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## Research Article

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**Dynamics of microbial-derived nitrogen to increasing straw addition in two typical arable soils in Northeast China**

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## Abstract

**Background and Aims** Microbial-derived nitrogen (N) is now recognized as an important contributor to the organic N pool in croplands, yet its dynamics under straw addition remain poorly quantified.

**Methods** We inoculated microorganisms from two typical arable soils (Alfisol and Mollisol) in Northeast China separately in  $^{15}\text{N}$ -containing M9 liquid media to generate labeled microorganisms. The harvested  $^{15}\text{N}$ -labeled microorganisms were subsequently introduced into their native soils for 288 days of incubation under four levels of straw addition: 0, 4, 8 and 12 t ha<sup>-1</sup> (S0, S4, S8 and S12), respectively.

**Results** The mineralization rate of microbial-derived N decreased with increasing straw addition (except for the Mollisol under S4), with a range of 0.008–0.113 d<sup>-1</sup> in the Alfisol and 0.026–0.051 d<sup>-1</sup> in the Mollisol. By the end, 38.45–57.15% of the labeled N was retained in the organic N pool in the Alfisol, whereas 72.03–78.33% was recovered from the NO<sub>3</sub><sup>-</sup>-N pool in the Mollisol. Straw addition significantly increased the labeled N stored in the organic N pool in the Alfisol and had little effect in the Mollisol. When the function of biotic processes on the microbial-derived N retention or supply is relatively weak in the soil, abiotic processes will fill the deficit and play a compensatory role.

**Conclusion** The utilization strategies of microbial-derived N differ between the two soils—the Alfisol tends to maintain its original organic form, while Mollisol tends to convert it into mineral N pool.

**Keywords:** Soil microorganisms, Microbial necromass,  $^{15}\text{N}$  tracing, Straw return, Clay minerals

## Introduction

Soil organic matter (SOM) contains multiple nutrients, such as carbon (C), nitrogen (N) and phosphorus (P), which are important for plant growth and microbial activities (Lavallee et al. 2020). The stabilization of SOM is important for mitigating climate change and maintain soil fertility (Liang et al. 2019). Microbial necromass has received increasing attention in recent years because it contributes more than 50% of SOM (Wang et al.

2021), whereby necromass N contributes 30–80% to soil total N pool across different ecosystems (Fu et al. 2026; Mou et al. 2024; Wang et al. 2026). Driven by China's strong policy support for straw return, the straw incorporation rate has risen steadily over the past decades (Zhao et al. 2018). However, to date, there is little information about the dynamics of microbial-derived N to increasing straw application rates.

In agricultural system, less than 50% of the N in crops is derived from current-year fertilizer inputs (Yan et al. 2019), indicating that plants are supplied with N derived from SOM to a larger extent. The recycling of microbial necromass is important for supplying N to crops (Holz et al. 2025; Pausch et al. 2024). Ammonium ( $\text{NH}_4^+$ ) released from decomposing necromass is subjected to multiple transformation pathways (Villarino et al. 2023), as it occupies a central position in the soil N cycle, bridging biotic (microbial immobilization and nitrification) and abiotic processes (clay fixation) (Nannipieri and Paul 2009). Competition for  $\text{NH}_4^+$  occurs between heterotrophic microorganisms and nitrifying bacteria when soil N is limiting (Xiao et al. 2021). It is generally believed that nitrifying bacteria have a lower competitive ability for  $\text{NH}_4^+$  than heterotrophic microorganisms do, especially when the C source is adequate (Xia et al. 2025). In addition, 2:1 clay minerals, such as vermiculite, hydromica and montmorillonite, can abiotically immobilize  $\text{NH}_4^+$  at interlayer sites (Nieder et al. 2011). When the  $\text{NH}_4^+$  concentration gradient between the clay interlayer and outside is large, fixed  $\text{NH}_4^+$  will be released, thus providing available N for living microorganisms and plants (Mengel et al. 1990). The above two biotic processes (microbial immobilization and nitrification) are important driving forces of fixed  $\text{NH}_4^+$  release (Xia et al. 2023). The outcome of competition among different processes affects the subsequent availability and stability of the fertilizer-N stored in microbial biomass and necromass in soil. Consequently, clarifying how biotic and abiotic processes interplay and govern the fate of microbial-derived N is essential for maintaining the sustainable N provisioning capacity of soil.

Returning straw to the field is a vital practice for enhancing SOM and achieving C neutrality in

45 agroecosystems. The application of straw can stimulate heterotrophic microorganisms, thereby promoting  
46 microbial immobilization (Cao et al. 2020). This process facilitates mid- to long-term N stabilization by the  
47 formation of chemically resistant mineral-associated organic matter or microbial necromas (Meng et al. 2024).  
48 While existing studies have focused predominantly on the turnover of microbial-derived C (Liu et al. 2024;  
49 Yang et al. 2024), a critical knowledge gap persists regarding how straw affects the mineralization and  
50 subsequent transformation of microbial-derived N in soil. Adding organic material with a high C:N ratio (e.g.,  
51 maize straw) may promote the preferential utilization of fresh organic C by heterotrophic microorganisms,  
52 which diminishes the decomposition of native organic matter, resulting in a negative priming effect of straw  
53 (Chen et al. 2014). However, to meet growth demands, microorganisms may also adopt an N-mining strategy  
54 during straw decomposition, accelerating the degradation of inherent soil organic N and showing a positive  
55 priming effect (Song et al. 2022). These conflicting mechanisms introduce uncertainty in the direction of straw's  
56 effect on organic N mineralization (promoting vs. inhibiting), which may be related to the amount of organic C  
57 input (Liu et al. 2023). To date, the dose effect of straw addition on microbial-derived N mineralization remains  
58 unclear. Our limited understanding currently restricts the development of appropriate straw management  
59 strategies (Wu et al. 2023). Therefore, clarifying the response of microbial-derived N mineralization to  
60 increasing straw addition amount is beneficial for accurately predicting its availability in soil under different  
61 straw return regimes, providing a basis for formulating reasonable straw application policies in Northeast China.

62       Among the various factors, physical protection by soil minerals is recognized as one of the most important  
63 factors influencing the turnover of microbial necromass (Wang et al. 2020b). Microbial necromass accumulation  
64 is positively correlated with the content of clay (Wang et al. 2026). The Fe/Al oxide coating on the surface of  
65 clay minerals enhances microbial necromass stabilization through organo–mineral association (Durn et al. 2019).  
66 2:1 clay mineral has a larger specific surface area than 1:1 clay mineral, and provides more potential adsorption

sites (Rakhsh et al. 2017). Microbial necromass associated with montmorillonite and illite have a slower mineralization rate than that associated with kaolinite (Wang et al. 2024). In addition, the microbial community composition may change with organic matter input, which is related to a shift in their substrate from SOM to newly introduced straw (Xiao et al. 2015). Compared with bacteria, fungi are more susceptible to straw incorporation because of their irreplaceable role in decomposing recalcitrant compounds of straw (Guo et al. 2026; Sun et al. 2022). Therefore, the mineralization of microbial-derived N may differ in soils containing distinct clay contents and harboring different microbial communities (Gunina et al. 2017).

In this study, we inoculated microorganisms isolated from two typical arable soils in Northeast China, which differ in terms of C content, clay content and  $\text{NH}_4^+$ -fixing capacity, into M9 liquid media containing labeled  $^{15}\text{N}$ . The M9 liquid media was centrifuged after three days incubation to obtain  $^{15}\text{N}$  labeled microorganisms. Previous studies investigating microbial necromass decomposition usually used autoclaving or UV light sterilization procedure to obtain necromass (Buckeridge et al. 2022; Wang et al. 2024). However, these sterilization treatments may substantially alter the cellular structure and chemical composition of the necromass (Berns et al. 2008), potentially confounding subsequent decomposition dynamics. Moreover, selective labeling a few species may not adequately reflect the diversity and functional complexity of microorganisms in natural soils (Wang et al., 2020a; Wang et al., 2020b). To overcome these limitations, we harvested all microbial groups capable of growing in M9 media as labeled microorganisms, without any sterilization. This makes it accessible to preserve the original cellular structure of the microbial necromass and investigate the turnover of microbial necromass when living microorganisms are involved. The harvested labeled microorganisms were subsequently introduced into their native soils for 288 days of incubation at four straw addition rates: 0, 4, 8 and  $12 \text{ t ha}^{-1}$  (S0, S4, S8 and S12), respectively. Here, we evaluated the effects of straw addition on the mineralization, transformation and distribution of microbial-derived N in two soils via the  $^{15}\text{N}$  isotope tracing

technique, addressing two main hypotheses: (i) the mineralization rate of microbial-derived N decreases with increasing straw addition; (ii) soil with a higher clay content has a slower mineralization rate of microbial-derived N.

