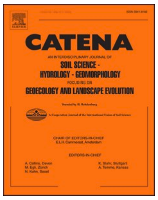
Catena 246 (2024) 108456

Contents lists available at ScienceDirect

Catena

journal homepage: www.elsevier.com/locate/catena



Impacts of conversion of cropland to grassland on the C-N-P stoichiometric dynamics of soil, microorganisms, and enzymes across China: A synthesis

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ARTICLE INFO

Keywords:
Cropland to grassland conversion
Soil stoichiometry
Microbial C-N-P stoichiometry
Enzyme C-N-P stoichiometry

ABSTRACT

In response to escalating land degradation, the conversion of cropland to grassland has emerged as a crucial mitigation strategy. This conversion has a significant influence on the stoichiometry of soil, microorganisms, and enzymes, specifically in relation to carbon (C), nitrogen (N), and phosphorus (P). A *meta*-analysis was conducted with 371 observations from 122 articles investigating the impacts of cropland to grassland conversion on the C-N-P stoichiometric dynamics of soils, microorganisms, and enzymes across China. The findings revealed that conversion significantly increased soil C:P (9.0%), soil N:P (5.6%), microbial C:N (15.5%), and notably, microbial C:P by 57.9%. This substantial increase in microbial C:P indicates that microbial communities are highly responsive to land use conversion. Contrastingly, the enzyme C:P ratio decreased by 19.8%, suggesting microbial adaptation to changing nutrient availability. The duration of conversion was positively correlated with soil C:P and N:P ratios, implying that relative P availability may decrease as conversion progresses. However, duration was negatively correlated with microbial C:P. Environmental factors such as clay content, mean annual temperature, and mean annual precipitation were positively correlated with microbial C:N and negatively correlated with microbial N:P, while soil pH was inversely correlated with microbial C:N. These results suggest the substantial influence of cropland to grassland conversion on soil, microbial, and enzyme stoichiometry, with particularly pronounced effects on microbial communities. The observed shifts in stoichiometric ratios suggest changes in nutrient cycling and availability following conversion. While these changes are primarily attributed to

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https://doi.org/10.1016/j.catena.2024.108456
Received 7 September 2023; Received in revised form 30 September 2024; Accepted 5 October 2024

the land use conversion, we acknowledge that alterations in management practices, such as reduced fertilization, likely contribute to the observed stoichiometric shifts. Our findings emphasize the importance of considering both environmental factors and management practices when implementing grassland conversion initiatives.

1. Introduction

Since the 20th century, climate change has exacerbated environmental degradation, contributing to reduced vegetation cover and exacerbating soil degradation, which directly impacts an estimated 1.5 billion people globally (Cui et al., 2019a; Xu et al., 2020). To counteract this, vegetation restoration measures, such as the conversion of degraded cropland to grassland, have been implemented globally, China being a notable participant (Tang et al., 2022; Zheng et al., 2022). Efforts to transform degraded croplands into grasslands have resulted in an increase of approximately 0.3 million hectares in grassland area over the past two decades in China (NFGA, 2019). Previous studies have reported various effects of cropland to grassland conversion on soil, microbial, and enzyme stoichiometry. Yang et al. (2021) found that conversion increased soil enzyme activities, while Liu and Wang (2020) observed increases in the ratios of soil organic C to total nitrogen (C:N) and soil organic C to available phosphorus (C:P). Zhang et al. (2019) reported changes in microbial biomass C:N:P ratios following conversion, suggesting shifts in microbial nutrient limitations. However, the magnitude and direction of these changes have been inconsistent across studies.

Soil carbon (C), nitrogen (N), and phosphorus (P) cycles are critical components of soil health and ecosystem function, and are significantly impacted by the conversion of cropland to grassland (Allison et al., 2007; Li et al., 2016; Liu et al., 2018). The conversion from cropland to grassland alters both biotic and abiotic conditions, leading to changes in vegetation community composition, soil environmental conditions, and C, N, and P contents (Bohoussou et al., 2022; Yang et al., 2021). For instance, a *meta*-analysis reported that converting cropland to grassland increased soil organic C (SOC) content by 36.9 % at 0 to 20 cm depth (Song et al., 2014). Changes in the stoichiometric ratios of these elements (C:N:P) can provide insights into soil nutrient dynamics and organic matter cycling. While not direct indicators of soil fertility, these ratios can reveal important information about the state of organic matter decomposition and potential nutrient limitations (Liu and Wang, 2020; Manzoni et al., 2012; Song et al., 2014). Understanding how converting cropland to grassland affects soil nutrients is crucial for assessing soil health during ecological restoration. Changes in nutrient ratios can indicate nutrient use efficiency or potential imbalances. Monitoring these changes provides insights into soil recovery and helps refine restoration strategies.

The conversion to grassland from cropland can significantly influence soil properties, including an increase in soil microbial biomass and diversity, enhancing soil enzyme activity (Kim et al., 2023; Manzoni et al., 2012; Mori et al., 2023; Yu et al., 2019). Soil microbes play a central role in ecosystem nutrient cycling and organic matter decomposition, influencing soil C conversion and nutrient regulation. Indicators such as microbial C, N, and P contents (MBC, MBN, and MBP) and their stoichiometric ratios can provide reliable assessments of soil quality and offer insights into ecosystem productivity (Allison et al., 2007; Pan et al., 2022). Additionally, the increase in microbial biomass and nutrients post-conversion provides the substrate for microbial secretion of various extracellular enzymes.

Extracellular enzymes secreted by microbes break down complex organic compounds, leading to an increase in soil extracellular enzyme activity post-conversion (Allison et al., 2007; Tang et al., 2022). These enzymes further break down plant matter and residues into SOC, stimulating further soil enzyme secretion. Extracellular enzyme stoichiometric ratios can portray the balance of microbial metabolism and estimate the equilibrium between microbial nutrient demand and soil nutrient supply, thereby shedding light on energy flow in ecosystems (Cui et al., 2019b; Yang et al., 2021). However, the utilization of enzyme C:N:P stoichiometry for inferring soil microbial nutrient limitation needs careful interpretation, and should be employed as a supporting measure in nutrient limitation assessments rather than a driving factor (Mori et al., 2023). Therefore, further investigation is required to understand how cropland-to-grassland conversion alters microbial and enzyme stoichiometry ratios.

The “Conversion of Cropland to Forest and Grassland Program” project, implemented by the Chinese government in 1999, aimed at improving the ecological environment and achieving sustainable development. This project led to improvements in ecosystem services and has significant impacts on terrestrial ecosystem C cycles (Peng et al., 2007; Yu et al., 2020; Zeng et al., 2020). Studies have shown that soil C stocks increase after cropland conversion to grassland, while they decrease upon grassland reclamation (Zhang et al., 2021; Zhang et al., 2015). Additionally, the reclamation of mine soils with forest and hay enhanced water infiltration capacity and water-stable aggregates at the lower depths (Shrestha and Lal, 2008). Therefore, understanding soil, enzyme, and microbial C-N-P stoichiometric responses during grassland restoration efforts is essential for optimizing these processes, such as terrestrial ecosystem carbon cycles and ecosystem services.

