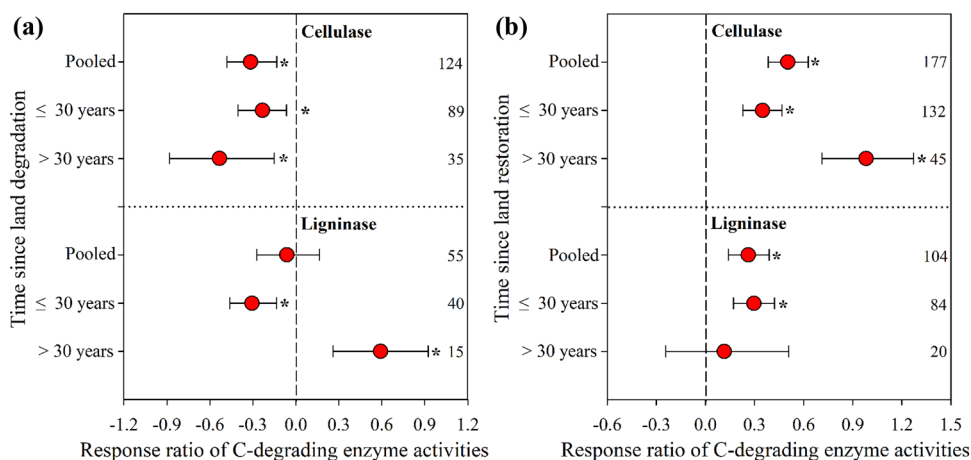


Figure 3. The response ratios of cellulase and ligninase activities to the time since **a** land degradation and **b** restoration. The error bars represent 95% confidence interval (CI). If the CI did not overlap with zero, a response was considered to be significant. The numbers next to the CI bars are sample sizes, and the asterisks indicate significant response. Studies are grouped by the duration of land-use change (≤ 30 and > 30 years).

short-term land degradation significantly decreased its activity by 26.3%, whereas long-term land degradation significantly increased its activity by 80.7% (Figure 3a). Similarly, the positive effect of short-term land restoration on cellulase activities was smaller ($Q_M = 42.89$, $P < 0.001$) than that of long-term land restoration (Figure 3b). For ligninase, short-term land restoration significantly increased its activity by 34.6%, while it showed no response to long-term land restoration (Figure 3b).

Effects of Land Degradation and Restoration on the Ratio of Ligninase to Cellulase

Based on the whole database, it indicated that land degradation increased the ligninase-to-cellulase ratio by 24.1% (but insignificant). In contrast, land restoration significantly decreased it by 46.0% (Figure 4b). There were significant heterogeneities in the response of ligninase-to-cellulase ratio to short- and long-term land degradation and restoration, respectively (Table S1; Figure 4a, b).

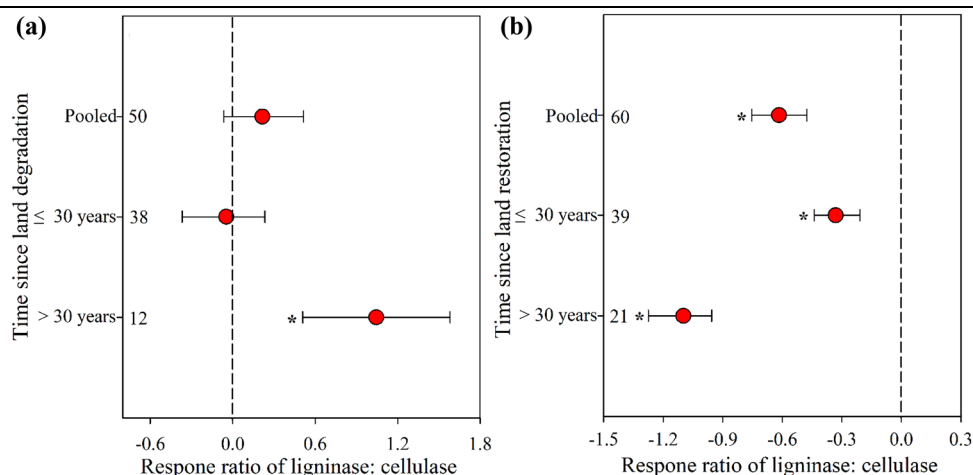


Figure 4. The response ratios of ligninase-to-cellulase ratio to the time since **a** land degradation and **b** restoration. The error bars represent 95% confidence interval (CI). If the CI did not overlap with zero, a response was considered to be significant. The numbers next to the CI bars are sample sizes, and the asterisks indicate significant response. Studies are grouped by the duration of land-use change (≤ 30 and > 30 years).