## Materials and methods

### *Study site*

Two typical arable soils, the Alfisol and Mollisol in Northeast China, which differ in organic C content, clay content and  $\text{NH}_4^+$ -fixing capacity, were selected for the experiments. In comparison, the organic C and clay contents are greater for the Mollisol than for the Alfisol, whereas the  $\text{NH}_4^+$ -fixing capacity is greater for the Alfisol than for the Mollisol. The soil textures of the Alfisol and Mollisol at depths of 0–15 cm are silt loam and clay loam, respectively. The main physical and chemical properties of the two soils are shown in Table 1. Both soils were sampled at a depth of 0–15 cm from the surface, passed through a 2-mm sieve after the removal of large root and vegetation, homogenized, and air dried. The Alfisol was collected from the area of a long-term field experiment at the Shenyang Experimental Station of the Institute of Applied Ecology, Liaoning Province, China (41° 32' N, 123° 23' E). This site has an annual mean temperature of 7–8 °C. The sampling plot has been under a continuous soybean–maize–maize 3-year rotation since 1990, with annual inputs of 150, 25, and 60 kg  $\text{ha}^{-1}$  of N, P, and K, respectively. Mollisol soil was collected from a long-term field experiment in Harbin city, Heilongjiang Province, China (45° 30' N, 126° 29' E). The annual average temperature at this site is 4–5 °C. This site has been continuously planted with maize for more than 8 years, with annual inputs of 210, 40, and 45 kg  $\text{ha}^{-1}$  of N, P, and K, respectively.

**Table 1** Basic properties of the studied soils

| Soil type | Chemical properties | Mechanical composition (%) |
|-----------|---------------------|----------------------------|
|-----------|---------------------|----------------------------|

|          | Total C<br>(g kg <sup>-1</sup> ) | Total N<br>(g kg <sup>-1</sup> ) | Available P<br>(mg kg <sup>-1</sup> ) | Available K<br>(mg kg <sup>-1</sup> ) | pH  | Sand<br>(>50µm) | Silt<br>(2-50µm) | Clay<br>(<2µm) |
|----------|----------------------------------|----------------------------------|---------------------------------------|---------------------------------------|-----|-----------------|------------------|----------------|
| Alfisol  | 10.8                             | 0.9                              | 7.2                                   | 86.8                                  | 5.7 | 16.2            | 59.6             | 24.1           |
| Mollisol | 17.6                             | 1.5                              | 13.1                                  | 195.7                                 | 5.2 | 27.9            | 43.8             | 28.3           |

Note: Soil total C and N were determined by an Element Analyzer; available P was extracted with 0.5 M sodium bicarbonate in a 1:20 suspension and quantified by the Olsen method; available K was extracted with 1 M ammonium acetate in a 1:10 suspension following the flame photometer method; pH was determined in a 1:2.5 soil:water suspension using an electrode pH meter; and mechanical composition was measured by the pipette method.

## ***Experimental design***

### *Preparation of <sup>15</sup>N-labeled microorganisms*

The microorganisms in both soils were separately inoculated in M9 liquid media containing <sup>15</sup>N tracer to obtain <sup>15</sup>N-labeled microorganisms, which were composed of living biomass and necromass (Alef 1995; Wang et al. 2024). The M9 liquid medium was composed of 17.1 g Na<sub>2</sub>HPO<sub>4</sub>·12H<sub>2</sub>O, 3.0 g KH<sub>2</sub>PO<sub>4</sub>, 0.5 g NaCl, 1.2 g (<sup>15</sup>NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> (50.16 atom% <sup>15</sup>N), 2 ml MgSO<sub>4</sub>·7H<sub>2</sub>O (1 mol/L), 1 ml CaCl<sub>2</sub> (1 mol/L) and 20 ml glucose (20%) per liter of distilled water at pH 7.0 (Table S1). The microbial cells were harvested at stationary phase by centrifugation (10000 rpm, 10 min), followed by three washes with phosphate buffer solution (PBS; Table S2). Each wash procedure included the addition of PBS, vortexing for 1 min, centrifuging (10000 rpm, 10 min) and discarding the supernatant. Afterwards, the harvested microbial cells were freeze-dried. Finally, 2–3 g of labeled microorganisms (the remaining dry residues) were obtained and stored at 4 °C until they were introduced into their native soils. Approximately 80 mg of the labeled microorganisms was sampled for determination of their C and N contents, <sup>15</sup>N atom% and microbial composition. The labeling efficiency was 99.8% and 97.5% for the

127 microorganisms added to the Alfisol and Mollisol, respectively.

#### 128 *Incubation experiment*

129 The incubation experiment included four levels of maize straw application: no straw addition (S0) and low-  
130 level (4 t ha<sup>-1</sup>, S4), moderate-level (8 t ha<sup>-1</sup>, S8) and high-level (12 t ha<sup>-1</sup>, S12) straw addition rates. The soil was  
131 rewetted and preincubated at 25 °C for two weeks to restore soil microbial activity. Afterwards, the labeled  
132 microorganisms were applied to their native soils. Maize straw (C:N ratio of 55) was ground and passed through  
133 a 1-mm sieve, and then fully mixed with the soils. The soil water content was adjusted to 20% for both soils.  
134 Finally, 100 g (dry weight) of soil was weighed into 200 ml polyethylene bottles for each replicate. Each  
135 treatment was repeated three times and destructive samples were taken on days 0.5, 3, 12, 36, 72, 144, and 288  
136 of incubation. A total of 168 bottles (two soils × four amounts of straw addition × three replicates × seven  
137 samplings) were placed in a constant temperature incubator and incubated at 25 °C in the dark. The bottles were  
138 vented for 30 min every three days. Any soil moisture lost during the incubation was replenished by adding  
139 deionized water.

#### 140 *Chemical analysis*

141 Inorganic N was extracted with 2 M KCl at a ratio of 30 g fresh soil to 100 ml solution. The exchangeable NH<sub>4</sub><sup>+</sup>-  
142 N and NO<sub>3</sub><sup>-</sup>-N in the 2 M KCl extracts were measured by a flow injection analyzer (TRAACS 2000 Bran and  
143 Luebbe, Germany). The <sup>15</sup>N atom% of exchangeable NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N were analyzed by using the diffusion  
144 method described by Sun et al. (2016). Briefly, the ammonia derived from NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N was separately  
145 trapped in two 2.5 M KHSO<sub>4</sub>-containing glass fibres by successively adding MgO and Devarda's alloy to the 2  
146 M KCl extract.

147 Soil microbial biomass N was determined by chloroform fumigation extraction (Brookes et al. 1985).  
148 Specifically, 30 g of fresh soil was fumigated with chloroform for 24 h while another 30 g of fresh soil was

incubated without chloroform, and then both soil samples were extracted with 100 ml of 0.5 M K<sub>2</sub>SO<sub>4</sub>. Biomass N was calculated by subtracting the dissolved N in the nonfumigated extract from that in the fumigated extract and was corrected by an extraction efficiency factor of 0.45 (Jenkinson 1988). The N contents of the 0.5 M K<sub>2</sub>SO<sub>4</sub> extracts were determined by steam distillation upon digestion with sulfuric acid. The <sup>15</sup>N atom% of biomass N was analyzed by a diffusion method, in which volatile ammonia was trapped with 2.5 M KHSO<sub>4</sub> by simultaneously adding MgO and Devarda's alloy to 0.5 M K<sub>2</sub>SO<sub>4</sub> extracts.

The content and <sup>15</sup>N atom% of fixed NH<sub>4</sub><sup>+</sup>-N were determined by a modified method of Beuters and Scherer (2012). Two grams of the air-dried soil (sieved through a 100-mesh sieve) was treated with 40 ml of KOBr, washed with 0.5 M KCl three times, oven-dried at 60 °C, and ground to pass through a 0.15-mm sieve. Approximately 30 mg of processed soil was used, and its N content and <sup>15</sup>N abundance were determined by a stable isotope ratio mass spectrometer (Delta plus XP).

The microbial composition of the labeled microorganisms was determined by a gas chromatography. The total C (TC) and total N (TN) contents of the labeled microorganisms and soils were determined by an Element Analyzer. The <sup>15</sup>N abundance of different N pools and bulk soils were determined by a stable isotope ratio mass spectrometer (Delta plus XP).