The main objectives of this study were to (1) determine the responses of soil, microbial, and enzyme C-N-P stoichiometry to cropland to grassland conversion; and (2) assess the effects of environmental (climate and soil conditions) and management factors (restoration duration) on their changes following the conversion. We hypothesized that: (1) the conversion of cropland to grassland would lead to increased soil carbon content accumulation and changes in nutrient dynamics, resulting in a) an increase in soil C:P and N:P ratios due to enhanced C sequestration and reduced P availability; b) shifts in microbial and enzyme stoichiometry, reflecting adaptations to changing resource availability; (2) environmental factors, particularly mean annual precipitation and restoration duration, would significantly influence the magnitude and direction of changes in C-N-P stoichiometry following conversion.

2. Materials and methods

2.1. Data collection and screening

We utilized the Web of Science database (https://www.webofknowledge.com/) to conduct an extensive literature search on studies investigating the effects of conversion of cropland to grassland on soil, microbial, and enzyme stoichiometric ratios across China. The search captured studies published from January 1990 to November 2021. The keywords employed in this search included terms such as “conversion of cropland to grassland”, “grassland restoration”, “grassland revegetation”, “conversion of agricultural land to grassland”, “soil stoichiometry”, “soil chemistry”, “soil stoichiometric ratio”, “soil C, N, P stoichiometric ratio”, “soil C:N”, “soil C:P”, “soil N:P”, “microbial stoichiometric ratio”, “microbial C:N”, “microbial C:P”, “microbial N:P”, “enzyme C-N-P stoichiometric ratio”, “enzyme C:N”, “enzyme C:P”, OR “enzyme N:P” AND “China” OR “Chinese”. These terms were used in various combinations to maximize the breadth of the search. The initial keyword search yielded 631 articles.

The articles collected from the initial search were then rigorously screened based on the following criteria: (1) both the control group (degraded cropland) and the treatment group (cropland subjected to conversion measures) clearly demonstrated the impact of conversion on soil stoichiometric ratios; (2) conversion was defined as a change in land use from cropland to grassland, and soil, microbial, and enzyme stoichiometric ratios were characterized as the C:N, C:P, and N:P ratios in soil, microbes, and enzymes: (3) at least two of the three elements (C, N, and P) needed to be present in the literature; (4) in studies involving multiple treatments, only the results of the conversion treatment were recorded; (5) the experiments had to be replicated at least three times to ensure the reliability of the results. Our study selection criteria focused on the conversion treatment itself, rather than comparing different management practices. As such, while changes in management practices (including fertilization) likely occurred as part of the land use conversion, our data do not allow us to separate these effects from those of vegetation change. Following the application of our screening criteria, a final set of 122 peer-reviewed publications was obtained for further analysis and synthesis in this study.

2.2. Database preparation

The C-N-P stoichiometric response ratios for soil, microorganisms, and enzymes (Table 1) were gathered either by utilizing GetData Graph Digitizer (https://getdata-graph-digitizer.com/, version 2.26) or extracted directly from tables and text in the selected articles. For instances where multiple fallow treatments were present within a study, we compiled the soil, enzyme, and microbial stoichiometric response ratios for the entire experiment as well as for each individual fallow treatment, provided that the necessary data were accessible. To account for variations in initial soil conditions, we also summarized the ratios of C:N, C:P, and N:P for both cropland (control) and converted grassland (treatment) sites (Table S1). However, we note that our ability to analyze trends based on initial element contents was limited, as not all studies in our *meta*-analysis reported individual C, N, and P contents.

From this process, we extracted a total of 371 observations from 122 distinct studies. In this study, we analyzed data on soil P, including both total P and available P. When discussing P limitation, we primarily focus on AP as it represents the form of P directly accessible to plants and microorganisms.

Simultaneously, we collected additional supplementary information including the mean annual temperature (MAT), mean annual precipitation (MAP), soil characteristics (for instance, soil texture with a focus on clay content, and soil pH), and the duration of conversion. If the studies did not provide coordinates (latitude and longitude), we retrieved this data through Google Earth (https://www.google.com/earth/), using the site information provided in the respective study. Similarly, if climate records (MAT and MAP) were not included in the study, we obtained this data from the National Centers for Environmental Information (NCEI, https://www.ncei.noaa.gov/), using the location of the experimental site for reference. In cases where soil characteristics were not provided in the study, we sought alternative data from the Harmonised World Soil Database (HWSD: http://www.fao.org/land–water/land/land-governance/land-resources-planning-toolbox/category/details/en/c/1028012/).

Table 1
The abbreviations of soil, microbial and enzyme C-N-P stoichiometric response ratios.

Abbreviation	Description
$RR_{\mathrm{SC/N}}$	Soil C:N response ratio
$RR_{\mathrm{SC/P}}$	Soil C:P response ratio
$RR_{\mathrm{SN/P}}$	Soil N:P response ratio
$RR_{\mathrm{MBC/N}}$	Microbial C:N response ratio
$RR_{\mathrm{MBC/P}}$	Microbial C:P response ratio
$RR_{\mathrm{MBN/P}}$	Microbial N:P response ratio
$RR_{En\mathrm{C/N}}$	Enzyme C:N response ratio
$RR_{En\mathrm{C/P}}$	Enzyme C:P response ratio
$RR_{En\mathrm{N/P}}$	Enzyme N:P response ratio

2.3. Meta-analysis

To reduce estimation bias and improve accuracy, the natural log response ratio (ln*RR*) was used to study the effect of conversion of cropland to grassland on the C-N-P stoichiometry of the plant-soil-enzyme system (Hedges et al., 1999). It was calculated as:

$$RR = ln(X_t/X_c) = ln(X_t) - ln(X_c) \tag{1}$$

where *RR* is the response ratio of individual observations; X_t and X_c are the means of the experimental and control group variables, respectively.

The variance (v) was calculated as follows:

$$v = \frac{S_t^2}{n_t S_t^2} + \frac{S_c^2}{n_c S_c^2} \tag{2}$$

where S_t and S_c are standard errors for the experimental and control groups, respectively; n_t and n_c are sample sizes for the experimental and control groups, respectively.

Effect sizes for individual observations were calculated using "metafor" package (Viechtbauer, 2010). A random effects model was used to calculate the mean of the response ratio (RR_{++}), 95 % confidence interval (CI) and its standard error S (RR_{++}).

$$RR_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{ki} W_{ij}RR_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{ki} W_{ij}}\# \tag{3}$$

$$95\%CI = RR_{++} \pm 1.96S(RR_{++})\# \tag{4}$$

$$S(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{ki} W_{ij}}}\# \tag{5}$$

If the 95 % CI overlaps with 0, conversion does not lead to differences in individual observations between the experimental and control groups. For 95 % CI $>$ 0, conversion has a positive effect on individual observations, while for 95 % CI $<$ 0 is a negative effect.

Weighting factors were calculated as follows:

$$w_{ij} = \frac{1}{\vartheta_i + \sigma^2}\# \tag{6}$$

where ϑ_i and σ^2 are the variance of the data in the i^{th} study and the random variables present between studies, respectively.

During data compilation, we observed that a small number of observations exhibited extreme values, such as soil C:N ratios below 1. While these values are untypical, suggesting N content exceeds C content, they may represent unique soil conditions resulting from specific environmental factors or intensive management practices (e.g., large nitrogen fertilization). Excluding these data points without definitive evidence of error could introduce bias and reduce the comprehensiveness of our *meta*-analysis. To ensure that these extreme values did not disproportionately influence our results, we conducted a sensitivity analysis excluding observations with C:N ratios below 1. The findings from this analysis indicated that the exclusion did not significantly alter the overall patterns or conclusions of our study.

