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1 **Dynamics and fate of atmospherically deposited nitrogen in two tropical montane**
2 **forests over three years**

3
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32
33 **Highlights**

34
35 1. $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ tracers were applied to two tropical montane forests to explore
36 the fates and redistribution of atmospherically deposited N over three years.

37
38 2. More than 60% of ^{15}N tracer was retained within the two forests even after three
39 years.

40
41 3. Ecosystem ^{15}N retention was not significantly different between two study forests
42 and between two N forms.

43
44 4. ^{15}N tracer was redistributed over time from the organic soil layer to plants and

45 mineral soil.

46

47 5. Proportionally more ^{15}N was distributed to mineral soil and plant in tropical forests
48 while more to organic soil layer in temperate forests.

49

50 **Abstract**

51

52 The effects of nitrogen (N) deposition on forest ecosystems largely depends on its fates
53 after entering the ecosystems. Several studies have addressed the fates of N deposition
54 using ^{15}N tracers, but long-term fate and redistribution of deposited N in tropical forests
55 remains unknown. In this study, we applied ^{15}N tracers to examine the fates of deposited
56 ammonium (NH_4^+) and nitrate (NO_3^-), separately, over three years in a primary and a
57 secondary tropical montane forests in southern China. Three months after ^{15}N tracer
58 addition, over 60% of ^{15}N was retained in our study tropical forests, and the ecosystem
59 retention did not change significantly over the study period. From three months to three
60 years, the ^{15}N recovery in plants increased from 10% to 19% and 13% to 22% in the
61 primary and secondary forests, respectively, while ^{15}N recovery in the organic soil layer
62 decreased from 16% to 2% and 9% to 2% over time. Mineral soil retained 50% and 35%
63 in the primary and secondary forests of ^{15}N , with retention being stable over time. We
64 found no significant difference in ecosystem retention between two N forms, but plants
65 retained more $^{15}\text{NO}_3^-$ than $^{15}\text{NH}_4^+$ and the organic layer retained more $^{15}\text{NH}_4^+$ than
66 $^{15}\text{NO}_3^-$. Mineral soil did not differ in $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ retention. Compared to
67 temperate forests, proportionally more ^{15}N was distributed to mineral soil and plant in
68 our study tropical forests. Overall, our results indicate that atmospherically deposited
69 of both NH_4^+ and NO_3^- is lost within the first three months, and then can be retained
70 steadily over a relatively longer term within the ecosystem, with retained N being
71 redistributed to plants and mineral soil over time from organic soil layer. As a result,
72 we suggest that this N retention may benefit tropical montane forest growth and
73 enhance carbon sequestration from the atmosphere.

74

75 **Key words:** N deposition; N retention and redistribution; Long-term fate; Tropical
76 montane forests; ^{15}N tracer; Ammonium and nitrate

77

78 **Introduction**

79

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

89 of N deposition on forest ecosystems largely depend on whether and where the
90 deposited N is retained within ecosystems.

91
92 The ^{15}N tracer method is the only approach currently available to trace and quantify the
93 fate and (re)distribution of deposited N over multi-year periods in forest ecosystems
94 (Nadelhoffer et al., 1999a; Templer et al., 2012). Many studies have examined the fate
95 of various forms of ^{15}N added to forest ecosystems (Feng et al., 2008; Templer et al.,
96 2012; Gurmesa et al., 2016; Goodale, 2017; Liu et al., 2017a; Liu et al., 2017b; Wang
97 et al., 2018; Li et al., 2019). However, most studies tracked the deposited N for no more
98 than one year and primarily in temperate and boreal forests (see Templer et al., 2012),
99 and they reported that the fate of deposited N varied between temperate and tropical
100 forests, with most added ^{15}N ended up in the organic soil layer in temperate and boreal
101 forests (Feng et al., 2008; Templer et al., 2012; Goodale, 2017; Liu et al., 2017a; Li et
102 al., 2019) whereas plants and mineral soil were more important sinks in tropical and
103 subtropical forests (Gurmesa et al., 2016; Liu et al., 2017b; Wang et al., 2018). Despite
104 these numerous studies, the long-term retention dynamics of deposited N is uncertain
105 since N initially retained in the organic soil layer and mineral soil may redistribute to
106 woody plants (Goodale, 2017), or be lost from the ecosystem (Preston & Mead, 1994;
107 Wessel et al., 2013). To date, only several studies in temperate forests have traced the
108 distribution of deposited N more than two years (Preston & Mead, 1994; Nadelhoffer
109 et al., 2004; Krause et al., 2012; Wessel et al., 2013; Goodale, 2017; Li et al., 2019).
110 However, the long-term retention dynamics of deposited N in tropical forest ecosystems
111 are poorly understood. Tropical forests cover approximately 12% of the earth's land
112 area and play a vital role in sustaining global climate and regulating global N and C
113 cycles (Field et al., 1998; Phillips et al., 1998). Nitrogen deposition has substantially
114 increased in the tropics (Galloway et al., 2008; Bejarano-Castillo et al., 2015; Cusack
115 et al., 2016; Ackerman et al., 2019). Thus, it is critical to study the long-term fate of
116 deposited N in tropical forests to predict how these ecosystems respond to N deposition.

117
118 Previous short-term ^{15}N tracer studies have suggested that deposited $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$
119 may have different fates since NH_4^+ is more preferable uptake by soil microbes or
120 immobilized in mineral soil while NO_3^- is more prone to leaching and gaseous loss
121 (Providoli et al., 2006; Jacob & Leuschner, 2015; Liu et al., 2017a; Wang et al., 2018).
122 However, most of long-term ^{15}N tracer studies focused on $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$ separately
123 or $^{15}\text{NH}_4^{15}\text{NO}_3$ (Providoli et al., 2005; Wessel et al., 2013; Gurmesa et al., 2016;
124 Goodale, 2017), the different fates of deposited NH_4^+ and $^{15}\text{NO}_3^-$ were seldom compared
125 for the same forests over multi-year time scales (Preston et al., 1990; Preston & Mead,
126 1994; Nadelhoffer et al., 2004; Li et al., 2019), especially in tropical forests.
127 Furthermore, few studies have been carried out on different forests within a given site
128 (Nadelhoffer et al., 2004; Li et al., 2019). There may be differences in the patterns of
129 N retention in forests with different successional status due to different species
130 composition and N status (Li et al., 2019).