### ***Calculations***

Here, we clarify that the following calculation equations are based on one basic assumption: the harvested labeled microorganisms are comprised of only microbial biomass and necromass. Hereafter, the 'microbial-derived N' was used to represent the content of N derived from the <sup>15</sup>N-labeled microorganisms to simplify the expression.

The microbial-derived N content in each N pool was calculated using the equation (1).

$$^{15}\text{N}_{\text{xpool}} = \text{N}_{\text{xpool}} \times \text{ape}_{\text{xpool}}(\%) / \text{ape}_{\text{tracer}}(\%) \quad (1)$$

171 where  $^{15}\text{N}_{\text{xpool}}$  represents the microbial-derived N content in the related N pool ( $\text{mg kg}^{-1}$ );  $\text{N}_{\text{xpool}}$  represents  
172 the N content of the related N pool ( $\text{mg kg}^{-1}$ );  $\text{ape}_{\text{xpool}}(\%)$  represents the excess  $^{15}\text{N}$  atom% in the related N  
173 pool; and  $\text{ape}_{\text{tracer}}(\%)$  represents the excess  $^{15}\text{N}$  atom% in the labeled microorganisms applied to soils.

174 The recovery of  $^{15}\text{N}$  in each N pool was calculated using the equation (2).

$$175 \text{ Recovery}(\%) = ^{15}\text{N}_{\text{xpool}}/M_0 \times 100\% \quad (2)$$

176 where  $M_0$  is the initial  $^{15}\text{N}$  input.

177 The microbial-derived N content in the nonmicrobial organic N (NMON) pool was calculated by  
178 subtracting the sum of the labeled  $^{15}\text{N}$  content in the  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ , biomass N and fixed  $\text{NH}_4^+$  pools from  
179 the total labeled  $^{15}\text{N}$  content in the soil (Rutherford and Juma 1992).

180 To predict the availability of microbial-derived N over a long time scale, a single-component first-order  
181 exponential model (Stanford and Smith 1972) was used to simulate the amount of labeled N mineralization, i.e.,  
182 the sum of labeled N present in the exchangeable  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$  and fixed  $\text{NH}_4^+\text{-N}$  pools. The model is  
183 expressed as follows.

$$184 y(t) = M \cdot [1 - \exp(-k \cdot t)] \quad (3)$$

185 where  $y(t)$  is the amount of mineralized labeled microorganisms at time  $t$ ;  $M$  is the mineralization potential  
186 of labeled microorganisms in the soil; and  $k$  is the mineralization rate constant. In this way,  $M/M_0$  is  
187 calculated to determine the proportion of labeled microorganisms that has been mineralized.

### 188 ***Statistical analysis***

189 The following analyses were conducted in R 4.5.2 (R 2025). The experiment employed a design with three  
190 independent replicates per treatment and destructive sampling at each sampling time. Analysis of variance  
191 (ANOVA) was conducted within each soil with treatment and incubation days as fixed factors, including two-  
192 way interactions (*car* package). Pairwise comparisons between the two soils at same treatment were carried out

193 using a t-test (*emmeans* package). One-way ANOVA was performed separately for each soil to test the effect of  
 194 the straw addition rate on the recovery of labeled <sup>15</sup>N at the end of incubation. Correlation (*psych* package) and  
 195 relative importance (*relaimpo* package) analyses were used to explore key factors influencing the transformation  
 196 of microbial-derived N. Partial least squares path modeling (PLS–PM) (*plspm* package) was used to study the  
 197 relative strengths of the effects of biotic and abiotic processes on the retention and supply of microbial-derived  
 198 N. *P* value of 0.05 was considered to indicate statistical significance.

199 **Results**

200 *Initial composition of the <sup>15</sup>N-labeled microorganisms*

201 The average N contents of the labeled microorganisms were 9.87% and 7.78% for the Alfisol and Mollisol,  
 202 respectively (Table 2). The labeled microorganisms for both soils were primarily bacteria, and the sum of gram-  
 203 negative and gram-positive bacteria accounted for 84.71% and 83.49% in the Alfisol and Mollisol, respectively,  
 204 whereas fungi accounted for a small proportion. The initial labeled N inputs (*M*<sub>0</sub>) were 9.80 mg kg<sup>-1</sup> and 8.06  
 205 mg kg<sup>-1</sup> for the Alfisol and Mollisol, respectively.

206 **Table 2** Chemical and microbial composition of the <sup>15</sup>N-labeled microorganisms

| Soil type                       |                           | Alfisol | Mollisol |
|---------------------------------|---------------------------|---------|----------|
| Chemical properties             | N (g kg <sup>-1</sup> )   | 0.99 a  | 0.78 b   |
|                                 | C (g kg <sup>-1</sup> )   | 4.65 a  | 3.63 b   |
|                                 | C:N                       | 4.71 a  | 4.66 b   |
|                                 | Atom% <sup>15</sup> N (%) | 50.08 a | 48.93 b  |
| Microbial community composition | Gram Negative (%)         | 77.95 b | 82.82 a  |
|                                 | Gram Positive (%)         | 6.76 a  | 0.67 b   |
|                                 | Anaerobe (%)              | 5.74 a  | 0.88 b   |
|                                 | AM Fungi (%)              | 1.29 a  | 0.32 b   |
|                                 | Fungi (%)                 | 0.44 a  | 0.39 a   |
|                                 | Actinomycetes (%)         | 1.50 a  | 0.28 b   |

|                                            |                        |        |        |
|--------------------------------------------|------------------------|--------|--------|
| Initial $^{15}\text{N}$ input<br>( $M_0$ ) | (mg kg <sup>-1</sup> ) | 9.80 a | 8.06 b |
|--------------------------------------------|------------------------|--------|--------|

Note:  $M_0$  is the initial labeled  $^{15}\text{N}$  input (mg kg<sup>-1</sup>). Different lowercase letters in a row indicate significant differences at the 5% level between soils.

### *Dynamics of labeled $^{15}\text{N}$ in different N pools*

The labeled  $^{15}\text{N}$  in the exchangeable  $\text{NH}_4^+$ -N pool remained low in the Alfisol and changed within a small range during the incubation, whereas it constituted a sizable amount in the Mollisol from day 0.5 to day 12 (Fig. 1a and b). The labeled  $^{15}\text{N}$  in the  $\text{NO}_3^-$ -N pool for two soils increased rapidly during the early period of incubation, slightly decreased during the middle period, and then increased during the latter period (Fig. 1c and d). The labeled  $^{15}\text{N}$  in the biomass N pool increased at the early period of incubation but then gradually decreased in both soils (Fig. 1e and f). There was an obvious decrease in the content of labeled  $^{15}\text{N}$  in the fixed  $\text{NH}_4^+$ -N pool at the early period and the latter period of incubation (Fig. 1g and h). Straw addition significantly decreased the average content of labeled  $^{15}\text{N}$  in  $\text{NO}_3^-$ -N pool, and it further decreased with increasing straw addition for two soils (Table S3). In contrast, straw addition increased the average content of labeled  $^{15}\text{N}$  in the biomass N pool for two soils, except for S12 in the Alfisol. Besides, straw addition decreased the average content of labeled  $^{15}\text{N}$  in the exchangeable  $\text{NH}_4^+$ -N pool of the Mollisol but had no significant effect in the Alfisol. Straw addition had no significant effect on the average content of labeled  $^{15}\text{N}$  in the fixed  $\text{NH}_4^+$ -N pool of the two soils.