2.4. Statistical analysis

Publication bias was evaluated using Rosenthal's weighted method (Rosenberg, 2005). To assess the relationships between environmental factors (such as soil pH, clay content, MAT, MAP, and management factors (e.g., restoration duration) with soil, microbial, and enzyme C-N-P stoichiometry, we applied Pearson's correlation analysis using the "corrr" package (Jackson et al., 2016). Additionally, relationships among the *RR* of soil, microbial, and enzyme C-N-P stoichiometry were examined.

Meta-regression analysis was conducted using the "metaphor" package, employing the restricted maximum likelihood (RMLE) method with the Knapp and Hartung (KH) adjustment (Viechtbauer, 2010). This analysis explored linear or quadratic associations between the *RR* of soil, microbial, and enzyme C-N-P stoichiometry with grassland restoration duration or MAP. Although *meta*-regression was conducted to explore variable relationships, the R^2 values were often low, which is typical in ecological studies due to natural variability. We interpret these results cautiously, using them to show trends rather than make strong predictions.

Furthermore, piecewise structural equation modeling (SEM) was utilized to determine the effects of grassland restoration on soil, microbial, and enzyme C-N-P stoichiometry in conjunction with other environmental factors (e.g., soil pH, clay content, MAT, and MAP) and management factors (e.g., restoration duration). Significance levels were set at $P < 0.05$ for all statistical tests, all statistical analyses and visualizations were performed using R (version 3.4.2).

3. Results

3.1. Soil, microbial and enzyme stoichiometric ratios in response to conversion of cropland to grassland

Conversion of cropland to grassland had various effects on soil, microbial and enzyme C-N-P stoichiometric ratios (Table 2). On average, the conversion increased soil C:N, soil C:P, soil N:P, microbial C:P, and microbial N:P, while it decreased microbial C:N, enzyme C:N, enzyme C:P and enzyme N:P (Table 2).

Conversion of cropland to grassland significantly increased $RR_{\mathrm{SC/P}}$ and $RR_{\mathrm{SN/P}}$ by 9.0 % and 5.6 %, respectively, but had no significant effect on $RR_{\mathrm{SC/N}}$ (Fig. 1). The conversion significantly increased $RR_{\mathrm{MBC/N}}$ and $RR_{\mathrm{MBC/P}}$ by 15.5 % and 57.9 %, respectively, while there was no significant effect on $RR_{\mathrm{MBN/P}}$ (Fig. 1). In addition, the conversion significantly decreased $RR_{\mathrm{EnC/P}}$ by 19.8 %, while there was no significant effect on $RR_{\mathrm{EnC/N}}$ and $RR_{\mathrm{EnN/P}}$ (Fig. 1).

3.2. Factors influencing stoichiometry response to conversion of cropland to grassland

In the conversion of cropland to grassland, the response ratios of soil, microbial, and enzymatic C-N-P stoichiometry were affected by factors such as clay content, experiment duration, MAP, MAT, and pH (Fig. 2). Out of these, the $RR_{\mathrm{SC/N}}$ exhibited a low correlation with all factors (Fig. 2a). Duration displayed the strongest positive correlation with the $RR_{\mathrm{SN/P}}$ (correlation coefficient, $r = 0.93$, $P < 0.01$) and $RR_{\mathrm{SC/P}}$ (0.90, $P < 0.01$), while negative correlation with the $RR_{\mathrm{MBC/P}}$ (−0.58, $P < 0.05$). However, pH was highly negatively correlated with the $RR_{\mathrm{MBC/N}}$ (−0.83, $P < 0.01$). Clay, MAP, and MAT showed a positive correlation with the $RR_{\mathrm{MBC/N}}$ (0.83, 0.83, 0.83, $P < 0.01$) and $RR_{\mathrm{EnN/P}}$ (0.70, 0,69, 0.69, $P < 0.01$), but a negative correlation with $RR_{\mathrm{MBN/P}}$ (−0.58, −0.63, −0.63, $P < 0.05$, Fig. 2a).

The stoichiometry of soil, enzymes, and microbes also interacted with each other (Fig. 2b). The most significant and highest positive correlation was found between the $RR_{\mathrm{SN/P}}$ and $RR_{\mathrm{SC/P}}$ (correlation coefficient, $r = 0.94$, $P < 0.001$). The correlation between the $RR_{\mathrm{EnC/P}}$ and $RR_{\mathrm{EnC/N}}$ (0.77, $P < 0.01$) followed, which was greater than the correlation between the $RR_{\mathrm{EnC/P}}$ and $RR_{\mathrm{EnN/P}}$ (0.64, $P < 0.05$). However, the $RR_{\mathrm{MBN/P}}$ showed the strongest negative correlation with the $RR_{\mathrm{MBC/N}}$ (−0.63, $P < 0.05$). The $RR_{\mathrm{MBC/P}}$ had a slightly lower negative correlation with the $RR_{\mathrm{SN/P}}$ (−0.60, $P < 0.05$), followed by the correlation between the $RR_{\mathrm{EnN/P}}$ and $RR_{\mathrm{SC/N}}$ (−0.58, $P < 0.05$).

3.3. Correlation analysis between soil, enzyme and microbial stoichiometric response ratios

The correlation between $RR_{\mathrm{MBC/N}}$ and $RR_{\mathrm{ENC/N}}$ indicated that low MAP and long duration were associated with lower $RR_{\mathrm{MBC/N}}$ and $RR_{\mathrm{ENC/N}}$ values (Fig. 3c). In contrast, higher MAP and shorter duration were associated with higher $RR_{\mathrm{MBC/N}}$ and $RR_{\mathrm{ENC/N}}$ values (Fig. 3c). Furthermore, $RR_{\mathrm{ENC/N}}$ decreased with the increase of the duration (Fig. 4e). The correlation between $RR_{\mathrm{SC/P}}$ and $RR_{\mathrm{MBC/P}}$ suggested that low MAP and longer duration generally resulted in higher $RR_{\mathrm{SC/P}}$ values (Fig. 3d). These patterns in stoichiometric ratios may suggest shifts in relative nutrient availability, but direct claims about element limitations should be made cautiously.

SEM demonstrated that increasing soil stoichiometric response ratios (RR_{SS}) led to a decrease in microbial stoichiometric response ratios (RR_{MS}, Fig. 5), but an increase in enzyme stoichiometric response ratios (RR_{ES}). Additionally, certain environmental factors also influenced these response ratios. Specifically, clay content and pH had a positive impact on RR_{MS} ($P < 0.05$). Similarly, increments in duration and MAP increased RR_{SS} and RR_{ES} ($P < 0.05$), respectively. While the explanatory power of individual factors was relatively low (R^2 ranging from 3 % to 12 %).

4. Discussion

4.1. Effect of conversion of cropland to grassland on soil C-N-P stoichiometry

This study found that the response ratio of soil stoichiometry was ranked as C:P > N:P > C:N (Fig. 6). This is likely driven by the rate at which soil C content increased, which surpassed that of N, while the change in P content was not significant (Liu et al., 2018; Xu et al., 2022). In particular, a significant increase in both $RR_{\mathrm{SC/P}}$ (9.0 %) and $RR_{\mathrm{SN/P}}$ (5.6 %) was observed with conversion of cropland to grassland, which appears to stem from increases in SOC and total N coupled with a decrease in soil available P content (Wang et al., 2023; Yang et al., 2021; Zhang et al., 2021). These dynamics also elucidate why $RR_{\mathrm{SC/P}}$ exceeded $RR_{\mathrm{SN/P}}$.