More specifically, short-term land degradation had no effect on the ligninase-to-cellulase ratio, while long-term land degradation significantly increased it (Figure 4a). The decline in the ligninase-to-cellulase ratio induced by short-term land restoration was lower ($Q_M = 112.27$, $P < 0.001$) than that induced by long-term land restoration (Figure 4b).

Effects of land degradation and restoration on SOC content

In general, our analysis suggested that land degradation significantly decreased SOC content by

35.7% (Figure S2a; Figure 5a) and that land restoration significantly increased it by 86.3% (Figure S2b; Figure 5b). The heterogeneities also existed in the response of SOC content to the short- and long-term land degradation and restoration (Table S1). The long-term land degradation decreased SOC content to a greater extent ($Q_M = 11.47$, $P < 0.001$) compared to that of the short-term land degradation. On the contrary, the response of SOC content to long-term land restoration was more positive than ($Q_M = 51.56$, $P < 0.001$) short-term land restoration.

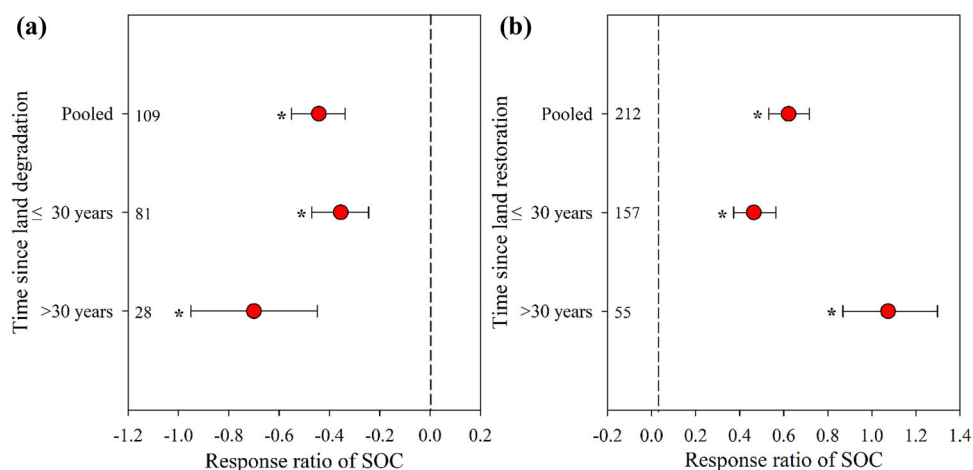


Figure 5. The response ratios of soil organic carbon (SOC) content to the time since **a** land degradation and **b** restoration. The error bars represent 95% confidence interval (CI). If the CI did not overlap with zero, a response was considered to be significant. The numbers next to the CI bars are sample sizes, and the asterisks indicate significant response. Studies are grouped by the duration of land-use change (≤ 30 and > 30 years).

Factors driving the response of ligninase-to-cellulase ratio and SOC content

Linear regression analysis revealed that the ligninase-to-cellulase ratio was positively correlated with the time since land degradation (Figure S4a), but was negatively correlated with the time since land restoration (Figure S4b). The responses of SOC content were negatively correlated with the response of specific enzyme activity and ligninase-to-cellulase ratio under both land degradation and restoration (Figure 6a–d). The slopes of the linear equations between land degradation and restoration were no significant difference ($P > 0.05$), which suggested that the magnitude of decrease or increase in SOC content caused by shifts in C-degrading enzymes activities under land degradation and restoration is almost the same. The SEM analysis also confirmed the tight relationship between ligninase-to-cellulase ratio and SOC content when accounting for multiple drivers of SOC dynamics simultaneously under land degradation and restoration, respectively (Figure 7a–d).

DISCUSSION

Through a global data synthesis based on 138 studies, our study provides a comprehensive assessment of the effect of land degradation and restoration on C-degrading enzymes activities and their associations with SOC dynamics. Our analysis suggests that land degradation decreased the cellulase activity but had no significant influence on ligninase activity, while land restoration enhanced both cellulase and ligninase activities with stronger effect on cellulase activity. As a result, the ratio of ligninase to cellulase increased under land degradation and decreased under land restoration. More importantly, the response of SOC content to land degradation and restoration was tightly correlated with the shifts in ligninase-to-cellulase ratio and specific enzyme activity. These findings are of important value for understanding the underlying mechanisms of SOC dynamics under land-use changes.

