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Short Communication

Calculation of fungal and bacterial inorganic nitrogen immobilization rates in soil

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ABSTRACT

Microbial inorganic nitrogen (N) immobilization is an important mechanism in the retention of N in soils. However, as a result of the high diversity and complexity of soil microorganisms, there is still no effective approach to measuring the respective immobilization rates of inorganic N by fungi and bacteria, which are the two dominant microbial communities in soils. We propose a mathematical framework, combining the experimentally measurable gross inorganic N immobilization rate and proxies for fungal and bacterial inorganic N immobilization rates, to quantify the respective immobilization rates of inorganic N by fungal and bacterial communities in soil. Our approach will help to unravel the mechanisms of microbial N retention in soils.

The microbial immobilization of inorganic nitrogen (N) has a vital role in controlling the size of the soil inorganic N pool and is therefore an important mechanism for the retention of N in ecosystems (Davidson et al., 1992; Stark and Hart, 1997; Zogg et al., 2000; Zhang et al., 2013). Through this immobilization process, inorganic N in soil is converted to microbial biomass N and subsequently re-mineralized or converted to stable organic N, eventually reducing the risk of N losses from soil (Recous et al., 1990; Tahovská et al., 2013; Zhang et al., 2019). As the dominant microorganisms in soil, fungi and bacteria are probably the main participants in inorganic N immobilization (Myrold and Posavatz, 2007; Boyle et al., 2008; Bottomley et al., 2012). Given the distinct physiologies, morphologies, lifestyles and quantities of these two microbial groups in soil (Six et al., 2006; Lauber et al., 2008; Rousk and Bååth, 2011; Waring et al., 2013), the relative importance of fungi and bacteria in soil inorganic N immobilization is likely to be unequal (Myrold and Posavatz, 2007; Bottomley et al., 2012; Li et al., 2019). However, as a result of the high diversity and complexity of soil microorganisms, quantifying the respective rates of immobilization of inorganic N by fungal and bacterial communities in soil is challenging (Fierer, 2017; Li et al., 2019, 2020), although the gross inorganic N immobilization rate can be measured using well-established ^{15}N isotope techniques (e.g., the ^{15}N pool dilution method) (Murphy et al., 2003; Cheng et al., 2017).

Amino sugars, which are important constituents of microbial cell walls, have different origins in microorganisms. Among the amino sugars identified in microorganisms, muramic acid (MurN) originates exclusively from bacterial peptidoglycan, whereas glucosamine (GlcN) is mainly in the form of chitin in fungal cell walls (Parsons, 1981; Zhang and Amelung, 1996; Amelung, 2001). Based on their microbial source specificity, stable isotope probing based on amino sugars (^{15}N-AS-SIP) has been developed to disentangle the immobilization processes of inorganic N by fungi and bacteria in soils (He et al., 2006, 2011a, 2011b; Liang and Balser, 2010; Reay et al., 2019a, 2019b).

This approach has recently been extended to indicate the inorganic N immobilization rates of fungal and bacterial communities in soils (Li et al., 2019, 2020). More specifically, given the relatively long

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persistence of amino sugars in soils (mean turnover time >2 years, much longer than that of the living microorganisms) (Glaser et al., 2006; Derrien and Amelung, 2011; Liu et al., 2016), the newly formed ^{15}N-labeled amino sugars are considered to be stable in soil even after cell death (Glaser et al., 2004; Gunina et al., 2017). The fungal-derived ^{15}N-GlcN and bacterial-derived ^{15}N-MurN synthesis rates within a short period of incubation after ^{15}N tracer addition have therefore been used as proxies for the rates of immobilization of inorganic N by fungi and bacteria, respectively (Li et al., 2019, 2020). To further obtain the actual inorganic N immobilization rates by fungi and bacteria, the respective contents of MurN and GlcN in the bacterial and fungal biomass, and the turnover rates of cell N-containing components (including MurN and GlcN) are required. However, mainly as a result of the variation in the composition of N-containing components of diverse microbial species, but also within each species under different growth conditions, the actual contents of GlcN and MurN in the respective biomasses of fungi and bacteria in soil are almost unobtainable (Glaser et al., 2004; Appuhn and Joergensen, 2006; Engelking et al., 2007; Joergensen, 2018). It is also still unclear how fast do the cell N-containing components turn over intracellularly and extracellularly in soil (Engelking et al., 2007; Ma and Kazanci, 2014; Gunina et al., 2017; Dippold et al., 2019). As a consequence, directly converting the synthesis rates of ^{15}N-labeled amino sugars specific for fungi and bacteria to the actual inorganic N immobilization rates in soil is challenging.