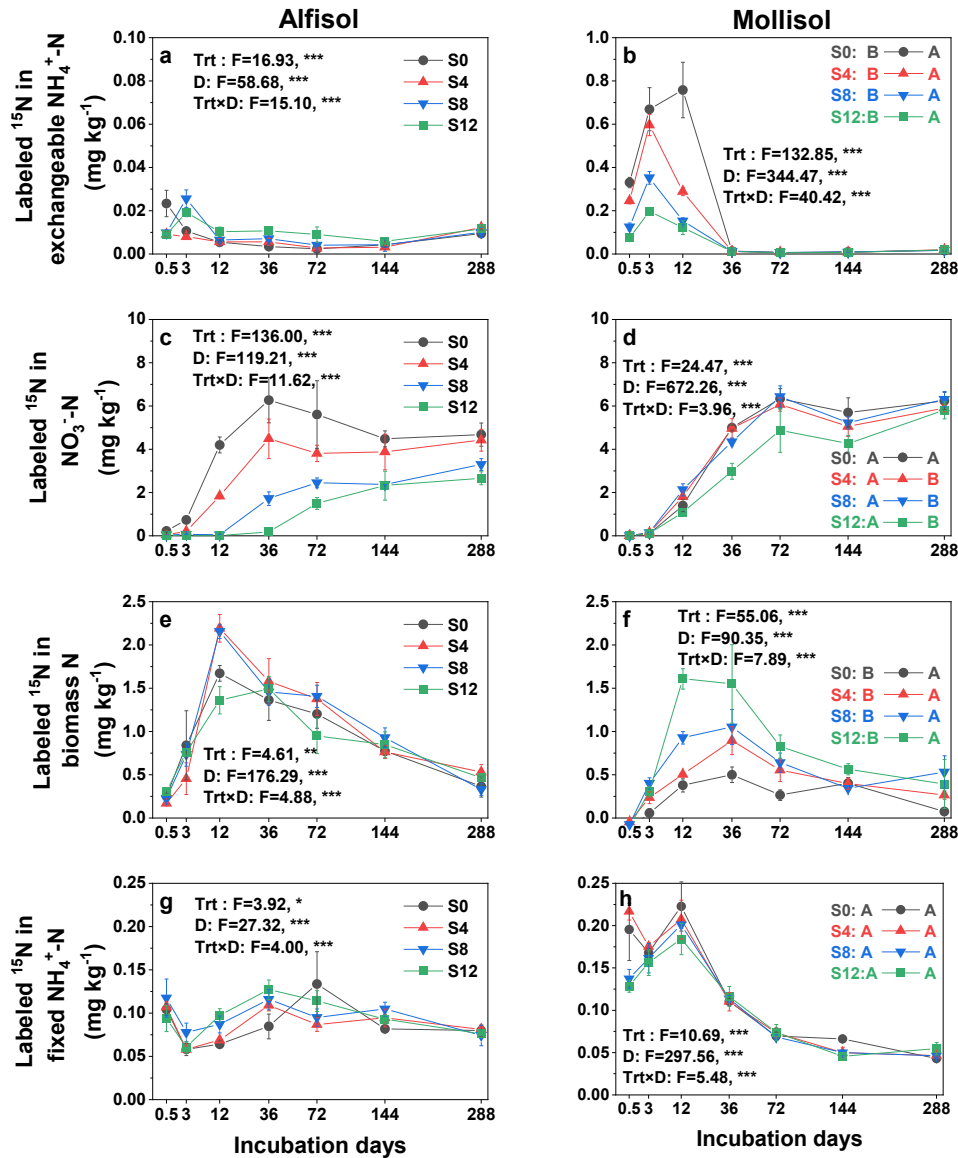
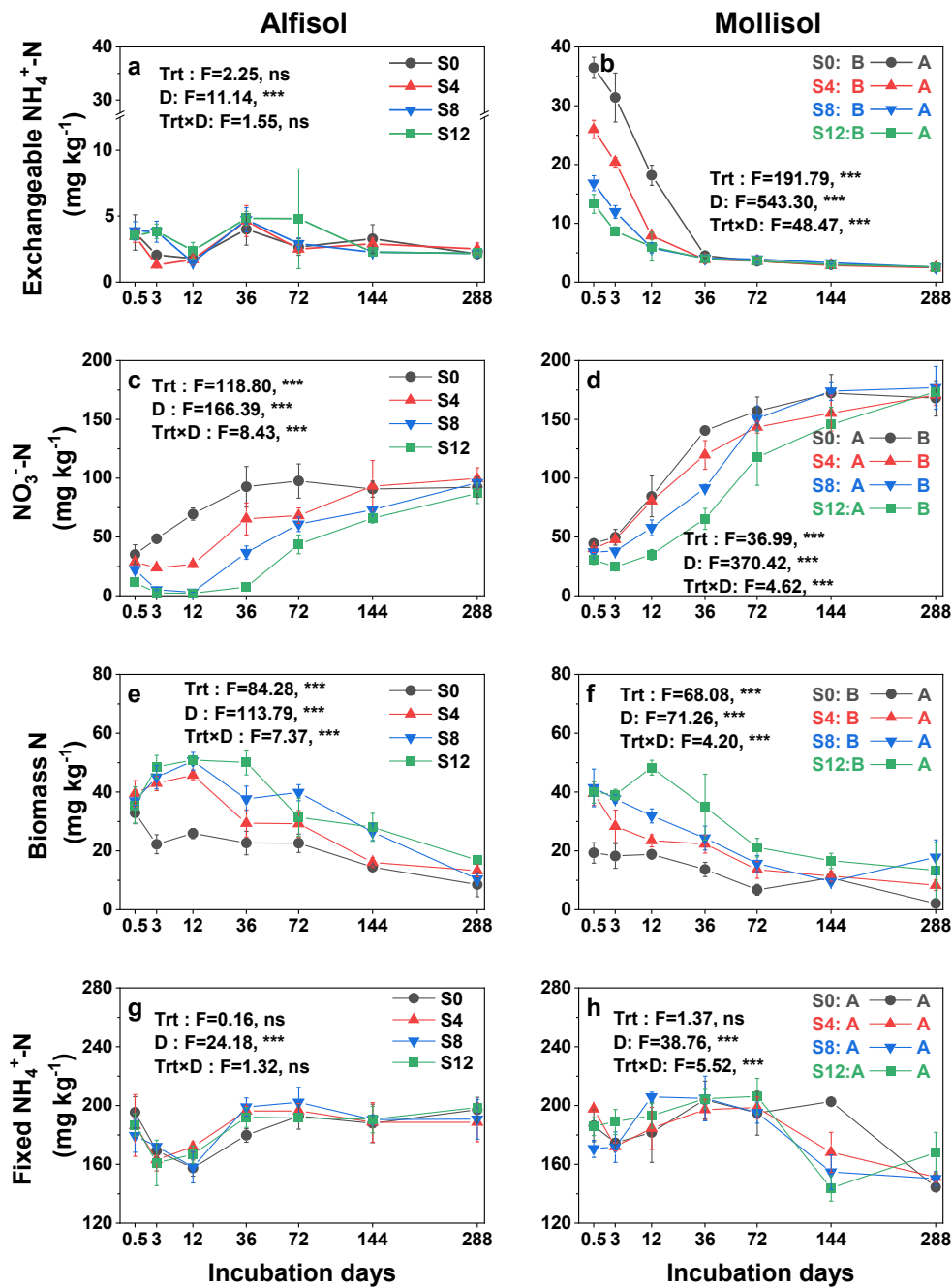


**Fig. 1** Dynamics of labeled  $^{15}\text{N}$  in different N pools

Note: Vertical bars represent the standard deviations of the means ( $n=3$ ). S0, no straw; S4, low straw addition rate ( $4 \text{ t ha}^{-1}$ ); S8, medium straw addition rate ( $8 \text{ t ha}^{-1}$ ); S12, high straw addition rate ( $12 \text{ t ha}^{-1}$ ). Two-way ANOVA was performed for each soil separately; Trt, treatment (S0, S4, S8 and S12); D, days of incubation; Trt  $\times$  D, the interaction between treatment and days of incubation; \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . A t-test was conducted between the two soil types for the same treatment, and the results are shown on the right plots; different uppercase letters on ends of short lines indicate significant differences between Alfisol (left side) and Mollisol (right side) ( $P < 0.05$ ).



232  
233 **Fig. 2** Dynamics of different N pools in soil

234 Note: Vertical bars represent the standard deviations of the means (n=3). S0, no straw; S4, low amount of straw  
235 addition ( $4\text{ t ha}^{-1}$ ); S8, medium amount of straw addition ( $8\text{ t ha}^{-1}$ ); S12, high amount of straw addition ( $12\text{ t ha}^{-1}$ ).  
236 Two-way ANOVA was performed for each soil separately; Trt, treatment (S0, S4, S8 and S12); D, days of  
237 incubation; Trt × D, the interaction between treatment and days of incubation; \* $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p <$

238 0.001. A t-test was conducted between the two soil types for the same treatment, and the results are shown on  
239 the right plots; different uppercase letters on ends of short lines indicate significant differences between Alfisol  
240 (left side) and Mollisol (right side) ( $P<0.05$ ).

