Received: 22 July 2020 | Accepted: 16 January 2021

DOI: 10.1111/gcb.15526

Global Change Biology WILEY

PRIMARY RESEARCH ARTICLE

Dynamics and multi-annual fate of atmospherically deposited nitrogen in montane tropical forests

Ang Wang[1] | Dexiang Chen[2] | Oliver L. Phillips[3] | Per Gundersen[4] | Xulun Zhou[1,5] | Geshere A. Gurmesa[1] | Shanlong Li[1] | Weixing Zhu[6] | Erik A. Hobbie[7] | Xueyan Wang[8] | Yunting Fang[1,9,10]

[1]CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China

[2]Hainan Jianfengling Forest Ecosystem National Field Science and Observation Station, Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangzhou, China

[3]School of Geography, University of Leeds, Leeds, UK

[4]Department of Geosciences and Natural Resource Management, University of Copenhagen, Frederiksberg C, Denmark

[5]School of Resources and Civil Engineering, Northeastern University, Shenyang, China

[6]Department of Biological Sciences, Binghamton University, The State University of New York, Binghamton, NY, USA

[7]Earth Systems Research Center, Morse Hall, University of New Hampshire, Durham, NH, USA

[8]School of Energy and Water Resources, Shenyang Institute of Technology, Fushun, China

[9]Qingyuan Forest CERN, Shenyang, China

[10]Key Laboratory of Stable Isotope Techniques and Applications, Shenyang, Liaoning Province, China

Correspondence
Yunting Fang, Institute of Applied Ecology, Chinese Academy of Sciences, 72 Wenhua Road, Shenyang 110016, China.
Email: fangyt@iae.ac.cn

Funding information
Liaoning Vitalization Talents Program, Grant/Award Number: XLYC1902016; Strategic Priority Research Program of the Chinese Academy of Sciences, Grant/Award Number: XDA23070103; National Natural Science Foundation of China, Grant/Award Number: 31901134, 41773094, 31770498, 41811530305 and 41773071; National Key Research and Development Program of China, Grant/Award Number: 2016YFA0600802; Key Research Program of Frontier Sciences of Chinese Academy of Sciences, Grant/Award Number: QYZDB-SSW-DQC002; K.C. Wong Education Foundation, Grant/Award Number: GJTD-2018-07; Scientific Research Foundation of the Educational Department of Liaoning Province, Grant/Award Number: L201908

Abstract

The effects of nitrogen (N) deposition on forests largely depend on its fate after entering the ecosystem. While several studies have addressed the forest fate of N deposition using ^{15}N tracers, the long-term fate and redistribution of deposited N in tropical forests remains unknown. Here, we applied ^{15}N tracers to examine the fates of deposited ammonium (NH_4^+) and nitrate (NO_3^-) separately over 3 years in a primary and a secondary tropical montane forest in southern China. Three months after ^{15}N tracer addition, over 60% of ^{15}N was retained in the forests studied. Total ecosystem retention did not change over the study period, but between 3 months and 3 years following deposition ^{15}N recovery in plants increased from 10% to 19% and 13% to 22% in the primary and secondary forests, respectively, while ^{15}N recovery in the organic soil declined from 16% to 2% and 9% to 2%. Mineral soil retained 50% and 35% of ^{15}N in the primary and secondary forests, with retention being stable over time. The total ecosystem retention of the two N forms did not differ significantly, but plants retained more $^{15}NO_3^-$ than $^{15}NH_4^+$ and the organic soil more $^{15}NH_4^+$ than NO_3^-. Mineral soil did not differ in $^{15}NH_4^+$ and $^{15}NO_3^-$ retention. Compared to temperate forests, proportionally more ^{15}N was distributed to mineral soil and plants in these tropical forests. Overall, our results suggest that atmospherically deposited NH_4^+ and NO_3^- is rapidly lost in the short term (months) but thereafter securely retained within the ecosystem, with retained N becoming redistributed to plants and mineral soil from the

organic soil. This long-term N retention may benefit tropical montane forest growth and enhance ecosystem carbon sequestration.

KEYWORDS
^{15}N tracer, ammonium and nitrate, long-term fate, N deposition, N retention and redistribution, tropical montane forests

1 | INTRODUCTION

Nitrogen (N) is a limiting nutrient that affects primary productivity and ecosystem functions in many terrestrial ecosystems (Vitousek & Howarth, 1991). However, reactive N emitted from human activities such as fossil fuel burning and fertilizer use has tripled N deposition to the Earth's terrestrial ecosystems over recent decades (Ackerman et al., 2019; Yu et al., 2019). Increased N deposition could reduce N limitation and promote plant growth in N-limited forest ecosystems. However, once N inputs exceed biotic and abiotic sinks for N, increased deposition can induce ion imbalances, reduce biodiversity, and acidify soil and water due to losses of nitrate (Aber et al., 2003; Du et al., 2019; Gundersen et al., 1998; Niu et al., 2016). The effects of N deposition on forest ecosystems largely depend on whether—and where—the deposited N is retained within ecosystems.

The ^{15}N tracer method is the only approach currently available to trace and quantify the fate and (re)distribution of deposited N over multiyear periods in forest ecosystems (Nadelhoffer et al., 1999; Templer et al., 2012). Many studies have examined the fate of various forms of ^{15}N added to forest ecosystems (Feng et al., 2008; Goodale, 2017; Gurmesa et al., 2016; Li et al., 2019; Liu, Peng, et al., 2017; Liu, Yu, et al., 2017; Templer et al., 2012; Wang et al., 2018). Most of these, largely located in temperate and boreal forests (see Templer et al., 2012), showed most added ^{15}N ending up in the organic soil (Feng et al., 2008; Goodale, 2017; Li et al., 2019; Liu, Peng, et al., 2017; Templer et al., 2012). But few temperate studies traced the distribution of deposited N for more than 2 years (Goodale, 2017; Krause et al., 2012; Li et al., 2019; Nadelhoffer et al., 2004; Preston & Mead, 1994; Wessel et al., 2013), and the three ^{15}N tracer studies in tropical and subtropical forests suggest instead that plants and mineral soil sinks are more important (Gurmesa et al., 2016; Liu, Yu, et al., 2017; Wang et al., 2018). The long-term retention dynamics of deposited N remains especially uncertain as N initially retained in the organic soil and mineral soil may redistribute to woody plants (Goodale, 2017) or be lost from the ecosystem altogether (Preston & Mead, 1994; Wessel et al., 2013). This challenge is greatest in the tropics, where there has been least work even though tropical forests cover approximately 12% of the Earth's land area (Pan et al., 2013) and play a vital role in sustaining global climate and regulating global N and C cycles (Field et al., 1998; Phillips et al., 1998). Nitrogen deposition has, moreover, substantially increased in the tropics (Ackerman et al., 2019; Bejarano-Castillo et al., 2015; Cusack et al., 2016; Galloway et al., 2008). Thus it is critical to study the long-term fate of deposited N in tropical forests to predict better how these ecosystems will respond to N deposition.

Previous short-term ^{15}N tracer studies have suggested that deposited $^{15}NH_4^+$ and $^{15}NO_3^-$ may have different fates since NH_4^+ is preferred for uptake by soil microbes or immobilized in mineral soil while NO_3^- is more prone to leaching and gaseous loss (Jacob & Leuschner, 2015; Liu, Peng, et al., 2017; Providoli et al., 2006; Wang et al., 2018). However, most long-term ^{15}N tracer studies focused on $^{15}NH_4^+$ or $^{15}NO_3^-$ separately or did not differentiate (Goodale, 2017; Gurmesa et al., 2016; Providoli et al., 2005; Wessel et al., 2013); thus, the different fates of deposited $^{15}NH_4^+$ and $^{15}NO_3^-$ were seldom compared for the same forests over multiple years (Li et al., 2019; Nadelhoffer et al., 2004; Preston et al., 1990; Preston & Mead, 1994). Furthermore, while we may expect differences in the patterns of N retention in forests with different successional status due to different species composition and N status (Li et al., 2019), few studies have compared different forests in a given site (Li et al., 2019; Nadelhoffer et al., 2004).

In this study, for the first time, we applied $^{15}NH_4^+$ and $^{15}NO_3^-$ tracers to explore the long-term patterns and mechanisms of retention of deposited NH_4^+ versus NO_3^- in tropical forests. Two forests with different species composition and N status (Wang et al., 2014) were selected, a primary and a secondary tropical montane forest in southern China. Our main objectives were to test: (1) the mechanisms and patterns of retention and redistribution of deposited N over 3 years, and (2) how different N forms (NH_4^+ vs. NO_3^-) and forests (primary vs. secondary) influence patterns of retention and redistribution of ^{15}N. We hypothesized that: (H1) Tropical montane forests would lose the experimentally added ^{15}N over time due to rapid N turnover (e.g., via litter decomposition resulting in more N loss via leaching or gaseous emission); (H2) Plants would become a more important sink for N over time as the initially retained ^{15}N tracer is remineralized from organic matter; (H3) Plants would retain more NO_3^- than NH_4^+ while soils (organic soil and mineral soil) retain more NH_4^+ than NO_3^-; (H4) ^{15}N retention would be lower in the primary forest than in the secondary forest due to the relatively higher N availability of the primary forest (Wang et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Site description

Our study was conducted in the Jianfengling National Natural Reserve, on Hainan Island, southern China. The region is characterized by tropical monsoon climate, with a wet season (from May

to October) and a dry season (from November to April). Between 2009 and 2018, annual precipitation averaged 2414 mm (from 1637 to 3458 mm), and the mean annual temperature was 19.7°C. For this study, we selected two major tropical montane forest types: a primary forest (18°43′47″N, 108°53′23″E, elevation 893 m) and a secondary forest (18°44′41″N, 108°50′57″E, elevation 935 m). Total inorganic N deposition in bulk precipitation was 6.7 kg N ha^{-1} $year^{-1}$, with the ratio of NH_4^+/NO_3^- being 1, and no fertilization had ever been previously applied.