131
132 In this study, for the first time, we applied $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ tracers to explore the

133 long-term patterns and mechanisms of retention of deposited NH_4^+ versus NO_3^- in
134 tropical forests. Two forests with different species composition and N status (Wang et
135 al., 2014), a primary and a secondary tropical montane forests in southern China, were
136 selected. Our main objectives were to test: 1) the mechanisms and patterns of retention
137 and redistribution of deposited N over three years, and 2) how different N forms (NH_4^+
138 versus NO_3^-) and forests (primary versus secondary) influence patterns of retention and
139 redistribution of ^{15}N . We hypothesized that: (H1) Tropical montane forests would lose
140 the experimentally added ^{15}N over time due to the rapid N turnover. Even though
141 tropical montane forests are considered to be N-limited (Matson et al., 1999), a previous
142 study shows that in a primary montane forest about 40% of the deposited N was lost
143 during the first year, presumably through rapid hydrologic or gaseous pathways under
144 the hot and humid climate (Wang et al., 2018); (H2) Plants would become a more
145 important sink for N over time as the re-mineralization of organic matter those had
146 initially retained in ^{15}N tracer; (H3) Plants would retain more NO_3^- than NH_4^+ while
147 soil (organic soil layer and mineral soil) retain more NH_4^+ than NO_3^- ; (H4) We expected
148 lower ^{15}N retention in the primary forest due to its relatively higher N status than the
149 secondary forest (Wang et al., 2014).

151 **Methods and materials**

153 *Site description*

154
155 Our study was conducted in the Jianfengling National Natural Reserve, on Hainan
156 Island, southern China. The region is characterized by tropical monsoons climate, with
157 a wet season (from May to October) and a dry season (from November to April).
158 Between 2009 and 2018, annual precipitation averages 2414 mm (from 1637 mm to
159 3458 mm), and the mean annual temperature was 19.7 °C. For this study, we selected
160 two major tropical montane forests: a primary forest (18°43'47"N, 108°53'23"E,
161 elevation 893 m) and a secondary forest (18°44'41"N, 108°50'57"E, elevation 935 m).
162 Total inorganic N deposition in bulk precipitation was 6.7 kg N ha⁻¹ yr⁻¹, with the ratio
163 of $\text{NH}_4^+/\text{NO}_3^-$ being 1, and no fertilization had ever been previously applied.

164
165 The primary forest has never been disturbed by human activities and is dominated by
166 *Mallotus hookerianus*, *Gironniera subaequalis*, *Cryptocarya chinensis*, *Nephel*
167 *iumtopengii* and *Cyclobalanopsis patelliformis*. The secondary forest has developed
168 naturally after a clear-cutting in the 1960s and mainly consists of *Castanopsis*
169 *tonkinensis*, *Schefflera octophylla*, *Psychotria rubra* and *Blastus cochinchinensis*. The
170 soil is an acidic lateritic yellow, well-drained soil with the porosity of 52% in the
171 primary forest and 47% in the secondary forest. Soil pH was 4 in both forests. Soil
172 texture is similar between the two forests, being sandy clay loam with 57.1% sand, 18.2%
173 silt, and 24.7% clay in the primary forest and with 53.8% sand, 12.1% silt, and 34.1%
174 clay in the secondary forest (Fang et al., 2004; Luo et al., 2005).

176 *Experimental design*

177

178 In each forest, three separate plots (20 m × 20 m each) were randomly selected. Each
179 plot was divided into two (10 m × 20 m each), with each subplot receiving a solution
180 of either $^{15}\text{NH}_4\text{NO}_3$ or $\text{NH}_4^{15}\text{NO}_3$. In April 2015 and 2016, ^{15}N tracer solutions were
181 sprayed directly on the forest floor using backpack sprayers in the primary forest (Wang
182 et al., 2018) and in the secondary forest to simulate N deposition during the rainfall,
183 respectively. In the primary forest, the quantity of applied ^{15}N tracers was 25 mg ^{15}N
184 m^{-2} as 99.14 atom% $^{15}\text{NH}_4\text{NO}_3$ and 99.21 atom% $\text{NH}_4^{15}\text{NO}_3$. In the secondary forest,
185 the labelling method was similar to that used in the primary forest, but the ^{15}N tracer
186 levels were doubled to 50 mg ^{15}N m^{-2} to increase the ^{15}N signal further above
187 background levels and trace the long-term fate of deposited N. Yet, the added ^{15}N tracer
188 is relatively small compared to N deposition and ecosystem N pool. Thus, the added
189 ^{15}N tracer can substantially increase the concentration of ^{15}N above its natural
190 abundance in all ecosystem pools with minimal disturbance of ecosystem N cycling.
191 The fate of ^{15}N tracer in the first year was reported previously for the primary forest
192 (Wang et al., 2018) and submitted to review for the secondary forest along with the
193 results from 12 other forests (Gurmesa et al., submitted). Here, we reported the fates
194 after three years and compared them with those in the first three months and years and
195 other temperate forests.

196

197 *Sampling and chemical analysis*

198

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

214

215 All plant and organic soil layer samples were oven-dried at 65 °C to constant weight.
216 Mineral soil from each plot was passed through a 2 mm mesh to remove fine roots and
217 coarse fragments and then air-dried at room temperature. All samples were ball-milled
218 and analyzed for ^{15}N abundance and total N and total C concentrations by elemental
219 analyzer-isotope ratio mass spectrometry at the Institute of Applied Ecology (Elementar
220 Analysen Systeme GmbH, Hanau, Germany; IsoPrime100, IsoPrime limited, Stockport,

221 UK). Calibrated D-glutamic, glycine, acetanilide and histidine were used as references.
222 The analytical precision for $\delta^{15}\text{N}$ was better than 0.2‰.

223

224 ***Calculation and Statistical analysis***

225

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

233

234 The ^{15}N tracer recovery in all sampled components of ecosystem was estimated using
235 ^{15}N tracer mass balances as the following (Nadelhoffer & Fry, 1994):

236

$$237 \quad {}^{15}\text{N}_{\text{rec}} = \frac{(\text{atom}\% {}^{15}\text{N}_{\text{sample}} - \text{atom}\% {}^{15}\text{N}_{\text{ref}}) \times \text{N}_{\text{pool}}}{(\text{atom}\% {}^{15}\text{N}_{\text{tracer}} - \text{atom}\% {}^{15}\text{N}_{\text{ref}}) \times \text{N}_{\text{tracer}}} \times 100\%$$

238

239 where $^{15}\text{N}_{\text{rec}}$ = percent of ^{15}N tracer recovered in the labelled N pool; N_{pool} = N pool of
240 each ecosystem compartment; $\text{atom}\% {}^{15}\text{N}_{\text{sample}}$ = atom percent ^{15}N in the labelled
241 sample; $\text{atom}\% {}^{15}\text{N}_{\text{ref}}$ = atom percent ^{15}N in the reference sample (non- ^{15}N labelled);
242 and $\text{atom}\% {}^{15}\text{N}_{\text{tracer}}$ = atom percent ^{15}N of added tracer; N_{tracer} = the mass of ^{15}N in the
243 ^{15}N tracer applied to the plot.