241 Overall, the dynamics of  $\text{NO}_3^-$ -N and fixed  $\text{NH}_4^+$ -N were similar to those of labeled  $^{15}\text{N}$  in corresponding pools,  
242 whereas exchangeable  $\text{NH}_4^+$ -N and biomass N differed (Fig. 2). Specifically, exchangeable  $\text{NH}_4^+$ -N and biomass  
243 N generally tended to decrease during the early period of incubation (Fig. 2a, b, e and f), opposite to the  
244 increasing trend of labeled  $^{15}\text{N}$  in corresponding N pools (Fig. 1a, b, e and f). The average exchangeable  $\text{NH}_4^+$ -  
245 N and  $\text{NO}_3^-$ -N contents were greater in the Mollisol than in the Alfisol, whereas the average biomass N contents  
246 were greater in the Alfisol than in the Mollisol (Table S4). For both soils, the average  $\text{NO}_3^-$ -N content decreased  
247 with increasing straw addition, whereas the average biomass N contents increased (Table S4). We additionally  
248 set up a blank control without any addition of labeled microorganisms or straw addition. The results revealed  
249 that Alfisol had a higher biomass N content, but Mollisol had a faster rate of  $\text{NO}_3^-$ -N production (Fig. S1).

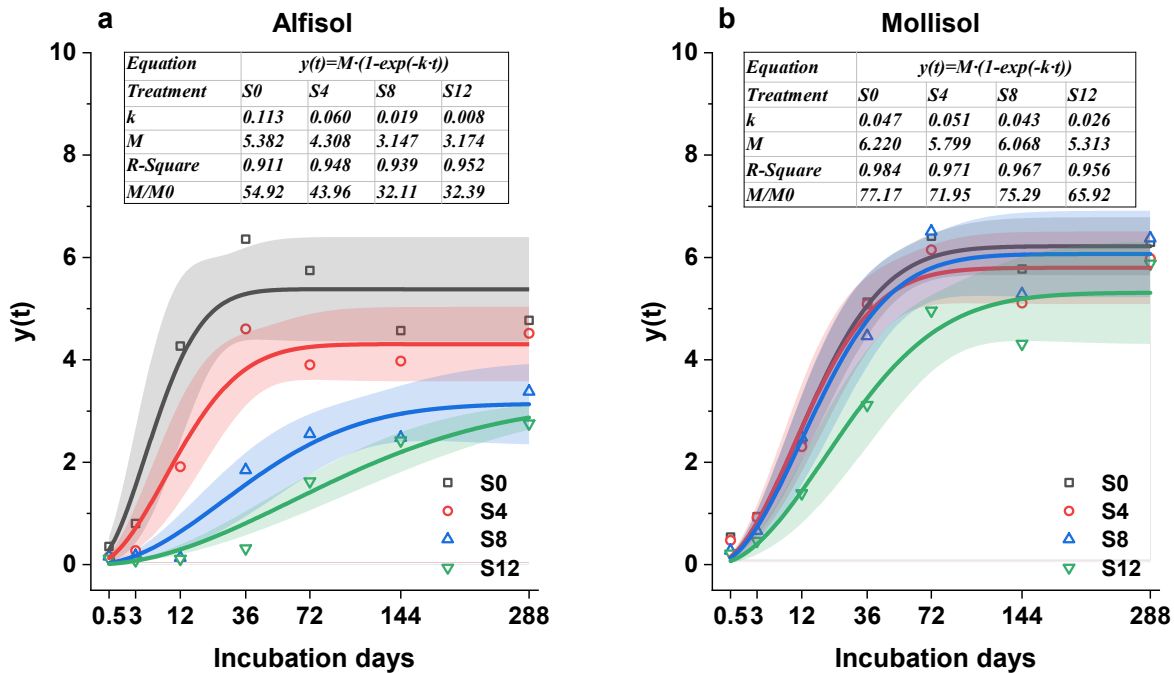


**Fig. 3** Scatterplot of the accumulated amount of microbial-derived N mineralization in the two soils

Note:  $y(t)$  is the accumulated mineralized amount of labeled N at time  $t$ , and the unit is  $\text{mg kg}^{-1}$ ;  $M$  is the mineralization potential of microbial-derived N and the unit is  $\text{mg kg}^{-1}$ ;  $k$  is the rate constant of mineralization, and the unit is  $\text{d}^{-1}$ ; and  $M/M_0$  is the proportion of microbial-derived N that has been mineralized (%). The curves are results of the first-order exponential model, and shading shows the confidence intervals. S0, no straw; S4, low straw addition rate ( $4 \text{ t ha}^{-1}$ ); S8, medium straw addition rate ( $8 \text{ t ha}^{-1}$ ); S12, high straw addition rate ( $12 \text{ t ha}^{-1}$ ).

The high R-square values for the simulated microbial-derived N mineralization indicated that the exponential model fitted the measured results well (Fig. 3). For the Alfisol, the mineralization rate ( $k$ ) of microbial-derived N ranged from  $0.008 \text{ d}^{-1}$  to  $0.113 \text{ d}^{-1}$  and decreased with increasing straw addition (Fig. 3a). For the Mollisol,  $k$  ranged from  $0.026 \text{ d}^{-1}$  to  $0.051 \text{ d}^{-1}$  and decreased under S8 and S12 but slightly increased under S4 (Fig. 3b). The mineralization potential ( $M$ ) of microbial-derived N ranged from  $3.147 \text{ mg kg}^{-1}$  to  $5.382 \text{ mg kg}^{-1}$  in the

Alfisol and from 5.313 mg kg<sup>-1</sup> to 6.220 mg kg<sup>-1</sup> in the Mollisol (Fig. 3). For both soils, the addition of straw decreased the value of M, but this decreasing effect was nonlinear with the straw addition rate. The mineralized proportions (M/M<sub>0</sub>) of microbial-derived N were 32.11–54.92% and 65.92–77.17% in the Alfisol and Mollisol, respectively.

**Recovery of labeled <sup>15</sup>N in soil**

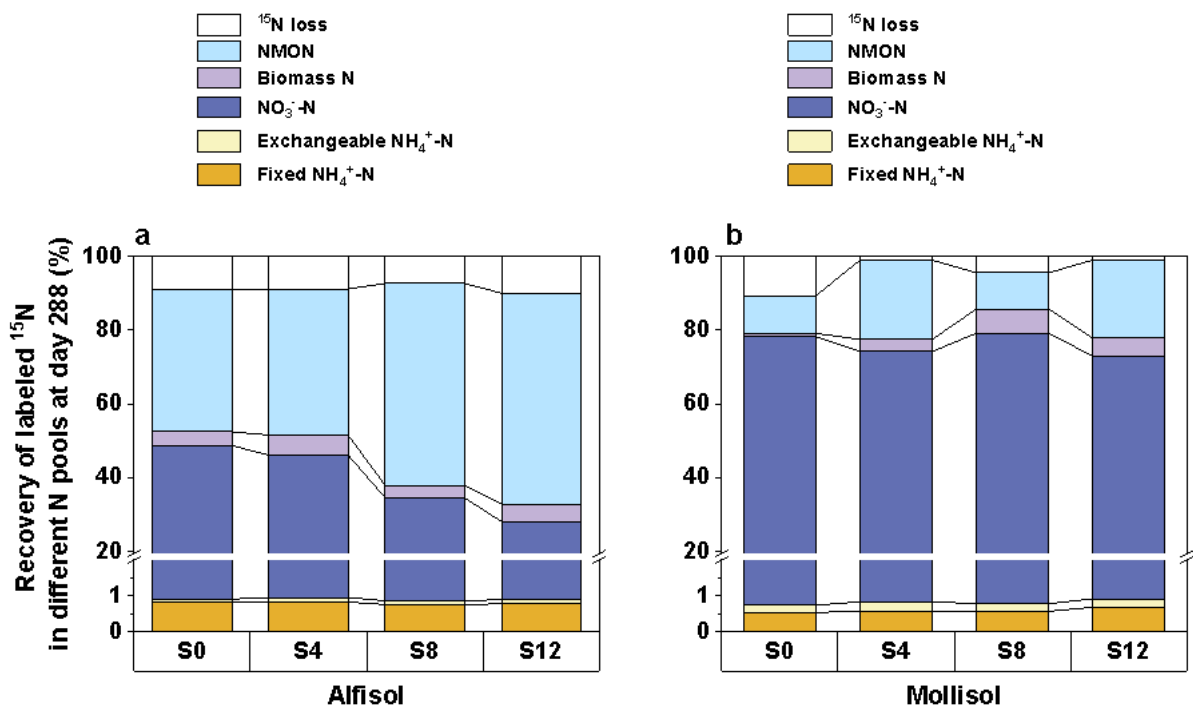


**Fig. 4** Recovery of labeled <sup>15</sup>N from different N components at the end of incubation

Note: S0, no straw; S4, low straw addition rate (4 t ha<sup>-1</sup>); S8, medium straw addition rate (8 t ha<sup>-1</sup>); S12, high straw addition rate (12 t ha<sup>-1</sup>).

