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Impact of manure on soil biochemical properties: a global synthesis

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Abstract

Manure application mitigates land degradation and improves soil fertility. Despite many individual studies on manure effects, a comprehensive overview of its consequences for a broad range of soil properties is lacking. Through a meta-analysis of 521 observations spanning the experiments from days after pulse addition up to 113 years with continues manure input, we quantified and generalized the average responses of soil biochemical properties depending on climatic factors, management, soil, and manure properties. Large increase of pools with fast turnover (microbial carbon (C) and nitrogen (N): +88% and +84%, respectively) compared to stable organic matter pools (+27% for organic C, and +33% of total N) reflects acceleration of C and N cycles and soil fertility improvement. Activities of enzymes acquiring C-, energy-, N-, phosphorus- and sulfur were 1.3-3.3 times larger than those in soil without manure for all study durations included. Soil C/N ratio remained unaffected, indicating the stability of coupled C and N cycles. Microbial C/N ratio decreased, indicating a shift towards bacterial domination, general increase of C and N availability and acceleration of element cycling. Composted manure or manure without mineral fertilizers induced the greatest increase compared to non-composted manure or manure with mineral fertilizers, respectively, in most biochemical properties. The optimal manure application rate for adjusting proper soil pH was 25 Mg ha^{-1} year^{-1}. Among manure types, swine manure caused the greatest increase of N-cycle-related properties: microbial N (+230%), urease (+258%) and N-acetyl-β-D-glucosaminidase (+138%) activities. Manure application strategies should avoid P and N losses and pollution via runoff, leaching or gaseous emissions due to fast mineralization and priming of soil organic matter. In conclusion, manure application favors C accumulation and accelerates nutrient cycling by providing available organic substances and nutrients and thus increasing enzyme activities.

Keywords: Soil nutrients; Manure; Soil organic matter; Soil leaching; Enzyme activities; Meta-analysis

Introduction

Soils are key reservoirs of global biodiversity and are the basis of global food production (FAO, 2015). The increasing human population combined with shrinking agricultural land further highlights the necessity to maintain soil health and quality (Thangarajan et al., 2013). Arable soils are being rapidly degraded due to erosion, structure degradation, nutrient depletion, loss of soil organic carbon (SOC) and other threats (Fan et al., 2012; Pu et al., 2019). In the Anthropocene, manure that is mainly excreted by animals or derived from plant residues is an environmentally friendly soil amendment to remediate soil degradation and thereby increase the stability of crop production and agroecosystem functioning (Liu et al., 2020; Mandal et al., 2020). Manure application not only increases aggregate stability and soil porosity (Haynes and Naidu, 1998; Karami et al., 2012) and decreases bulk density (Edmeades, 2003), but also improves the soil biochemical properties (Jiang et al., 2018; Luo et al., 2018a; Saha et al., 2008a).

Manure application increases SOC and nutrient contents (e.g., nitrogen (N), phosphorus (P)) (Liang et al., 2014; Nicolas et al., 2012; Ros et al., 2006; Zhang et al., 2015). For instance, field application of cattle manure for 46 years increased the SOC and total nitrogen (TN) contents by ca. 34% and 31%, respectively (Giacometti et al., 2014). Swine manure application at a rate of 41 Mg ha^{-1} for 15 years increased the total P content from 123 to 458 mg kg^{-1} (Zhang et al., 2015). Application of poultry manure (Tejada, 2009) or composted cattle manure (Zaller and Köpke, 2004) increased the microbial C by more than 200% or 27%, respectively. Despite the positive effects of manure on soil microbial indices, great variability in the response of soil biochemical properties after manure application exists, especially for enzyme activities (Foster et al., 2016). For instance, positive effects of green manure (i.e., *Trifolium pratense,* L. and *Brassica napus*, L.) or composted cattle manure on β-glucosidase, urease, phosphatase, dehydrogenase and sulfatase were observed (Tejada et al., 2008; Tripathy et al., 2008), while a negative response of chitinase to green and composted swine manure was found in a 6-month field experiment (Liu et al., 2017). In contrast to the positive/negative responses, Giacometti et al. (2014) found no response of acid phosphatase activities to a 46-year application of green/cattle manure. In particular, the observed contradictory effects of manure application on enzymes that are involved in the C cycle indicate that different C sources may be depleted by fertilization, which affects the activity of enzymes involved in the C cycle. While each of these results makes sense individually, they do not fit together into a consistent theory across a broad range of soils and management systems. Abundant unexplained responses seen in some systems but not in others suggest a major knowledge gap and the necessity of multi-meta-analysis (Gurevitch et al., 2018).

Despite a wide range of studies on the influence of manure application on soil biochemical parameters (Luo et al., 2018; Kallenbach and Grandy, 2011; Maillard et al., 2014; Thangarajan et al., 2013; Webb et al., 2010(Kallenbach and Grandy, 2011), there are only rare attempts to provide a more comprehensive, mechanistic understanding based on soil characteristics (Jiang et al., 2018). For instance, by analyzing the impacts of manure application on soil microbial C and N in croplands, Ren et al. (2018) found a positive correlation between annual C and N input from manure and microbial C and N, respectively. A recent study using a large database more accurately identified the effects of manure on SOC, TN and biological parameters compared to mineral fertilizers (Luo et al., 2018a). However, the conclusion by Luo et al. (2018), which showed that manure application results in increase of soil enzyme activities, is vulnerable to uncertainty in the calculation of average extracellular enzyme activities. The averaging of extracellular enzyme activities that are used as proxies of a specific substrate or nutrient acquisition is based on an assumption that the sum of the major C- or nutrient acquiring enzyme activities is a better indicator of the total C- or nutrient acquisition than are individual enzymes (Bell et al., 2014). However, this approach masks the diverse responses of individual enzymes that are involved in the same nutrient cycle. For instance, in a northwestern Himalayan ecosystem, continuous application of composted cattle manure at rates of 3700 and 5500 kg ha^{-1} increased the alkaline phosphatase but caused a decline in the acid phosphatase activity (Saha et al., 2008a). In addition, recent meta-analyses (Luo et al., 2018; Maillard et al., 2014) did not differentiate manure-only application from the application of manure combined with mineral fertilizers. Considering both strategies together led to inaccurate quantification of the manure’s effect on soil organic matter and biochemical properties (Luan et al., 2019). The effects of manure chemical composition (i.e., the C and N contents, the C/N ratio) on microbe-mediated soil functioning were not evaluated but were proposed for future investigation (Luo et al., 2018b). These characteristics (e.g., types, forms of production and application) are critical in maintaining soil fertility, but their roles in controlling soil properties have yet to be summarized (Ali et al., 2019; Maillard et al., 2014). Thus, a more comprehensive evaluation of manure application’s effects on soil biochemical properties was required from both agronomic and environmental perspectives. This helps us understand the consequences of agricultural management strategies for food production.