244

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

249

$$250 \quad \text{NUE}_{\text{dep}} = {}^{15}\text{N}_{\text{recovery in wood}} \times (\text{C/N})_{\text{wood}}$$

251

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

258

259 **Results**

260

261 ***Ecosystem nitrogen pools and $\delta^{15}\text{N}$ in the two forests***

262

263 The total ecosystem N pool was about 7700 kg N ha⁻¹ in the primary forest and 7100

264 kg N ha⁻¹ in the secondary forest (excluding soils below 40 cm) (Table 1). The N pools
265 of trees were 2200 kg N ha⁻¹ in the primary forest and 1700 kg N ha⁻¹ in the secondary
266 forest, accounting for 95% of the total plant N pool in both forests. Total soil N pools
267 down to 40 cm depth were about 5500 kg N ha⁻¹ and 5400 kg N ha⁻¹ in the primary and
268 the secondary forest, respectively. There were 82 kg N ha⁻¹ and 68 kg N ha⁻¹ in the forest
269 floor in the primary and the secondary forests, accounting for only about 1% of the total
270 ecosystem N pools. The N pools in the major ecosystem compartments did not differ
271 between the two forests, except that the N pool in 0-10 cm mineral soils in the primary
272 forest was significantly higher than that in the secondary forest (Table 1).

273

274 The $\delta^{15}\text{N}$ values of different ecosystem compartments did not differ between two forests
275 before labelling, except in tree stems. Plants $\delta^{15}\text{N}$ varied from -1.8‰ to 0.3‰ in the
276 primary forest and from -1.7‰ to 0.8‰ in the secondary forest (Figure 1, Table S1 and
277 S2). The $\delta^{15}\text{N}$ of organic soil layer averaged -0.4‰ in the primary forest and -1.1‰
278 in the secondary forest, respectively. The $\delta^{15}\text{N}$ of mineral soil was always positive and
279 increased with soil depth in both forests (Figure 1).

280

281 After the ¹⁵N tracer addition, the $\delta^{15}\text{N}$ increased in all ecosystem pools of the two forests
282 (Figure 1, Table S1 and S2). However, the temporal patterns of $\delta^{15}\text{N}$ in different
283 ecosystem pools varied. The $\delta^{15}\text{N}$ of tree components and shrubs increased over time
284 (from -1.8‰ to 48.3‰ in the primary forest and from -1.5‰ to 84.8‰ in the secondary
285 forest) while the $\delta^{15}\text{N}$ of herbs, fine roots, and organic soil layer peaked at three months
286 and then decreased (Figure 1, Table S1 and S2). For 0-40 cm mineral soils, $\delta^{15}\text{N}$ also
287 increased three months after ¹⁵N tracer addition but did not change significantly from
288 three months to three years.

289

290 There were major differences in ¹⁵N abundance in the receiving ecosystem components
291 between ¹⁵NH₄⁺ and ¹⁵NO₃⁻. In the two forests, the $\delta^{15}\text{N}$ of tree foliage and branches
292 were significantly lower under ¹⁵NH₄⁺ labelling (4.2‰ to 18.6‰ in the primary forest
293 and 17.3‰ to 63.3‰ in the secondary forest) than under ¹⁵NO₃⁻ labelling (21.4‰ to
294 38.8‰ in the primary forest and 44.1‰ to 84.8‰ in the secondary forest) from three
295 months to three years (Figure 1, Table S1 and S2). In contrast, the $\delta^{15}\text{N}$ of the organic
296 soil layer was consistently higher under ¹⁵NH₄⁺ labelling than under ¹⁵NO₃⁻ labelling.
297 However, there were no significant differences in $\delta^{15}\text{N}$ of herbs and mineral soils
298 between ¹⁵NH₄⁺ and ¹⁵NO₃⁻ labelling in the primary forest. In the secondary forest, the
299 $\delta^{15}\text{N}$ of 0-10 cm mineral soils was significantly higher under ¹⁵NH₄⁺ than under ¹⁵NO₃⁻
300 labelling three months to one year after ¹⁵N tracer addition, but this difference
301 disappeared at three years after the ¹⁵N tracer addition.

302

303 ***Total ecosystem recovery***

304

305 Three months after ¹⁵N tracer addition, the total ecosystem recovery in the primary
306 forest was 60.4% and 59.1% with ¹⁵NH₄⁺ and ¹⁵NO₃⁻ labelling, respectively, and 63.8%
307 and 48.0% in the secondary forest (Figure 2, Table S3 and S4). One year after ¹⁵N tracer

308 addition, the total ecosystem recovery in the primary forest was 58.5% and 64.5% with
309 $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ labelling, respectively, and 60.9% and 59.7% in the secondary forest
310 (Figure 2, Table S3 and S4). Three years after ^{15}N tracer addition, the ^{15}N recovery in
311 the primary forest under $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ labelling was 67.9% and 73.7%,
312 respectively, and 61.0% and 57.1% in secondary forest (Figure 2, Table S3 and S4).
313 The change in the total ecosystem recovery over time was minor considering the
314 uncertainties in estimating the ^{15}N recovery. In addition, neither the tracer form nor the
315 forest type significantly affected the total ecosystem recovery of added ^{15}N (Table S6).

316

317 *^{15}N tracer redistribution in different ecosystem components*

318

319 There was no significant difference in plant ^{15}N recovery between two forests over time
320 (Table S6). In both forests, ^{15}N recovery in plants increased from three months to three
321 years after ^{15}N tracer addition. The ^{15}N recovery in plants in the primary forest increased
322 from 6.4% to 12.6% with $^{15}\text{NH}_4^+$ labelling and from 13.7% to 26.0% with $^{15}\text{NO}_3^-$
323 labelling ($P < 0.05$, Table S3). The ^{15}N recovery in plants in the secondary forest
324 increased from 12.1% to 21.3% with $^{15}\text{NH}_4^+$ labelling and from 13.8% to 22.1% with
325 $^{15}\text{NO}_3^-$ labelling ($P < 0.05$, Table S4). However, the temporal patterns of ^{15}N recovery
326 differed greatly among different plant components (Figure 3, Table S3, and S4). The
327 ^{15}N recovery in herbs and fine roots decreased with time in both forests, whereas
328 recovery in tree components and shrubs increased with time. Moreover, in the primary
329 forest, significantly more ^{15}N was recovered in plants after the $^{15}\text{NO}_3^-$ tracer addition
330 than after $^{15}\text{NH}_4^+$ addition at all sampling times. However, ^{15}N recovery in plant
331 compartments in the secondary forest did not differ significantly between $^{15}\text{NO}_3^-$ and
332 $^{15}\text{NH}_4^+$ labelling.