Mathematical approach can be used to explore solutions when experimental manipulations are currently impossible (Bennett et al., 2019). To bypass the intractable problem mentioned above, we propose a mathematical framework to estimate the conversion coefficients between fungal and bacterial inorganic N immobilization rates and their respective proxies by combining the gross inorganic N immobilization rate with proxies for the respective inorganic N immobilization rates of fungi and bacteria. In this way, we can obtain the respective immobilization rates of inorganic N by fungal and bacterial communities in soil.

Calculation of fungal and bacterial inorganic N immobilization rates

Our proposed calculation is based on the assumption that fungi and bacteria are the dominant participants in soil microbial inorganic N immobilization. If both the gross inorganic N immobilization rate (measured by ^{15}N isotope techniques) and the proxies for inorganic N immobilization rates of fungi and bacteria (measured by ^{15}N-AS-SIP) have been measured on n soil samples ($n \geq 2$), then the respective immobilization rates of inorganic N by fungal and bacterial communities can be calculated.

The measured variables are:

$G = \begin{bmatrix} G_1 \\ G_2 \\ \vdots \\ G_n \end{bmatrix}$: gross microbial inorganic N (NH_4^+ or NO_3^-) immobilization rates for n samples (mg N kg^{-1} day^{-1});

$F = \begin{bmatrix} F_1 \\ F_2 \\ \vdots \\ F_n \end{bmatrix}$: fungal-derived ^{15}N-GlcN synthesis rates for n samples (mg N kg^{-1} day^{-1});

$B = \begin{bmatrix} B_1 \\ B_2 \\ \vdots \\ B_n \end{bmatrix}$: bacterial-derived ^{15}N-MurN synthesis rates for n samples (mg N kg^{-1} day^{-1}).

The two parameters to be estimated are:

K_F: the conversion coefficient from the fungal-derived ^{15}N-GlcN synthesis rate to the fungal inorganic N immobilization rate;

K_B: the conversion coefficient from the bacterial-derived ^{15}N-MurN synthesis rate to the bacterial inorganic N immobilization rate.

Using the ^{15}N-labeled amino sugars synthesis rates and conversion coefficients, the estimated fungal and bacterial inorganic N immobilization rates (mg N kg^{-1} day^{-1}) are, respectively, calculated as:

$$R_F = K_F \times F \quad (1)$$

and

$$R_B = K_B \times B \quad (2)$$

Their sum is therefore the estimated gross microbial inorganic N immobilization rate (mg N kg^{-1} day^{-1}):

$$\widehat{G} = R_F + R_B = K_F \times F + K_B \times B$$

The measured gross microbial inorganic N immobilization rate results are included in the equation:

$$G = \widehat{G} + e = K_F \times F + K_B \times B + e$$

where e is the estimation error. This equation can be rewritten in a matrix format:

$$G = [F \quad B] \begin{bmatrix} K_F \\ K_B \end{bmatrix} + e$$

Alternatively,

$$\begin{bmatrix} G_1 \\ G_2 \\ \vdots \\ G_n \end{bmatrix} = \begin{bmatrix} F_1 & B_1 \\ F_2 & B_2 \\ \vdots & \vdots \\ F_n & B_n \end{bmatrix} \begin{bmatrix} K_F \\ K_B \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ \vdots \\ e_n \end{bmatrix}$$

If we let $K = \begin{bmatrix} K_F \\ K_B \end{bmatrix}$ and $X = \begin{bmatrix} F_1 & B_1 \\ F_2 & B_2 \\ \vdots & \vdots \\ F_n & B_n \end{bmatrix}$, we obtain:

$$G = X K + e$$

The least-squares estimators that minimize the sum of the squared residuals are given in the following (see Appendix for the detailed derivation) (Wackerly et al., 2014):

$$\widehat{K} = \left(X^T X\right)^{-1} X^T G \quad (3)$$

To illustrate how this approach works, we calculated the soil nitrate (NO_3^-) immobilization rates of fungi and bacteria using the gross NO_3^- immobilization rates reported by Zhang et al. (2013) and the ^{15}N-labeled amino sugars synthesis rates reported by Li et al. (2019).