Here, we generalized studies worldwide that report the effects of manure application on SOC, TN, microbial C and N and activities of seven enzymes (i.e., C-cycling: β-1,4-glucosidase; energy-acquiring: dehydrogenase; N-cycling: urease, N-acetyl-β-D-glucosaminidase; P-cycling: acid and alkaline phosphatase; S-cycling: sulfatase). The impacts of key explanatory variables were evaluated, i.e., climatic factors (mean annual temperature (MAT), mean annual precipitation (MAP)), soil properties (initial soil pH, type (e.g. Alfisols, Entisols and so on), texture), management (alone or combined with mineral fertilizers, field or lab, duration) and manure characteristics (type (e.g. cattle, swine and so on), composted or non-composted, dry or wet application). The relationships between basic manure chemical composition (i.e., C, N, P, and K contents and their stoichiometry) and their impact on soil properties were a specific focus. Our main objectives were to (1) comprehensively evaluate and quantify the effects of manure on soil biochemical properties, (2) verify the reliability of using the average extracellular enzyme activities as proxies of a specific substrate or nutrient acquisition and (3) clarify the influence of the above-mentioned explanatory variables on manure impacts. We hypothesized that (1) the activity of enzymes involved in acquisition of the same element may respond differently to manure application because of their different functions in complex C and nutrient cycles; (2) the combined application of mineral fertilizers with manure lowers the impact of manure on soil biochemical properties; and (3) manure characteristics significantly effect soil properties.

2. Materials and methods

2.1 Data collection and extraction

The database *ISI Web of Science* was used to search for primary literature that had been published prior to June 2019. The search terms were (“manure" or "poultry*" or "dairy*" or "swine*”), (“enzyme activity" or "enzyme activities”) and “soil*”. The literature had to meet the following criteria to be included in the final database: (i) the study involved application of manure to soil and the manure type was clearly stated; (ii) control plots without manure application were included for comparison with the treatment that had received manure; (iii) the literature investigated the activities of enzymes related to organic carbon (OC) or nutrient cycles; (iv) the means, standard deviation (SD) and replicate numbers were reported. For the literature using standard error (SE), the SD was calculated by SD=SE×$n^{0.5}$, where n represents number of replicates.

In total, 92 studies, including 521 observations, satisfied the criteria (Fig. 1). The means and SDs of the SOC and TN contents, the microbial C and N and the soil pH were also extracted. For the first time and in contrast to previous reviews, seven enzymes, including six hydrolases and one oxidoreductase, were selected and evaluated (Table S1). Furthermore, manure characteristics, soil properties, climatic factors and management were also compiled (Table S2) and considered to be explanatory variables because they may affect the impact of manure on enzyme activities. For studies without information about climate parameters, the MAT and MAP were derived from the WorldClim (http://worldclim.org/version1) using the provided coordinates and ArcGIS 10 software (Hijmans et al., 2005) (Fig. 1). These continuous explanatory variables were further divided into categorical variables (Table S2). Because, in some cases, the manure was produced by mixing several ingredients, the manure types were classified based on the main ingredient. For example, if the paper clearly stated that cattle dung accounted for the largest proportion of manure, it was assigned to the “Cattle” group. When the largest proportion was not presented, the literature was assigned to the “Farmyard” group. Moreover, when the paper reported that fresh, liquid or wet manure was used in their experiment, the data was grouped as “wet”; when the paper stated that solid or dry manure was used in the study, the data was marked as “dry”. When the paper reported that they used composted or non-composted manure, the data was grouped as “composted” or “non-composted”, respectively. Long-term field experiments were included to be more representative of real life, while the lab or short-term experiments provide information of the immediate impact of manure application. Some explanatory variables were not available for all studies, which resulted in missing categories for some factors. For instance, studies on the response of β-glucosidase activity to manure application in sandy soil were absent, therefore only results on sandy loam, sandy clay loam, loam, clay loam, clay and silt soils are available. For alkaline phosphatase activity, however, data for sand, sandy loam, sandy clay loam, loam, clay loam and clay soil can be presented.

The reference or control groups were soil without manure application, but this does not necessarily mean soil without mineral fertilization. When only manure was applied, the control group was unfertilized (null-treatments, no mineral fertilizers). When manure was applied with mineral fertilizers, the control group received application of mineral fertilizers alone (Table S3). Both comparisons can help us more accurately quantifying the effect of manure than previous studies (e.g. Luo et al., 2018; Maillard et al., 2014). Data represented in the tables or text of the literature were collected directly. Data illustrated as figures were extracted using g3data (v.1.5.1) software (https://directory.fsf.org/wiki/G3data).

2.2. Data analysis and statistics

When soil organic matter content was reported, it was converted to SOC content by dividing by a conversion factor of 2.0 (Pribyl, 2010). When the pH ($CaCl_2$) was used, an estimated pH (H_2O) was determined as follows: pH (H_2O) =1.65 + [0.86 × pH ($CaCl_2$)] (Augusto et al., 2008). Similarly, the pH (KCl) was converted to pH (H_2O) using the following equation: pH (H_2O) = -1.95 + 11.58×$\log_{10}$[pH (KCl)] (Kabała et al., 2016).