333

334 The temporal pattern of ^{15}N recovery in the organic soil layer differed from the patterns
335 of the plant pools. In both forests, ^{15}N recovery was high in the organic soil layer three
336 months after the ^{15}N tracer addition (21.0% and 11.7% with $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ labelling
337 in the primary forest, and 13.0% and 4.5% in the secondary forest), but declined
338 significantly over time afterward (Figure 2, Table S3 and S4). In addition, ^{15}N recovery
339 in the organic soil layer was higher for $^{15}\text{NH}_4^+$ than for $^{15}\text{NO}_3^-$ tracer in both forests
340 (Table S6), but the difference between the two decreased over time.

341

342 Mineral soil was the dominant sink for the added ^{15}N tracer (Figure 2, Table S3 and S4).
343 In the primary forest, 33.0% and 33.7% of the ^{15}N was found in the mineral soil after
344 three months with $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ labelling, and that recovery was 53.5% and 46.3%
345 after three years. However, soil retention of ^{15}N in the secondary forest did not change
346 significantly over time, with 37.6% and 33.2% of the ^{15}N being retained in the mineral
347 soil after three years under $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ labelling. The recovery of ^{15}N declined
348 with soil depth in two forests, with the highest ^{15}N recovery being observed in the 0-10
349 cm (26.6% and 21.9% with $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ labelling in the primary forest and 22.9%
350 and 19.2% in the secondary forest). Nevertheless, substantial amounts of ^{15}N were also
351 retained at 10-20 cm and 20-40 cm depth. Overall, ^{15}N recovery in mineral soil did not

352 differ significantly between $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ treatments in either forest (Table S3 and
353 S4).

354

355 **Discussion**

356

357 *Temporal patterns of total ecosystem recovery compared to temperate forests*

358

359 Our results indicated that large quantities of ^{15}N (about 40%) were lost only during the
360 first growing season, and from three months to three years, there was no significant
361 change in total ecosystem recovery. These results contradicted our first hypothesis that
362 the amount of ^{15}N retained in tropical montane forests over longer periods would
363 decrease substantially through leaching and gaseous loss. The potential mechanism for
364 the rapid initial losses might be that ^{15}N might be absorbed physically on the litter and
365 surface mineral soil and therefore lost through physical processes such as leaching or
366 erosion caused by heavy rain in the first few months after ^{15}N labelling (Wang et al.,
367 2018; Li et al., 2019). In addition, this pattern of initial losses in the first few months is
368 similar to that observed in several temperate forest experiments (Figure 4), suggesting
369 that total long-term ecosystem retention might be determined by the initial loss. A
370 recent long-term study also suggested that ^{15}N initially retained would remain in
371 temperate forests while newly deposited N would be lost from the system (Veerman et
372 al., 2020). We speculate that ^{15}N initially retained after the first few months might be
373 converted to organic forms and then enters the ecosystem internal N cycling.

374

375 The observed total ecosystem recovery of 70% and 60% of ^{15}N in the primary and
376 secondary tropical montane forests three years after the ^{15}N tracer addition (Table S3
377 and S4) were comparable to the mean recovery reported by long-term ^{15}N studies in
378 temperate forests which are considered to be N-limited (Figure 4, on average 58%, n =
379 8, t test, $P = 0.935$). Synthesis results of ^{15}N tracer studies have suggested that total
380 ecosystem retention is positively correlated with soil C/N represented ecosystem N
381 status (Vitousek et al., 1998; Templer et al., 2012). The soil C/N (11) in the studied
382 forests being within the range of that in temperate forests (9.7 to 29.6, Table S5),
383 suggesting that the N retention capacity in the studied tropical montane forests is
384 comparable to temperate forests over the long-term. In addition, the net primary
385 production (NPP) in the primary and secondary forests is about 4.5 and 8.3 Mg C ha^{-1}
386 yr^{-1} according to field inventory (Jiang, 2016). If the average C/N of 230 was used, 35
387 to 64 $\text{kg N ha}^{-1} \text{yr}^{-1}$ at least was needed to sustain the NPP. Thus, about 80% - 90% N
388 sustaining the NPP comes from soil N pool and is inner-recycled. We, therefore,
389 conclude that both the primary and secondary tropical montane forests we studied have
390 a conservative N cycle, where N is tightly recycled within these ecosystems once after
391 the atmospherically deposited inorganic N was transformed into organic form.

392

393 *Distribution of ^{15}N in different ecosystem components*

394

395 The distribution patterns of deposited N in the studied tropical forests differed

396 substantially from temperate and boreal forests, with larger fractions of added ^{15}N found
397 in plants and mineral soils than is the case with temperate and boreal forests where the
398 organic soil layer is a much more important sink (Figure 4, t-test, $P < 0.05$). This
399 difference in the patterns of ^{15}N distribution can be attributed to the differences between
400 tropical and temperate forests in climate (e.g., mean annual temperature and
401 precipitation), mass and decomposition rate of organic soil layers (Templer et al., 2012).
402 The thin organic soil layer and fast decomposition of litter in tropical forests due to high
403 temperature and precipitation might be release the ^{15}N retained and facilitate plant N
404 uptake (Wang et al., 2018). In contrast, thicker organic soil layers (and lower rainfall)
405 hamper the transfer of ^{15}N to mineral soil in temperate and boreal forests (Buchmann
406 et al., 1996; Gundersen, 1998; Koopmans et al., 1996; Nadelhoffer et al., 1999a;
407 Providoli et al., 2006; Liu et al., 2017a; Li et al., 2019). Our results also suggested that
408 the ^{15}N recovery in soil organic layer was positively correlated to the soil organic layer
409 mass ($R^2 = 0.88$, $P < 0.001$) (Figure S1, Table S5), further supporting these mechanisms.