At the end of the incubation, the total recoveries of labeled <sup>15</sup>N in soils were in a range of 89.29–98.96% (Table S5), indicating that only a small proportion of the labeled N left from soil system in the form of gases (NH<sub>3</sub>, N<sub>2</sub>O, etc.) during the incubation. In the Mollisol, the main destination for labeled <sup>15</sup>N under the four treatments was the NO<sub>3</sub><sup>-</sup>-N pool, but in the Alfisol, the primary destination for labeled <sup>15</sup>N shifted from the NO<sub>3</sub><sup>-</sup>-N pool to the NMON pool with increasing straw addition (Fig. 4). The recoveries of labeled <sup>15</sup>N in the NMON pool were

only 9.78–21.47% for the Mollisol, which were significantly lower than the 38.45–57.15% for the Alfisol (Table S5). In comparison, a relatively small fraction of labeled  $^{15}\text{N}$  was recovered in the fixed  $\text{NH}_4^+\text{-N}$  pool; however, its recoveries were still greater than those of the exchangeable  $\text{NH}_4^+\text{-N}$  pool in both soils (Fig. 4, Table S5).

*Correlation and relative importance analyses*

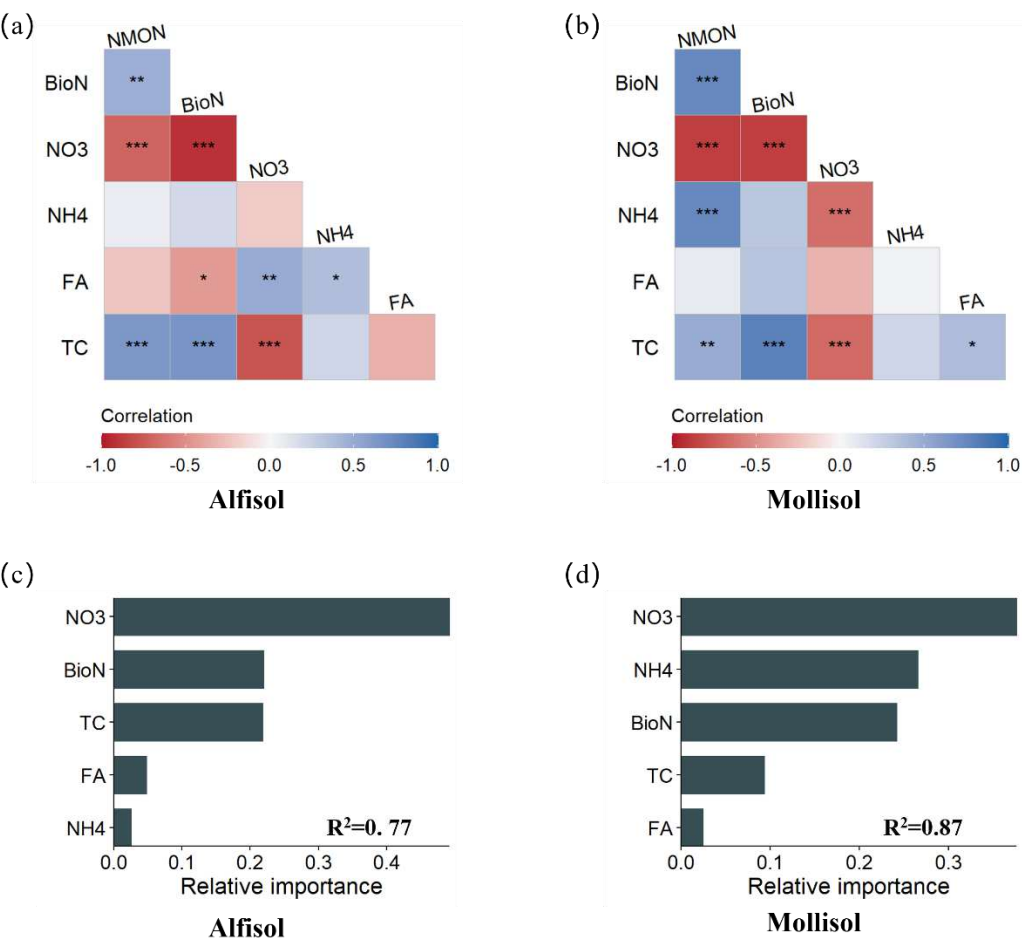


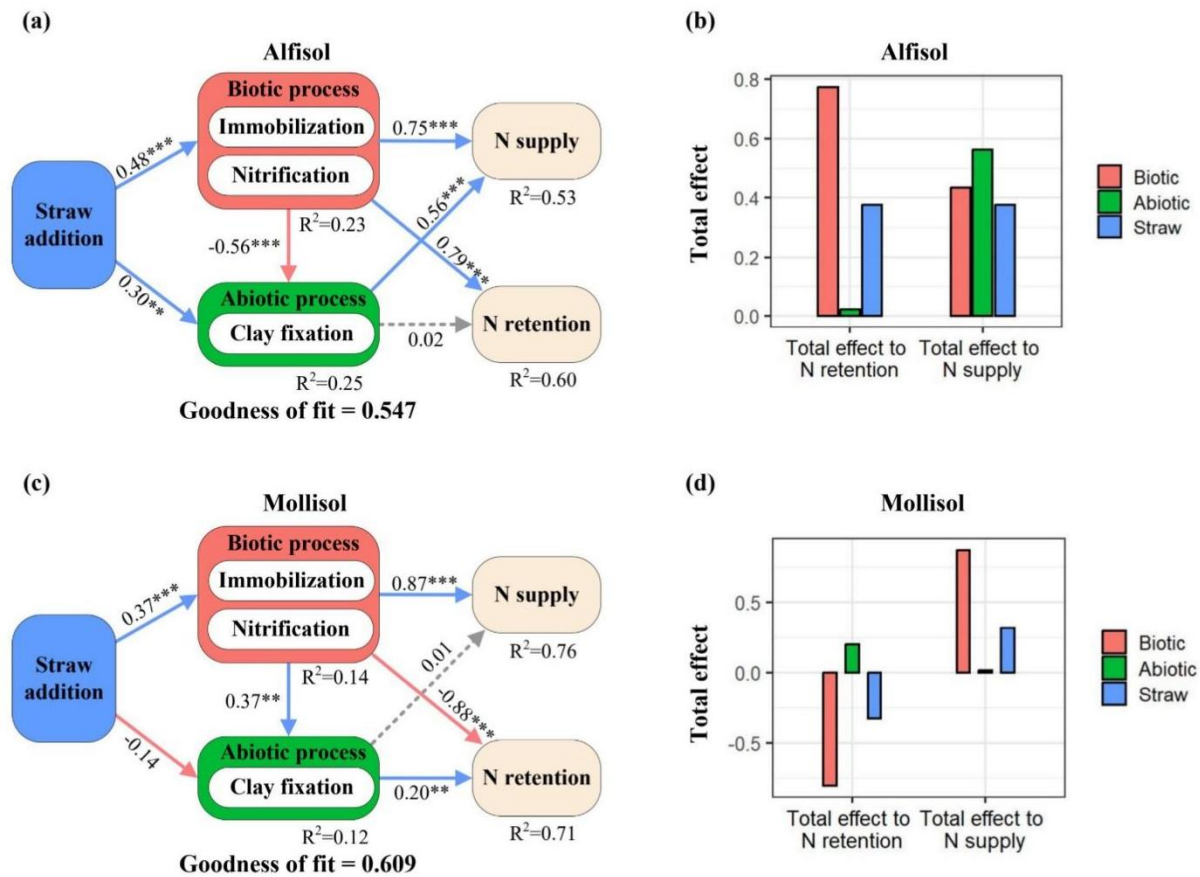
**Fig. 5** Correlation and relative importance of soil factors to microbial-derived NMN

Note: NMN, nonmicrobial organic N. BioN and FA represent biomass N and fixed  $\text{NH}_4^+$ , respectively.

The correlation analysis revealed that microbial-derived NMN was significantly positively correlated with biomass N and TC contents but was significantly negatively correlated with  $\text{NO}_3^-\text{-N}$  content in the two soils (Fig. 5a and b). Relative importance analysis revealed that the  $\text{NO}_3^-\text{-N}$  content was the most important factor influencing the microbial-derived NMN for two soils, and the biomass N content was another important

289 influencing factor (Fig. 5c and d). In addition, the TC content was an important influencing factor in the Alfisol,  
 290 whereas in the Mollisol, the exchangeable  $\text{NH}_4^+$ -N content was more important than the TC content.