Effect size was calculated as the natural log of the response ratio (RR) (Hedges et al., 1999):

$$\mathrm{lnRR} = \ln\left(\frac{\overline{\mathrm{X}}_{\mathrm{T}}}{\overline{\mathrm{X}}_{\mathrm{C}}}\right) \tag{1}$$

where $\overline{\mathrm{X}_{\mathrm{C}}}$ and $\overline{\mathrm{X}_{\mathrm{T}}}$ are the means of a variable in the control and manure-applied soil, respectively. Normality of the variables was tested using the Shapiro-Wilk test. The positive or negative lnRR represented an increase or decrease of the variable in response to manure application. The variance of lnRR was determined as follows (Curtis and Wang, 1998; Ren et al., 2018):

$$\mathrm{V}_{\mathrm{lnRR}} = \frac{\mathrm{S}_{\mathrm{T}}^2}{\mathrm{n}_{\mathrm{T}}\overline{\mathrm{X}}_{\mathrm{T}}^2} + \frac{\mathrm{S}_{\mathrm{C}}^2}{\mathrm{n}_{\mathrm{C}}\overline{\mathrm{X}}_{\mathrm{C}}^2} \tag{2}$$

where S_C and S_T are the SDs of the variables in the control and manure-applied treatment, respectively. n_C and n_T are the sample sizes of the variables in the control and manure-applied treatment, respectively. To elucidate the overall effect of the manure application, the weighted mean response ratio (lnRR_{++}) was determined as follows by using a random-effects model (Curtis and Wang, 1998; Ren et al., 2018):

$$\mathrm{lnRR}_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}\mathrm{w}_{ij}\mathrm{lnRR}_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{n}\mathrm{w}_{ij}} \tag{3}$$

where m is the number of compared groups, *j* is the number of comparisons in the *i*th group, and *w* is the weight of lnRR (i.e., $w_{ij}=1/\mathrm{V}_{\mathrm{lnRRij}}$). The SEs of lnRR_{++} were calculated as follows:

$$s(lnRR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{n}w_{ij}}} \tag{4}$$

Accordingly, the percentage change can be derived by the equation [(exp(lnRR_{++})-1) × 100%]. When 95% confidence intervals (CIs) overlap zero, the impact of the manure application on the soil enzyme activities or other parameters is significant. Otherwise, the result is insignificant. During the categorical moderators' analysis, the significance of the heterogeneities between groups ($Q_{between}$) and within groups (Q_{within}) was applied by using the Chi-square test. A *p* value of $Q_{between}$ smaller than 0.05, for instance, represents the significant heterogeneity of the effect size between categories of individual explanatory variables. The meta-analysis was performed in MetaWin 2.1 (Rosenberg et al., 2000).

The manure C/N, C/P and N/P ratios were calculated by considering studies that reported any two elements simultaneously. The manure OC, TN, TP and TK compositions were also calculated by including papers that reported each single element, which resulted in a larger database than that of the elemental ratios. All data of the contents of OC and nutrients in manure and in soil are presented in mg kg^{-1} or g kg^{-1}. To present the effects of manure and to show the changes compared to the control soil without manure, the data are presented as percentage increase or decrease compared to the control soil. The soil C/N ratio, microbial C/N ratio and the ratio of alkaline phosphatase to acid phosphatase activities in the manure-treated and control group were also correlated using linear regression. Statistical differences in soil C/N ratio and microbial C/N ratio between the manure-treated and control soils were tested using Student's *t*-test ($p < 0.05$). The soil ΔpH was calculated by subtracting the value of the manure-treated group from the value of the control. The relationship between the initial soil pH and ΔpH was then established. Furthermore, Spearman's correlation coefficients were calculated to analyze the relationships between the effect sizes of enzyme activities, SOC, TN, microbial C, microbial N and continuous explanatory variables (i.e., initial soil pH, MAT, MAP and duration of manure application) since not all variables were normally distributed ($p > 0.05$). These analyses were performed in SigmaPlot 12.5 software (Systan Software Inc.).

3. Results

3.1 Manure characteristics

Green manure has the highest OC content (407 ± 24 g kg^{-1}; all data presented on a dry-weight basis) compared to that of the other manure types (Fig. 2, left). The TN content in cattle manure is the lowest (15 ± 2 g kg^{-1}) among all manure types. In contrast, the TP content is the lowest in green manure (2.6 ± 0.5 g kg^{-1}). The unique OC, TN and TP compositions in green manure result in the highest ratios: C/N=42±8.1, C/P=221±32, N/P=12±3.8 (Fig. 2, right). The OC content and nutrient compositions of composted manure were nominally lower than those of non-composted manure (Fig. 2). Composted manure has nominally higher TN (18 ± 2.2 g kg^{-1}) and TP (11 ± 3.4 g kg^{-1}) than non-composted manure ($p > 0.05$). This leads to nominally lower C/N (20 ± 2.6) and C/P (60 ± 22) ratios in composted manure ($p > 0.05$).

3.2 Effects of manure application on soil properties

Manure application increased SOC and TN contents by 27 ± 4.2% and 33 ± 8.7% (Fig. 3) compared to soil without manure. Microbial C and N increased by 88 ± 6.3% and 84 ± 11%, respectively. No significant shifts of the soil C/N ratio were found (Fig. 4, left), but the microbial C/N ratio decreased from 9.49 ± 0.34 to 7.64 ± 0.44 after manure application ($p < 0.0001$, Fig. 4, right). For experiments applying swine manure, the microbial C/N ratio decreased from 8.9 ± 0.5 in the control group to 5.6 ± 0.5 in the manure-treated group.

The ΔpH was negatively correlated with the initial soil pH (p<0.01, Fig. 5). The x-intercept value is approximately 7.47, which indicates that the soil pH will increase when the initial soil pH is lower than 7.47 and decrease when the initial soil pH is higher.

Manure application to clay loam soil induced nominally larger effect sizes of SOC and TN (Fig. 6). Microbial C and N contents had larger effect sizes when manure was applied to sandy loam and sandy clay loam (Fig. 7). Applying manure in the lab led to larger increases of SOC, TN, and microbial C and N contents than those in the field (Figs. 6 and 7).