The primary forest has never been disturbed by human activities and is dominated by *Mallotus hookerianus*, *Gironniera subaequalis*, *Cryptocarya chinensis*, *Nephel iumtopengii*, and *Cyclobalanopsis patelliformis*. The secondary forest has developed naturally after a clear-cutting in the 1960s and mainly consists of *Castanopsis tonkinensis*, *Schefflera octophylla*, *Psychotria rubra*, and *Blastus cochinchinensis*. Among these dominant species, trees associated with ectomycorrhizal symbiosis include *C. patelliformis* and *C. tonkinensis*, while those with arbuscular symbiosis include *M. hookerianus*, *C. chinensis*, *N. iumtopengii*, *S. octophylla*, *P. rubra*, and *B. cochinchinensis*. The soil is an acidic, well-drained lateritic yellow soil with porosity of 52% in the primary forest and 47% in the secondary forest. Soil pH was 4 in both forests. Soil texture is sandy clay loam in the two forests, with 57.1% sand, 18.2% silt, and 24.7% clay in the primary forest and 53.8% sand, 12.1% silt, and 34.1% clay in the secondary forest (Fang et al., 2004; Luo et al., 2005).

2.2 | Experimental design

In each forest, three separate plots (20 m × 20 m each) were randomly selected. Each plot was divided into two subplots (10 m × 20 m each), with each subplot receiving a solution of either $^{15}NH_4NO_3$ or $NH_4{}^{15}NO_3$. In April 2015 and 2016, ^{15}N tracer solutions were sprayed directly on the forest floor using backpack sprayers in the primary forest (Wang et al., 2018) and in the secondary forest to simulate N deposition during rainfall, respectively. In the primary forest, the quantity of applied ^{15}N tracers was 25 mg ^{15}N m^{-2} as 99.14 atom% $^{15}NH_4NO_3$ and 99.21 atom% $NH_4{}^{15}NO_3$. In the secondary forest, the labeling method was similar to that used in the primary forest, but the ^{15}N tracer levels were doubled to 50 mg ^{15}N m^{-2} to increase the ^{15}N signal further above background levels and allow us to trace the long-term fate of deposited N. The added ^{15}N tracer is very small compared to N deposition and ecosystem N pools (<0.01%). Thus, the added ^{15}N tracer can substantially increase the concentration of ^{15}N above its natural abundance in all ecosystem pools with minimal disturbance of ecosystem N cycling. The fate of ^{15}N tracers in the first year was reported previously for the primary forest (Wang et al., 2018) and was submitted to review for the secondary forest along with the results from 12 other forest sites (Gurmesa et al., 2021). Here, we report the fate of deposited N after 3 years and compare these with the first 3 months and 1 year as well as temperate forests.

2.3 | Sampling and chemical analysis

Samples were taken from the edges to minimize edge effects. Major plant components and soil layers were sampled prior to ^{15}N tracer application at 3 months, 1 year, and 3 years after ^{15}N tracer application. In the primary forest, samples were also collected at 1 week and 1 month after ^{15}N labeling. For plant samples, foliage and branches of trees and shrubs were sampled from common species in each subplot. Bark and wood (3 cm of an exterior portion) were sampled using an increment corer from trees with a diameter at breast height above 5 cm. Herbs and the organic soil (mainly consisting of undecomposed plant materials on the soil surface) were sampled using a 20 cm × 20 cm iron frame. Six samples taken randomly in each subplot were mixed into one composited sample. Mineral soil samples were taken using an auger (2.5 cm inner diameter) and divided into three layers (0–10, 10–20, and 20–40 cm depth). Six soil cores taken randomly in each subplot were mixed into one composite soil by soil depth. Living fine roots (<2 mm, 0–40 cm depth) were hand-sorted from separate composite soil samples (taken using an auger of 5 cm inner diameter), and then cleaned with deionized water.

All plant and organic soil samples were oven-dried at 65°C to constant weight. Mineral soil from each plot was passed through a 2-mm mesh to remove fine roots and coarse fragments and then air-dried at room temperature. All samples were ball-milled and analyzed for ^{15}N abundance and total N and total C concentrations by elemental analyzer-isotope ratio mass spectrometry at the Institute of Applied Ecology (Elementar Analysen Systeme GmbH; IsoPrime100, IsoPrime Ltd). Calibrated D-glutamic, glycine, acetanilide, and histidine were used as references. The analytical precision for $\delta^{15}N$ was better than 0.2‰.

2.4 | Calculation and statistical analysis

Dry masses of tree or shrub compartments were estimated using allometric equations of mixed species (Chen et al., 2010; Zeng et al., 1997). Dry masses of herbs, organic soil samples, and fine roots were calculated by the weight of the harvested samples. Nitrogen pools of the different tree or shrub tissues, herbs, litters, and fine roots were calculated by multiplying dry mass and N concentration of each measured component. Soil N pools were calculated by multiplying soil bulk density at different soil layers, soil depth, and the corresponding N concentration.

The ^{15}N tracer recovery in all sampled components of ecosystem was estimated using ^{15}N tracer mass balances as follows (Nadelhoffer & Fry, 1994):

$$^{15}N_{rec} = \frac{(\text{atom}\,\%\,{}^{15}N_{sample} - \text{atom}\,\%\,{}^{15}N_{ref}) \times N_{pool}}{(\text{atom}\,\%\,{}^{15}N_{tracer} - \text{atom}\,\%\,{}^{15}N_{ref}) \times N_{tracer}} \times 100\,\%,$$

where $^{15}N_{rec}$ is the percent of ^{15}N tracer recovered in the labeled N pool, N_{pool} is the N pool of each ecosystem compartment, atom%

$^{15}N_{sample}$ is the atom percent ^{15}N in the labeled sample, atom% $^{15}N_{ref}$ is the atom percent ^{15}N in the reference sample (non-^{15}N labeled), atom% $^{15}N_{tracer}$ is the atom percent ^{15}N of added tracer, and N_{tracer} is the mass of ^{15}N in the ^{15}N tracer applied to the plot.

The carbon sequestration efficiency stimulated by N deposition (NUE_{dep}) was estimated using the ^{15}N recoveries of tree woody biomass (including branch, bark, stem, and coarse root of trees) and their corresponding C/N ratios, by the following standard stoichiometry approach of Nadelhoffer, Emmett, et al. (1999):

$$NUE_{dep} = \sum_{i=1}^{n} \left[{}^{15}N_{rec,i} \times (C/N)_i \right],$$

where $^{15}N_{rec,i}$ is the ^{15}N recoveries in branch, bark, stem, and coarse root of trees; and $(C/N)_i$ is the C/N ratio of branch, bark, stem, and coarse root of trees, assuming that C/N ratios are unchanged under the current N deposition.

The differences in ^{15}N abundance and ^{15}N recovery between the treatments at each sampling time were tested by the analysis of independent *t*-tests. Repeated-measures ANOVA was used to test the differences in ^{15}N abundance and ^{15}N recovery over time together with forest types and N forms. All analyses were conducted using the SPSS software (version 19.0; SPSS Inc.) with the significance threshold set at $p \leq 0.05$.

3 | RESULTS

3.1 | Ecosystem nitrogen pools and $\delta^{15}N$ in the two forests

The total ecosystem N pool was about 7700 kg N ha^{-1} in the primary forest and 7100 kg N ha^{-1} in the secondary forest (excluding soils below 40 cm; Table 1). The N pool of trees was 2100 kg N ha^{-1} in the primary forest and 1700 kg N ha^{-1} in the secondary forest, accounting for 95% of the total plant N pool in both forests. The total soil N pool down to 40 cm depth was about 5500 kg N ha^{-1} in the primary forest and 5300 kg N ha^{-1} in the secondary forest. The forest floor had 82 kg N ha^{-1} in the primary forest and 68 kg N ha^{-1} in the secondary forest, accounting for only about 1% of the total ecosystem N pools. The N pools in the major ecosystem compartments did not differ between the two forests (Table 1).

The $\delta^{15}N$ values of different ecosystem compartments did not differ between the two forests before labeling, except in tree stems. Plant $\delta^{15}N$ varied from −1.8‰ to −0.2‰ in the primary forest and from −1.7‰ to 0.6‰ in the secondary forest (Figure 1; Tables S1 and S2). The $\delta^{15}N$ of the organic soil averaged −0.4‰ in the primary forest and −1.1‰ in the secondary forest. The $\delta^{15}N$ of mineral soil was always positive and increased with soil depth in both forests (Figure 1).