Both studies investigated the effect of land conversion from forest to agriculture on the soil NO_3^- immobilization in subtropical zones of China, which are located in two adjacent provinces: Fujian Province (Zhang et al., 2013) and Guangdong Province (Li et al., 2019). Soils in both studies are classified in the Ultisol group according to USDA soil taxonomy. In the practical application, the gross NO_3^- immobilization rates and the ^{15}N-labeled amino sugars synthesis rates should be simultaneously derived from the same soils and hence are estimating immobilization for the same microbial communities. Due to the unavailability of such data at this stage, the results in Table 1 based on these two similar but separate studies (Zhang et al., 2013; Li et al., 2019) are presented as an illustrative example of the concepts, rather than as reliable estimates. For simplicity, only the mean rates for forest and agricultural lands were used in this example ($n = 2$).

The conversion coefficients were obtained by substituting the measured gross NO_3^- immobilization rates and the ^{15}N-labeled amino sugars synthesis rates into Equation (3). In this illustrative example, the calculated coefficients were the integrated conversion coefficients of

Table 1
An illustration of the method of calculating soil fungal and bacterial NO_3^- immobilization rates under different land use scenarios. The gross NO_3^- immobilization rates (G) were obtained from Zhang et al. (2013). The synthesis rates of fungal-derived ^{15}N-GlcN (F) and bacterial-derived ^{15}N-MurN (B) were calculated based on data provided in Li et al. (2019) (see Table S1 for the calculation of F and B). These values are presented as an illustrative example, rather than as reliable estimates.

Land use	G	F	B	K_F	K_B	R_F	R_B
	mg N kg^{-1} day^{-1}					mg N kg^{-1} day^{-1}	
Woodland	0.47	0.0303	0.0022	13.78	23.83	0.42	0.05
Agriculture	0.10	0.0057	0.0009	13.78	23.83	0.08	0.02

Note: K_F and K_B are the conversion coefficients between F, B and the NO_3^- immobilization rates of fungi (R_F) and bacteria (R_B), respectively.

both soils studied, i.e. woodland soil and agriculture soil. The fungal and bacterial NO_3^- immobilization rates were then calculated using Equations (1) and (2). A summary of measured data and estimated values is provided in Table 1.

The results showed that the NO_3^- immobilization rates of fungi in woodland and agricultural soils were about 8.4 and four times those of bacteria, indicating that fungi dominated the microbial NO_3^- immobilization in the studied soil (Table 1). Compared with woodland soil, fungal and bacterial NO_3^- immobilization rates in agriculture soil were lowered by 0.34 and 0.03 mg N kg^{-1} day^{-1}, respectively, which suggests that the decrease in the fungal NO_3^- immobilization rate dominates the decrease in the gross soil microbial NO_3^- immobilization caused by the land use change.

The conversion coefficients mainly depend on the composition and activity of the soil microbial community. Given the possibly large differences in the microbial communities of different ecosystems, the conversion coefficients may differ among these ecosystems. Therefore, future extensive experimental studies are needed to further validate and constrain the application of this approach to different ecosystems. This approach could be separately applied to each specific ecosystem of similar microbial community, to examine how the conversion coefficients vary in different circumstances. We speculate that the greater difference in the microbial communities between different ecosystems, the larger difference in the conversion coefficients, and vice versa. However, on account of the concept of biological homeostasis (Sterner and Elser, 2002) and the high diversity and variability of soil microorganisms, it is likely that the conversion coefficients fluctuate in a narrow range across many different ecosystems.

Advantages and limitations of this approach

Understanding the microbially mediated N cycling processes in soil is central to unraveling soil N retention mechanisms and has ramifications for reducing N losses and managing ecosystem productivity. As a result of the high diversity and complexity of microbial communities, quantifying the process rates of different microbial groups has been a great challenge, especially in soil (Stres and Tiedje, 2006; Bardgett and Van Der Putten, 2014; Fierer, 2017). Our approach provides an effective way to mathematically, rather than mechanically, quantify the relative importance of fungal and bacterial communities in soil inorganic N immobilization. It circumvents the bottleneck of directly measuring or estimating the inorganic N immobilization rates of fungi and bacteria in soil, i.e., the infeasibility of directly converting the synthesis rates of ^{15}N-labeled amino sugars specific for fungi and bacteria to the actual inorganic N immobilization rates in soil due to the reasons described earlier. The experimentally accessible gross inorganic N immobilization rate and proxies of fungal and bacterial inorganic N immobilization rates are utilized by the mathematical framework to estimate the conversion coefficients between fungal and bacterial inorganic N immobilization rates and their respective proxies. The conversion coefficients obtained inherently take into account both the actual contents of GlcN and MurN in the respective biomasses of fungi and bacteria and the turnover of cell N-containing components in the studied soil. Because the rationale and mathematical derivation are universal, our method may also be applicable to other environmental systems, such as freshly colonized organic substrates (Appuhn and Joergensen, 2006).