3.3 Effects of manure application on enzyme activities

Manure application increased the activities of β-1,4-glucosidase (B-glu), dehydrogenase (Deh), acid and alkaline phosphatase (Acp and Akp), N-acetyl-β-D-glucosaminidase (Nag), urease (Ure) and sulfatase by 147 ± 15%, 114 ± 10%, 39 ± 6%, 112 ± 12%, 58 ± 13%, 104 ± 8.7% and 228 ± 19%, respectively (Fig. 3). All the enzyme activities showed either an increase or no change in response to the manure application for all conditions (i.e., climatic factors, soil properties, management and manure characteristics) (Fig. 8, S1-S3). The largest effect sizes for almost all the enzyme activities were found within the MAT and MAP ranges of 10-20 °C and 250-1000 mm compared with those of other ranges. The exception was Acp and Akp, which showed lower effect sizes in the MAP range of 250-1000 mm compared to that in the MAP range of >1000 mm (Fig. S2). Among all soil types, manure application to Mollisols induces the largest responses of SOC (59%) and TN (77%). Almost all enzyme activities showed the greatest increase when manure was applied to Entisols (Fig. 8, S1-S3). Most enzyme activities had the largest effect sizes when the initial soil pH was in the range of 6-8. In particular, the effect size of Akp decreased when the initial soil pH increased (p<0.001, Table 1, Fig. S2, right). Manure application to sandy loam or sandy clay loam soil induced relatively larger effect sizes of almost all enzyme activities compared to those of other soils (Figs. 8, S1-S3). One exception is for Acp activity, which had the largest effect size when manure was applied in clay loam soil (Fig. S2 left).

Field and lab-controlled conditions had similar effects on B-glu (~148%) and Deh (~110%) (Fig. 8). The field experiment induced larger increases of Akp (148±5.6%) and Sul (286±17%) than did the lab experiment, but applying manure in the lab led to larger increases of Ure, Nag and Acp than those in the field (Figs. S1-S2). When the manure application was combined with mineral fertilizers (i.e., only N, only P, N+P, P+K and N+P+K), the manure effects on all the enzyme activities were lower than those of the application with manure alone. The composted manure application induced larger effect sizes of most enzyme activities. Swine manure had the largest effect sizes on Ure (258 ± 39%) and Nag (138 ± 31%) (i.e., N-cycling-related parameters, Fig. S1).

The Akp/Acp ratio is an indicator for soil pH adjustment. A significant linear relation was found for Akp/Acp ratio between soil without manure and soil with manure (Fig. 9 left). The mean Akp/Acp ratios in soil without manure and soil with manure are 0.80±0.17 and 0.86±0.14, respectively. Manure application rate (Mg ha^{-1} year^{-1}) was correlated with the ΔAkp/Acp ratio (here, ΔAkp/Acp ratio = (Akp/Acp ratio in soil with manure) - (Akp/Acp ratio in soil without manure)) and a quadratic relationship was found (p < 0.0001; Fig. 9, right).

3.4 Correlations between the effect sizes of SOC, TN, microbial C and N, all enzyme activities and the continuous explanatory variables

The effect sizes of nearly all enzyme activities showed that they were positively correlated ($p<0.05$, Table 1). Especially, B-glu, Ure and Deh were significantly correlated with other enzymes (Table 1). Microbial C was the most pronounced property that positively correlated with the enzyme activity changes ($p<0.05$) (except Sul) as compared to SOC, TN and microbial N.

Among the continuous explanatory variables, MAP was negatively correlated with most of the factors involved in N-cycling-related properties (i.e., TN, microbial N, Ure and Nag) ($p<0.01$), and Akp and Deh increased with the increasing MAP ($p<0.001$). The effect sizes of activities of β-glu, Ure, Sul and Deh decreased with the duration of continuous manure input ($p<0.05$).

4. Discussion

4.1 Overall effects of manure application

Soil OC and TN contents increased by 27 ± 4.2% and 33 ± 8.7% (Fig. 6), respectively, with manure application. These increases as shown in Fig. S4 are greater than the impact induced by mineral fertilizers (0.1-8.4% for SOC and 15% for TN; Geisseler et al., 2017; Geisseler and Scow, 2014; Jian et al., 2016; Xiao et al., 2018). This greater effect of manure can be partly due to the C (206-407 g kg^{-1}) and N (13-22 g kg^{-1}) contained in the manure. In addition, manure application can also lower the soil bulk density and increase the porosity and water holding capacity (Eden, 2017). This, together with the loading of OC and nutrients from manure, affects the microbiome and plant growth, which in turn will increase the C input via rhizodeposition and litter input (Liu et al., 2017). Even though the data for other soil nutrients (P and K) were not reviewed, manuring increased soil nutrients status (Fig. 2, left). In addition, microbial C and N also strongly increased by 88 ± 6.3% and 84 ± 11%, respectively, mainly because of the increased resource availability and physical soil properties for microbial growth following manure application (Chen et al., 2009; de Graaff et al., 2019). The larger increase of microbial C or N compared to the SOC or TN increase implies a higher ratio of microbial C or N to SOC or TN in manured soils, respectively, which could reflect increased soil organic matter quality (Friedel et al., 2006). This highlights the remarkable consequences of manure application for the long-term improvement of soil fertility and the acceleration of C and N cycles (Gan et al., 2013; Schjønning et al., 2018; Luce et al., 2011).

Soil C/N ratios remained stable with manure application, which indicated the stability of the coupled C and N cycles. An exceptional decline of the soil C/N ratio was common for experiments (as shown in Fig. 4 (left), as indicated by the red color) shorter than 21 days (Kizilkaya, 2008; Kizilkaya and Hepsen, 2007). Mancinelli et al. (2013) reported a decreasing soil C/N ratio after applying green manure for 0.5-4.5 months, and suggested that the incorporation of legume biomass into soil was the main reason, due to its low C/N ratio (Mancinelli et al., 2013). However, a two-year study in leguminous green manure-based cropping systems showed no strong change in the soil C/N ratio (Astier et al., 2006). Based on our large database, green manure application has no strong impact on the soil C/N ratio (Fig. 4, left), even though it has the largest C/N ratio (i.e., 42 ± 8.1) compared to that of other manure types. The quality (e.g., the C/N ratio) of manure applied to soil controls soil N_2O emissions with a negative relation with C/N ratio (Huang et al., 2004). The application of manure with a lower C/N ratio might accelerate N mineralization rates and cause greater N_2O emissions, thus indicating the likelihood of greater and faster N losses. When the C/N ratio is larger (e.g. >25), the N mineralization activity declines due to increased microbial N immobilization. In both cases, the soil C and N cycles remain coupled, and the application of manure with different C/N ratios induced no shift in the soil C/N ratio. This stable soil C/N ratio can also be explained by the fine and stable mineral-associated organic matter, which represents the major portion of total soil organic matter and responds slowly to management practices (Cotrufo et al., 2019; Gentsch et al., 2015; Samson et al., 2020).