TABLE 1 Dry mass, nitrogen pool size, nitrogen concentration, and carbon:nitrogen ratio (C/N) of major ecosystem components before adding ^{15}N tracer in the two tropical montane forests. Values in parentheses are 1 SE (n = 3)

	Dry mass (Mg ha^{-1})		N pool (kg ha^{-1})		%N		C/N	
Ecosystem components	Primary	Secondary	Primary	Secondary	Primary	Secondary	Primary	Secondary
Tree								
Foliage	11 (1)	10 (0.2)	188 (24)	168 (3)	1.69 (0.03)	1.72 (0.03)	28.4 (0.5)	28.2 (0.5)
Branch	80 (14)	65 (2)	481 (87)	415 (10)	0.61 (0.02)	0.65 (0.02)	76.6 (2.1)	78.3 (1.8)
Bark	32 (5)	26 (0.5)	189 (29)	185 (4)	0.66 (0.05)	0.71 (0.05)	74.3 (4.1)	82.6 (4.0)
Stem	289 (52)	234 (6)	578 (104)	399 (10)	0.18 (0.01)	0.17 (0.01)	318.9 (24.8)	326.5 (14.8)
Coarse root	167 (37)	130 (4)	670 (146)	533 (17)	0.40 (0.01)[a]	0.41 (0.01)[a]	197.7 (13.4)[a]	202.4 (9.3)[a]
Subtotal	579 (109)	465 (12)	2106 (390)	1700 (43)				
Shrub	0.4 (0.1)	0.7 (0.1)	5 (0.9)	7 (0.3)	1.23 (0.1)	1.19 (0.03)	45.9 (3.2)	52.9 (1.4)
Herb	0.1 (0.0)	0.05 (0.01)	2 (0.6)	0.8 (0.2)	1.76 (0.2)	1.51 (0.19)	24.0 (2.0)	27.8 (4.5)
Fine root	5 (1)	3 (0.4)	55 (12)	33 (5)	1.20 (0.1)	1.01 (0.06)	40.8 (2.5)	46.1 (2.8)
Plant subtotal	584 (110)	469 (12)	2168 (399)	1743 (47)				
Organic soil	6 (0.5)	6 (0.4)	82 (7)	68 (5)	1.31 (0.04)	1.21 (0.03)	33.2 (1.0)	36.4 (1.0)
Mineral soil								
0–10 cm	1134 (18)	1085 (82)	2154 (35)	1844 (139)	0.19 (0.01)	0.17 (0.02)	12.0 (0.6)	11.8 (0.5)
10–20 cm	1204 (58)	1106 (53)	1445 (70)	1328 (64)	0.12 (0.02)	0.12 (0.02)	10.9 (0.4)	11.4 (0.2)
20–40 cm	2651 (161)	2397 (31)	1856 (113)	2158 (28)	0.07 (0.01)	0.09 (0.01)	10.0 (0.3)	10.9 (0.2)
Soil subtotal	4989 (207)	4588 (152)	5455 (165)	5329 (213)				
Ecosystem total	5579 (307)	5064 (145)	7705 (557)	7140 (189)				

[a]Roots of trees were not sampled separately due to the highly destructive for sampling them. The N concentration and C/N of tree root was estimated by the mean value of branch and stem.

After ^{15}N tracer addition, $\delta^{15}N$ increased in all ecosystem pools in both forests (Figure 1; Tables S1 and S2). However, the temporal patterns of $\delta^{15}N$ in different ecosystem pools varied greatly. The $\delta^{15}N$ of tree components and shrubs increased over time (from −1.8‰ to 47.9‰ in the primary forest and from −1.5‰ to 83.6‰ in the secondary forest) while the $\delta^{15}N$ of herbs, fine roots, and organic soil peaked at 3 months and then decreased (Figure 1; Tables S1 and S2). For 0–40 cm mineral soils, $\delta^{15}N$ also increased 3 months after ^{15}N tracer addition but did not change significantly from 3 months to 3 years.

There were major differences in ^{15}N abundance in ecosystem components between labeling treatments with $^{15}NH_4^+$ and $^{15}NO_3^-$. In both forests, the $\delta^{15}N$ of tree foliage and branches for the period from 3 months to 3 years was significantly lower with $^{15}NH_4^+$ labeling (4.4‰ to 18.1‰ in the primary forest and 17.6‰ to 37.8‰ in the secondary forest) than with $^{15}NO_3^-$ labeling (22.1‰ to 38.5‰ in the primary forest and 43.0‰ to 83.6‰ in the secondary forest) from 3 months to 3 years (Figure 1; Tables S1 and S2). In contrast, the $\delta^{15}N$ of the organic soil was consistently higher for $^{15}NH_4^+$ labeling than $^{15}NO_3^-$ labeling. However, there were no significant differences in $\delta^{15}N$ of herbs and mineral soils between $^{15}NH_4^+$ and $^{15}NO_3^-$ labeling in the primary forest. In the secondary forest, the $\delta^{15}N$ of 0–10 cm mineral soil was significantly higher for $^{15}NH_4^+$ than $^{15}NO_3^-$ labeling at 3 months and 1 year after ^{15}N tracer addition, but this difference had disappeared by the 3-year point.

3.2 | Total ecosystem recovery

Three months after ^{15}N tracer addition, the total ecosystem recovery in the primary forest was 60.4% and 59.1% with $^{15}NH_4^+$ and $^{15}NO_3^-$ labeling, respectively, and 63.8% and 48.0% in the secondary forest (Figure 2; Tables S3 and S4). One year after ^{15}N tracer addition, the total ecosystem recovery in the primary forest was 58.5% and 64.5% with$^{15}NH_4^+$ and $^{15}NO_3^-$ labeling, respectively, and 60.9% and 59.8% in the secondary forest (Figure 2; Tables S3 and S4). Three years after ^{15}N tracer addition, the ^{15}N recovery in the primary forest under $^{15}NH_4^+$ and $^{15}NO_3^-$ labeling was 67.9% and 73.7%, respectively, and 61.0% and 57.1% in the secondary forest (Figure 2; Tables S3 and S4). The change in the total ecosystem recovery over time was not significant considering the uncertainties in estimating ^{15}N recovery. In addition, neither tracer form nor forest type significantly affected total ecosystem recovery of added ^{15}N (Table S6).

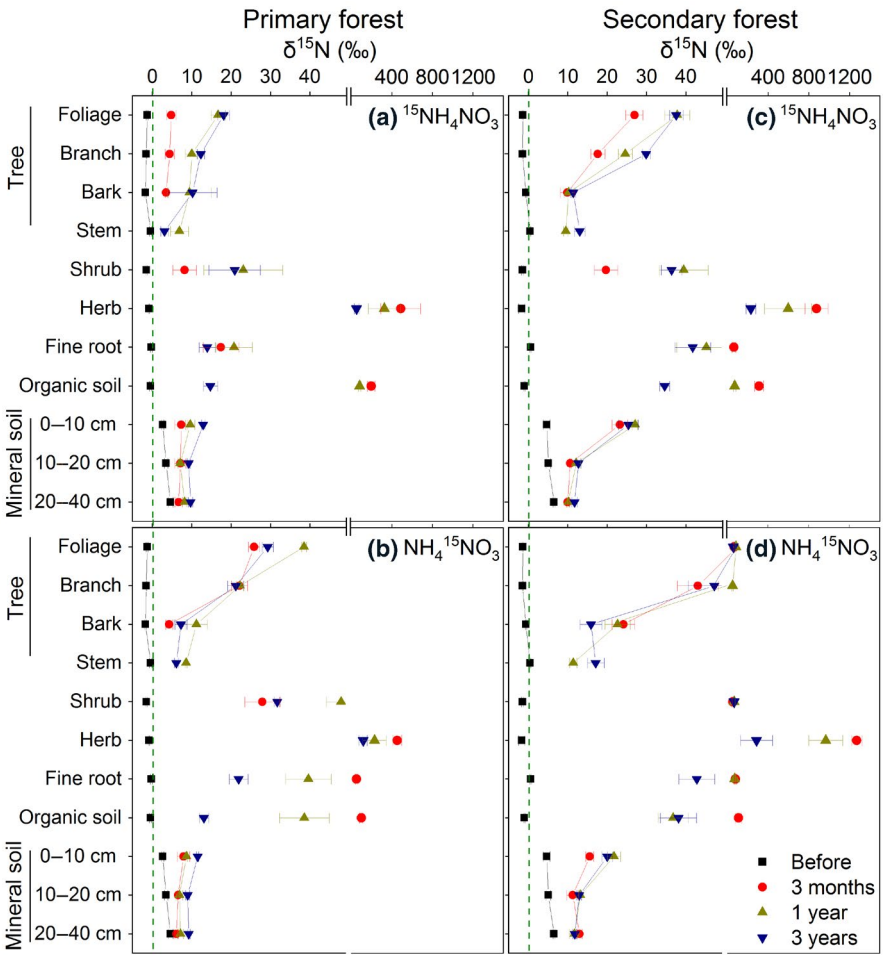

FIGURE 1 Mean $\delta^{15}N$ values of major ecosystem compartments in the (a, b) primary and (c, d) secondary tropical forests before ^{15}N labeling and 3 months, 1 year, and 3 years after ^{15}N labeling. Error bars are standard error of the mean (n = 3). The $\delta^{15}N$ values after ^{15}N labeling cannot be compared directly between the two forests, since the ^{15}N addition was doubled in the secondary forest compared to the primary forest to increase the precision of measurements