The relative stability of soil C:N ratios observed in our study warrants careful interpretation within the context of land use change. While we found less dramatic changes in soil C:N compared to C:P and N:P ratios, it's important to note that land use changes can indeed impact soil C:N ratios. Soil C:N ratios are influenced by multiple factors, including vegetation type, management practices, and environmental conditions. In grassland ecosystems, the C:N ratio of plant inputs can vary depending on species composition, with legumes typically having lower C:N ratios than grasses (Spehn et al., 2002). The apparent stability of soil C:N ratios in our study could be attributed to: balanced changes in C and N cycling following conversion (Deng et al., 2016); time lag in soil

Table 2
The effects of conversion of cropland to grassland on the response ratios of soil, microbial, and enzyme C-N-P stoichiometry.

	$RR_{\mathrm{SC/N}}$	$RR_{\mathrm{SC/P}}$	$RR_{\mathrm{SN/P}}$	$RR_{\mathrm{MBC/N}}$	$RR_{\mathrm{MBC/P}}$	$RR_{\mathrm{MBN/P}}$	$RR_{\mathrm{EnC/N}}$	$RR_{\mathrm{EnC/P}}$	$RR_{\mathrm{EnN/P}}$
Minimum	−1.00	−0.71	−2.46	−3.39	−1.51	−1.98	−2.79	−3.16	−2.24
Maximum	2.38	1.40	1.18	1.78	1.53	2.82	1.27	2.41	3.11
Median	0.03	0.15	0.14	−0.06	0.21	0.00	−0.02	−0.37	−0.06
Mean	0.05	0.16	0.06	−0.06	0.18	0.05	−0.05	−0.30	−0.18
SD	0.40	0.42	0.53	0.63	0.69	0.75	0.74	0.97	0.81
CV	7.62	2.61	9.07	−9.89	3.77	14.06	−13.78	−3.27	−4.51

Note: SD, standard deviation; CV, coefficient of variation.

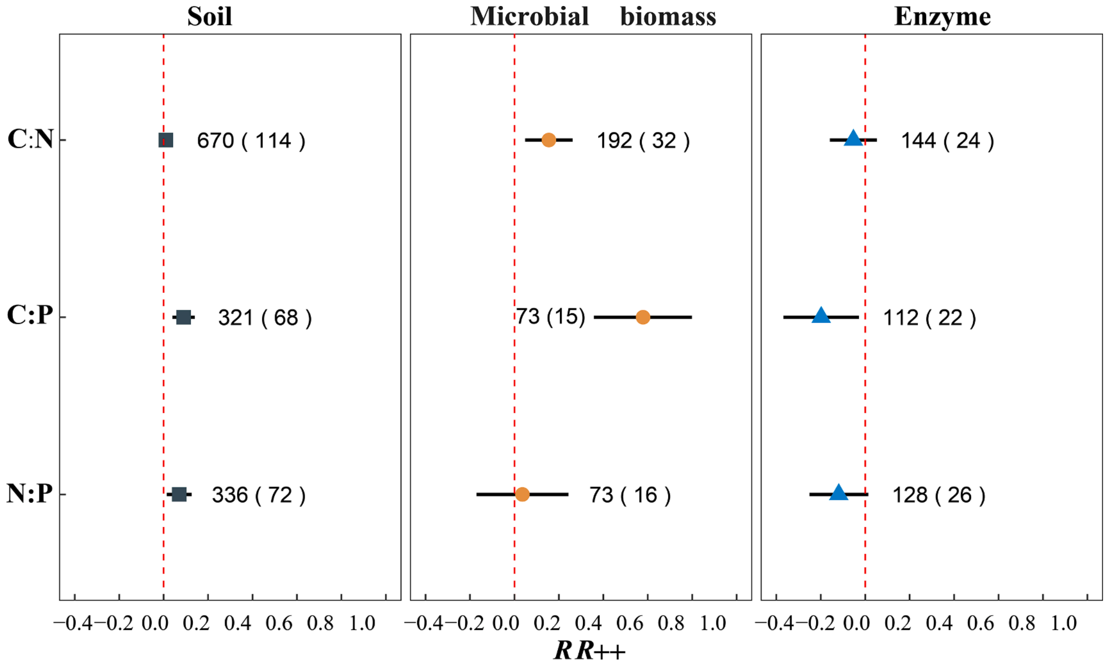
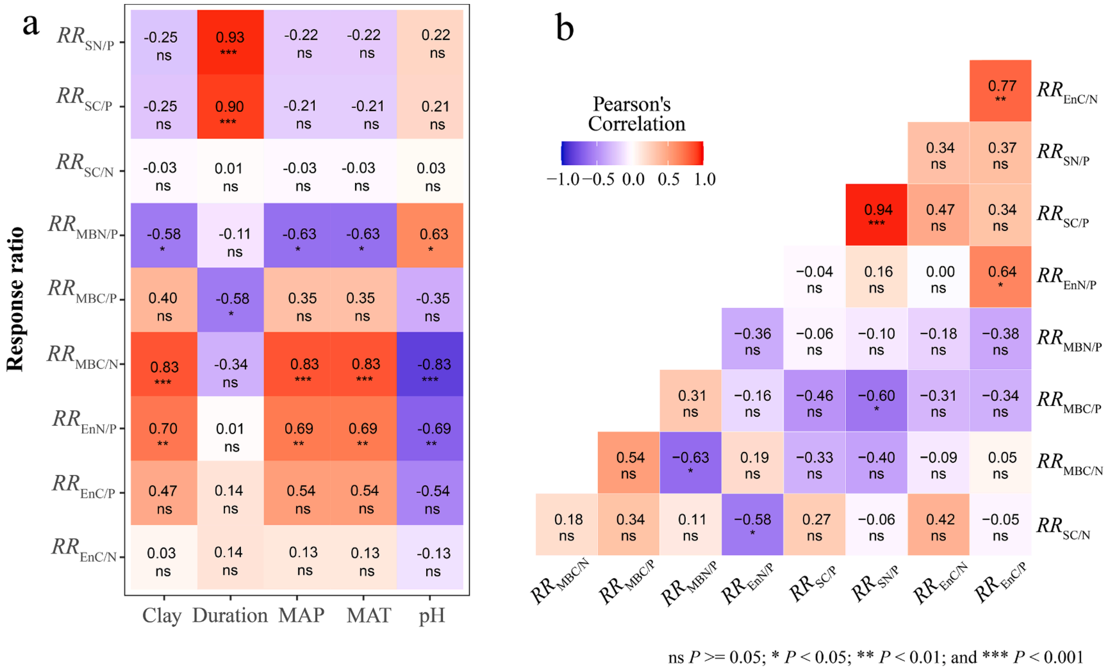


Fig. 1. The effects (weighted response ratio, RR_{++}) of conversion of cropland to grassland on the C-N-P stoichiometry of soil, microbes, and enzymes. Note: Points with error bars represent overall means and 95 % confidence intervals (CIs). Numbers in parentheses indicate the sample size.