Unlike the soil C/N ratio, microbial C/N decreased after manure application, especially for swine manure (as indicated by the green color in Fig. 4, right). Such a response of microbial C and N indicates greater N immobilization. In particular, the decrease in microbial C/N ratio suggests a shift in microbial community towards bacterial dominance because of their lower C/N ratio compared to that of fungal biomass (Six et al., 2006). Long-term and continuous increases in bacterial biomass following manure application, instead of fungal biomass, have been well documented (Marschner et al., 2003; Peacock et al., 2001; Rousk and Bååth, 2007). In addition, the C/N ratio of various manure types was a determinant of the microbial C/N ratio or fungal to bacterial growth, with lower C/N ratios of manure (e.g., swine manure) being more beneficial to bacterial growth than to fungal growth (Grosso et al., 2016; Zornoza et al., 2016).

Manure application increased enzyme activities, and this increase was enzyme-specific, even for enzymes that are involved in the cycling of the same element, which confirms our first hypothesis. For instance, Acp increased by approximately 40% with manure application, while the increase of Akp reached 110%. The same phenomenon occurred for Nag (+59%) and Ure (+106%). Acp is produced by both plants and microbes, but Akp originates from soil bacteria, fungi and fauna (Dinkelaker and

Marschner, 1992; Tarafdar and Claassen, 1988). This contributed to the greater increase of Akp activity in manure-treated soil compared to the control group (no manure application, see Table S3). Consequently, the summation or averaging of major C (or nutrient) acquiring enzyme activities (as used in Luo et al., 2018 and Jian et al., 2016) as an indicator of the total C (or nutrient) acquisition is problematic. Such summation or averaging approaches disregard the specific functions of individual enzymes. For instance, despite Nag and Ure both being involved in the N cycle, they catalyze different reactions. Nag is mainly responsible for chitin hydrolysis, which is a constituent of the cell walls or structural tissues of fungi, with the end product being acetyl-glucosamine (Rodriguez-Kabana et al., 1983). In contrast, Ure participates in the hydrolysis of urea to NH_3 (Fisher et al., 2017). The response ratios of almost all enzymes are positively correlated, which illustrates the convergence of ratios of specific C, N and P acquisition activities as 1:1:1 (Sinsabaugh et al., 2008). Therefore, instead of calculating the sum or average of the enzyme activities, we propose that the response of one or two enzyme activities (e.g., B-glu, Ure and Deh) to manure application can partly reflect the response of others ($p<0.001$). For accurate quantification, however, it is necessary to identify the responses individually or develop a more proper index to reflect the response.

Soil sulfatase activity showed the greatest increase (i.e., 228 ± 19%) with manure application. To our knowledge, it is the first time that the response of the soil sulfatase activity to manure application has been generalized. Sulfatase catalyzes the hydrolysis of sulfate esters of complex macromolecules, and plays an important role in the transformation of organic sulfates to inorganic form (i.e., SO_4^{2-}) (Acosta-Martínez and Tabatabai, 2000). The release of SO_4^{2-} is especially crucial for sulfur supply in agricultural soils that do not receive pollutant sulfur deposition from the atmosphere

(Turner et al., 2016). This greatest response of sulfatase activity may be induced by input of substrates (e.g. ester sulfate) and stimulated by microbial growth under manure application (Bandick and Dick, 1999; Giacometti et al., 2014; Piotrowska and Wilczewski, 2012).

The response ratio of most enzymes was not correlated with that of SOC but was positively related to the microbial C (Table 1). Consequently, the effects of manure on enzyme activities were more closely related to the enzyme producers i.e., microbes (Le Bayon and Binet, 2006). Manure was applied at the beginning, but SOC was generally measured at the end of each growing season for the studies with longer duration (> 1 growing season). At the sampling time for the SOC analyses, the labile organic matter from manure had mostly decomposed. The remaining soil organic matter is thus mainly comprised of more recalcitrant materials, which are not the primary substrate for hydrolytic enzymes. This explains the absence of significant relationships between the responses of the SOC content and enzyme activities after manure application.

4.2 Soil pH and its influence on the manuring effect

The soil pH is one of the most important properties regulating enzyme activities and synthesis (Dick et al., 2000) by controlling the microbial community composition (Rousk et al., 2009; Zhalnina et al., 2014) and mediating nutrient availability (Sinsabaugh et al., 2008). Manure application can increase the pH buffering capacity (Shi et al., 2019), thus indicating that its application will adjust the soil pH to the neutral range (i.e., acidification of alkaline soil or alkalization of acidic soil) (Fig. 5). This is crucial because most plants grow best near neutral pH (i.e., 6.5-7.5), and the response of microbial activities to manure application was the strongest in this range (Figs. 7, 8, S1-S3). This buffering capacity is one of the substantial advantages of applying manure compared to mineral fertilizers, which commonly strongly lower the soil pH because of the nutrient uptake and release of protons (Richter et al., 1994). Even though manure application may also acidify soil by ammonia volatilization or nitrification, addition of several cations (e.g. Ca^{2+}, Mg^{2+}) contributes to buffer the soil solution (Zhang et al., 2015). In addition, bacterial growth decreases at lower pH (e.g., ~4.5) much faster than fungal growth (Grosso et al., 2016; Rousk et al., 2009). Manure application, on the contrary, mitigates the decrease of bacterial growth but slows the growth of fungi by increasing the soil pH to the neutral range. This further supports our finding that manure applications narrow the microbial C/N ratio, and our related argument that manured soils are more conducive to bacterial than fungal growth.