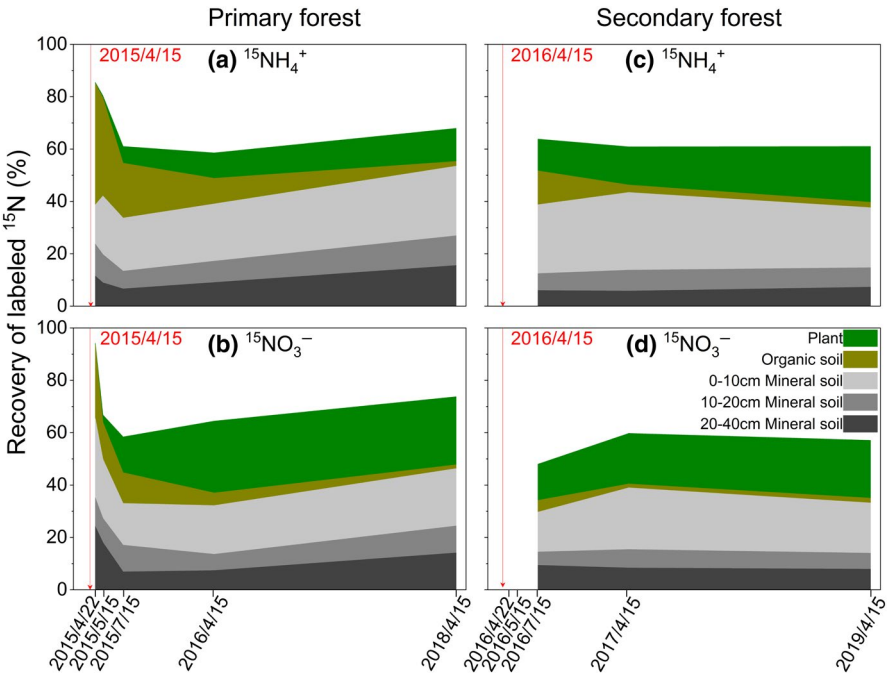

FIGURE 2 ^{15}N recovery in plants, organic soil, and mineral soil in the (a, b) primary and (c, d) secondary forests at 3 months, 1 year, and 3 years after ^{15}N labeling. Labeling date was April 15, 2015 (primary forest) and April 15, 2016 (secondary forest). ^{15}N recovery 1 week and 1 month after ^{15}N tracer addition was only available for the primary forest and only trees and shrubs were included as plants

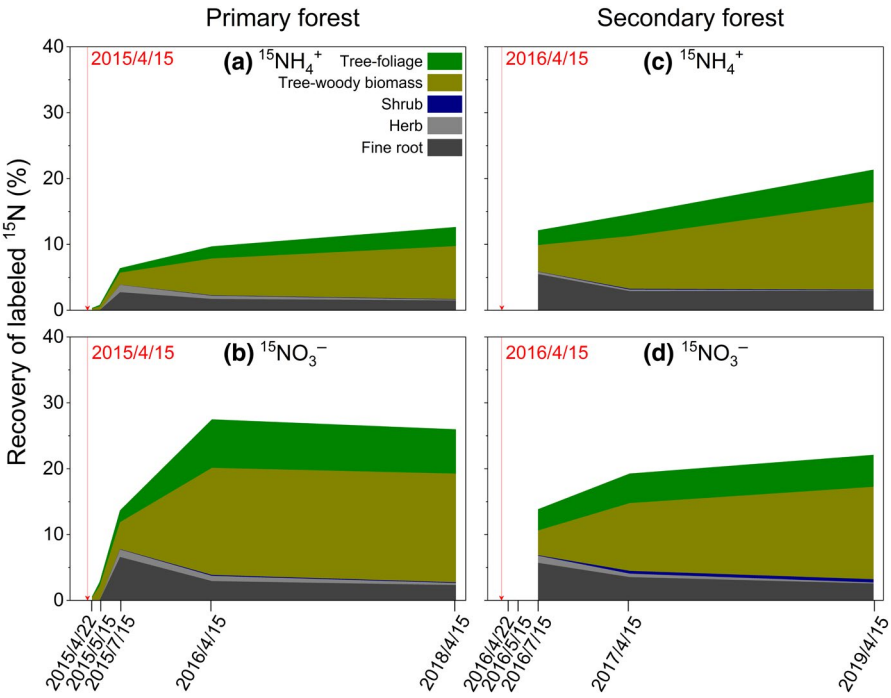

FIGURE 3 ^{15}N recovery in different plant compartments 3 months, 1 year, and 3 years after ^{15}N labeling in the (a, b) primary and (c, d) secondary forests. "Tree-woody biomass" includes branch, bark, stem, and root of trees. Labeling date was April 15, 2015 (primary forest) and April 15, 2016 (secondary forest). ^{15}N recovery 1 week and 1 month after ^{15}N tracer addition was only available for the primary forest and only trees and shrubs were included as plants. ^{15}N recovery in stems and roots of trees was only measured for 1 and 3 years after ^{15}N tracer addition

3.3 | ^{15}N tracer redistribution in different ecosystem components

There was no significant difference in plant ^{15}N recovery between the two forests over time (Table S6). In both forests, ^{15}N recovery in plants increased from 3 months to 3 years after ^{15}N tracer addition. The ^{15}N recovery in plants in the primary forest increased from 6.4% to 12.6% with $^{15}NH_4^+$ labeling and from 13.7% to 26.0% with $^{15}NO_3^-$ labeling ($p < 0.05$; Table S3). The ^{15}N recovery in plants in the secondary forest increased from 12.1% to 21.3% with $^{15}NH_4^+$ labeling and from 13.8% to 22.1% with $^{15}NO_3^-$ labeling ($p < 0.05$; Table S4). However, the temporal patterns of ^{15}N recovery differed greatly among different plant components (Figure 3; Tables S3 and S4). The ^{15}N recovery in herbs and fine roots decreased with time in both forests, whereas recovery in tree components and shrubs increased with time. Moreover, in the primary forest, significantly more ^{15}N was recovered in plants at all sampling times after $^{15}NO_3^-$ tracer addition than after $^{15}NH_4^+$ addition (Table S3). However, ^{15}N recovery in plant compartments in the secondary forest did not differ significantly between $^{15}NO_3^-$ and $^{15}NH_4^+$ labeling (Table S4).

The temporal pattern of ^{15}N recovery in the organic soil differed from the patterns of the plant pools. In both forests, ^{15}N recovery was high in the organic soil 3 months after ^{15}N tracer addition (21.0% with $^{15}NH_4^+$ labeling and 11.7% with $^{15}NO_3^-$ labeling in the primary forest and 13.0% and 4.5% in the secondary forest), but declined significantly over time afterward (Figure 2; Tables S3 and S4). In addition, ^{15}N recovery in the organic soil was higher for $^{15}NH_4^+$ than for $^{15}NO_3^-$ tracer in both forests (Table S6) but the difference between the two decreased over time.

Mineral soil was the dominant sink for the added ^{15}N tracer (Figure 2; Tables S3 and S4). In the primary forest, 33.0% of ^{15}N was found in the mineral soil after 3 months with $^{15}NH_4^+$ labeling and 33.7% with $^{15}NO_3^-$ labeling, and that recovery was 53.5% and 46.3% after 3 years. However, soil retention of ^{15}N in the secondary forest did not change significantly over time, with 37.6% and 33.2% of the ^{15}N retained in the mineral soil after 3 years under $^{15}NH_4^+$ and $^{15}NO_3^-$ labeling. The recovery of ^{15}N declined with soil depth in two forests, with the highest ^{15}N recovery observed in the 0–10 cm depth (26.6% and 21.9% with $^{15}NH_4^+$ and $^{15}NO_3^-$ labeling in the primary forest and 22.9% and 19.2% in the secondary forest). Nevertheless, substantial amounts of ^{15}N were also retained at 10–20 and 20–40 cm depths. Overall, ^{15}N recovery in mineral soil did not differ significantly between $^{15}NH_4^+$ and $^{15}NO_3^-$ treatments in either forest (Tables S3 and S4).

4 | DISCUSSION

4.1 | Temporal patterns of total ecosystem recovery compared to temperate forests

Our results indicated that while 40% of applied ^{15}N was lost during the first growing season, total ecosystem recovery did not then change significantly from 3 months to 3 years. These results contradicted our first hypothesis that the amount of ^{15}N retained in tropical montane forests over longer periods would decrease substantially through leaching and gaseous loss. One additional potential mechanism for the rapid initial losses might be ^{15}N was absorbed physically on the litter and surface mineral soil and therefore lost through abiotic processes such as leaching or erosion caused by heavy rain in the first few months after ^{15}N labeling (Li et al., 2019; Wang et al., 2018). In addition, this pattern of initial losses in the first few months is similar to that observed in several temperate forest experiments (Figure 4), suggesting that total long-term ecosystem retention might be determined by the initial loss. A recent long-term study also suggested that ^{15}N initially retained would remain in temperate forests while newly deposited N would be lost from the system (Veerman et al., 2020). We speculate that ^{15}N initially retained after the first few months might be converted to organic forms and then enters the ecosystem's internal N cycling.

The observed total ecosystem recovery values of 70% and 60% of ^{15}N in the primary and secondary tropical montane forests 3 years after ^{15}N tracer addition (Tables S3 and S4) are comparable to the mean recovery (Figure 4; 66 ± 8%, n = 8) reported by long-term ^{15}N studies in temperate forests which are considered to be N-limited (t-test, p = 0.95). The net primary production (NPP) in our primary and secondary forests is about 4.5 and 8.3 Mg C ha^{-1} $year^{-1}$ (Jiang, 2016). If the average C:N ratio of 230 was used, then 35–64 kg N ha^{-1} $year^{-1}$ was needed to sustain the NPP. Thus, about 80%–90% of the N needed to sustain the NPP comes from the soil and is internally recycled. We therefore conclude that both the primary and secondary tropical montane forests we studied have a conservative N cycle, where N is tightly recycled within these ecosystems once the atmospherically deposited inorganic N is transformed into the organic form, just as they are generally considered to be N-limited (Brookshire et al., 2012; Matson et al., 1999).