a

	Clay	Duration	MAP	MAT	pH
$RR_{SN/P}$	-0.25 ns	0.93 ***	-0.22 ns	-0.22 ns	0.22 ns
$RR_{SC/P}$	-0.25 ns	0.90 ***	-0.21 ns	-0.21 ns	0.21 ns
$RR_{SC/N}$	-0.03 ns	0.01 ns	-0.03 ns	-0.03 ns	0.03 ns
$RR_{MBN/P}$	-0.58 *	-0.11 ns	-0.63 *	-0.63 *	0.63 *
$RR_{MBC/P}$	0.40 ns	-0.58 *	0.35 ns	0.35 ns	-0.35 ns
$RR_{MBC/N}$	0.83 ***	-0.34 ns	0.83 ***	0.83 ***	-0.83 ***
$RR_{EnN/P}$	0.70 **	0.01 ns	0.69 **	0.69 **	-0.69 **
$RR_{EnC/P}$	0.47 ns	0.14 ns	0.54 ns	0.54 ns	-0.54 ns
$RR_{EnC/N}$	0.03 ns	0.14 ns	0.13 ns	0.13 ns	-0.13 ns

b

$RR_{MBC/N}$	$RR_{MBC/P}$	$RR_{MBN/P}$	$RR_{EnN/P}$	$RR_{SC/P}$	$RR_{SN/P}$	$RR_{EnC/N}$	$RR_{EnC/P}$	
							0.77 **	$RR_{EnC/N}$
						0.34 ns	0.37 ns	$RR_{SN/P}$
					0.94 ***	0.47 ns	0.34 ns	$RR_{SC/P}$
				−0.04 ns	0.16 ns	0.00 ns	0.64 *	$RR_{EnN/P}$
			−0.36 ns	−0.06 ns	−0.10 ns	−0.18 ns	−0.38 ns	$RR_{MBN/P}$
		0.31 ns	−0.16 ns	−0.46 ns	−0.60 *	−0.31 ns	−0.34 ns	$RR_{MBC/P}$
	0.54 ns	−0.63 *	0.19 ns	−0.33 ns	−0.40 ns	−0.09 ns	0.05 ns	$RR_{MBC/N}$
0.18 ns	0.34 ns	0.11 ns	−0.58 *	0.27 ns	−0.06 ns	0.42 ns	−0.05 ns	$RR_{SC/N}$

ns $P >= 0.05$; * $P < 0.05$; ** $P < 0.01$; and *** $P < 0.001$

Fig. 2. Correlation analysis of a) factors affecting response ratio (*RR*) of soil, enzyme, and microbial stoichiometry and b) correlation between *RR* of soil, enzyme, and microbial stoichiometry in response to conversion of cropland to grassland. Duration: time since conversion from cropland to grassland; MAP: mean annual precipitation; MAT: mean annual temperature; Clay: clay content; pH: soil acidity. Other abbreviations are defined in Table 1.

organic matter turnover (De Deyn et al., 2008; Zhang et al., 2021); microbial processing converging organic matter towards a constrained C:N ratio (Cotrufo et al., 2013).

The observed increases in soil C:P (9.0 %) and N:P (5.6 %) ratios after converting cropland to grassland suggest a relative decline in P availability compared to C and N. This shift hints at possible P limitation (Du et al., 2020), influenced by several factors: (1) P excess in croplands, where P fertilization can lead to P accumulation that gradually depletes after conversion due to the cessation of fertilization (MacDonald et al., 2011); (2) increased P uptake during vegetation restoration, as diverse plant communities establish and absorb more P, especially in the early stages (Xu et al., 2020; Yang et al., 2021); (3) changes in P cycling, where soil physical and chemical properties alter, affecting P availability through shifts in mineralization, organic matter, and pH (Allison et al., 2007; An et al., 2013); and (4) management practices, such as reduced tillage and fertilization, which can impact P availability and cycling (An et al., 2013). These changes in stoichiometric ratios highlight the complex factors influencing nutrient dynamics during land-use change (Du et al., 2020).

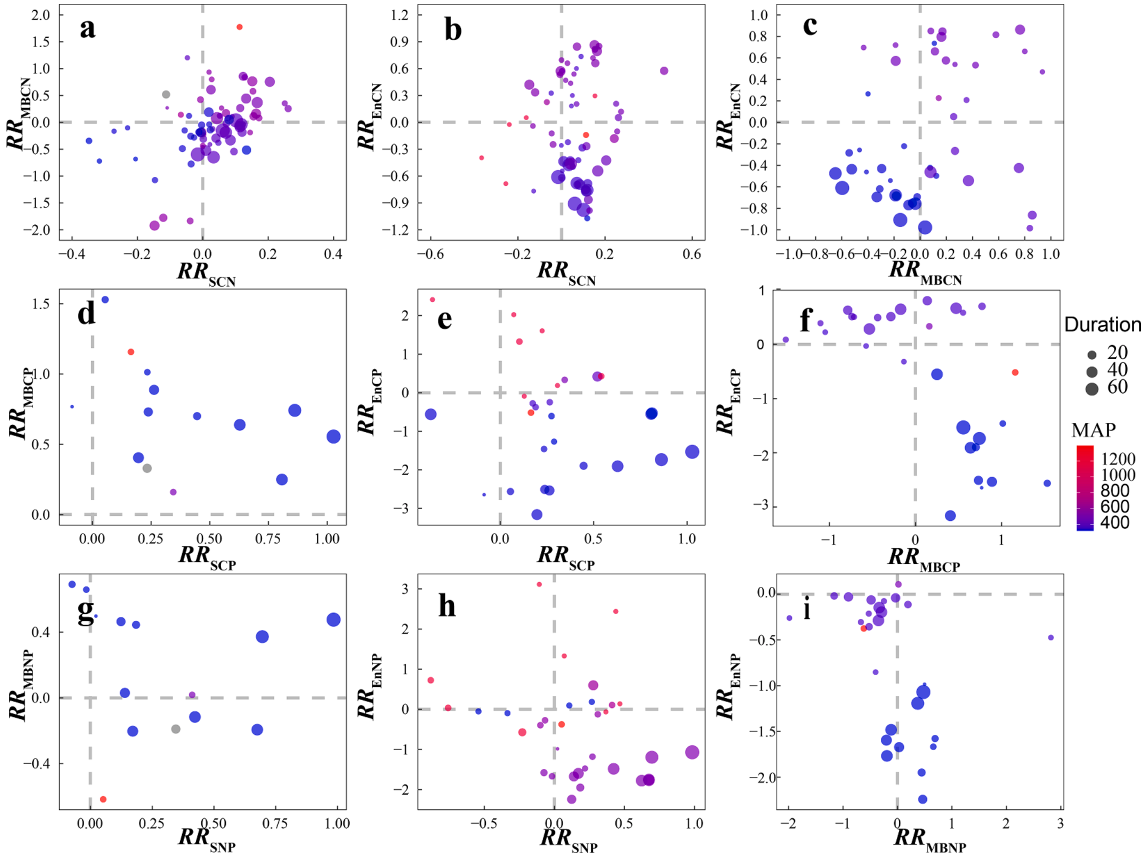


Fig. 3. Plot of the interaction between soil, enzyme, and microbial C-N-P stoichiometric response ratios (*RR*). The dashed gray lines indicate the *RR* = 0 lines for both the *x* and *y* axes, marking the threshold for positive and negative effects, and dividing the plot into quadrants. The interactive effects of mean annual precipitation (MAP) and restoration duration are represented by the size of the dots and the color gradient. For example, when both $RR_{\mathrm{SC/N}}$ or $RR_{\mathrm{MBC/N}}$ fall within the positive and negative partitions, this suggests consistent carbon (C) and nitrogen (N) limitations, respectively. The meaning of other abbreviations is shown in Table 1.