410
411 Over a longer time scale, the deposited N is recycled and redistributed among the plant,
412 organic soil layer, and mineral soil in the studied tropical forests. Consistent with our
413 second hypothesis, the ^{15}N recovery increased in plants after three years (Figure 3),
414 indicating that deposited N that was initially retained in mineral soil and organic soil
415 layer over the long term has become available for plant uptake and assimilation (Wessel
416 et al., 2013; Goodale, 2017; Li et al., 2019). Earlier studies have also suggested that ^{15}N
417 tracer immobilized by microorganisms was slowly released to soil solution and then
418 assimilated by plants (Zogg et al., 2000; Zak et al., 2004). In our results, ^{15}N recovery
419 in shrubs and all tree components increased with time, but decreased in herbs and fine
420 roots (Figure 3), suggesting that assimilated N was transferred from active plant pools
421 to stable plant pools (Nadelhoffer et al., 2004; Goodale, 2017; Li et al., 2019). The
422 carbon sequestration efficiency of plants (NUE_{dep}) was estimated to be 14 and 18 kg C
423 per kg N for primary and secondary forest after three years, which is within the range
424 of values in temperate forests (Wang et al., 2018) and higher than the values estimated
425 for tropical forests (9 kg C per kg N, De Vries et al., 2014). According to a nutrient
426 addition experiment in the studied forests (Zhou, 2013), N addition enhanced
427 aboveground biomass carbon pool (NUE_{dep} by 24-35 kg C per kg N and 11 kg C per kg
428 N in the primary and secondary forests, respectively). Together, these results suggest
429 that over time more deposited N will be increasingly retained in high C/N ratio tree
430 components and therefore enhance N deposition-induced carbon sequestration
431 (Nadelhoffer et al., 1999a, b; Goodale, 2017).

432
433 In contrast to the pattern in the plants, the organic soil layer ^{15}N recovery declined from
434 three months (4.5% to 21.0%) to three years (1.5% to 2.1%), especially so in the
435 primary forest (Figure 2, Table S3 and S4). We attribute this to fast litter turnover in
436 tropical forests, resulting in the small capacity of organic soil layer to retain the added
437 ^{15}N (Gurmesa et al., 2016; Liu et al., 2017b; Wang et al., 2018). The ^{15}N initially
438 retained in organic soil layer could be transferred to the mineral soil, or released and
439 assimilated by plants (Wessel et al., 2013; Veerman et al., 2020). In numerous studies

440 in temperate forests, ^{15}N recovery decreased over time in the organic soil layer, which
441 was attributed to litter decomposition, physical leaching or downward transport by soil
442 fauna (Nadelhoffer et al., 2004; Goodale, 2017; Li et al., 2019).

443

444 In the mineral soils, there was no significant change in ^{15}N recovery from three months
445 to three years (Figure 2 and 4). The mineral soil was still the largest sink for deposited
446 N after three years. The long-term persistence of ^{15}N in mineral soil might be attributed
447 to the incorporation of ^{15}N into stable soil organic matter (SOM) pools (Perakis & Hedin,
448 2001; Goodale et al., 2015; Veerman et al., 2020). Previous studies have demonstrated
449 that inorganic N could be immobilized in the organic N pool through microbial
450 accumulation, condensation of N in microbial enzymes with phenolic compounds, or
451 abiotic reactions of inorganic N with soil organic matter (Johnson, 1992; Johnson et al.,
452 2000; Lewis & Kaye, 2012; Goodale et al., 2015; Liu et al., 2017a; Fuss et al., 2019),
453 while inputs of high C/N woody debris would also promote the immobilization of ^{15}N
454 by microbes (Lajtha, 2020). Moreover, the deposited N retained in mineral soil may
455 promote soil organic carbon accumulation in the studied forests which have the
456 conservative N cycle (Manzoni et al., 2017; Zhou et al., 2019). The nutrient addition
457 experiment in the studied forests also found that N addition enhanced soil organic
458 carbon pool (Zhou, 2013).

459

460 *Different fates of $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$*

461

462 In present study, total ecosystem retention did not differ significantly between $^{15}\text{NH}_4^+$
463 and $^{15}\text{NO}_3^-$ (Figure 2, Table S6), indicating that deposited NH_4^+ and NO_3^- can be
464 retained equally by the studied forest. Nonetheless, the patterns of ^{15}N distribution
465 within ecosystems (plants, organic soil layer and mineral soil) did differ, which might
466 be the potential reason for the similar total ecosystem ^{15}N recovery. Consistent with
467 many previous ^{15}N -field studies (Nadelhoffer et al., 2004; Feng et al., 2008; Sheng et
468 al., 2014; Liu et al., 2017a; Wang et al., 2018; Li et al., 2019), our results indicate that
469 deposited NO_3^- is more efficiently used by plants compared to NH_4^+ . The higher
470 recovery $^{15}\text{NO}_3^-$ in plants than $^{15}\text{NH}_4^+$ could be attributed to its higher mobility, so that
471 $^{15}\text{NO}_3^-$ can move more easily to the root surface and be assimilated by plants (Jacob &
472 Leuschner, 2015). Additionally, NO_3^- is more important in balancing cation uptake (e.g.,
473 K^+ , Ca^{2+} and Mg^{2+}) than NH_4^+ (Hoffmann et al., 2007). In contrast, NH_4^+ is likely
474 retained on cation exchange sites in soil organic matter and clay particles or
475 preferentially taken up by soil microbes (Gebauer et al., 2000; Providoli et al., 2006;
476 Jacob & Leuschner, 2015; Liu et al., 2017a). Furthermore, plant uptake of NO_3^- would
477 avoid direct competition for NH_4^+ with microbes (Kuzyakov & Xu, 2013). However,
478 these difference in tree components were less prevalent in the long-term, indicating that
479 both deposited $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ are slowly redistributed to stable plant pools over
480 time.

481

482 In our results, retention in the organic soil layer was significantly higher for $^{15}\text{NH}_4^+$
483 than for $^{15}\text{NO}_3^-$ (Table S6), which is consistent with previous studies (Corre &

484 Lamersdorf, 2004; Feng et al., 2008; Liu et al., 2017a; Li et al., 2019). Many studies
485 have demonstrated that forest floor microbes prefer NH_4^+ to NO_3^- due to its lower
486 energy cost during assimilation (Recous et al., 1990). Moreover, NO_3^- has greater
487 mobility than NH_4^+ and leaches readily to mineral soils. In the primary forest, the
488 organic soil layer was the major sink for deposited N (46%) under $^{15}\text{NH}_4^+$ labelling at
489 one week after ^{15}N tracer addition while 65% of ^{15}N was retained in mineral soil under
490 $^{15}\text{NO}_3^-$ labelling (Figure 2), further supporting this mechanism. However, ^{15}N recovery
491 three years after ^{15}N tracer addition in the organic soil layer did not differ between the
492 two N forms. Fast decomposition of litter in tropical forests is a possible mechanism
493 for similar retention patterns after three years. Both deposited NH_4^+ and NO_3^- could
494 over the three years be finally transferred to the mineral soil, or released and assimilated
495 by plants in the growing season (Nadelhoffer et al., 2004; Goodale, 2017; Li et al.,
496 2019).