Differential Response of Cellulase and Ligninase to Land Degradation and Restoration

Consistent with our first hypothesis, our analysis suggests that the cellulase activity was significantly

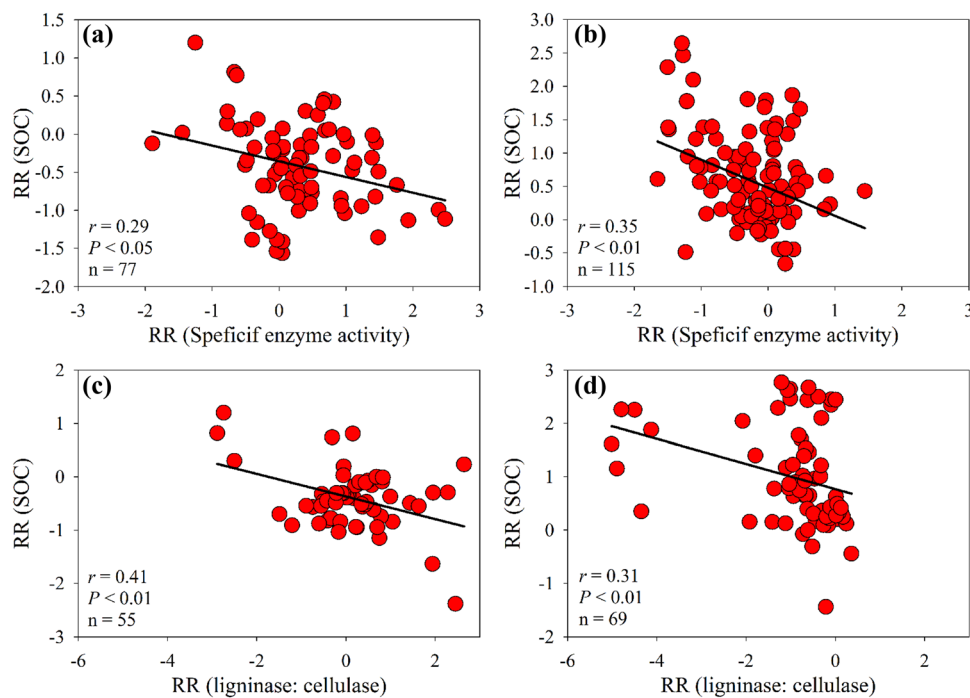


Figure 6. Coordinated changes between soil organic carbon (SOC) content and C-degrading enzyme activities. Linear relationships between the response ratio of SOC and the response ratio of specific enzyme activity under **a** land degradation and **b** restoration. Linear relationships between the response ratio of SOC and the response ratio of ligninase to cellulase under **c** land degradation and **d** restoration.