This neutralizing effect of manure also explains the negative relationship between the response of Akp and the initial soil pH (i.e., the soil pH before manure was applied, ranging from 4.5-8.6 in this study) (p<0.001). The activity of Akp increases with the increasing soil pH and has an optimum of ~9.0 (Ekenler and Tabatabai, 2003; Koncki et al., 2005). When the initial soil pH is high and alkaline, the Akp activity is already high, and thus the manure application will induce only a slight increment in activity. Accordingly, manuring can cause a large increment of Akp activity by increasing the pH of acidic soils. In contrast, the increment of Acp increases with the increasing initial soil pH (Fig. S2, left). The contrasted responses of Acp and Akp activities also explain the effect of manure on adjusting the Akp/Acp ratio: In acidic soil, manure application will induce a greater increment of Akp than Acp and thus increase the Akp/Acp ratio; in alkaline soil, the increment of Acp will be greater than Akp, thus inducing a decrease in the Akp/Acp ratio (Fig. 9 left).

The Akp/Acp ratio of 0.50 was proposed as the proper Akp/Acp target ratio for crop production (Dick et al., 2000). Manure application may increase the Akp/Acp ratio up to 0.86 ± 0.14 (Fig. 9 left), which is 0.36 units higher than the suggested target ratio (i.e., 0.5). This indicates that the effect of manure application on crop production may be limited. Large manure input improves soil productivity (Edmeades, 2003), so we hypothesize that manure application rate may influence the Akp/Acp ratio. The quadratic relationship between manure application rate and ΔAkp/Acp ratio suggests that, to bring the Akp/Acp ratio in soil without manure from 0.80 to the target ratio of 0.5, the manure application rate should correspond to 25 Mg ha^{-1} year^{-1} (Fig. 9, right). Consequently, a manure application rate of ~25 Mg ha^{-1} year^{-1} would bring the Akp/Acp ratio to the target level for optimal crop production. However, it is still inappropriate to set this rate as the global best rate, even though the data were extracted from studies with different climate, manure types and soil types (e.g. Li et al., 2012; Liang et al., 2015; Saha et al., 2008b; Tamilselvi et al., 2015). To reach a global best rate, much larger database is required.

4.3 Effects of soil, climate, management and manure-related factors on the soil biochemical properties

4.3.1 Climate factors

For most soil enzyme activities, the response to manure was the greatest in the MAT range of 10-20 °C, thus indicating that the optimal temperature for soil enzyme function is at this range. By comparison, MAP did not greatly influence the soil properties and enzyme activities, except for the phosphatases, which showed the strongest response to manure application at sites with MAP > 1000 mm. This specific response can be related to strong P limitation because of strong rate of weathering and leaching (Richardson et al., 2004). High P demand of soil prompts the hydrolysis of organic P to available phosphates by increasing phosphatase activities. The negative correlation between soil initial pH and MAP (p<0.001) suggests that the soil acidity increases with precipitation. As discussed earlier, manure addition may help maintaining soil pH closer to neutrality. This, in turn, could help regulate P availability in P-deficient soils.

4.3.2 Soil properties

Mollisols are among the most fertile soils and are rich in organic matter (Eswaran et al., 2012). Therefore, extra supplies from manure are mostly preserved in Mollisols following manure application and induced the largest SOC and TN increase. However, Mollisols are under severe threat, as they are intensively cultivated for agricultural production (Hatfield et al., 2017; Liu et al., 2012). In the present study, manure application appeared to have some potential to maintain or remediate fertility of degraded Mollisols.

The strongest increase of enzyme activities after manure application was observed in Entisols. Manure application to Entisols strongly stimulated microbial activities because Entisols are young soils (Kolb et al., 2009). Entisols are poorly developed and are mostly dominated by sand and low organic carbon content, which results in a low cation exchange capacity and weak nutrient retention (Franco-Andreu et al., 2017; Lehmann and Schroth, 2003; Mancinelli et al., 2013). Therefore, stimulation of microbial activities by manure in Entisols increases the risk of nutrient losses from leaching if manure is applied in the absence of plant nutrient uptake.

The greatest increase of microbial C and N and almost all soil enzyme activities, as influenced by manure application, occurs in sandy loam or sandy clay loam soils. Both soils are conducive to microbial and plant growth due to its better drainage than that of clay or silty soil and greater nutrient-retaining capacity than sandy soil. An organic amendment has been found to have greater improvement on the physical properties of coarser-textured soil compared to that of finer-textured soil (e.g., hydraulic conductivity, water retention capacity, bulk density, aggregation and aggregate stability) (Aggelides and Londra, 2000; Candemir and Gülser, 2011). This suggests that manure application to sandy loam or sandy clay loam soil plays the greatest role in soil fertility improvements and nutrient cycles. One exceptional greatest increase was Acp activity in clay loam soil when manure was applied. As was shown in our database, most of the sampling points (i.e., 19, Fig. S2 left) to calculate the effect size of Acp activity in clay loam soil are from Liang et al., 2015. They attributed the strong increase of Acp activity to the strong secretion of Acp by roots. However, this does not explain the lower response in other soils and thus further investigations are required.

4.3.3 Management characteristics

Larger increases of SOC, TN, and microbial C and N following manure application were observed in the lab-controlled conditions than in the field, thus indicating that lab studies may overestimate manure effects. Laboratory experiments include pot trials, controlled dark incubation and greenhouse trials. Experimental durations are shorter than those of field experiments, lasting from days to one year (Franco-Andreu et al., 2017; Nicolas et al., 2012; Tripathy et al., 2008). In the short term, a relatively slow decomposition of organic matter and abundant labile organic compounds in manure may contribute to the extreme increase. This argument is also supported by the greater increase of SOC, TN and microbial C when the experimental duration is within 0.1 year. Higher temperature is generally common for experiments under controlled conditions compared to field experiments (Max et al., 2012; Xu et al., 2019). This may also contribute to the overestimation of manure effects on microbial C and N contents.