497

498 Surprisingly, ^{15}N recovery in mineral soil did not differ between $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$
499 considering the uncertainties in estimating the mineral soil N pools (Table S3-S4 and
500 S6), in contrast to previous studies (Nadelhoffer et al., 2004; Feng et al., 2008; Sheng
501 et al., 2014; Liu et al., 2017a; Liu et al., 2017b; Li et al., 2019). This might be attributed
502 to the conservative N cycle of the studied tropical montane forests. A previous study
503 also suggested that both $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ can be incorporated into stable soil organic
504 matter and hence resulting in similar long-term “equilibrium” patterns of $^{15}\text{NH}_4^+$ and
505 $^{15}\text{NO}_3^-$ retention in N-poor forests (Perakis & Hedin, 2001). Added $^{15}\text{NH}_4^+$ can be
506 immobilized by soil microbes or incorporated into cation exchange sites in soil organic
507 matter (SOM) and clays (Perakis & Hedin, 2001; Zhu & Wang, 2011; Lewis & Kaye,
508 2012; Templer et al., 2012). The NO_3^- could also be incorporated to particulate and
509 mineral-associated SOM fractions through abiotic or biotic processes (Matus et al.,
510 2019; Fuss et al., 2019). For example, dissimilatory nitrate reduction to ammonium
511 (DNRA) has been hypothesized to play a key role in the retention of bioavailable N in
512 forests from high rainfall areas (Silver et al., 2001; Huygens et al., 2007; Templer et al.,
513 2008; Gao et al., 2016).

514

515 *Difference between the two forests*

516

517 In our study, both tropical montane forests have low N status (Wang et al., 2014), as
518 indicated by low rates of atmospheric N deposition and persistent ecosystem retention
519 (Figure 2), but the primary forest was initially somewhat more N-rich than the
520 secondary forest (Wang et al., 2014). However, there was no significant difference in
521 ecosystem N retention between two forests over time (Table S6), which contradicted
522 our fourth hypothesis that lower ^{15}N retention in the primary forest due to its relatively
523 higher N status than the secondary forest. Although there were differences in labelling
524 time and the amount of ^{15}N tracer between the two forests, the similarity in N retention
525 pattern were not due to the inconsistent experimental designs. The precipitation varied
526 between two years and the precipitation in the first three months after ^{15}N labelling in
527 the primary forest (Year 2015) was larger than that in the secondary forest (Year 2016)

528 (Figure S2). Moreover, twice as much tracer was applied to the secondary forest (50
529 mg $^{15}\text{N m}^{-2}$) as to the primary forest (25 mg $^{15}\text{N m}^{-2}$). However, our results suggested
530 that about 40% of ^{15}N were lost only during the first three months in the two forests,
531 and from three months to three years, there was no significant change in total ecosystem
532 recovery (Figure 2). Thus, the differences in precipitation and the amount of ^{15}N tracer
533 could not affect the patterns of ^{15}N retention in the two forests. We therefore suggested
534 that succession status did not strongly affect total ecosystem recovery nor the
535 distribution patterns of added ^{15}N in our two tropical forests.

536 537 **Conclusions**

538
539 In this study, we presented the first analysis of the fates of deposited NH_4^+ and NO_3^-
540 over three years for two tropical montane forests. More than 60% of ^{15}N was retained
541 in both primary and secondary tropical montane forests one as well as three years after
542 ^{15}N tracer addition, indicating persistent ecosystem retention of deposited N in these
543 forests. Although total ecosystem ^{15}N recovery did not change significantly with time,
544 the deposited N became redistributed within the forests. The retention and
545 retranslocation patterns in plants, organic soil layers, and mineral soil differed between
546 $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ tracer in the two forests. More $^{15}\text{NO}_3^-$ than $^{15}\text{NH}_4^+$ was retained by
547 plants and the total ^{15}N recovery attributed to plants increased over time. In contrast to
548 long-term retention in plants, the organic soil layer was a transient sink for deposited N
549 and more $^{15}\text{NH}_4^+$ was retained here. The mineral soil was the largest ecosystem sink for
550 deposited N. It was surprising that the ^{15}N recovery of mineral soil remained relatively
551 steady in study forests over time and that ^{15}N recovery in mineral soil did not differ
552 between the two N forms. Neither forest types nor N forms significantly affected total
553 ecosystem N retention. Overall, our results suggest that deposited N is redistributed to
554 more stable plant and soil pools over time. Critically, our results indicate that roughly
555 60% of the deposited N was still retained within tropical montane forests after three
556 years, from which we expect the retained N to benefit tropical forest growth and
557 enhance carbon sequestration.

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560
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570 571 **References**

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817

818 **Table 1** Dry mass, nitrogen pool, total nitrogen concentration and carbon: nitrogen ratio (C/N) of major ecosystem components before adding ¹⁵N
 819 tracer in the two tropical montane forests. Values in parentheses are one standard error (n = 3). Different lowercase superscript letters within a row
 820 represent statistically significant ($P \leq 0.05$) differences.

Ecosystem components	Dry mass (Mg ha ⁻¹)		N pool (kg ha ⁻¹)		%N		C/N	
	Primary	Secondary	Primary	Secondary	Primary	Secondary	Primary	Secondary
Tree								
Foliage	11 (1)	10 (0.2)	188 (24)	167 (3)	1.69 (0.03)	1.72 (0.03)	28.4 (0.5)	28.2 (0.5)
Branch	80 (14)	65 (2)	481 (87)	419 (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)	188 (4)	0.66 (0.05)	0.71 (0.05)	74.3 (4.1)	82.6 (4.0)
Stem	289 (52)	234 (6)	578 (104)	396 (10)	0.18 (0.01)	0.17 (0.01)	318.9 (24.8)	326.5 (14.8)
Root	167 (37)	130 (4)	670 (146)	530 (17)	0.40 (0.01) *	0.41 (0.01) *	197.7 (13.4) *	202.4 (9.3) *
Subtotal	579 (109)	465 (12)	2105 (390)	1701 (43)				
Shrub	0.4 (0.1)	0.7 (0.1)	5 (0.9)	8 (1)	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)	0.7 (0.2)	1.76 (0.2)	1.51 (0.19)	24.0 (2.0)	27.8 (4.5)
Root								
< 2 mm	5 (1)	3 (0.4)	55 (12)	34 (4)	1.20 (0.1)	1.01 (0.06)	40.8 (2.5)	46.1 (2.8)
2-10mm	8 (0.4)	5 (2)	62 (3)	37 (10)	0.77 (0.1)	0.69(0.04)	64.7 (4.2)	68.9 (4.1)
Plant subtotal	592 (110)	475 (14)	2228 (395)	1781 (60)				
Organic soil layer	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 (18)	2154 ^a (35)	1830 ^b (18)	0.19 (0.01)	0.17 (0.02)	12.0 (0.6)	11.8 (0.5)
10-20 cm	1204 (58)	1106 (21)	1445 (70)	1364 (25)	0.12 (0.02)	0.12 (0.02)	10.9 (0.4)	11.4 (0.2)
20-40 cm	2651 (161)	2397 (80)	1856 (113)	2198 (63)	0.07 (0.01)	0.09 (0.01)	10.0 (0.3)	10.9 (0.2)
Soil subtotal	4995 (208)	4594 (135)	5537 (171)	5395 (115)				
Ecosystem total	5587 (532)	5069 (25)	7768 (965)	7164 (110)				