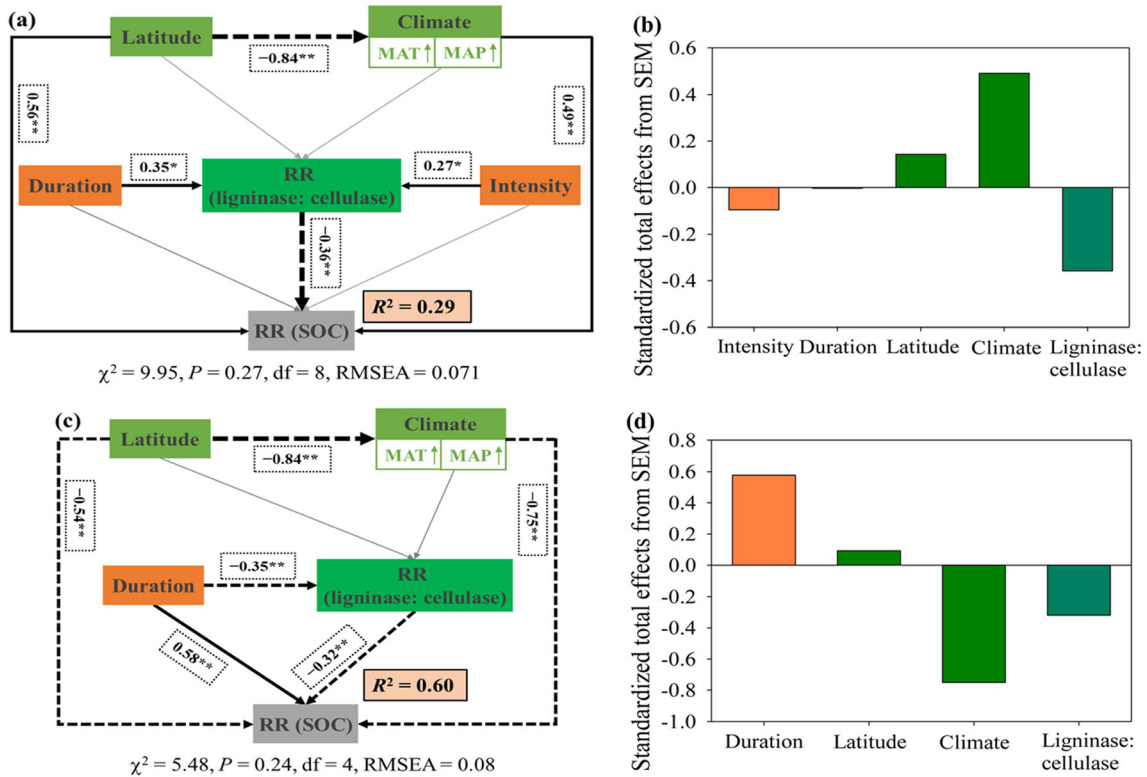


Figure 7. Structural equation model (SEM) analysis of the multivariate effects on the response of soil organic carbon (SOC) content to **a** land degradation and **b** restoration, respectively. Black solid and dotted arrows indicate positive and negative relationships, respectively. Gray arrows represent tested, but not significant paths. The arrow width is proportional to the strength of the relationship. The symbols \uparrow indicate a positive relationship between the variables and the first component from the principal component analysis (PCA), respectively. Abbreviations: MAT, mean annual temperature; MAP, mean annual precipitation; SOC, soil organic carbon; TN, total nitrogen. Goodness-of-fit statistics for the model are shown below the model * $P < 0.05$; ** $P < 0.01$. Bar graphs represent the standardized total effects (sum of direct and indirect effects) derived from SEM on the response of SOC content to **c** land degradation and **d** restoration.

decreased under land degradation, but not for ligninase activity (Figure 1a). In contrast, land restoration increased both cellulase and ligninase activities with greater effect on cellulase activity (Figure 1b). This differential response can be tracked back to the following reasons: Firstly, the cellulases are generally associated with decomposition of relatively labile C pools, while the ligninases are considered to be the proxy to decompose the recalcitrant C pools (Sinsabaugh and Follstad Shah 2012; Margida and others 2020; Chen and others 2020). The shifts in substrate availability were accompanied with land degradation and restoration. Our results show that land degradation was usually associated with loss of labile substrate (Figure S3a), leading to the negative response of cellulase activity to land degradation. Meanwhile, the proportion of recalcitrant C pools is found to be increased under land degradation (Solomon and others 2007; Dieckow and others 2009; Wang and others 2020a). Under this circumstance, microor-

ganisms may shift to utilize the recalcitrant C pools (that is, lignin and polyphenols) to meet their energy acquirement by the production of ligninase (Jian and others 2016; Takriti and others 2018). Contrary to land degradation, increasing plant litter input and root exudates under land restoration can release the resource limitation of microorganisms (Yu and others 2017; Shao and others 2019; Li and others 2020). In this case, microorganisms may invest energy in cellulase production to acquire labile resources rather than ligninase production, because the synthesis of ligninase incurs higher energy cost compared with cellulase (Jian and others 2016; Takriti and others 2018).

Secondly, the shifts in microbial biomass and community composition under land degradation and restoration could also affect the response of cellulase and ligninase activities. The production of enzyme is positively correlated with microbial biomass (Pition and others 2020), and land degradation was associated with reduction in the

microbial biomass (Figure S3a). As a result, the cellulase activity would decrease with microbial biomass. Several studies found that land degradation increased the relative abundance of fungi (Li and others 2019; Wang and others 2020b), especially the relative abundance of *Basidiomycota* (Wang and others 2020b). These microbial communities are widely recognized as their stronger ability to produce ligninase (Romani and others 2006; Cusack and others 2011; van der Wal and others 2013). Meanwhile, the oligotrophic communities are always associated with a higher investment in extracellular enzymes to decompose the complex resources (Malik and others 2019; Piton and others 2020). Thus, land degradation was associated with the decrease of microbial biomass (Figure S3a), but the ligninase activity remain unchanged. However, copiotrophic taxa such as *Proteobacteria* and *Actinobacteria* became more common with the restoration time (Zhang and others 2016; Shao and others 2019). These taxa had a higher potential to produce cellulase compared with other groups within bacteria (Trivedi and others 2016; Wang and others 2020c).