4.2. *Effect of conversion of cropland to grassland on microbial and enzymatic C-N-P stoichiometry*

Conversion from cropland to grassland resulted in significant changes in the soil microbial stoichiometry. Specifically, the conversion led to a significant increase in soil microbial C:N (15.5 %) and C:P (57.9 %), while microbial N:P remained relatively stable (Fig. 1). This differential response may be attributed to land use changes, which alter vegetation type and quantity, leading to enhanced litter inputs, root secretions, and an overall increase in organic matter content (An et al., 2013; Li et al., 2019). These conditions provide nutrient sources that stimulate rapid microbial reproduction, thereby amplifying the C and N content of the soil microbial biomass (An et al., 2013; Zheng et al., 2022).

Conversely, the P content of the microbial biomass remains relatively stable despite the increases in soil organic matter, MBC, and MBN. This suggests that the increased soil organic matter, which leads to the rise in MBC and MBN, does not contain sufficient P to affect MBP contents. Our findings support this inference, showing that the conversion decreased soil available P content by 26 %. The unchanging content of MBP despite an increase in soil organic matter may be due to the initial low P contents of the degraded croplands that were converted to grasslands. These grasslands, likely not receiving any additional P fertilizer, may still retain the low P contents from their cropland state. Furthermore, the observed decrease in available P following conversion from cropland to grassland could be attributed to several factors: (1) increased P uptake by plants as diverse vegetation establishes in grasslands (Kim et al., 2023); (2) changes in P cycling that store more P in less available organic forms (Allison et al., 2007; Cotrufo et al., 2013); and (3) reduced P inputs since grasslands usually receive little fertilization compared to croplands. Thus, even with an increase in soil organic matter, the limited P availability may restrict the increase in MBP, resulting in a relative P limitation within the microbial community (Li et al., 2019; Wang et al., 2023; Xu et al., 2022).

Notably, the magnitude of change in microbial C:P (57.9 %) following conversion far exceeds that of soil C:P (9.0 %) suggesting that microbial communities are acutely responsive to the conversion and microbial communities would be seriously affected by P limitation following the conversion. The substantial difference between microbial and soil stoichiometric changes could hint at the intricate mechanisms driving microbial adaptation to nutrient limitations. Furthermore, it may provide insight into the complex microbial responses to land use changes, which could be crucial for improving our understanding of microbial ecology in the context of ecological restoration efforts.

Conversion from cropland to grassland resulted in a significant decrease in the enzyme C:P ratio (19.8 %) while there were no significant effects observed on enzyme C:N and N:P (Fig. 1). This decline in enzyme C:P ratio can be attributed to the increased activities of phosphatase following the conversion (Liu et al., 2018; Yang et al., 2021). Phosphatase is instrumental in decomposing organic P, liberating it for uptake by plants or microorganisms (Yan et al., 2023).

The reasons for the increased phosphatase activity following conversion can be attributed to two primary factors: (1) an increase in soil organic matter. The conversion of cropland to grassland typically results in higher contents of soil organic matter, which serves as a reservoir of P and a substrate for phosphatase, its increase leads to elevated phosphatase activity; (2) changes in plant community composition. Grasslands, dominated by grasses, have a different root structure than crops.

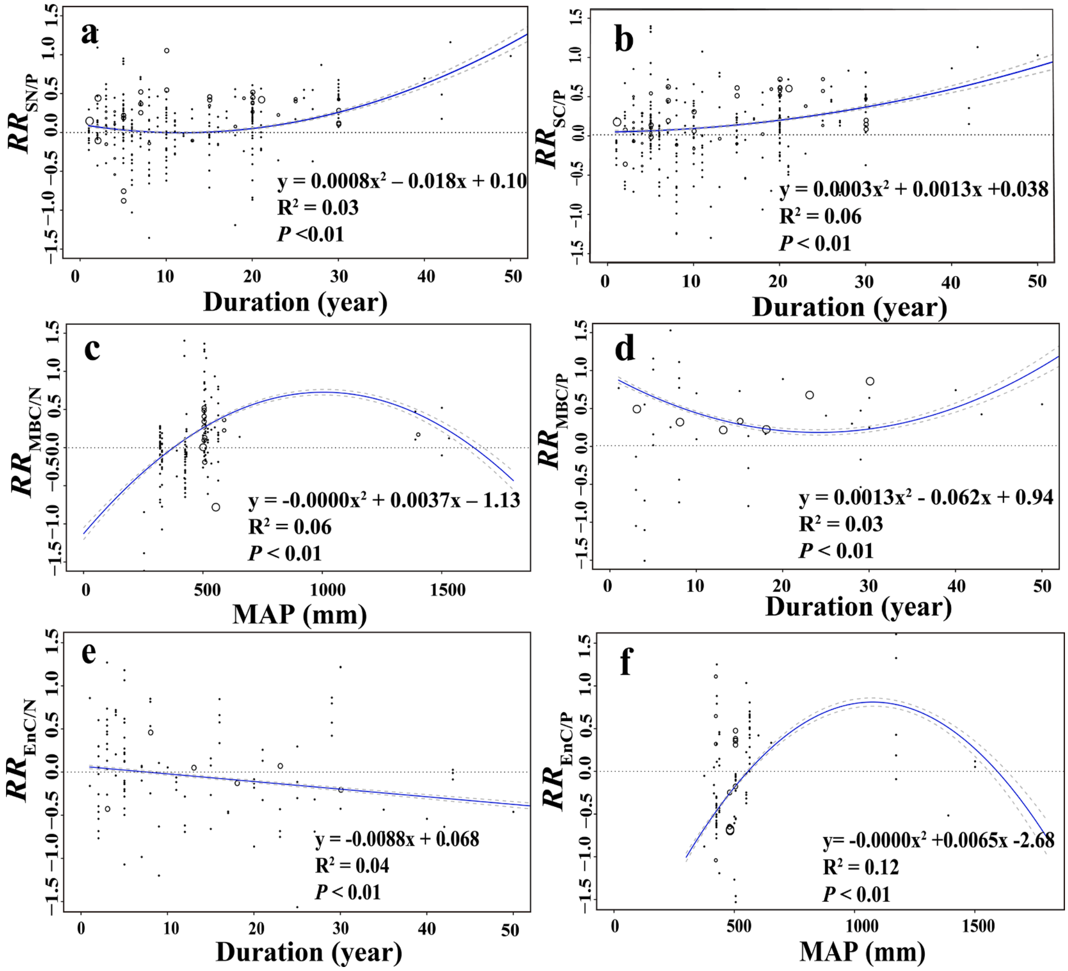


Fig. 4. Scatter plot of response ratio (*RR*) of soil, enzyme and microbial C-N-P stoichiometry against a, b, d, e) duration and c, f) mean annual precipitation (MAP). The solid purple line represents the weighted regression line based on variance-weighted least squares. The dash lines shows the 95% confidence interval around the regression line. The circles indicate the *RR* of each observation. The circle size is proportional to the precision of the *RR*. For a description of the abbreviations, refer to Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