The combined application of manure with mineral fertilizers lowers the manure effects on soil biochemical properties, which is in accordance with the second hypothesis. The major benefit of enzyme production is the release of organic monomers or nutrients that microbes and plant roots can take up. Evolutionary-economic mechanisms of enzyme production suggest that microbial communities function similarly to economic units, maximizing their productivity by allocating resources to extracellular C-, N-, and P-releasing enzymes, depending on the substrate quality and nutrient limitations (Allison et al., 2011). Thus, excessive mineral fertilization suppresses the need for enzyme expression. Compared with the effects of mineral fertilizers (e.g., N, P and N+P) on soil biochemical properties, as shown by previous studies (Jian et al., 2016; Luo et al., 2018), the effect of manure + mineral fertilizers was much larger. This means that even though mineral fertilizer attenuates the influence of manure on soil biochemical properties, the combined effect of manure + mineral fertilizers is still stronger than the application of mineral fertilizers alone. Nevertheless, the greater increase of soil biochemical properties in the manure-alone application did not represent the optimal conditions for plant growth. Long-term use of manure was found to have a similar influence on crop production compared to mineral fertilizers when applied at equivalent N rates (Celestina et al., 2019; Chen et al., 2018; Edmeades, 2003). This could be because the high competition for nutrients between microbes and plants following manure addition may slow plant growth, although it improves the soil fertility (Kuzyakov and Xu, 2013; Liu et al., 2017).

4.3.4 Manure characteristics

Composted manure had nominally lower C content but nominally larger N and P contents than non-composted manure, thus composting increased the nutrient content and decreases the C/N and C/P ratios (Fig. 2, right). Composting reduces pathogens and parasites, weakens seed viability and suppresses soil-borne plant diseases (Larney and Hao, 2007; Mehta et al., 2013). Composting also contributes to humification of organic residues, which are more beneficial for plant growth (Cavagnaro, 2015; Mehta et al., 2013; Quilty and Cattle, 2011). These special characteristics of composts cause a greater increase of microbial C and of all enzyme activities compared with non-composted manure, revealing stronger organic matter decomposition and nutrient cycling following composted manure application.

Regarding manure types, swine manure application resulted in the greatest increase of N-cycling-related parameters (i.e., microbial N (230%), Ure (258%) and Nag (138%) activities). This implies that swine manure strongly stimulates N mineralization. This may be explained by the relatively low C/N ratio of swine manure (~12 ± 0.9), which induces a decrease in the soil microbial C/N ratio and increases the N demand of microbes (Grosso et al., 2016; Nicolardot et al., 2001). These results, in accordance with the third hypothesis, emphasize the importance of manure characteristics (e.g. manure types, composted or non-composted) for manure effects on soil biochemical properties.

4.4 Environmental implications and perspectives

Given that enormous amounts of manure are produced globally, it is necessary to promote nutrient recycling by using manure resources instead of synthetic or nonrenewable mineral fertilizers (Powers et al., 2019). In comparison with previous studies on mineral fertilizers (Jian et al., 2016; Luo et al., 2018), our review demonstrates that manure application is more beneficial for soil fertility. However, manure application does not guarantee better crop production, as suggested by the high Akp/Acp ratio found after manuring (i.e., ~0.86 > the Akp/Acp target ratio of 0.5; Fig. 9 left). The quadratic relationship (Fig. 9 right) suggested that a manure application rate of 25 Mg ha^{-1} $year^{-1}$ is optimal pertaining to crop growth and soil fertility. Dick et al. (2000) suggested that manuring with additional lime treatment can also help in reducing the Akp/Acp ratio (Dick et al., 2000).

The addition of composted manure, and manure in the absence of fertilizers, had a greater effect on most biochemical properties than non-composted manure or manure in the presence of fertilizers (Fig. 10). Manure application to Entisols also shows a strong response in comparison to other soils. Swine manure application, especially, may increase the risk of N loss due to its greater effect on N mineralization. Therefore, incorrect timing or strategy of manure application may increase N losses and pollution via NO_3^- leaching or gaseous emissions due to rapid organic matter mineralization in the absence of plant N uptake (Xia et al., 2017). P addition to soil by manuring may also threaten water quality because of the role of P in eutrophication of water resources (Tabbara, 2003). Some contaminants (e.g. phthalic acid esters, heavy metals and so on) toxic to microbes and enzymes may also be introduced into soil following manure application (He et al., 2015; Tejada et al., 2011). The presence of antibiotic residues, human pathogens and so on may also pose potential health risks to public health (Venglovsky et al., 2009). Consequently, the identification of these potential threats to soil and plant growth before manure application is crucial and should be taken into consideration when designing agricultural management strategies. Furthermore, other important parameters (e.g. soil depth, tillage systems; Shirani et al., 2002; Zaller and Köpke, 2004) may also have significant influence on the manure effect and therefore should be included in further investigation.

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Supporting information

Supporting information was illustrated in Table S1-S3 and Figure S1-S4.

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Figure captions:

Fig. 1. Global distribution of manure studies included in the meta-analysis. “MAT” represents mean annual temperature; “MAP” represents mean annual precipitation. The MAT-MAP inset shows the climatic conditions for all locations.

Fig. 2. Average organic carbon (OC), total nitrogen (TN) and total phosphorus (TP) contents (**left**) and C/N/P stoichiometric ratios (**right**) of various manure types. Green manure, farmyard manure, cattle manure, swine manure and poultry manure were illustrated according to their relatively larger database. The numbers in the parentheses represent the sample size. “Composted” represents composted manure and “Not-composted” represents non-composted manure. Whiskers show standard error (±SE).

Fig. 3. Weighted effect sizes of manure application on SOC, TN, microbial C and N contents as well as enzyme activities. The number in the parentheses besides each property is the sample size. The thinner black lines were drawn to separate C-, energy-, N-, P- and S-acquiring enzymes. SOC and TN represent soil organic carbon and total nitrogen contents. Whiskers represent 95% confidence intervals. A weighted effect of 1.0 means percentage change of the concentration or activity level is 171.8% by calculating [(exp(1)-1) × 100%].

Fig. 4. Relationship of soil C/N (**left**) and microbial C/N (**right**) between soil without and with manure. Manure types are differentiated with colors. The numbers in the parentheses represent the sample size. The large solid symbols are the means of the small semitransparent ones. Whiskers represent standard errors of means. Black continuous lines are 1:1 lines, and dashed lines reflects the linear regression. The linear regression lines were forced through the origin to reflect whether the ratio of (C/N in soil with manure) to (C/N in soil without manure) is close to 1.0.

Fig. 5. Relationships between ΔpH and initial soil pH. Positive ΔpH values show increase of soil pH (decreased acidity) after manure application.

