



Review Paper

Patterns and mechanisms of responses by soil microbial communities to nitrogen addition



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ABSTRACT

Anthropogenic nitrogen (N) deposition is expected to increase substantially and continuously in the future. Soil N availability regulates microbial communities and the decomposition and formation of soil organic matter, which have great impacts on global carbon (C) cycling. We conducted a meta-analysis based on 454 N-addition experiments in order to synthesize the patterns and mechanisms of responses by soil microbial communities to N addition in various biomes (i.e., boreal forest, temperate forest, tropical/subtropical forest, grassland, and desert). Results showed that the effects of N addition on the total microbial biomass varied depending on biome types, methodologies (fumigation–extraction technique vs. total phospholipid fatty acid), and N-addition rates. Nitrogen addition consistently decreased the microbial C:N and fungi to bacteria ratio (F:B), but increased Gram positive bacteria to Gram negative bacteria ratio (GP:GN) among biome types and N-addition rates. Nitrogen addition increased soil N availability and thereby resulted in soil acidification. Regression technique and principal component analyses showed that the shifts in the F:B and GP:GN mainly resulted from enhanced N availability due to N addition rather than soil acidification. When the N addition rate is lower than 100 kg N ha⁻¹ year⁻¹, about ten times higher than of global normal rate, the positive response of microbial growth was found. Overall, these findings revised the previous notion that N addition inhibited the microbial growth. Microbial species shifts might accentuate or mitigate the effects of alterations in microbial biomass at the ecosystem level, highlighting the critical role of microbial community composition in soil ecosystem functions under N deposition scenarios.

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1. Introduction

Anthropogenic nitrogen (N) deposition is expected to increase substantially and continuously in the future (Dentener et al., 2006; Galloway et al., 2008). The worldwide N deposition has the potential to constrain the accumulation of anthropogenic CO₂ in the Earth's atmosphere by increasing ecosystem carbon (C) storage, thereby slowing the pace of climate warming (LeBauer and Treseder, 2008; Xia and Wan, 2008; Zak et al., 2017). Soil microbes, regulated by soil N availability, are capable of changing the terrestrial C cycling by decomposition and formation of soil organic matter (SOM) (Cotrufo et al., 2013; Xu et al., 2016, 2017). For

example, the substrate with a high N content can be rapidly decomposed by microorganisms at the initial stage, resulting in large accumulation of microbial products and concomitant formation of stable SOM. In contrast, for the substrate with a low N content, more C tends to be respired rather than stored in soils as stable SOM (Manzoni et al., 2012; Cotrufo et al., 2013; Xu et al., 2014). However, it remains unclear how N addition regulates soil microbial biomass and community composition among various terrestrial ecosystems, which constrains our understanding of soil C cycling in response to N deposition.

Nitrogen addition is supposed to increase microbial biomass via increasing the C or/and N resource availability. Specifically, most terrestrial ecosystems in the world are limited by N, as evidenced by the positive responses of above-ground (29% increase; LeBauer and Treseder, 2008) and below-ground plant growth (35.5% increase; Xia and Wan, 2008) to N additions. Besides the quantity of

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litter inputs, N addition can significantly increase litter N concentration by 36% at the global scale (Yuan and Chen, 2015). Several previous meta-analyses reported that N addition increased soil N availability and dissolved organic C by more than 110% and 10%, respectively (Liu and Greaver, 2010; Lu et al., 2011a, b; Yue et al., 2016). Nevertheless, N addition also results in soil acidification, leading to leaching of base cations (e.g., Mg^{2+} , Ca^{2+} , and Na^+) and mobilization of Al^{3+} (Treseder, 2008). Consequently, microbial growth may be constrained due to the reduced availability of Mg^{2+} , Ca^{2+} , or Na^+ and the toxicity of Al^{3+} in soils (Treseder, 2008; Chen et al., 2015).

Microbial community composition is also sensitive to variations in soil N availability and soil pH (Six et al., 2006; Högberg et al., 2007; Rousk et al., 2010; Fanin et al., 2013; Waring et al., 2013; Mooshammer et al., 2014; Zechmeister-Boltenstern et al., 2015; Zhou and Wang, 2015). Fungi dominates in the decomposition of the SOM with a low nutrient content, because their nutrient demands and metabolic activities are low, compared to bacteria (Fierer et al., 2003; Mooshammer et al., 2014; Zechmeister-Boltenstern et al., 2015; Zhou et al., 2017a). Consequently, N addition may decrease the fungi to bacteria ratio (F:B). Meanwhile, the soil acidification induced by N addition is likely to increase the F:B, because fungi have higher adaptability of the soils with high H^+ concentration than bacteria (Högberg et al., 2007; Rousk et al., 2010; Chen et al., 2015) due to their thick and interlinked peptidoglycan cell wall (Schimel et al., 2007; Nielsen and Ball, 2015). Through these two opposite processes, the ultimate effect of N addition on soil microbial biomass and community composition remains unclear and needs validation across different ecosystems.