291 *Path analysis of the retention and supply of microbial-derived N*



292 **Fig. 6** Partial least squares path modelling analysis (PLS-PM)

294 Note: Model outer blocks include biotic processes, abiotic processes, N supply and N retention. Overall model  
 295 fitness was determined by goodness of fit (GoF). Path coefficients and explained variability ( $R^2$ ) were calculated.  
 296 The blue paths indicate positive effects, and the red paths indicate negative effects. Path coefficients along grey  
 297 dashed lines indicate no significant difference from zero. \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

298 A PLS-PM model was adopted to elucidate the relationships among biotic processes, abiotic processes, N  
 299 retention and N supply (Fig. 6). In terms of microbial-derived N retention or supply, biotic processes had a

higher total effect on N retention than N supply in the Alfisol, and had a higher total effect on N supply than N retention in the Mollisol. The situation of abiotic processes is exactly the opposite of biotic processes in two soils. However, biotic processes still played a dominant role in microbial-derived N retention for two soils, and abiotic processes were more important for microbial-derived N supply in the Alfisol than in the Mollisol. In addition, abiotic processes were negatively affected by biotic processes in the Alfisol and positively in the Mollisol, leading to the opposite effect of biotic process through indirect paths on the retention and supply of microbial-derived N in the two soils. Straw addition had a greater effect on the retention and supply of microbial-derived N in the Alfisol than in the Mollisol.

## **Discussion**

### ***Mineralization of microbial-derived N***

Our findings revealed that the straw addition rate strongly influenced the mineralization rate of microbial-derived N (Fig. 3). The addition of straw decreased the mineralization rate ( $k$ ) of microbial-derived N in both types of soil (except for the Mollisol under S4), which partially supported the first hypothesis. During the early period of incubation, microbial immobilization was promoted by straw addition via supplying available C, but the subsequent decrease in biomass N suggested substantial microbial mortality (Fig. 2e and f). Accordingly, labeled  $^{15}\text{N}$  in the NMON pool increased during the latter period (Fig. S2), indicating that microbial necromass accumulated in soil as microbial demand for N decreased with the decreasing available C. Therefore, the rapid reimmobilization of mineralized  $^{15}\text{N}$  induced by straw addition may be the main reason for the decreasing effect of straw on microbial-derived N mineralization in this study. Similarly, a 13-year field study reported that straw incorporation increased mineral-associated organic N via enhanced N assimilation and subsequent necromass-N formation (Tang et al. 2026). Besides, a field study conducted in Northeast China found that the proportion of fungal necromass to total necromass in soil increased with the incorporation of maize straw (Sun et al. 2022).

Compared with bacterial necromass, fungal necromass is more stable and less prone to decomposition (Schweigert et al. 2015). This may be an underlying reason for the slower mineralization rate of microbial-derived N with straw addition in this study. However, direct measurement of microbial necromass (e.g., via amino sugar biomarkers) would be necessary to confirm this interpretation in future studies.

Compared with S0, an unexpected increase in the mineralization rate of microbial-derived N occurred within the Mollisol under S4 treatment (Fig. 3), which may be attributed to a positive priming effect of straw addition at a low rate. Similarly, when soil available N is low but the N demand of plants is high, C-exudation from plant roots provide an energy source that stimulates microorganisms to mine more N from SOM in the rhizosphere soil (Kuzyakov 2000; Pausch et al. 2024). These results indicated that organic C addition at a low amount may promote the mineralization of soil organic N (Santangeli et al. 2023). Conclusively, the response of microbial-derived N mineralization to increasing straw addition is nonlinear in the Mollisol. Blagodatskaya and Kuzyakov (2008) also proposed that the linear increase in the positive priming effect with exogenous organic C addition occurs only when the amount of added C is less than 15% of the microbial biomass C. Hence, there may be a threshold straw addition rate for a positive priming effect on necromass N mineralization. However, this threshold effect of straw addition did not occur in the Alfisol, which might be related to its low mineral N content. It has been reported that soil N availability critically modulates the direction of priming effect and N addition can mitigate the negative priming effect of straw addition (Cui et al. 2024). Thus, the threshold of straw addition for a positive priming effect may increase as soil available N increases within a certain range, and further research is needed for verification.

Regarding S0 treatment for two soils, the mineralization rate of microbial-derived N was greater in the Alfisol ( $0.113 \text{ d}^{-1}$ ) than in the Mollisol ( $0.047 \text{ d}^{-1}$ ) (Fig. 3). In addition, it has been reported that in the absence of exogenous organic C addition, the mineralization rates of microbial necromass N in the substrates of

montmorillonite, illite and kaolinite were 0.022 d<sup>-1</sup>, 0.044 d<sup>-1</sup> and 0.067 d<sup>-1</sup>, respectively (Wang et al. 2024), similar with our result. Hence, our findings supported the second hypothesis, which may be explained by the following reasons. First, the Mollisol has a relatively high content of clay particles, which can provide adsorption sites for organic compounds and thus protect the absorbed microbial necromass from mineralization (Slimani et al. 2023; Wang et al. 2026c). Second, the relatively low content of exchangeable NH<sub>4</sub><sup>+</sup>-N in the Alfisol may induce faster decomposition of microbial necromass by living microorganisms to meet their demand for N sources (Cui et al. 2020). The average biomass N content in the Alfisol was greater than that in the Mollisol (Fig. 2, Table S4), in accordance with this mechanism. Third, 30 years of soybean–maize–maize rotation of the Alfisol may lead to higher enzyme activity, especially for acquiring N, while the Mollisol was continuously planted with maize (Luo et al. 2024). Therefore, the mineralization rate of microbial-derived N is soil-type-specific (Han et al. 2023),.

#### ***Distribution of microbial-derived N***

The high recoveries of labeled <sup>15</sup>N in soil TN at the end of incubation (Table S5) supported the idea that the organic N derived from microorganisms contributed to the replenishment of the N stock in soil (Buckeridge et al. 2022). Unexpectedly, compared with the Alfisol, the Mollisol failed to retain a higher proportion of labeled N in the organic N pool (Fig. 4, Table S5), which was inconsistent with the view that soil clay content positively affects the contribution of microbial necromass to SOM (Chang et al. 2024). The Mollisol was characterized by high N availability and nitrification (Fig. S1), which may have resulted in the establishment of a nitrification trap (Koch and Sessitsch 2024). Consequently, <sup>15</sup>N-NH<sub>4</sub><sup>+</sup> released from the slowly mineralized necromass in the Mollisol was immediately converted to NO<sub>3</sub><sup>-</sup>, which was less readily assimilated by heterotrophic microorganisms, resulting in its accumulation in the NO<sub>3</sub><sup>-</sup>-N pool in the Mollisol (Fig. 4). Similarly, in a 231-day incubation with high-fertility forest soil from northern China, more than 50% of the labeled necromass N

366 was recovered in the  $\text{NO}_3^-$ -N pool (Wang et al. 2020b). In their 803-day in-situ experiment, most of labeled  
367 necromass N was utilized by plant (Wang et al. 2020a), demonstrating the significance of biotic processes in  
368 soil N supply. These findings highlighted that the slow mineralization of microbial-derived N, coupled with its  
369 subsequent fast nitrification, established a dual-purpose mechanism for N retention and supply in fertile, clay-  
370 rich soils (e.g. Mollisol).

371 In the Alfisol, the relatively lower clay content rendered microbial necromass more vulnerable to rapid  
372 initial mineralization. Moreover, the microorganisms in the Alfisol were in an N-starved state, maintaining a  
373 high MBN to acquire available N in the soil (Fig. S1). The released  $^{15}\text{N-NH}_4^+$  was quickly reimmobilized by  
374 heterotrophic microorganisms in the Alfisol, forming a tight mineralization-reimmobilization cycle (Schimel  
375 and Bennett 2004). In addition, the relatively weak nitrification in the Alfisol further extended the window for  
376 heterotrophic microorganisms to capture mineralized  $^{15}\text{N-NH}_4^+$  (Kuzuyakov and Xu 2013). Thus, the labeled  $^{15}\text{N}$   
377 predominantly resided in the organic N pool in the Alfisol (Fig. 4). A 10-year field experiment, conducted at the  
378 sampling site of Alfisol, demonstrated a continuous increase in the ratio of fertilizer-N sequestered in microbial  
379 necromass to soil TN, which reached 82% by the final year (Zhou et al. 2023). These results highlighted the  
380 strong microbial internal N cycle in the Alfisol, different from the pattern of microbial-derived N turnover in  
381 the Mollisol. Moreover, our previous incubation experiments on the same two soils demonstrated that fixed  
382  $\text{NH}_4^+$ -derived N was stored predominantly as  $\text{NO}_3^-$ -N in the Alfisol, but as organic N in the Mollisol (Xia et al.  
383 2023; Xia et al. 2025), partitioned differently from microbial-derived N. This divergence reflects the distinct  
384 patterns of microbial utilization of added N between soils, suggesting that the Mollisol meets its N demand  
385 mainly through organic N mineralization, whereas the Alfisol relies more heavily on exogenous mineral N.

