



## Nitrogen functional gene activity in soil profiles under progressive vegetative recovery after abandonment of agriculture at the Puding Karst Critical Zone Observatory, SW China



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### ARTICLE INFO

#### Keywords:

Nitrogen functional genes  
Soil profile  
Vegetation recovery  
Karst ecosystems  
Nitrate  
Phosphorus

### ABSTRACT

At the end of the 20th century, China launched the ‘Grain-for-Green’ Project (GGP) that recommended the abandonment of low-yielding sloping farmland (> 15°) prone to soil degradation by erosion, to allow recovery through natural vegetative regeneration. The effect of this policy on soil nitrogen (N) cycling, as fertilization applications are also withdrawn after abandonment, is poorly understood. A space-for-time approach was applied to investigate the responses of nitrogen functional genes (NFGs) in soil profiles (surface to bedrock) associated with progressive vegetative recovery (sloping farmland > recently abandoned sloping farmland > secondary forest > primary forest) at the Puding Karst Critical Zone Observatory in Guizhou province, southwest China. Coincident soil chemical properties (dissolved organic carbon (DOC), nitrate (NO<sub>3</sub><sup>-</sup>-N), ammonium (NH<sub>4</sub><sup>+</sup>-N), available inorganic phosphorus (AP), soil organic carbon (SOC), total nitrogen (TN) and total phosphorus (TP)) were also quantified. We found that the absolute abundance of NFGs significantly varied according to the phase of vegetation recovery, and that concentrations of AP and NO<sub>3</sub><sup>-</sup>-N were the best explanatory variables. The external N from fertilizer application promoted the absolute abundances of ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB) in sloping farmland. The relative abundances of *chiA* (associated with decomposition) increased with soil depth across all vegetation recovery phases. The relative abundances of *chiA* and *nifH* (associated with N fixation) accounted for the largest proportion (58–72%) of the measured NFGs, indicating that active N-acquisition increased along the vegetation recovery gradient. The ratios of (*chiA* + *nifH*)/(AOA + AOB) and the sums of (*nirK* + *nirS*) were larger in the forest soil than those of sloping farmland and abandoned sloping farmland, implying a greater capacity for N storage potential, though accompanied by increased gas N emission potential, in the karst forest ecosystems. Our results provide a new and comprehensive understanding of soil N cycling potentials at the microscale in degraded and recovering karst ecosystems.

### 1. Introduction

Karst landscapes cover around 15% of the world's land surface, arising through the dissolution of soluble rocks (i.e. limestone, dolomite, and gypsum) by rainfall (He et al., 2008; Zhu et al., 2012). Karst ecosystems are considered fragile because the soils that overlie the steeply sloping topography are usually thin, coarse, erosive and

degenerative (He et al., 2008; Zhu et al., 2012). The karst region of southwest China is one of the largest in the world, covering ~550,000 km<sup>2</sup> (Liang et al., 2015; Liu et al., 2016a) with about 20% located in Guizhou province (Peng and Wang, 2012). Extensive soil degradation in this region has been caused by rapid intensification of agriculture in the last 50 years (Liang et al., 2015; Liu et al., 2016a). Subsequently, the focus of the ‘Grain-for-Green’ Project (GGP;

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<https://doi.org/10.1016/j.soilbio.2018.07.004>

Received 9 December 2017; Received in revised form 4 July 2018; Accepted 7 July 2018

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introduced at the beginning of the 20th century) in the karst region of southwest China has been on the restoration of ecosystem integrity by allowing low-yielding cropland on slopes greater than 15° to revert to 'natural' vegetation (Zhang et al., 2015; Wang et al., 2017).

Soil microorganisms are key drivers of ecosystem nitrogen (N) cycling (Levy-Booth et al., 2014). Nitrogen (N<sub>2</sub>) fixation, decomposition-ammonification, nitrification, and denitrification are the primary microbiological processes associated with N supply, leaching, and transformation in soil systems (Levy-Booth et al., 2014; Fig. S1). The abundance of nitrogen functional genes (NFGs) can be used to determine the predominant N cycling pathways active in soils (Fig. S1). Both N fixation and organic matter decomposition are responsible for the acquisition of bioavailable N at the expense of energy or soil organic matter (SOM), which can be assessed using *nifH* and *chiA* genes, respectively (Rösch et al., 2002; Lindsay et al., 2010; Tang et al., 2017). Analyses of the *amoA* gene, which is the first and rate-limiting step of autotrophic nitrification, has been applied extensively to study the activity of ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) in soil systems (Levy-Booth et al., 2014; Tang et al., 2016). During denitrification, the reduction of NO<sub>2</sub> to NO is catalyzed by nitrite reductases encoded by *nirS* or *nirK*, and related to soil N loss via N<sub>2</sub>O greenhouse gas emission (Levy-Booth et al., 2014).

The abundance ratios of NFGs have been used as indicators of changes in soil N cycling (Henderson et al., 2010; Tang et al., 2017; Wang et al., 2017; Zhang et al., 2017). The relationships between the ratios of the abundances of (*nirK* + *nirS*) to *nosZ* and actual N<sub>2</sub>O emissions have been studied (Henderson et al., 2010; Wang et al., 2014), and the relationships between *nifH*/(AOA + AOB) ratios and N transformation rates have also been evaluated (Wang et al., 2017; Zhang et al., 2017). The sums of (*nirK* + *nirS*) have been used as a proxy for the gaseous N emission potential from the soils (Tang et al., 2016, 2017). However, the dynamic microbial N cycle is interlinked network of coincident processes (Tang et al., 2016; Wang et al., 2017). Thus, to obtain a comprehensive understanding of N transformations in soils it is necessary to consider the contribution of all of the different key stages of the soil N cycle.