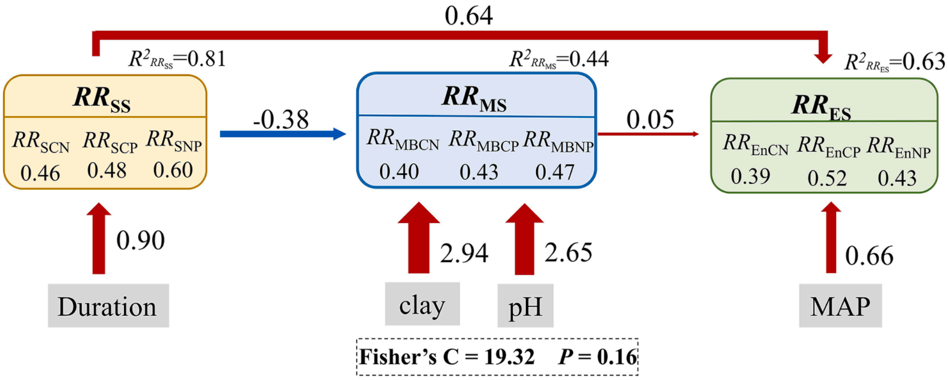


Fig. 5. Structural equation modelling (SEM) of the direct and indirect effects of environmental conditions and duration on soil, microbial and enzyme stoichiometric response ratios (RR_{SS}, RR_{MS}, RR_{ES}). Red and blue arrows indicate positive and negative correlations, respectively. Arrow width is proportional to the strength of the correlation. The numbers next to the arrows are significant normalized path coefficients. R^2 indicates the variance of dependent variable explained by the model. MAP, mean annual precipitation; clay, clay grain content; pH, acidity; Duration, duration of conversion of cropland to grassland. The meaning of other abbreviations is shown in Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The extensive root systems and higher density of root hairs of grasses allow better access to P in the soil, leading to a surge in phosphatase activity (Zhang et al., 2019).

The heightened phosphatase activity and the resulting decrease in enzyme C:P ratio may reflect an adaptation of soil microbial communities to P limitation in the soil. This highlights the importance of P in maintaining soil fertility in the conversion. Consequently, understanding the enzymatic C-N-P stoichiometry could provide valuable insights into managing soil fertility and enhancing soil C sequestration in the process of grassland restoration. It can also guide us to balance the

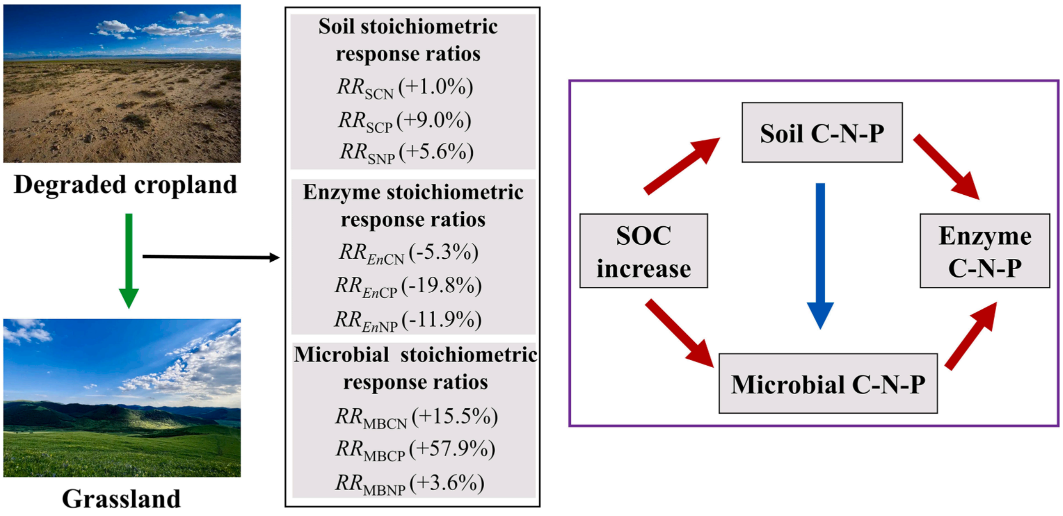


Fig. 6. Conceptual figure of the effects of conversion of cropland to grassland on microbial, soil and enzymatic C-N-P stoichiometry. Red and blue arrows indicate positive and negative correlations, respectively. Numbers in gray boxes indicate the percentage change following conversion of cropland to grassland. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

nutrient availability and hence the plant growth and C uptake in such ecosystems.

4.3. Effect of duration of conversion of cropland to grassland on soil-microbial-enzyme C-N-P stoichiometry

Our findings indicate a positive correlation between soil C:P, soil N:P, and the duration of conversion from cropland to grassland (Fig. 2a). This trend suggests that as grassland conversion progresses, P limitation intensifies. On the contrary, our finding indicated a negative correlation between microbial C:P and the duration of conversion. A possible explanation could be that the increase rate in MBC following the conversion may decrease as time passes. This pattern could be an additional indication of P limitation in the converted grassland, as a slower MBC increase rate may be due to the lack of sufficient P for microbial growth and activity (Yan et al., 2023). It is crucial to verify this hypothesis by investigating if the increase rates in MBC indeed reduce as the conversion duration extends.

The efficacy of conversion in improving soil nutrients is region-dependent (Yu et al., 2018). Changes in vegetation succession and plant species influence the input of soil nutrients, which could consequently modify soil C, N, and P content to a certain degree (Sun et al., 2021). As organic matter escalates with the duration of conversion, microbial C, N, and P increase, leading to an upsurge in enzyme secretion to decompose the growing organic matter, and subsequently altering soil enzyme stoichiometric ratios (Allison et al., 2007; Cui et al., 2019b; Yang et al., 2021). Therefore, prolonging the conversion duration considerably improves soil nutrient content, encourages N and P fixation, enhances microbial and enzyme activity, and aids in restoring degraded arable land. However, it also underscores the challenge of managing P limitation during this process, necessitating more focused strategies for efficient grassland restoration.

4.4. Influence of environmental conditions on stoichiometric response ratios

The structural equation model revealed significant effects of environmental variables, particularly soil attributes like clay content and pH, on soil, enzyme, and microbial stoichiometry.

Clay content showed a positive correlation with $RR_{MBC/N}$, which can be explained by several mechanisms: (1) surface area effect: higher clay content provides increased surface area for microbial colonization and nutrient adsorption. This can lead to enhanced microbial activity and biomass production, potentially favoring C accumulation over N (Allison et al., 2007); (2) physical protection: clay particles can physically protect organic matter from decomposition, leading to higher C retention in microbial biomass (Six et al., 2006); (3) nutrient availability: clay minerals can adsorb and retain nutrients, particularly ammonium N, potentially leading to localized N limitation and higher C:N ratios in microbial biomass (Rousk and Baath, 2011).

Soil pH demonstrated an inverse correlation with $RR_{MBC/N}$. This relationship can be attributed to several pH-dependent processes: (1) nutrient availability: in acidic conditions (lower pH), the availability of certain nutrients, particularly P, may be reduced due to increased binding with aluminium and iron oxides. This can lead to nutrient imbalances affecting microbial stoichiometry (Kunhikrishnan et al., 2016); (2) microbial community composition: pH is a major driver of microbial community structure. Lower pH often favors fungal dominance over bacteria. Fungi typically have higher C:N ratios than bacteria, which could explain the increased $RR_{MBC/N}$ at lower pH (Rousk and Baath, 2011); (3) enzyme activity: soil pH affects the activity and stability of extracellular enzymes. Changes in enzyme activity can alter the rate and efficiency of organic matter decomposition, potentially affecting the $RR_{MBC/N}$ (Sinsabaugh et al., 2008).