4.2 | Distribution of ^{15}N in different ecosystem components

The distribution patterns of deposited N in these two tropical forests differed substantially from temperate and boreal forests, with larger fractions of added ^{15}N found in plants and mineral soils than in temperate and boreal forests where the organic soil is an important sink for N (Figure 4; t-test, $p < 0.05$). This difference in patterns of ^{15}N distribution can be attributed to the differences between tropical and temperate forests in climate (e.g., mean annual temperature and precipitation), decomposition rate of litter, and mass of organic soil layer (Templer et al., 2012). The thin organic soil layer and fast decomposition of litter in tropical forests due to high temperature and precipitation might facilitate the rapid plant N uptake of ^{15}N initially retained in the organic soil (Wang et al., 2018). In contrast, thicker organic soil layer (and lower rainfall) hamper the transfer of ^{15}N to mineral soil in temperate and boreal forests (Buchmann et al., 1996; Gundersen, 1998; Koopmans et al., 1996; Li et al., 2019; Liu, Peng, et al., 2017; Nadelhoffer, Downs, et al., 1999; Providoli et al., 2006). Our results also suggested that the ^{15}N recovery in organic soil was positively correlated with the mass of the organic soil layer (n = 9, R^2 = 0.88, $p < 0.001$; Figure S1; Table S5), further supporting these mechanisms.

Over a longer time scale, the deposited N was recycled and redistributed among the plants, organic soil, and mineral soil in the tropical forests studied. Consistent with our second hypothesis, ^{15}N recovery increased in plants after 3 years (Figure 3), indicating that deposited N that was initially retained in mineral soil and organic soil has slowly become available for plant uptake and assimilation (Goodale, 2017; Li et al., 2019; Wessel et al., 2013). Earlier studies have also suggested that ^{15}N tracer immobilized by microorganisms was slowly released to soil solution and then assimilated by plants (Zak et al., 2004; Zogg et al., 2000). In our results, ^{15}N recovery increased with time in shrubs and all tree components but decreased in herbs and fine roots (Figure 3), suggesting that assimilated N was transferred from active plant pools

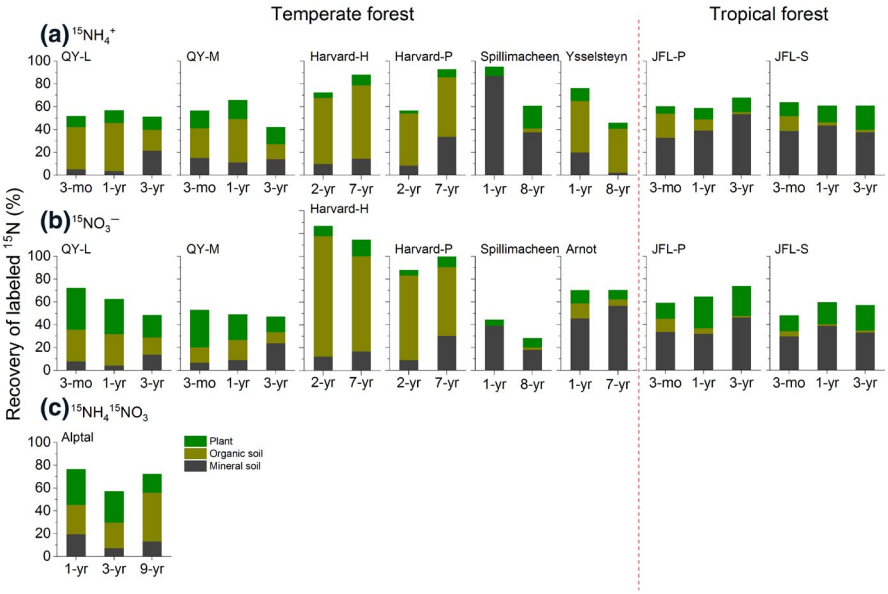

FIGURE 4 ^{15}N recovery (%) in the two tropical forest ecosystems studied compared with studies from temperate forests with (a) $^{15}NH_4^+$ labeling, (b) $^{15}NO_3^-$ labeling, and (c) $^{15}NH_4{}^{15}NO_3$ labeling. Only forests for which ^{15}N recovery has been determined for at least 3 years were analyzed. Details of site characteristics are provided in Table S5. JFL-P and JFL-S represent primary forest and secondary forest in Jianfengling (current study); QY-L and QY-M represent larch forest and mixed forest in Qingyuan (Li et al., 2019); Harvard-H and Harvard-P represent oak forest and red pine forest at Harvard Forest (Nadelhoffer et al., 2004; Nadelhoffer, Downs, et al., 1999); Spillimacheen (Preston et al., 1990; Preston & Mead, 1994); Ysselsteyn (only $^{15}NH_4^+$ labeling; Wessel et al., 2013); Arnot (only $^{15}NH_4^+$ labeling; Goodale, 2017); Alptal ($^{15}NH_4{}^{15}NO_3$ labeling; Krause et al., 2012; Providoli et al., 2005; Schleppi et al., 1999)

to stable plant pools (Goodale, 2017; Li et al., 2019; Nadelhoffer et al., 2004). The carbon sequestration efficiency of plants (NUE_{dep}) was estimated to be 14 and 18 kg C/kg N for primary and secondary forest after 3 years, which is within the range of values in temperate forests (Wang et al., 2018) and higher than values previously estimated for tropical forests (9 kg C/kg N; De Vries et al., 2014). According to a nutrient addition experiment in our study site (Zhou, 2013), N addition enhanced aboveground biomass carbon pool (NUE_{dep} was 24–35 kg C/kg N in the primary forest and 11 kg C/kg N in the secondary forest). Together, these results suggested that over time deposited N will be increasingly retained in high C:N ratio tree components and therefore enhance N deposition-induced carbon sequestration (Goodale, 2017; Nadelhoffer, Downs, et al., 1999; Nadelhoffer, Emmett, et al., 1999).

In contrast to the pattern in plants, the organic soil ^{15}N recovery declined from 3 months (16.4% in the primary forest and 8.8% in the secondary forest) to 3 years (1.6% in the primary forest and 2.0% in the secondary forest), with a greater decline in the primary forest (Figure 2; Tables S3 and S4). We attribute this to fast litter turnover in tropical forests, resulting in the small capacity of organic soil to retain the added ^{15}N (Gurmesa et al., 2016; Liu, Yu, et al., 2017; Wang et al., 2018). The ^{15}N initially retained in the organic soil could be transferred to the mineral soil, or released and assimilated by plants (Veerman et al., 2020; Wessel et al., 2013). In numerous studies in temperate forests, ^{15}N recovery decreased over time in the organic soil, which was attributed to litter decomposition, physical leaching, or downward transport by soil fauna (Goodale, 2017; Li et al., 2019; Nadelhoffer et al., 2004).

In mineral soils, ^{15}N recovery did not change significantly from 3 months to 3 years (Figures 2 and 4). The mineral soil was still the largest sink for deposited N after 3 years. The long-term persistence of ^{15}N in mineral soil has been attributed to the incorporation of ^{15}N into stable soil organic matter (SOM) pools (Goodale et al., 2015; Perakis & Hedin, 2001; Veerman et al., 2020). Previous studies have demonstrated that inorganic N could be incorporated into the organic N pool through microbial accumulation, condensation of N in microbial enzymes with phenolic compounds, or abiotic reactions of inorganic N with SOM (Fuss et al., 2019; Goodale et al., 2015; Johnson, 1992; Johnson et al., 2000; Lewis & Kaye, 2012; Liu, Peng, et al., 2017), while inputs of high C/N woody debris would also promote the immobilization of ^{15}N by microbes (Lajtha, 2020). Given the conservative N cycle in these forests, the deposited N retained in mineral soil may promote soil organic carbon accumulation (Manzoni et al., 2017; Zhou et al., 2019).

4.3 | Different fates of $^{15}NH_4^+$ and $^{15}NO_3^-$

The total ecosystem retention did not differ significantly between $^{15}NH_4^+$ and $^{15}NO_3^-$ (Figure 2; Table S6), indicating that deposited NH_4^+ and NO_3^- can be retained equally by these tropical forests. Nonetheless, the patterns of ^{15}N distribution within ecosystems (plants, organic soil and mineral soil) differed. Consistent with

many previous ^{15}N-field studies (Feng et al., 2008; Li et al., 2019; Liu, Peng, et al., 2017; Nadelhoffer et al., 2004; Sheng et al., 2014; Wang et al., 2018), our results indicated that deposited NO_3^- is more readily taken up by plants compared to NH_4^+. The higher recovery of $^{15}NO_3^-$ in plants than $^{15}NH_4^+$ could be attributed to the higher mobility of nitrate, so that $^{15}NO_3^-$ can move readily to the root surface and be assimilated by plants (Jacob & Leuschner, 2015). Additionally, NO_3^- is more important in balancing cation uptake (e.g., K^+, Ca^{2+}, and Mg^{2+}) than NH_4^+ (Hoffmann et al., 2007). In contrast, NH_4^+ is likely retained on cation exchange sites in SOM and clay particles or preferentially taken up by soil microbes (Gebauer et al., 2000; Jacob & Leuschner, 2015; Liu, Peng, et al., 2017; Providoli et al., 2006). Furthermore, plant uptake of NO_3^- would avoid direct competition for NH_4^+ with microbes (Kuzyakov & Xu, 2013). However, these differences between $^{15}NH_4^+$ and $^{15}NO_3^-$ were less prevalent in the long term, indicating that both deposited $^{15}NH_4^+$ and $^{15}NO_3^-$ are slowly redistributed to stable plant pools over time.