821
 822 Notes: *Root of trees was not sampled due to the highly destructive. The N concentration and C/N of tree root was estimated by the mean value of branch and stem.
 823

824 **Legends for figures**

825

826 **Figure 1** Mean $\delta^{15}\text{N}$ values of major ecosystem compartments before and three months
827 after, one year after and three years after ^{15}N addition in two forests. Error bars are
828 standard error of the mean ($n = 3$).

829

830 **Figure 2** The ^{15}N recovery in plant, organic soil layer and mineral soil at three months,
831 one year and three years in the two study forests. Labelling date was April 15th, 2015
832 (primary forest) and April 15th, 2016 (secondary forest). ^{15}N recovery one week and one
833 month after ^{15}N tracer addition was only available for the primary forest and only trees
834 and shrubs were included as plants.

835

836 **Figure 3** The ^{15}N recovery in different plant compartments three months, one year and
837 three years after ^{15}N labelling in the two study forests. “Tree-woody biomass” includes
838 branch, bark, stem and root of trees. Labelling date was on April 15th, 2015 (primary
839 forest) and April 15th, 2016 (secondary forest). ^{15}N recovery one week and one month
840 after ^{15}N tracer addition was only available for the primary forest and only trees and
841 shrubs were included as plants. ^{15}N recovery in stems and roots of trees was only
842 measured for one year and three years after ^{15}N tracer addition.

843

844 **Figure 4** The ^{15}N recovery (%) in our two tropical forest ecosystems in comparison
845 with other studies from temperate forests. Only forests for which ^{15}N recovery has been
846 determined for at least three years were analyzed. Details of site characteristics are
847 provided in Table S5. Note: JFL-P and JFL-S represent primary forest and secondary
848 forest in Jianfengling (current study); QY-L and QY-M represent larch forest and mixed
849 forest in Qingyuan (Li et al., 2019); Harvard-H and Harvard-P represent oak forest and
850 red pine forest in Harvard (Nadelhoffer et al., 1999a; Nadelhoffer et al., 2004);
851 Spillimacheen (Preston et al., 1990; Preston & Mead, 1994); Ysselsteyn (only $^{15}\text{NH}_4^+$
852 labelling, Wessel et al., 2013); Arnot (only $^{15}\text{NO}_3^-$ labelling, Goodale, 2017); Alptal
853 ($^{15}\text{NH}_4^{15}\text{NO}_3$ labelling, Schlegger et al., 1999; Providoli et al., 2005; Krause et al., 2012).