Interestingly, the responses of cellulase and ligninase activities to the short- and long-term land degradation and restoration were significantly different (Table S1; Figure 3a, b). Microbial communities can change their community composition or shift their C use strategies to adapt to land-use change. However, the adaptation may take several decades owing to the legacy effect of land-use history (Janssen and others 2018; McGee and others 2020; Turley and others 2020). For instance, the conversion of natural forest or grassland to cropland is always accompanied with the breakdown of soil aggregates (Yamashita and others 2006; Davari and others 2020; Cavalcanti and others 2020), and then, a large amount of available substrates were released to the soil environment, which could alleviate the resource limitation for microorganism. As a consequence, it is possible that the cellulase activity decreased to a less extent and the ligninase activity was even suppressed under the short-term land-use change (Figure 3a; Luo and others 2019). As the labile substrates decreased with the conversion time (Figure S3a), microorganisms need to shift their C use strategy toward more recalcitrant C pools by producing ligninase. On the contrary, at the initial stage of secondary succession or the conversion of cropland to plantation, the oligotrophic groups may dominate the microbial communities (Zhang and others 2016; Shao and others 2019). It is likely that under this circumstance, microorganisms would be characterized with

acquisition strategy to produce extracellular enzymes to break down complex resources (Malik and others 2020; Ramin and Allison 2019). As the labile resources increased with succession (Figure S3b), the substantial energy investment in ligninase production to decompose complex substrates was no longer needed. That was likely why the ligninase activity was enhanced under the long-term land degradation and the short-term land restoration (Figure 3a, b).

Linkage Between Shifts in C-Degrading Enzyme and SOC Dynamics Under Land Degradation and Restoration

The increased specific cellulase and decreased ligninase enzyme activities were associated with land degradation and restoration, respectively (Figure 2a, b). These results suggested that microorganisms invested relatively more energy in enzyme production under land degradation, and conversely, invested relatively less energy in the production of enzyme under land restoration (Raiesi and Beheshti 2014; Sauvadet and others 2018; Piton and others 2020). A recent trait-based microbial strategy proposed that microbial metabolic investments in degradative enzyme production for resource acquisition can reduce the investment in microbial growth yield (Malik and others 2019; Malik and others 2020; Ramin and Allison 2019). Based on their definition, the microorganisms dwelling under land degradation conditions could be characterized with the resource acquisition strategy. Thus, the relatively higher investment in no-growth products (that is, enzymes) may lead to a relatively lower microbial residue formation under land degradation (Malik and others 2020). Since microbial residue and necromass could make up of the most part of SOC formation (Liang and others 2019; Zhu and others 2020), resource acquisition strategies under land degradation should contribute more to the decomposition and carbon loss through investment in enzyme production (Schimel and Schaeffer 2012; Kallenbach and others 2016; Malik and others 2020). In contrast, the absence of resource limitation under land restoration is expected to favor high-yield strategy which invest less energy in enzyme production and have higher microbial yield and thus contribute to the formation and accumulation of SOC (Malik and others 2020). The linearly negative relationship between the response of SOC content and specific enzyme activity under land degradation and restoration also confirmed this point (Figure 6a, b). Although the tight linkage

between the response of SOC content and enzyme activity can contribute to the explanation of dynamics of SOC under land degradation and restoration, shifts in the plant C inputs caused by land degradation and restoration can also play a major role. Thus, the relative contribution of the microbial enzyme activities to SOC dynamics under land degradation and restoration is still not very clear.

More importantly, the response of SOC content to land degradation and restoration was negatively correlated with changes in ligninase-to-cellulase ratios induced by land-use change (Figs. 6c, d, 7a, c). This result suggested that the increased ligninase-to-cellulase ratio under land degradation (Figure 4a) would be unfavorable to the accumulation of SOC. In contrast, the decreased ligninase-to-cellulase ratio (Figure 4b) could be beneficial to the accumulation of SOC under land restoration. The possible explanations for this phenomenon were listed as follows: First, microbial C use strategy shifts toward ligninase induced by land degradation could directly accelerate the decomposition of more complex or stable organic compounds. On the other hand, the depolymerization of the complex compounds could increase microbial accessibility to the protected labile compounds, such as lignin-encrusted C compounds (Thevenot and others 2010). This would also accelerate the degradation of labile SOC and leading to further SOC losses (Chen and others 2020). In contrast, relative lower ligninase activity under land restoration could lead to the enrichment of lignin-like compounds, which could contribute to the accumulation of SOC.