Fig. 6. Weighted effect sizes of SOC (**left**) and TN (**right**) depending on the key explanatory variables (i.e. climatic factors, soil properties, management, and manure characteristics). The number in the parentheses beside each property is the sample size. SOC and TN represent soil organic carbon and total nitrogen content. Whiskers represent 95% confidence intervals.

Fig. 7. Weighted effect sizes of microbial C (**left**) and microbial N (**right**) depending on the key explanatory variables (i.e. climatic factors, soil properties, management, and manure characteristics). The number in the parentheses beside each property is the sample size. Whiskers represent 95% confidence intervals.

Fig. 8. Weighted effect sizes of the activity of β-glucosidase (**left**) and dehydrogenase (**right**) depending on the key explanatory variables (i.e. climatic factors, soil properties, management, and manure characteristics). The number in the parentheses beside each property is the sample size. Whiskers represent 95% confidence intervals.

Fig. 9. Relationship of Akp/Acp ratio in soil without and with manure (left) and relationship between manure application rates (Mg ha^{-1} year^{-1}) and ΔAkp/Acp ratio (right). “Akp” means alkaline phosphatase activity; “Acp” means acid phosphatase activity. The values in the parentheses represent the mean and standard errors of Akp/Acp ratio in soil with and without manure. “n” means observation numbers. The red dashed lines are the 95% confidence bands. The value “0.5” on the left figure was proposed as the Akp/Acp target ratio with optimal pH for crop production (Dick et al., 2000). The value “-0.3” in the right figure was the difference between the proposed target ratio (i.e., 0.5) and mean Akp/Acp ratio in soil without manure (i.e., 0.8; mean of “X” in left figure) (i.e., 0.5-0.8=-0.3). ΔAkp/Acp ratio = (Akp/Acp ratio in soil with manure) - (Akp/Acp ratio in soil without manure).

Fig. 10. Impact of manure application on soil biochemical properties. The red upward and downward arrows represent the increase and decrease of soil biochemical properties. The

percentage in the parentheses shows the increment of soil biochemical properties. The embedded figure about pH illustrates the neutralizing effect of manure application on soil, which may be one reason for the microbial community shift. Manure application increases soil C accumulation and accelerates nutrient cycles, but it does not guarantee improvement in crop production because of strong nutrient immobilization.

Table 1 Spearman's rank correlation coefficients between response ratios of extracellular enzyme activities, SOC, TN, microbial C and N and continuous explanatory variables (MAP, MAT, pH and duration of trials).

	Soil properties				Enzyme activities							Experimental variables			
	SOC	TN	MBC	MBN	B-glu	Nag	Acp	Akp	Ure	Sul	Deh	MAT	MAP	Duration	Initial pH
SOC	▨	0.78 *** 71	0.31 * 69	▨	▨	▨	▨	0.46 * 27	▨	▨	0.49 *** 46	▨	-0.25 * 110	▨	▨
TN		▨	0.40 * 37	0.87 *** 12	▨	▨	▨	0.49 * 22	0.33 * 44	▨	0.43 * 25	▨	-0.28 * 71	▨	▨
MBC			▨	0.75 *** 55	0.4 *** 104	0.64 *** 31	0.76 *** 52	0.70 *** 64	0.50 *** 129	▨	0.61 *** 108	0.26 *** 159	▨	-0.21 ** 219	▨
MBN				▨	▨	0.74 *** 41	▨	▨	0.75 *** 34	▨	▨	▨	-0.61 *** 76	-0.61 *** 76	0.49 *** 61
B-glu					▨	0.50 *** 51	0.65 *** 78	0.48 *** 51	0.64 *** 154	0.90 *** 81	0.82 *** 79	▨	▨	▨	▨
Nag						▨	0.87 *** 14	▨	0.76 *** 38	0.60 * 15	0.69 * 8	▨	-0.37 ** 68	-0.43 *** 78	0.51 *** 57
Acp							▨	▨	0.54 *** 81	0.41 ** 51	0.57 *** 38	▨	▨	▨	▨
Akp								▨	0.66 *** 74	0.95 *** 37	0.85 *** 79	▨	0.42 *** 87	▨	-0.55 *** 76
Ure									▨	0.81 *** 79	0.80 *** 107	-0.19 * 165	-0.37 *** 166	-0.37 *** 244	0.44 *** 161
Sul										▨	0.87 ***	▨	▨	▨	▨

										▨	48	▨	▨	▨	▨
Deh											▨	▨	▨	▨	▨
MAT												▨	0.39 *** 369	-0.30 *** 357	0.36 *** 240
MAP													▨	0.13 ** 370	-0.48 *** 253
Duration														▨	-0.37 *** 353
Initial pH															▨

*=p<0.05, **=p<0.01, ***=p<0.001. First line stands for correlation coefficient, second line stands for significance, third line stands for sampling sizes. The hatched boxes indicate insignificant relation. “SOC”, “TN”, “MBC”, “MBN”, “B-glu”, “Nag”, “Acp”, “Akp”, “Ure”, “Sul” and “Deh” represent contents of soil organic carbon, total nitrogen, microbial carbon, microbial nitrogen, and activities of β-1,4-glucosidase, N-acetyl-β-D-glucosaminidase, acid and alkaline phosphatase, urease, sulfatase and dehydrogenase, respectively. “MAT” and “MAP” represent mean annual temperature and mean annual precipitation, respectively.

CRediT author statement

Shibin Liu and Jinyang Wang: Conceptualization, Methodology, Software, Validation; **Shibin Liu:** Data curation, Writing-Original draft preparation, Funding acquisition; **Bahar Razavi:** Visualization, Investigation; **Shengyan Pu:** Supervision, Funding acquisition; **Yakov Kuzyakov and Evgenia Blagodatskaya**: Writing-Reviewing and Editing.

Graphical abstract

Highlights:

1. Manure effects on soil biochemical properties were identified using meta-analysis
2. Manure-only application was differentiated from application of manure with mineral fertilizers
3. Averaging of enzyme activities should be avoided as it disregards specific functions of individual enzymes
4. Optimal manure application rate for adjusting best soil pH is 25 Mg ha^{-1} year^{-1}
5. Swine manure caused the greatest increase of N-cycle-related properties.