Regarding the $RR_{SC/N}$ stability, our results align with the concept of stoichiometric homeostasis in soil organic matter. This stability can be explained by several mechanisms: (1) microbial processing: microbes tend to maintain relatively constant $RR_{MBC/N}$, which influences the C:N ratio of the organic matter they produce during decomposition (Cleveland and Liptzin, 2007); (2) physicochemical stabilization: organic compounds with certain C:N ratios may be preferentially stabilized through associations with soil minerals (Cotrufo et al., 2013); (3) plant input quality: while the quantity of plant inputs may change with land use, the quality (C:N ratio) of inputs from a given plant functional type (e.g., grasses) may remain relatively constant (De Deyn et al., 2008).

The positive relationship between MAP and the RR_{ES} can be explained by: (1) nutrient leaching: higher rainfall can increase nutrient leaching, particularly of more mobile nutrients like nitrate. This can alter nutrient availability ratios in the soil, prompting microbes to adjust their enzyme production to acquire limiting nutrients (Sinsabaugh et al., 2008); (2) microbial activity: increased soil moisture from higher MAP can stimulate overall microbial activity, leading to greater enzyme production. However, the relative production of different enzymes may shift based on changing nutrient limitations (Allison et al., 2007; Cui et al., 2019b; Tang et al., 2022); (3) substrate availability: higher MAP often correlates with greater plant productivity, increasing the input of organic matter to soil. This can alter the quantity and quality of substrates available for enzymatic degradation, potentially shifting enzyme stoichiometry (Cotrufo et al., 2013; Sinsabaugh et al., 2008; Six et al., 2006). However, the low R^2 values (R^2 ranging from 3 % to 12 %) indicate the complexity of these ecological processes and suggest that additional factors, including potential interactions between variables and site-specific conditions, likely contribute substantially to the observed variability in stoichiometric responses.

4.5. Limitations and suggestions for further studies

One primary limitation of this study was the difficulty in collecting sufficient soil microbial and enzyme data to robustly support our hypotheses. Despite the clear patterns demonstrated by the data collected, the complexity of soil-microbial-enzyme interactions necessitates more extensive datasets for greater insights. Future research could increase sample size and diversity to verify and expand upon our findings.

It's important to note that our study design did not allow us to disentangle the effects of vegetation change from those of associated changes in management practices, such as fertilization. Typically, conversion from cropland to grassland involves not only a change in plant species but also alterations in soil management, including reduced or ceased fertilization. These management changes could contribute significantly to the stoichiometric shifts we observed. Future studies should aim to explicitly record and analyze the effects of management practices, particularly fertilization, to better understand the mechanisms driving stoichiometric changes during land use conversion.

Extrapolation of our results, focused on China, to other regions should be approached with caution due to variations in climate, soil, and land use conditions. There is a clear need for similar studies in other regions globally to validate the general applicability of our findings and understand region-specific patterns and mechanisms, particularly given the global extent and significance of land use changes.

In our dataset, we included a small number of observations with extreme stoichiometric ratios, such as soil C:N ratios below 1. These untypical values may reflect unique soil conditions arising from specific environmental factors or intensive management practices. For example, soils subjected to excessive nitrogen inputs from heavy fertilization or atmospheric deposition, industrial pollution can accumulate high contents of N relative to C (Johnson and Curtis, 2001; Smith and Paul, 2017; Wardle, 2008). Such conditions might occur in certain agricultural systems or regions with significant anthropogenic influence. Including these extreme values ensures a comprehensive representation of soil nutrient dynamics across diverse environments. However, it is crucial to interpret these values cautiously. Our sensitivity analysis, which excluded observations with extreme ratios, demonstrated that their inclusion did not significantly affect our overall findings. This outcome suggests that the extreme values do not unduly influence the conclusions of our study. Future studies focusing on the impacts of excessive nutrient inputs and other anthropogenic factors on soil nutrient balances could provide valuable insights.

Lastly, we identified a gap in studies and conclusive evidence on managing P limitation during cropland to grassland conversion. This highlights the need for further research into best management practices, such as timing and rates of P fertilizer application or use of P-solubilizing microbes (Silva et al., 2023; Sun et al., 2022; Yan et al., 2023), to mitigate nutrient imbalances and ensure the sustainability of such land conversions.

5. Conclusion

This *meta*-analysis investigated the impact of cropland to grassland conversion on soil, enzyme, and microbial C-N-P stoichiometry across China. The results revealed significant changes in stoichiometric ratios following conversion: soil C:P and N:P increased by 9.0 % and 5.6 % respectively, while microbial C:N and C:P increased by 15.5 % and 57.9 %. Conversely, enzymatic C:P decreased by 19.8 %. Environmental factors played crucial roles in these stoichiometric shifts. Soil clay content and pH positively influenced microbial stoichiometry, while mean annual precipitation affected enzyme stoichiometry. The duration of conversion positively influenced soil stoichiometric ratios, suggesting temporal dynamics in nutrient cycling post-conversion. Importantly, our findings indicate that microbial communities are highly responsive to land use conversion, as evidenced by the substantial increase in microbial C:P ratios. The decrease in enzyme C:P ratio suggests microbial adaptation to changing nutrient availability, particularly reduced P availability following conversion.

While our results demonstrate clear stoichiometric shifts, we acknowledge that these changes likely reflect the combined effects of vegetation change and alterations in management practices, particularly reduced fertilization in converted grasslands. Future research should aim to disentangle these effects and quantify their relative contributions to stoichiometric changes.

CRediT authorship contribution statement

Ying Li: Writing – original draft, Validation, Formal analysis, Data curation. **Jianhui Sang:** Writing – review & editing, Data curation. **Canwei Zou:** Writing – original draft. **Qingping Zhang:** Writing – review & editing, Software, Methodology, Conceptualization. **Qian Yang:** Writing – review & editing, Resources, Conceptualization. **Gang Xu:** Writing – review & editing, Validation, Software, Data curation. **Dong-Gill Kim:** Writing – review & editing, Validation, Conceptualization. **Matthew D. Denton:** Writing – review & editing, Conceptualization. **Carmen Rosa Carmona:** Writing – review & editing, Conceptualization. **Hongyang Zhao:** Writing – review & editing, Conceptualization. **Yanting Mao:** Writing – review & editing, Funding acquisition. **Liping Mao:** Writing – review & editing. **Keren Wu:** Writing – review & editing. **Bin Yao:** Writing – review & editing, Funding acquisition. **Jianming Xue:** Writing – review & editing, Conceptualization. **Wentao Sun:** Writing – review & editing. **Yangzhou Xiang:** Writing – review & editing, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Yuan Li:** Writing – review & editing, Visualization, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jianxiao Zhu:** Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This work was supported by the Natural Science Foundation of Gansu Province (22JR5RA455), Key talent project of Gansu Province for Jianxiao Zhu, Fundamental Research Funds for the Guizhou Provincial Science and Technology Projects (QKHJC-ZK[2022]YB335), Fundamental Research Funds for the Central Non-profit Research Institution of Chinese Academy of Forestry (CAFYBB2020ZE005), Scientific Research Fund Project of Guizhou Education University (2024YB002; 2024BSKQ003), and National Key Research and Development Program of China (2020YFF0305900).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2024.108456.

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