The application of organic and inorganic fertilizers to improve soil fertility and crop productivity have become common in intensive agriculture across China over the past several decades (Liu et al., 2016b), with profound effects on the natural N cycle in soils. For example, the abundance of *amoA* is inhibited after N applications greater than 224 kg N ha<sup>-1</sup> yr<sup>-1</sup> in temperate grassland ecosystems (Zhang et al., 2016), while the abundances of AOA and *nifH* increased with phosphorus (P) applications in pastures and forest ecosystems (Wakelin et al., 2009; Tang et al., 2016). Long-term fertilizer applications are known to have the greatest influence on nitrate reductase activity (*narG*) abundance, and least in paddy soil, indicated by nitric oxide reductase (*qnorB*) abundance (Chen et al., 2012). Recently, the N cycle in China has been under intense scrutiny because of the negative impacts on human and environmental health caused by overuse of mineral fertilizers considered in the context of the progressive disconnect between application rates and yield returns; thus, within the Chinese Government's current 5-year plan a stringent target 'Zero Increase Action Plan' for fertilizers by 2020 has been set (Liu et al., 2016b). The withdrawal of N fertilizer applications to soils in recovering karst systems under the GGP strategy is an example of its implementation and offers an opportunity for a comprehensive and systems-based analysis of this little studied aspect of N management in cultivated land in a vulnerable ecosystem.

Each phase in recovering karst ecosystems is characterized by a unique plant community, i.e. sloping farmland = crop monocultures; abandoned sloping cropland = grasses and non-woody herbaceous species; secondary forest = woody shrubs and small trees; primary forest = mature trees and under-story species (Table 1; Fig. S2). Plant community variations affect soil N cycling processes (Ribbons et al., 2016); for example, Lindsay et al. (2010) reported that woodland soils

had increased abundances of *nirK* compared to grassland soils. Above and below ground physiologies vary between plants, and inputs to soils from litter inputs and rhizodeposits and exudates may be plant-specific (Loeppmann et al., 2016; Williams et al., 2016), and microbial communities unique to the plant community may develop (i.e. 'home field advantage'; Austin et al., 2014; Li et al., 2014). Liang et al. (2014) observed that the diversity of soil microbial groups associated with ammonia oxidation varied across a vegetation succession and were significantly increased in a primary forest compared with grass tussock, woody shrub, and secondary forest vegetation. However, our understanding of the functional genes involved in N cycling under changing vegetation communities (succession) during long-term natural vegetation recovery is poor, especially in karst ecosystems.

Research on sub-soils has intensified recently but has focused primarily on the potential for C sequestration (e.g. Beniston et al., 2014; Gregory et al., 2016). Knowledge of the N cycle in deep soil horizons extending to the bedrock is critical to critical zone research but is sparse compared to that of surface horizons (generally < 30 cm) and varies between ecosystem. For example, the relative abundances of *nirS* were larger in surface horizons of tropical forest soils at the Luquillo Critical Zone Observatory in northeast Puerto Rico (Stone et al., 2015) and a spruce plantation forest ecosystem (Kandeler et al., 2009), but there were no changes in *nirS* and *nirK* abundances with soil depth in an estuary ecosystem (Lee and Kang, 2016). Soil C/N ratios were reported to decline with soil depth accompanied by reductions in *chiA* and *nifH* genes abundances associated with N acquisition, but increases in *amoA* genes responsible for energy acquisition, in order to balance the soil stoichiometry in a subtropical forest subsoil (Tang et al., 2017). There is very little information about microbial activity associated with N cycling in sub-surface soil horizons in karst ecosystems, which is important to fully understand the strength of N fluxes associated with complex karst hydrology.

In this study, we assessed the effects of GGP on NFG abundances (*nifH*, *chiA*, AOA, AOB, *nirK* and *nirS*) in soil profiles along a recovery gradient from sloping farmland > abandoned sloping farmland > secondary forest > primary forest at the Puding Karst Critical Zone Observatory in Guizhou Province, southwest of China. We hypothesized that:

- 1) total NFG abundances will increase along the recovery gradient as the soil microbial habitat environment changes due to the development of a permanent plant canopy and increased and persistent organic inputs from plant litter and roots,
- 2) *nifH* and *chiA* genes (associated with resource acquisition) and AOA and AOB genes (associated with energy acquisition) will be more abundant in surface soils due to larger organic matter contents and available N limitation due to competition from plants,
- 3) abundances of *nirK* and *nirS* genes (associated with denitrification) will be increased in deeper soil horizons due to increasing anaerobicity.

## 2. Materials and methods

### 2.1. Site description

The study sites were within the new Puding Karst Critical Zone Observatory (CZO) in Puding County, Guizhou Province, southwest China, established in June 2016 (Table 1; Fig. S2). The sites were Chenqi catchment (26°15'37"-26°15'40" N, 105°46'11"-105°46'29" E) and Tianlong Mountain (26°14'48"N, 105°45'51"E). The dominant geology in the CZO is limestone of the Guanling Formation of the Middle Triassic (Lu et al., 2014). The soil type is limestone soil according to Chinese soil general classification, which are similar to Mollic Inceptisols according to USDA Soil Taxonomy (Soil Survey Staff, 2010). The region experiences a typical subtropical monsoon climate (Peng and Wang, 2012), with a mean annual temperature of 15.1 °C and

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