To date, there have been eight meta-analyses regarding the effects of simulated N deposition on microbial biomass or/and community composition (i.e., Treseder, 2008; Janssens et al., 2010; Liu and Greaver, 2010; Lu et al., 2011a, b; Geisseler and Scow, 2014; Geisseler et al., 2016; Yue et al., 2016). However, no consistent conclusions have been reached yet. Five of the eight meta-analyses emphasized the central tendency of ecosystem C or N pools and associated C or N processes under N addition (Janssens et al., 2010; Liu and Greaver, 2010; Lu et al., 2011a, b; Yue et al., 2016). Two studies examined the responses of microbial biomass to N addition in agricultural systems (Geisseler and Scow, 2014; Geisseler et al., 2016). These seven studies predominantly focused on microbial biomass C (MBC) rather than community composition. Only one study synthesized the responses of both microbial biomass and community composition to N addition (Treseder, 2008), but her data set compiled almost one decade ago included only 29 studies. Moreover, about 89% of the Earth's vegetation receives N input of $<10 \text{ kg N ha}^{-1} \text{ year}^{-1}$ currently (Dentener et al., 2006). Summarizing from previous meta-analyses (LeBauer and Treseder, 2008; Xia and Wan, 2008; Janssens et al., 2010; Peng et al., 2017), however, simulated N deposition experiments were generally applied very high N addition rates. Given the N-addition experiments have been booming recently, it allows us to compile the global data and explore generalities of soil microbial communities in response to N addition across various ecosystems and geographical gradients, and figure out what is actually happening in ecosystems.

In this meta-analysis, we established a global data set by retrieving peer-reviewed papers published till November 2016, including 454 simulated N-deposition experiments from 134 papers that covered various natural ecosystems (i.e., boreal forest, temperate forest, tropical/subtropical forest, grassland, and desert; Text S1; Table S1; Figs. S1 and S2). Our objectives were to explore general responses of soil microbial communities to N addition and the underlying mechanisms.

2. Materials and methods

2.1. Sources of data

The peer-reviewed articles reporting effects of N addition on soil microbes in terrestrial ecosystems were collected globally by searching the Web of Science (<http://apps.webofknowledge.com>), Google Scholar (<https://scholar.google.com>), and China National Knowledge Infrastructure (CNKI, <http://www.cnki.net>) till November 2016. The keywords and terms used for the literature online-searching were “(nitrogen deposition OR nitrogen addition OR nitrogen enrichment OR nitrogen fertilizer OR nitrogen amendment OR nitrogen elevated) AND (microbial biomass OR microbial communities OR fungi OR bacteria) AND (soil)”. The articles satisfying the following criteria were included in this meta-analysis: (1) only field experiments were included; (2) experimental and control plots must be established within the same experimental site, i.e., same microclimate, vegetation and soil types between the treatments; and (3) the N addition rates were clearly reported. A total of 454 N addition experiments from 134 papers met the criteria above and were included in the meta-analysis (Text S1; Table S1; Figs. S1 and S2).

Similar to a previous meta-analysis by Treseder (2008), we only adopted the microbial biomass measured with the chloroform fumigation–extraction technique and the total phospholipid fatty acid (PLFA) analysis, which are the most commonly used methods for microbial biomass measurements. Therefore, microbial biomass C (MBC), microbial biomass N (MBN), and total PLFA were used to estimate the microbial total biomass. The biomass of fungi (the term of ‘fungi’ is referred to saprotrophic fungi in order to examine whether N addition reduces the abundance of decomposer fungi), bacteria, Gram positive bacteria (GP), Gram negative bacteria (GN), actinomycetes, and arbuscular mycorrhizal fungi were measured by taxa-specific PLFA. For the community composition, the data set included the microbial C:N, fungi to bacteria ratio (F:B), and Gram positive bacteria to Gram negative bacteria ratio (GP:GN).

The matched soil pH, soil organic C (SOC), soil total N, soil dissolved organic C (DOC), soil available N (aN, sum of NO_3^- and NH_4^+), and location (i.e., latitude and longitude) were also collected. Finally, the relevant environmental variables (mean annual temperature (MAT) and mean annual precipitation (MAP)) were also obtained directly from the papers, cited papers, or extracted from the data base at <http://www.worldclim.org/> using the location information if not reported.

2.2. Data acquisition and analysis

The raw data were obtained numerically from the tables, texts, or extracted from the figures in the original papers with the Origin 7.0 digital plugin (Digitize) software. If the mean and standard error (SE) were reported, then the standard deviation (SD) was calculated as:

$$SD = SE\sqrt{n} \quad (1)$$

where n is the sample size. If the mean and confidence interval (CI) were given, the SD was computed as:

$$SD = (CI_u - CI_l)\sqrt{n}/2Z_{\alpha/2} \quad (2)$$

where CI_u and CI_l are the upper and lower limits of 95% CI, respectively; and $Z_{\alpha/2}$ is the Z score for a given level of significance (i.e., 1.96 at $\alpha = 0.05$). In the cases that no SE, SD, or CI was reported, the SD was assigned as 1/10 of the mean (Luo et al., 2006).

To maximize the comparability, (1) we categorized the data into

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