Both mathematical and mechanistical approaches, complementing each other, contribute to the incremental developments in improving our understanding of inorganic N immobilization by fungi and bacteria in soil (Bennett et al., 2019). In this study, the conversion coefficients from the synthesis rates of ^{15}N-labeled amino sugars specific for fungi and bacteria to the actual inorganic N immobilization rates are currently unobtainable using mechanistic experiments. The mathematical approach we proposed provides an alternative and efficient way to address this issue. On the other hand, the establishment and improvement of mathematical models depend on the data obtained from mechanistic experiments. The mathematical approach proposed in this study not only relies on the results obtained from ^{15}N dilution and ^{15}N-AS-SIP techniques, but also needs to be validated in practice. That is, the conversion coefficients between soil fungal and bacterial inorganic N immobilization rates and their respective proxies need to be validated and constrained based on experimental data in various ecosystems.

This approach relies on the simplifying assumption that only fungi and bacteria are involved in soil microbial inorganic N immobilization. This assumption may not quite hold true, because Archaea may also contribute to inorganic N immobilization (Laughlin et al., 2009). Considering that Archaea contain GlcN, but not MurN (Joergensen, 2018), the contribution of Archaea, if any, is included in the fungal inorganic N immobilization rates by adopting our approach. Nevertheless, considering that Archaea account for less than <1% of the soil microbial biomass (Fierer, 2017), the errors caused by this assumption are probably trivial.

Apart from the presented approach, selective antibiotics targeted at protein synthesis have been used to estimate the relative importance of fungi and bacteria to inorganic N immobilization in soil (Boyle et al., 2008; Bottomley et al., 2012). However, as a result of the non-target effects, other unintended consequences, and the difficulties in determining the optimal dosage of inhibitors, the results obtained by this method may not adequately represent actual immobilization rates (Bailey et al., 2002; Ullah and Dijkstra, 2019). In contrast, without adding exogenous inhibitors into the soil, the results estimated by the proposed method should be closer to the actual situation. It should also be noted that both approaches are limited to distinguish fungi and bacteria, and cannot further disentangle the contribution of different microbial taxa of fungi or bacteria to microbial inorganic N immobilization in soil.

We identify several potential future research directions towards strengthening the applicability of this approach and further unraveling the underlying mechanisms of N retention in soils. First, the immobilization rate of inorganic N by fungi or bacterial in soil can be linked with the respective changes in fungal or bacterial community composition. Taking fungi as an example, future studies could set a range of fungal communities that have been taxonomically manipulated in the laboratory or correlated with field conditions. Through simultaneously obtaining the rates of fungal inorganic N immobilization and the composition of fungal communities, it would be possible to link the fungal community composition with the fungal inorganic N immobilization rates, and to further reveal the relative contributions of different fungal species in immobilization of inorganic N by fungi in soil. Moreover, it is also interesting to combine immobilization rates of inorganic N by fungal and bacterial communities with estimates of fungal and bacterial biomass to calculate the inorganic N immobilization rates per unit biomass in soil. Such a measure could indicate the individual activities of fungi or bacteria, which would help to further link inorganic N immobilization rates among distinct microbial taxa with different life-histories.

Conclusions

We propose a mathematical approach that combines the mechanically accessible gross inorganic N immobilization rate and proxies for fungal and bacterial inorganic N immobilization rates to quantify the inorganic N immobilization rates of fungal and bacterial communities in soil. This approach, although not without its limitations, allows us for the first time to disentangle the actual contribution of fungi and bacteria to the immobilization of N-containing substrates in soil. Promisingly, integrating both fungal and bacterial inorganic N immobilization rates into terrestrial ecosystem models (e.g., microbial models) will improve our ability to understand, predict and manage the N retention capacity in soils under different scenarios.

Declaration of competing interest

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

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Appendix A. Supplementary data

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