386 In addition, the recovery of the NMON pool in the Alfisol increased with the increasing straw addition rate,  
387 while the recovery of the  $\text{NO}_3^-$ -N pool decreased (Fig. 4, Table S5). The results are consistent with most studies

on straw addition and demonstrated the significant impact of organic C input on the redistribution of microbial-derived N in the Alfisol (Wang et al. 2026). However, straw addition had no significant effect on the recoveries of NMON and  $\text{NO}_3^-$ -N pools in the Mollisol (Fig. 4, Table S5). It is widely acknowledged that high-fertility soils have accumulated organic matter over long periods, and have developed complex and functionally stable microbial communities (Liu et al. 2020). Their well-developed microbial communities and N cycling are already capable of effectively processing and transforming incoming C and N (Xu et al. 2026). The nonsignificant effect of straw addition on microbial-derived N redistribution in Mollisol reflected the system's high stability and robust buffering ability. In contrast, microbial communities and N cycles in low-fertility soils are more susceptible to disturbances from external organic inputs (Jiao et al. 2025), resulting in a more pronounced effect on microbial-derived N redistribution. Therefore, straw return is conducive to increasing the storage of SOM, but in low-fertility soils, excessive application should be avoided as it may exacerbate mineral N supply limitations (Cheng et al. 2025).

#### ***Coupling relationship between biotic and abiotic processes***

Owing to the lower C:N ratio of microbial necromass than that of SOM, the labeled microorganisms were immediately decomposed and utilized by living microorganisms to meet the demand for N (Cui et al. 2020). With increasing incubation days, the labeled  $^{15}\text{N}$  in the  $\text{NO}_3^-$ -N pool began to increase, whereas that in the biomass N pool gradually decreased (Fig. 1c-f). It indicated that the competitive ability of heterotrophic microorganisms for  $\text{NH}_4^+$  decreases, whereas that of nitrifying bacteria increases with decreasing C availability (Huang et al. 2024). The strong negative correlation ( $p < 0.01$ ) between the biomass N and  $\text{NO}_3^-$ -N contents (Fig. 5a and b) strengthened the competitive relationship between heterotrophic microorganisms and autotrophic nitrifying bacteria (Xiao et al. 2020). This competition between the two microbial groups may be the reason for the release of labeled  $^{15}\text{N}$  resided in the fixed  $\text{NH}_4^+$  pool during the later period of incubation in both soils (Fig.

410 1g and h). Although the proportion of  $^{15}\text{N}$  recovered in the fixed  $\text{NH}_4^+$  pool was less than 1%, it was higher than  
411 that in the exchangeable  $\text{NH}_4^+$  pool (Fig. 4). It indicates that microbial derived N is beneficial for the restoration  
412 of fixed  $\text{NH}_4^+$  pool, especially when fixed  $\text{NH}_4^+$  content is relatively low after one growing season of crop. This  
413 mechanism is crucial for enhancing soil sustainable N supply capacity in arable soils dominated by 2:1 clay  
414 mineral (Yuan et al. 2025).

415 As suggested by the results of the PLS–PM analysis, the retention of microbial-derived N in the two soils  
416 was dominated by biotic processes (Fig. 6). Consistent with most studies, biotic processes always play a  
417 dominant role in the retention of N (Braun et al. 2018; Dong et al. 2025; Pan et al. 2017), regardless of whether  
418 the N comes from organic matter or from fertilizer. This study fills a gap in research on the supply and retention  
419 patterns of N derived from microorganisms in croplands. In contrast, the contribution of biotic processes to the  
420 N supply capacity of the Alfisol is lower than its contribution to N retention, while in the Mollisol, the situation  
421 is exactly the opposite (Fig. 6). For two soils, the abiotic processes precisely make up for the deficits of biotic  
422 processes in N supply or retention in each soil. That is to say, abiotic processes plays a compensatory role in the  
423 retention and supply of microbial-derived N. Thus, biotic and abiotic processes jointly act on the recycling of  
424 microbial-derived N in soil (Cao et al. 2020; Wang et al. 2019). Moreover, the direct effects of straw addition  
425 on the biotic and abiotic processes in the Alfisol were greater than those in the Mollisol (Fig. 6a and c),  
426 ultimately resulting in a higher total effect of straw addition in the Alfisol (Fig. 6b and d). This finding is in line  
427 with the previously discussed view that straw addition has a significant effect on the distribution of available N  
428 in low-fertility soil, whereas this impact is relatively limited in high-fertility soil.

429 Certainly, M9 medium is not suitable for the growth of all microbial communities (Alef 1995); therefore,  
430 the labeled microorganisms in this study cannot completely represent the microbial composition of the native  
431 soils. In addition, the experimental temperature in this study was higher than the annual mean temperature at

the two soil sampling sites, which may not reflect the actual situation in the field. Wang et al. (2020b) reported that necromass N accumulation increased with increasing temperature in the range of 10–25 °C because the microbial turnover and necromass N production were relatively higher than the increase in necromass N mineralization. Furthermore, the 288-day duration may not precisely predict the persistence of necromass N on a longer time scale. As reported in a long-term field study conducted in Northeast China, the mean residence time of microbial necromass in the Alfisol was approximately 30 years, and it increased to 40 years with maize straw mulching (Zhou et al. 2023). Nevertheless, the findings of this study still provide new insights into how the straw addition rate affects the dynamics of microbial-derived N, which is important for enhancing the understanding of mechanisms of microbial-derived N retention and supply. Moreover, previous studies have shown that approximately 30% of newly applied fertilizer-N is immobilized by microorganisms and that microbial biomass N mineralization is synchronized with crop N demand (Ma et al. 2020). The proportion of fertilizer N stored in microbial biomass and necromass is further increased with straw addition (Liu et al. 2024). Thus, our findings provide a theoretical basis for optimizing farmland nutrient management and, consequently, improving N use efficiency under straw return regime in Northeast China.

## **Conclusion**

In summary, the response of microbial-derived N mineralization to increasing straw addition is linearly decreasing in the Alfisol but nonlinear in the Mollisol, indicating that there may be a threshold for the positive priming effect of straw. Besides, compared with low-clay soil, soil with a relatively high clay content has a lower mineralization rate of microbial-derived N. When the function of biotic processes on microbial-derived N retention or supply is relatively weak in the soil, abiotic processes will fill the deficit and play a compensatory role. In addition, straw addition strongly affected the distribution of microbial-derived N in the Alfisol, significantly decreasing the recovery of  $\text{NO}_3^-$ -N with S8 and S12 treatments, whereas its effect was limited in

the Mollisol. Accordingly, returning 1/3 of crop straw (equivalent to 4 t ha<sup>-1</sup>) is recommended in low-fertility soils (e.g., Alfisol) in Northeast China to enhance soil N supply capacity, and returning total crop straw (equivalent to 12 t ha<sup>-1</sup>) is recommended in high-fertility soils (e.g., Mollisol) to sustain soil fertility and minimize N losses. Our findings provide mechanistic insights into microbial-derived N dynamics and highlight the need to incorporate soil-type-specific responses into straw-return management and Earth system models of N cycling.

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#### **Competing interests**

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.

#### **Author contributions**

All authors contributed to the study conception and design. Material preparation, data curation and visualization: Zhuqing Xia; Xinhui Zhang, Mengmeng Zhu, Yun Gao, Changrui Zhou; Formal analysis: Yu Ning, Shuo Wang; Methodology and conceptualization: Qiang Ma, Wantai Yu, Shuailin Li; Draft writing: Zhuqing Xia; Review and editing: all authors. Funding acquisition, project administration, resources and supervision: Qiang Ma and Wantai Yu. All authors read and approved the final manuscript.

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