1 **Calculation of fungal and bacterial inorganic nitrogen immobilization rates in** 2 **soil**

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22 **Abstract**

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

32 **Keywords:**

33 Amino sugars; fungi; bacteria; microbial inorganic N immobilization; ¹⁵N; stable
 34 isotope probing

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36 The microbial immobilization of inorganic nitrogen (N) has a vital role in controlling
 37 the size of the soil inorganic N pool and is therefore an important mechanism for the
 38 retention of N in ecosystems (Davidson et al 1992, Stark and Hart 1997, Zhang et al
 39 2013, Zogg et al 2000). Through this immobilization process, inorganic N in soil is
 40 converted to microbial biomass N and subsequently re-mineralized or converted to
 41 stable organic N, eventually reducing the risk of N losses from soil (Recous et al 1990,
 42 Tahovská et al 2013, Zhang et al 2019). As the dominant microorganisms in soil,

43 fungi and bacteria are probably the main participants in inorganic N immobilization
 44 (Bottomley et al 2012, Boyle et al 2008, Myrold and Posavatz 2007). Given the
 45 distinct physiologies, morphologies, lifestyles and quantities of these two microbial
 46 groups in soil (Lauber et al 2008, Rousk and Bååth 2011, Six et al 2006, Waring et al
 47 2013), the relative importance of fungi and bacteria in soil inorganic N
 48 immobilization is likely to be unequal (Bottomley et al 2012, Li et al 2019, Myrold
 49 and Posavatz 2007). However, as a result of the high diversity and complexity of soil
 50 microorganisms, quantifying the respective rates of immobilization of inorganic N by
 51 fungal and bacterial communities in soil is challenging (Fierer 2017, Li et al 2019, Li
 52 et al 2020), although the gross inorganic N immobilization rate can be measured using
 53 well-established ^{15}N isotope techniques (e.g., the ^{15}N pool dilution method) (Cheng
 54 et al 2017, Murphy et al 2003).

55 Amino sugars, which are important constituents of microbial cell walls, have different
 56 origins in microorganisms. Among the amino sugars identified in microorganisms,
 57 muramic acid (MurN) originates exclusively from bacterial peptidoglycan, whereas
 58 glucosamine (GlcN) is mainly in the form of chitin in fungal cell walls (Amelung
 59 2001, Parsons 1981, Zhang and Amelung 1996). Based on their microbial source
 60 specificity, stable isotope probing based on amino sugars (^{15}N -AS-SIP) has been
 61 developed to disentangle the immobilization processes of inorganic N by fungi and
 62 bacteria in soils (He et al 2006, He et al 2011a, He et al 2011b, Liang and Balser 2010,
 63 Reay et al 2019a, Reay et al 2019b).

64 This approach has now been extended to indicate the inorganic N immobilization

65 rates of fungal and bacterial communities in soils (Li et al 2019, Li et al 2020). More
66 specifically, given the relatively long persistence of amino sugars in soils (mean
67 turnover time >2 years, much longer than that of the living microorganisms) (Derrien
68 and Amelung 2011, Glaser et al 2006, Liu et al 2016), the newly formed ¹⁵N-labeled
69 amino sugars are considered to be stable in soil even after cell death (Glaser et al 2004,
70 Gunina et al 2017). The fungal-derived ¹⁵N-GlcN and bacterial-derived ¹⁵N-MurN
71 synthesis rates within a short period of incubation after ¹⁵N tracer addition have
72 therefore been used as proxies for the rates of immobilization of inorganic N by fungi
73 and bacteria, respectively (Li et al 2019, Li et al 2020). However, mainly as a result of
74 the variation in the composition of tissues of massive microbial species, but also
75 within each species under different growth conditions, the actual contents of GlcN
76 and MurN in the respective biomasses of fungi and bacteria in soil are almost
77 unobtainable (Appuhn and Joergensen 2006, Engelking et al 2007, Glaser et al 2004,
78 Joergensen 2018). It is also still unclear how fast do the cell N-containing components
79 turn over intracellularly and extracellularly in soil (Dippold et al 2019, Engelking et al
80 2007, Gunina et al 2017). As a consequence, converting the synthesis rates of
81 ¹⁵N-labeled amino sugars specific for fungi and bacteria to the actual inorganic N
82 immobilization rates in soil is challenging.

83 To bypass this intractable problem, we propose a mathematical framework to estimate
84 the conversion coefficients between fungal and bacterial inorganic N immobilization
85 rates and their respective proxies by combining the gross inorganic N immobilization
86 rate with proxies for the respective inorganic N immobilization rates of fungi and

87 bacteria. In this way, we can obtain the respective immobilization rates of inorganic N
88 by fungal and bacterial communities in soil.

89 **Calculation of fungal and bacterial inorganic N immobilization rates**

90 Our proposed calculation is based on the assumption that fungi and bacteria are the
91 dominant participants in soil microbial inorganic N immobilization. If both the gross
92 inorganic N immobilization rate and the proxies for inorganic N immobilization rates
93 of fungi and bacteria have been measured on n soil samples ($n \geq 2$), then the respective
94 immobilization rates of inorganic N by fungal and bacterial communities can be
95 calculated.