In our results, retention in the organic soil was significantly higher for $^{15}NH_4^+$ than for $^{15}NO_3^-$ (Table S6), which is consistent with previous studies (Corre & Lamersdorf, 2004; Feng et al., 2008; Li et al., 2019; Liu, Peng, et al., 2017). Many studies have demonstrated that forest floor microbes prefer NH_4^+ to NO_3^- due to the lower energy cost of ammonium during assimilation (Recous et al., 1990). Moreover, NO_3^- has greater mobility than NH_4^+ and leaches readily to mineral soils. In the primary forest, the organic soil was the major sink for deposited N (46%) under $^{15}NH_4^+$ labeling at 1 week after ^{15}N tracer addition while 65% of ^{15}N was retained in mineral soil under $^{15}NO_3^-$ labeling (Figure 2), further supporting this mechanism. However, ^{15}N recovery 3 years after ^{15}N tracer addition in the organic soil did not differ between the two N forms. Fast decomposition of litter in tropical forests is a possible mechanism for similar retention patterns over the long term. Both deposited NH_4^+ and NO_3^- over time could ultimately be transferred to the mineral soil or released and assimilated by plants (Goodale, 2017; Li et al., 2019; Nadelhoffer et al., 2004).

Surprisingly, ^{15}N recovery in mineral soil did not differ between $^{15}NH_4^+$ and $^{15}NO_3^-$ (Tables S3, S4 and S6), in contrast to previous studies (Feng et al., 2008; Li et al., 2019; Liu, Peng, et al., 2017; Liu, Yu, et al., 2017; Nadelhoffer et al., 2004; Sheng et al., 2014). We attribute this to the conservative N cycle of the tropical montane forests studied. A previous study also suggested that both $^{15}NH_4^+$ and $^{15}NO_3^-$ can be incorporated into stable SOM and hence result in similar long-term "equilibrium" patterns of $^{15}NH_4^+$ and $^{15}NO_3^-$ retention in N-poor forests (Perakis & Hedin, 2001). Added $^{15}NH_4^+$ can be immobilized by soil microbes or incorporated into cation exchange sites in SOM and clays (Lewis & Kaye, 2012; Perakis & Hedin, 2001; Templer et al., 2012; Zhu & Wang, 2011). The NO_3^- could also be incorporated into particulate-associated and mineral-associated SOM fractions through abiotic or biotic processes (Fuss et al., 2019; Matus et al., 2019). For example, dissimilatory nitrate reduction to ammonium has been hypothesized to play a key role in the retention of bioavailable N in forests from high rainfall areas (Gao et al., 2016; Huygens et al., 2007; Silver et al., 2001; Templer et al., 2008).

4.4 | Difference between the two forests

Both tropical montane forests have low N status (Wang et al., 2014), as indicated by low rates of atmospheric N deposition and persistent ecosystem retention (Figure 2), but the primary forest was initially somewhat more N-rich than the secondary forest (Wang et al., 2014). However, ecosystem N retention of the two forests was similar over time (Table S6), which contradicted our fourth hypothesis of lower ^{15}N retention in the primary forest due to its relatively higher N status than the secondary forest. Although the two forests were labeled with different amounts of ^{15}N and in different years (25 mg ^{15}N m^{-2} applied in 2015 to the primary forest and 50 mg ^{15}N m^{-2} applied in 2016 to the secondary forest), the similarity in N retention patterns was not due to experimental design. The precipitation in the first 3 months after ^{15}N labeling was higher in the primary forest (737 mm in 2015) than in the secondary forest (445 mm in 2016; Figure S2). Thus, while the secondary forest had more N applied and experienced less 3-monthly rainfall than the primary forest, our results suggest similar loss and retention dynamics of ^{15}N in both forests, with 40% lost during the first 3 months after ^{15}N labeling in the two forests and no significant change in total ecosystem recovery at 1 and 3 years' post-labeling (Figure 2). Differences in precipitation and the amount of ^{15}N tracer are therefore unlikely to have affected the patterns of ^{15}N retention in the two forests. We interpret this as indicating that successional status did not strongly affect total ecosystem recovery or the distribution patterns of added ^{15}N in these tropical forests.

5 | CONCLUSIONS

We have presented the first analysis of the fates of deposited NH_4^+ and NO_3^- over 3 years for two tropical montane forests. More than 60% of ^{15}N was retained in both primary and secondary tropical montane forests at 3 months, 1 year, and 3 years after ^{15}N tracer addition, indicating persistent ecosystem retention of deposited N in these forests. Although total ecosystem ^{15}N recovery did not change significantly with time, the deposited N became redistributed within the forests. The retention and retranslocation patterns in plants, organic soil, and mineral soil differed between $^{15}NH_4^+$ and $^{15}NO_3^-$ tracers in the two forests. More $^{15}NH_4^+$ than $^{15}NH_4^+$ was retained by plants and the total ^{15}N recovery attributed to plants increased over time. In contrast to long-term retention in plants, the organic soil was a transient sink for deposited N and more $^{15}NH_4^+$ was retained here. The mineral soil was the largest ecosystem sink for deposited N. It was surprising that the ^{15}N recovery of mineral soil remained relatively steady in the study forests over time and that ^{15}N recovery in mineral soil did not differ between the two N forms. Neither forest types nor N forms significantly affected total

ecosystem N retention. Overall, our results suggest that deposited N is redistributed to more stable plant and soil pools over time. Critically, our results also show that the majority of N was still retained within tropical montane forests 3 years after deposition. This leads to the expectation that the retained N is likely to benefit tropical forest growth and enhance carbon sequestration.

ACKNOWLEDGMENTS

This work was supported financially by the National Key Research and Development Program of China (2016YFA0600802), Key Research Program of Frontier Sciences of the Chinese Academy of Sciences (QYZDB-SSW-DQC002), K.C. Wong Education Foundation (GJTD-2018-07), Liaoning Vitalization Talents Program (XLYC1902016), the National Natural Science Foundation of China (41773094, 41811530305, 41773071, 31901134, and 31770498), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA23070103), and Scientific Research Foundation of the Educational Department of Liaoning Province (L201908). We thank many students and field staff for assisting with sampling and analyses. The work was jointly supported by the Jianfengling National Key Field Station.

CONFLICT OF INTEREST

The authors declare no competing financial interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Ang Wang https://orcid.org/0000-0002-9365-2926
Oliver L. Phillips https://orcid.org/0000-0002-8993-6168
Per Gundersen https://orcid.org/0000-0002-9199-4033
Geshere A. Gurmesa https://orcid.org/0000-0002-2340-6076
Weixing Zhu https://orcid.org/0000-0002-4274-6973
Erik A. Hobbie https://orcid.org/0000-0002-1629-6307
Yunting Fang https://orcid.org/0000-0001-7531-546X

REFERENCES

Aber, J. D., Goodale, C. L., Ollinger, S. V., Smith, M. L., Magill, A. H., Martin, M. E., Hallett, R. A., & Stoddard, J. L. (2003). Is nitrogen deposition altering the nitrogen status of northeastern forests? *BioScience*, *53*(4), 375–389. https://doi.org/10.1641/0006-3568(2003)053%5B0375:indatn%5D2.0.co;2

Ackerman, D., Millet, D. B., & Chen, X. (2019). Global estimates of inorganic nitrogen deposition across four decades. *Global Biogeochemical Cycles*, *33*(1), 100–107. https://doi.org/10.1029/2018GB005990

Bejarano-Castillo, M., Campo, J., & Roa-Fuentes, L. L. (2015). Effects of increased nitrogen availability on C and N cycles in tropical forests: A meta-analysis. *PLoS One*, *10*(12), e0144253. https://doi.org/10.1371/journal.pone.0144253

Brookshire, E. N. J., Hedin, L. O., Newbold, J. D., Sigman, D. M., & Jackson, J. K. (2012). Sustained losses of bioavailable nitrogen from montane tropical forests. *Nature Geoscience*, *5*(2), 123–126. https://doi.org/10.1038/ngeo1372

Buchmann, N., Gebauer, G., & Schulze, E. D. (1996). Partitioning of ^{15}N-labeled ammonium and nitrate among soil, litter, below-and above-ground biomass of trees and understory in a 15-year-old *Picea abies* plantation. *Biogeochemistry*, *33*(1), 1–23. https://doi.org/10.1007/BF00000967

Chen, D., Li, Y., Liu, H., Xu, H., Xiao, W. F., Luo, T. S., Zhou, Z., & Lin, M. (2010). Biomass and carbon dynamics of a tropical mountain rain forest in China. *Science China-life Sciences*, *53*, 798–810. https://doi.org/10.1007/s11427-010-4024-2

Corre, M. D., & Lamersdorf, N. P. (2004). Reversal of nitrogen saturation after long-term deposition reduction: impact on soil nitrogen cycling. *Ecology*, *85*(11), 3090–3104. https://doi.org/10.1890/03-0423

Cusack, D. F., Karpman, J., Ashdown, D., Cao, Q., Ciochina, M., Halterman, S., Lydon, S., & Neupane, A. (2016). Global change effects on humid tropical forests: Evidence for biogeochemical and biodiversity shifts at an ecosystem scale. *Reviews of Geophysics*, *54*(3), 523–610. https://doi.org/10.1002/2015RG000510

De Vries, W., Du, E., & Butterbach-Bahl, K. (2014). Short and long-term impacts of nitrogen deposition on carbon sequestration by forest ecosystems. *Current Opinion in Environmental Sustainability*, *9–10*, 90–104. https://doi.org/10.1016/j.cosust.2014.09.001

Du, E., Fenn, M. E., De Vries, W., & Ok, Y. S. (2019). Atmospheric nitrogen deposition to global forests: Status, impacts and management options. *Environmental Pollution*, *250*, 1044–1048. https://doi.org/10.1016/j.envpol.2019.04.014

Fang, J., Li, Y., Zhu, B., Liu, G., & Zhou, G. (2004). Community structures and species richness in the montane rain forest of Jianfengling, Hainan Island, China. *Biodiversity Science*, *12*, 29–43.