Second, the synthesis of ligninase incurs higher energy cost compared with cellulase (Jian and others 2016; Takriti and others 2018), and the ligninase-to-cellulase ratio has been found to be negatively correlated with microbial CUE (Takriti and others 2018). This suggested that more C could be respired by the synthesis of ligninase (Chen and others 2018a). However, for land restoration, the reverse applies. This explanation was supported by the increased ηCO_2 which was associated with land degradation (Figure S3a). Our results were also consistent with a recent finding that warming-induced C loss was positively correlated with warming-induced increases in ligninase-to-cellulase ratio (Chen and others 2020).

Uncertainties and Implications

The quantity and quality of C input change as well as the alteration of soil microenvironment induced

by land degradation and restoration were the main drivers of shifts in SOC accumulation (Poeplau and Don 2013; Lai and others 2016; Wiesmeier and others 2019; Ledo and others 2020; Luo and others 2020; Veldkamp and others 2020). These changes could also result in the alteration of soil microbial community composition and C use strategy (Shao and others 2019; Sun and Badgley 2019). Shifts in the microbial C use strategy (that is, the cellulase and ligninase activity and their relative proportions) could exert nonnegligible effects on SOC accumulation (Malik and others 2020; Ramin and Allison 2019). However, cautions should be taken because the associations between enzyme activities and SOC dynamics do not reveal causal relationships, and the cause-effects are challenging to be validated in such observational study. The casual relationships between microbial C use strategy and SOC dynamics should be verified under more controlled conditions. Additionally, the timescales of enzyme activities and SOC formation and degradation are mismatched, but these microbial indicators are of important values in explaining the SOC dynamics under environment change (Melillo and others 2017; Chen and others 2018b, 2020; Chen and Sinsabaugh 2021). Despite the limitations mentioned above, our study raises three important knowledge gaps. First, the C-degrading enzyme production can be regulated by microbial composition and the associated genes (Trivedi and others 2016). However, only few studies simultaneously investigated the response of microbial community composition and C-degrading enzymes activities to land-use change (Wang and others 2020b), and the association between them was rarely explored. Moreover, studies that directly investigate the relationship between gene and C-degrading enzyme production under land-use change are still lacking. Second, although the correlations of microbial CUE with the amount of enzymatic production and ligninase-to-cellulase ratio were well acknowledged (Takriti and others 2018; Malik and others 2019), studies that simultaneously measure these variables under land degradation or restoration were rare. We suggested future studies should conduct experiments and establish their relationships directly under land-use change. Finally, the shifts of soil nutrient status and their stoichiometry in response to land-use change can significantly impact the coenzymatic stoichiometry and consequently the microbial CUE (Sinsabaugh and others 2013; Mooshammer and others 2014). Future studies should comprehensively investigate the effect of land-use change on

the coenzymatic stoichiometry and its relationship with substrates status.

To conclude, our result identified the tight linkage between shifts in microbial C use strategy and SOC accumulation under land degradation and restoration scenarios. The upregulated production of ligninase by microorganisms compared with cellulase under land degradation would accelerate the decomposition of recalcitrant C pools. However, the decreased ligninase activity relative to cellulase activity associated with land restoration would contribute to the enrichment of lignin-like compounds and finally favor the accumulation of SOC. Meanwhile, the higher energy invested in enzyme production by microorganism (higher specific enzyme activity) to cope with resource limitation under land degradation could also contribute to the increased decomposition and C loss. In contrast, the lower investment in enzyme production by microorganism under land restoration can contribute to the C accumulation. Overall, the comprehensive assessment of the response of C-degrading enzyme activity to land degradation and restoration, as well as its close relationship with the alteration of SOC content provided by our meta-analysis, could contribute to the mechanistic understanding of SOC dynamics in response to land degradation and restoration, which was also useful for improving future models through including these microbial processes.

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AUTHOR CONTRIBUTIONS

JW, XC, YL and GL conceived and designed the study. JW, XC and WL performed research. JW, XC and WL analyzed the data. JW, XC and GL wrote the paper with contribution also from all other authors.

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