96 The measured variables are:

97 $G = \begin{bmatrix} G_1 \\ G_2 \\ \vdots \\ G_n \end{bmatrix}$: gross microbial inorganic N immobilization rates for n samples (mg N
98 $\text{kg}^{-1} \text{ day}^{-1}$);

99 $F = \begin{bmatrix} F_1 \\ F_2 \\ \vdots \\ F_n \end{bmatrix}$: fungal-derived ^{15}N -GlcN synthesis rates for n samples (mg N $\text{kg}^{-1} \text{ day}^{-1}$);

100 $B = \begin{bmatrix} B_1 \\ B_2 \\ \vdots \\ B_n \end{bmatrix}$: bacterial-derived ^{15}N -MurN synthesis rates for n samples (mg N kg^{-1}
101 day^{-1}).

102 The two parameters to be estimated are:

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

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

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

$$110 \quad R_F = K_F \times F \quad (1)$$

111 and

$$112 \quad R_B = K_B \times B \quad (2)$$

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

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

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

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

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

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

118 Alternatively,

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

119

120 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:

$$G = X K + e$$

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

$$123 \quad \hat{K} = (X^T X)^{-1} X^T G \quad (3)$$

124 To illustrate how this approach works, we calculated the soil nitrate (NO_3^-)
125 immobilization rates of fungi and bacteria using the gross NO_3^- immobilization rates
126 reported by Zhang et al (2013) and the ^{15}N -labeled amino sugars synthesis rates
127 reported by Li et al (2019). Both studies studied the effect of land conversion from
128 forest to agriculture on the soil NO_3^- immobilization in subtropical zones of China.
129 Ideally, the gross NO_3^- immobilization rates and the ^{15}N -labeled amino sugars
130 synthesis rates should be measured under the same experimental conditions such as
131 sampling sites. Due to the unavailability of such data, we roughly treat selected
132 studies as being conducted at the same sites. Therefore, the results in Table 1 are
133 presented as an illustrative example, rather than as reliable estimates. For simplicity,
134 only the mean rates for forest and agricultural lands were used in this example ($n = 2$).
135 The conversion coefficients were obtained by substituting the measured gross NO_3^-
136 immobilization rates and the ^{15}N -labeled amino sugars synthesis rates into Equation
137 (3). The fungal and bacterial NO_3^- immobilization rates were then calculated using
138 Equations (1) and (2). A summary of measured data and estimated values is provided
139 in Table 1.

140 The results showed that the NO_3^- immobilization rates of fungi in woodland and
141 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). Conversion to agricultural use led to decreases in the fungal and bacterial NO_3^- immobilization rates of 0.34 and 0.03 $\text{mg N kg}^{-1} \text{ day}^{-1}$, 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.

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 obtained from Li et al (2019) (see Table S1 for detailed calculations). 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
	$\text{mg N kg}^{-1} \text{ day}^{-1}$					$\text{mg N kg}^{-1} \text{ day}^{-1}$	
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.

Advantages and limitations of this approach

Understanding the microbially mediated N cycling processes in soil is central to

158 unraveling soil N retention mechanisms and has ramifications for reducing N losses
159 and managing ecosystem productivity. As a result of the high diversity and
160 complexity of microbial communities, quantifying the process rates of different
161 microbial groups has been a great challenge, especially in soil (Bardgett and Van Der
162 Putten 2014, Fierer 2017, Stres and Tiedje 2006). Our approach provides an effective
163 way to mathematically, rather than mechanically, quantify the relative importance of
164 fungal and bacterial communities in soil inorganic N immobilization. It circumvents
165 the bottleneck of directly measuring or estimating the inorganic N immobilization
166 rates of fungi and bacteria in soil. The experimentally accessible gross inorganic N
167 immobilization rate and proxies of fungal and bacterial inorganic N immobilization
168 rates are used to estimate the conversion coefficients between fungal and bacterial
169 inorganic N immobilization rates and their respective proxies. The conversion
170 coefficients obtained inherently take into account both the actual contents of GlcN
171 and MurN in the respective biomasses of fungi and bacteria and the turnover of cell
172 N-containing components in the studied soil. Because the rationale and mathematical
173 derivation are universal, our method may also be applicable to other environmental
174 systems, such as freshly colonized organic substrates (Appuhn and Joergensen 2006).
175 This approach relies on the simplifying assumption that only fungi and bacteria are
176 involved in soil microbial inorganic N immobilization. This assumption may not quite
177 hold true, because Archaea may also contribute to inorganic N immobilization
178 (Laughlin et al 2009). Considering that Archaea contain GlcN, but not MurN
179 (Joergensen 2018), the contribution of Archaea, if any, is included in the fungal

180 inorganic N immobilization rates by adopting our approach. Nevertheless, considering
181 that Archaea account for less than <1% of the soil microbial biomass (Fierer 2017),
182 the errors caused by this assumption are probably trivial.

183 **Conclusions**

184 We propose a mathematical approach that combines the mechanically accessible gross
185 inorganic N immobilization rate and proxies for fungal and bacterial inorganic N
186 immobilization rates (measured by ¹⁵N-AS-SIP) to quantify the inorganic N
187 immobilization rates of fungal and bacterial communities in soil. This approach,
188 although not without its limitations, allows us for the first time to disentangle the
189 actual contribution of fungi and bacteria to the immobilization of N-containing
190 substrates in soil. Promisingly, integrating both fungal and bacterial inorganic N
191 immobilization rates into terrestrial ecosystem models (e.g., microbial models) will
192 improve our ability to understand, predict and manage the N retention capacity in
193 soils under different scenarios (Waring et al 2013).

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