Feng, Z., Brumme, R., Xu, Y. J., & Lamersdorf, N. (2008). Tracing the fate of mineral N compounds under high ambient N deposition in a Norway spruce forest at Solling/Germany. *Forest Ecology and Management*, *255*(7), 2061–2073. https://doi.org/10.1016/j.foreco.2007.12.049

Field, C. B., Behrenfeld, M. J., Randerson, J. T., & Falkowski, P. (1998). Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science*, *281*(5374), 237–240. https://doi.org/10.1126/science.281.5374.237

Fuss, C. B., Lovett, G. M., Goodale, C. L., Ollinger, S. V., Lang, A. K., & Ouimette, A. P. (2019). Retention of nitrate-N in mineral soil organic matter in different forest age classes. *Ecosystems*, *22*(6), 1280–1294. https://doi.org/10.1007/s10021-018-0328-z

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R., Martinelli, L. A., Seitzinger, S. P., & Sutton, M. A. (2008). Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science*, *320*(5878), 889–892. https://doi.org/10.1126/science.1136674

Gao, W., Kou, L., Yang, H., Zhang, J., Müller, C., & Li, S. (2016). Are nitrate production and retention processes in subtropical acidic forest soils responsive to ammonium deposition. *Soil Biology and Biochemistry*, *100*, 102–109. https://doi.org/10.1016/j.soilbio.2016.06.002

Gebauer, G., Zeller, B., Schmidt, G., May, C., Buchmann, N., Colin-Belgrand, M., Dambrine, E., Martin, F., Schulze, E. D., & Bottner, P. (2000). The fate of ^{15}N-labelled nitrogen inputs to coniferous and broadleaf forests. *Carbon and nitrogen cycling in European forest ecosystems* (pp. 144–170). Springer. https://doi.org/10.1007/978-3-642-57219-7_7

Goodale, C. L. (2017). Multiyear fate of a ^{15}N tracer in a mixed deciduous forest: Retention, redistribution, and differences by mycorrhizal association. *Global Change Biology*, *23*(2), 867–880. https://doi.org/10.1111/gcb.13483

Goodale, C. L., Fredriksen, G., Weiss, M. S., McCalley, C. K., Sparks, J. P., & Thomas, S. A. (2015). Soil processes drive seasonal variation in retention of ^{15}N tracers in a deciduous forest catchment. *Ecology*, *96*(10), 2653–2668. https://doi.org/10.1890/14-1852.1

Gundersen, P. (1998). Effects of enhanced nitrogen deposition in a spruce forest at Klosterhede, Denmark, examined by moderate

NH_4NO_3 addition. *Forest Ecology and Management*, *101*, 251–268. https://doi.org/10.1016/S0378-1127(97)00141-2

Gundersen, P., Callesen, I., & De Vries, W. (1998). Nitrate leaching in forest ecosystems is related to forest floor CN ratios. *Environmental Pollution*, *102*(1), 403–407. https://doi.org/10.1016/S0269-7491(98)80060-2

Gurmesa, G. A., Lu, X., Gundersen, P., Mao, Q., Zhou, K., Fang, Y., & Mo, J. (2016). High retention of ^{15}N-labeled nitrogen deposition in a nitrogen saturated old-growth tropical forest. *Global Change Biology*, *22*(11), 3608–3620. https://doi.org/10.1111/gcb.13327

Gurmesa, G. A., Wang, A., Li, S., Peng, S., de Vries, W., Gundersen, P., Ciais, P., Phillips, P. L., Hobbie, E. A., Zhu, W., Nadelhoffer, K. J., Xi, Y., Bai, E., Sun, T., Chen, D., Zhou, W., Zhang, Y., Guo, Y., Zhu, J., … Fang, Y. (2021). Differential retention of deposited ammonium and nitrate affects the global forest carbon sink. *Nature* (in preparing to re-submit).

Hoffmann, A., Milde, S., Desel, C., Hümpel, A., Kaiser, H., Hammes, E., Piippo, M., Soitamo, A., Aro, E., Gerendás, J., Sattelmacher, B., & Hansen, U. (2007). N form-dependent growth retardation of *Arabidopsis thaliana* seedlings as revealed from physiological and microarray studies. *Journal of Plant Nutrition and Soil Science*, *170*, 87–97. https://doi.org/10.1002/jpln.200625032

Huygens, D., Rütting, T., Boeckx, P., Van Cleemput, O., Godoy, R., & Müller, C. (2007). Soil nitrogen conservation mechanisms in a pristine south Chilean Nothofagus forest ecosystem. *Soil Biology and Biochemistry*, *39*(10), 2448–2458. https://doi.org/10.1016/j.soilbio.2007.04.013

Jacob, A., & Leuschner, C. (2015). Complementarity in the use of nitrogen forms in a temperate broad-leaved mixed forest. *Plant Ecology & Diversity*, *8*(2), 243–258. https://doi.org/10.1080/17550874.2014.898166

Jiang, L. (2016). *Effects of nitrogen and phosphorus fertilization on carbon cycling of tropical montane rainforests in Hainan Island, China*. PhD theses, Peking University (in Chinese).

Johnson, D. W. (1992). Nitrogen retention in forest soils. *Journal of Environmental Quality*, *21*, 1–12. https://doi.org/10.2134/jeq1992.00472425002100010001x

Johnson, D. W., Cheng, W., & Burke, I. C. (2000). Biotic and abiotic nitrogen retention in a variety of forest soils. *Soil Science Society of America Journal*, *64*(4), 1503–1514. https://doi.org/10.2136/sssaj2000.6441503x

Koopmans, C., Tietema, A., & Boxman, A. (1996). The fate of ^{15}N enriched throughfall in two coniferous forest stands at different nitrogen deposition levels. *Biogeochemistry*, *34*(1), 19–44. https://doi.org/10.1007/BF02182953

Krause, K., Providoli, I., Currie, W. S., Bugmann, H., & Schleppi, P. (2012). Long-term tracing of whole catchment ^{15}N additions in a mountain spruce forest: measurements and simulations with the TRACE model. *Trees*, *26*(6), 1683–1702. https://doi.org/10.1007/s00468-012-0737-0

Kuzyakov, Y., & Xu, X. (2013). Competition between roots and microorganisms for nitrogen: Mechanisms and ecological relevance. *New Phytologist*, *198*(3), 656–669. https://doi.org/10.1111/nph.12235

Lajtha, K. (2020). Nutrient retention and loss during ecosystem succession: Revisiting a classic model. *Ecology*, *101*(1). https://doi.org/10.1002/ecy.2896

Lewis, D. B., & Kaye, J. P. (2012). Inorganic nitrogen immobilization in live and sterile soil of old-growth conifer and hardwood forests: Implications for ecosystem nitrogen retention. *Biogeochemistry*, *111*, 169–186. https://doi.org/10.1007/s10533-011-9627-6

Li, S., Gurmesa, G. A., Zhu, W., Gundersen, P., Zhang, S., Xi, D., Huang, S., Wang, A., Zhu, F., Jiang, Y., Zhu, J., & Fang, Y. (2019). Fate of atmospherically deposited NH_4^+ and NO_3^- in two temperate forests in China: Temporal pattern and redistribution. *Ecological Applications*, *29*(6). https://doi.org/10.1002/eap.1920

Liu, J., Peng, B., Xia, Z., Sun, J., Gao, D., Dai, W., Jiang, P., & Bai, E. (2017). Different fates of deposited NH_4^+ and NO_3^- in a temperate forest in northeast China: A ^{15}N tracer study. *Global Change Biology*, *23*, 2441–2449. https://doi.org/10.1111/gcb.13533

Liu, W., Yu, L., Zhang, T., Kang, R., Zhu, J., Mulder, J., Huang, Y., & Duan, L. (2017). In situ N-15 labeling experiment reveals different long-term responses to ammonium and nitrate inputs in N-saturated subtropical forest. *Journal of Geophysical Research: Biogeosciences*, *122*(9), 2251–2264. https://doi.org/10.1002/2017JG003963

Luo, T., Li, Y., Chen, D., Lin, M., & Sun, Y. (2005). A study on the soil properties of *Dacrycarpus imbricatus* Bl. plantation in tropical mountainous region in Hainan Island. *Natural Science Journal of Hainan University*, *23*(4), 340–346.

Manzoni, S., Čapek, P., Mooshammer, M., Lindahl, B. D., Richter, A., & Šantrůčková, H. (2017). Optimal metabolic regulation along resource stoichiometry gradients. *Ecology Letters*, *20*, 1182–1191. https://doi.org/10.1111/ele.12815

Matson, P. A., McDowell, W. H., Townsend, A. R., & Vitousek, P. M. (1999). The globalization of N deposition: Ecosystem consequences in tropical environments. *Biogeochemistry*, *46*(1–3), 67–83. https://doi.org/10.1007/978-94-011-4645-6_4

Matus, F., Stock, S., Eschenbach, W., Dyckmans, J., Merino, C., Najera, F., Koester, M., Kuzyakov, Y., & Dippold, M. A. (2019). Ferrous wheel hypothesis: Abiotic nitrate incorporation into dissolved organic matter. *Geochimica Et Cosmochimica Acta*, *245*, 514–524. https://doi.org/10.1016/j.gca.2018.11.020

Nadelhoffer, K. J., Colman, B. P., Currie, W. S., Magill, A., & Aber, J. D. (2004). Decadal-scale fates of ^{15}N tracers added to oak and pine stands under ambient and elevated N inputs at the Harvard Forest (USA). *Forest Ecology and Management*, *196*(1), 89–107. https://doi.org/10.1016/j.foreco.2004.03.014

Nadelhoffer, K. J., Downs, M. R., & Fry, B. (1999). Sinks for ^{15}N-enriched additions to an oak forest and a red pine plantation. *Ecological Applications*, *9*(1), 72–86. https://doi.org/10.1890/1051-0761(1999)009%5B0072:SFNEAT%5D2.0.CO;2

Nadelhoffer, K. J., Emmett, B. A., Gundersen, P., Kjønaas, O. J., Koopmans, C. J., Schleppi, P., Tietema, A., & Wright, R. F. (1999). Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature*, *398*(6723), 145–148. https://doi.org/10.1038/18205

Nadelhoffer, K. J., & Fry, B. (1994). Nitrogen isotope studies in forest ecosystems. In K. Lajtha & R. Michener (Eds.), *Stable isotopes in ecology* (pp. 22–44). Black-well Scientific.

Niu, S., Classen, A. T., Dukes, J. S., Kardol, P., Liu, L., Luo, Y., Rustad, L., Sun, J., Tang, J., Templer, P. H., Thomas, R. Q., Tian, D., Vicca, S., Wang, Y. P., Xia, J., & Zaehle, S. (2016). Global patterns and substrate-based mechanisms of the terrestrial nitrogen cycle. *Ecology Letters*, *19*(6), 697–709. https://doi.org/10.1111/ele.12591

Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 593–622. https://doi.org/10.1146/annurev-ecolsys-110512-135914

Perakis, S. S., & Hedin, L. O. (2001). Fluxes and fates of nitrogen in soil of an unpolluted old-growth temperate forest, southern Chile. *Ecology*, *82*(8), 2245–2260. https://doi.org/10.1890/0012-9658(2001)082%5B2245:FAFONI%5D2.0.CO;2

Phillips, O. L., Malhi, Y., Higuchi, N., Laurance, W. F., Núnez, P. V., Vásquez, R. M., Laurance, S. G., Ferreira, L. V., Stern, M., & Brown, S. (1998). Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science*, *282*(5388), 439–442. https://doi.org/10.1126/science.282.5388.439

Preston, C. M., Marshall, V. G., McCullough, K., & Mead, D. J. (1990). Fate of N-15-labeled fertilizer applied on snow at 2 forest sites in British-Columbia. *Canadian Journal of Forest Research*, *20*(10), 1583–1592.

Preston, C. M., & Mead, D. J. (1994). Growth-response and recovery of N-15-fertilizer one and 8 growing seasons after application to lodgepole pine in British-Columbia. *Forest Ecology*

and Management, *65*(2–3), 219–229. https://doi.org/10.1016/0378-1127(94)90172-4

Providoli, I., Bugmann, H., Siegwolf, R., Buchmann, N., & Schleppi, P. (2005). Flow of deposited inorganic N in two gleysol-dominated mountain catchments traced with $^{15}NO_3^-$ and $^{15}NH_4^+$. *Biogeochemistry*, *76*(3), 453–475. https://doi.org/10.1007/s10533-005-8124-1

Providoli, I., Bugmann, H., Siegwolf, R., Buchmann, N., & Schleppi, P. (2006). Pathways and dynamics of $^{15}NO_3^-$ and $^{15}NH_4^+$ applied in a mountain *Picea abies* forest and in a nearby meadow in central Switzerland. *Soil Biology and Biochemistry*, *38*(7), 1645–1657. https://doi.org/10.1016/j.soilbio.2005.11.019

Recous, S., Mary, B., & Faurie, G. (1990). Microbial immobilization of ammonium and nitrate in cultivated soils. *Soil Biology and Biochemistry*, *22*(7), 913–922. https://doi.org/10.1016/0038-0717(90)90129-N

Schleppi, P., Bucher-Wallin, L., Siegwolf, R., Saurer, M., Muller, N., & Bucher, J. (1999). Simulation of increased nitrogen deposition to a montane forest ecosystem: Partitioning of the added ^{15}N. *Water, Air, and Soil Pollution*, *116*(1–2), 129–134. https://doi.org/10.1023/A:1005206927764

Sheng, W., Yu, G., Fang, H., Jiang, C., Yan, J., & Zhou, M. (2014). Sinks for inorganic nitrogen deposition in forest ecosystems with low and high nitrogen deposition in China. *PLoS One*, *9*(2), e89322. https://doi.org/10.1371/journal.pone.0089322

Silver, W. L., Herman, D. J., & Firestone, M. K. (2001). Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. *Ecology*, *82*(9), 2410. https://doi.org/10.1890/0012-9658(2001)082%5B2410:DNRTAI%5D2.0.CO;2

Templer, P., Mack, M. C., Chapin III, F. S., Christenson, L., Compton, J., Crook, H., Currie, W., Curtis, C., Dail, D., & D'Antonio, C. (2012). Sinks for nitrogen inputs in terrestrial ecosystems: A meta-analysis of ^{15}N tracer field studies. *Ecology*, *93*(8), 1816–1829. https://doi.org/10.1890/11-1146.1

Templer, P. H., Silver, W. L., Pett-Ridge, J., DeAngelis, K. M., & Firestone, M. K. (2008). Plant and microbial controls on nitrogen retention and loss in a humid tropical forest. *Ecology*, *89*(11), 3030–3040. https://doi.org/10.1890/07-1631.1

Veerman, L., Kalbitz, K., Gundersen, P., Kjønaas, J., Moldan, F., Schleppi, P., van Loon, E. E., Schoorl, J., Wessel, W., & Tietema, A. (2020). The long-term fate of deposited nitrogen in temperate forest soils. *Biogeochemistry*, *150*(1), 1–15. https://doi.org/10.1007/s10533-020-00683-6

Vitousek, P. M., & Howarth, R. W. (1991). Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry*, *13*(2), 87–115. https://doi.org/10.1007/BF00002772

Wang, A., Fang, Y., Chen, D., Koba, K., Makabe, A., Li, Y., Luo, T., & Yoh, M. (2014). Variations in nitrogen-15 natural abundance of plant and soil systems in four remote tropical rainforests, southern China. *Oecologia*, *174*(2), 567–580. https://doi.org/10.1007/s00442-013-2778-5

Wang, A., Zhu, W., Gundersen, P., Phillips, O. L., Chen, D., & Fang, Y. (2018). Fates of atmospheric deposited nitrogen in an Asian tropical primary forest. *Forest Ecology and Management*, *411*, 213–222. https://doi.org/10.1016/j.foreco.2018.01.029

Wessel, W. W., Tietema, A., & Boxman, A. W. (2013). The fate of $^{15}NH_4^+$ labeled deposition in a Scots pine forest in the Netherlands under high and lowered NH_4^+ deposition, 8 years after application. *Biogeochemistry*, *113*(1–3), 467–479. https://doi.org/10.1007/s10533-012-9775-3

Yu, G., Jia, Y., He, N., Zhu, J., Chen, Z., Wang, Q., Piao, S., Liu, X., He, H., Guo, X., Wen, Z., Li, P., Ding, G., & Goulding, K. (2019). Stabilization of atmospheric nitrogen deposition in China over the past decade. *Nature Geoscience*, *12*(6), 424–429. https://doi.org/10.1038/s41561-019-0352-4

Zak, D. R., Pregitzer, K. S., Holmes, W. E., Burton, A. J., & Zogg, G. P. (2004). Anthropogenic N deposition and the fate of $^{15}NO_3^-$ in a northern hardwood ecosystem. *Biogeochemistry*, *69*(2), 143–157. https://doi.org/10.1023/B:BIOG.0000031045.24377.99

Zeng, Q., Li, Y., Chen, B., Wu, Z., & Zhou, G. (1997). *Management on tropical forest ecosystems*. 1997. China Forestry Press, 202 pp. (in Chinese).

Zhou, G., Xu, S., Ciais, P., Manzoni, S., Fang, J., Yu, G., Tang, X., Zhou, P., Wang, W., Yan, J., Wang, G., Ma, K., Li, S., Du, S., Han, S., Ma, Y., Zhang, D., Liu, J., Liu, S., … Chen, X. (2019). Climate and litter C/N ratio constrain soil organic carbon accumulation. *National Science Review*, *6*, 746–757. https://doi.org/10.1093/nsr/nwz045

Zhou, Z. (2013). *Effects of nitrogen and phosphorus additions on carbon cycling of tropical mountain rainforests in Hainan Island, China*. PhD theses, Peking University (in Chinese).

Zhu, W., & Wang, W. (2011). Does soil organic matter variation affect the retention of $^{15}NH_4^+$ and $^{15}NO_3^-$ in forest ecosystems? *Forest Ecology and Management*, *261*(3), 675–682. https://doi.org/10.1016/j.foreco.2010.11.024

Zogg, G. P., Zak, D. R., Pregitzer, K. S., & Burton, A. J. (2000). Microbial immobilization and the retention of anthropogenic nitrate in a northern hardwood forest. *Ecology*, *81*(7), 1858–1866. https://doi.org/10.1890/0012-9658(2000)081%5B1858:MIATRO%5D2.0.CO;2

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Wang A, Chen D, Phillips OL, et al. Dynamics and multi-annual fate of atmospherically deposited nitrogen in montane tropical forests. *Glob Change Biol*. 2021;00:1–12. https://doi.org/10.1111/gcb.15526