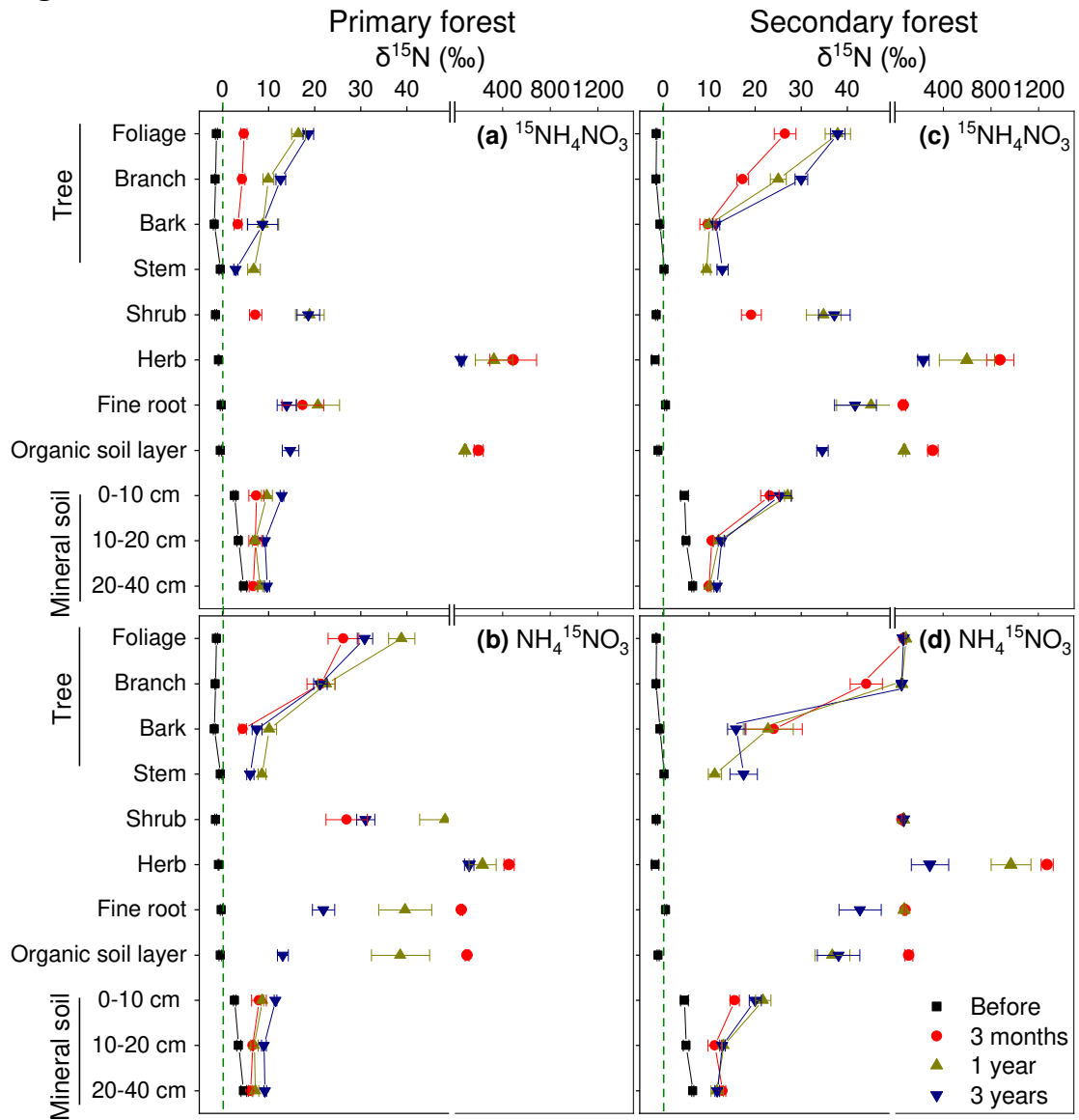


Figure 2

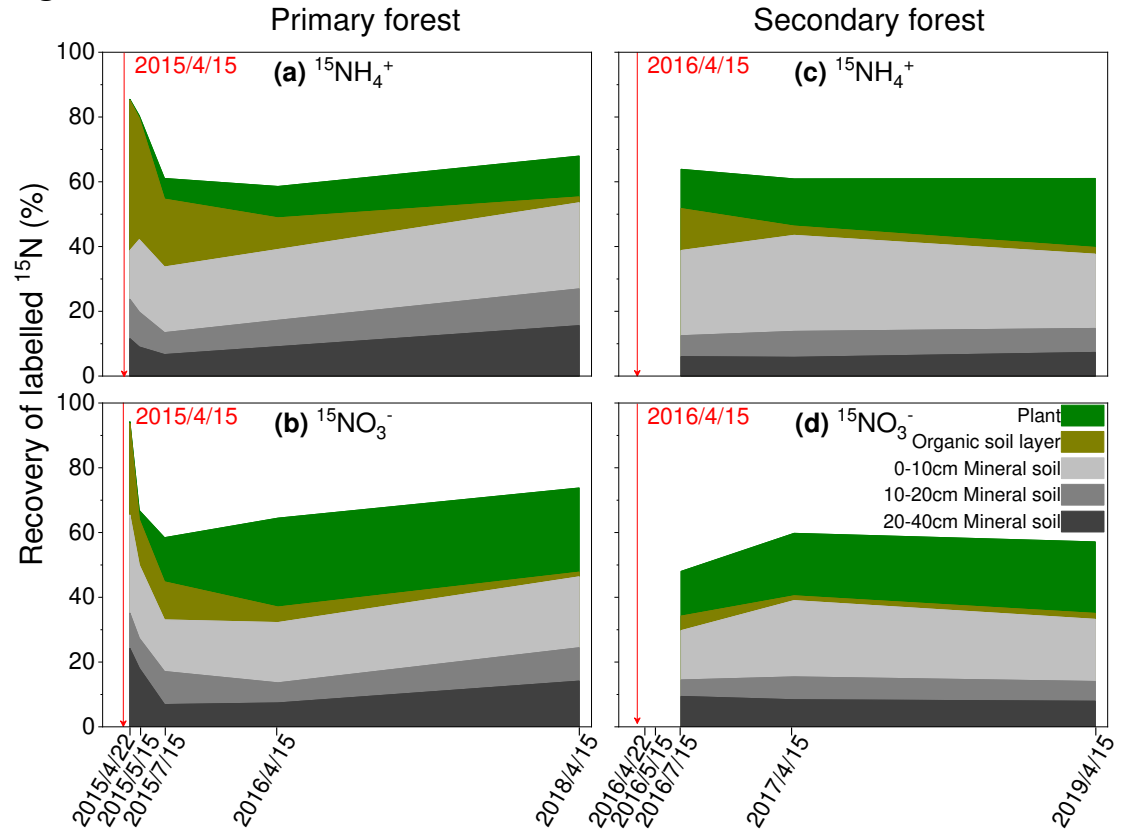
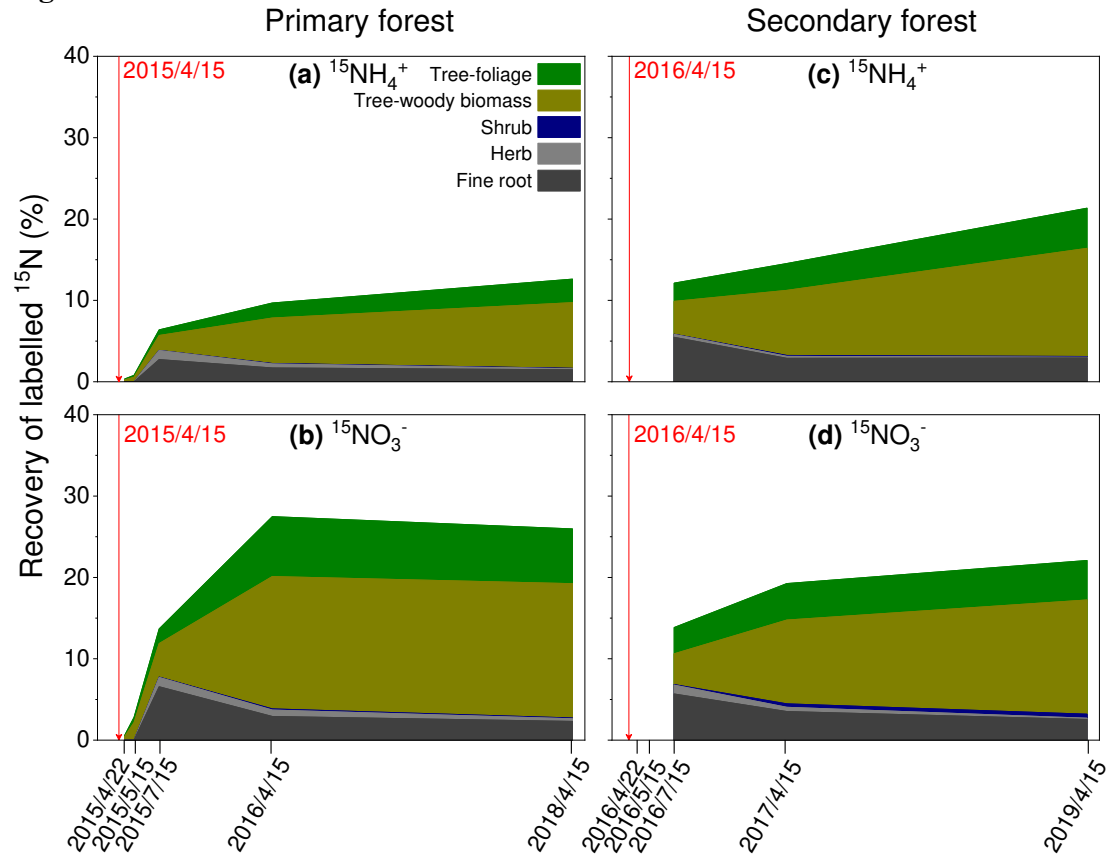
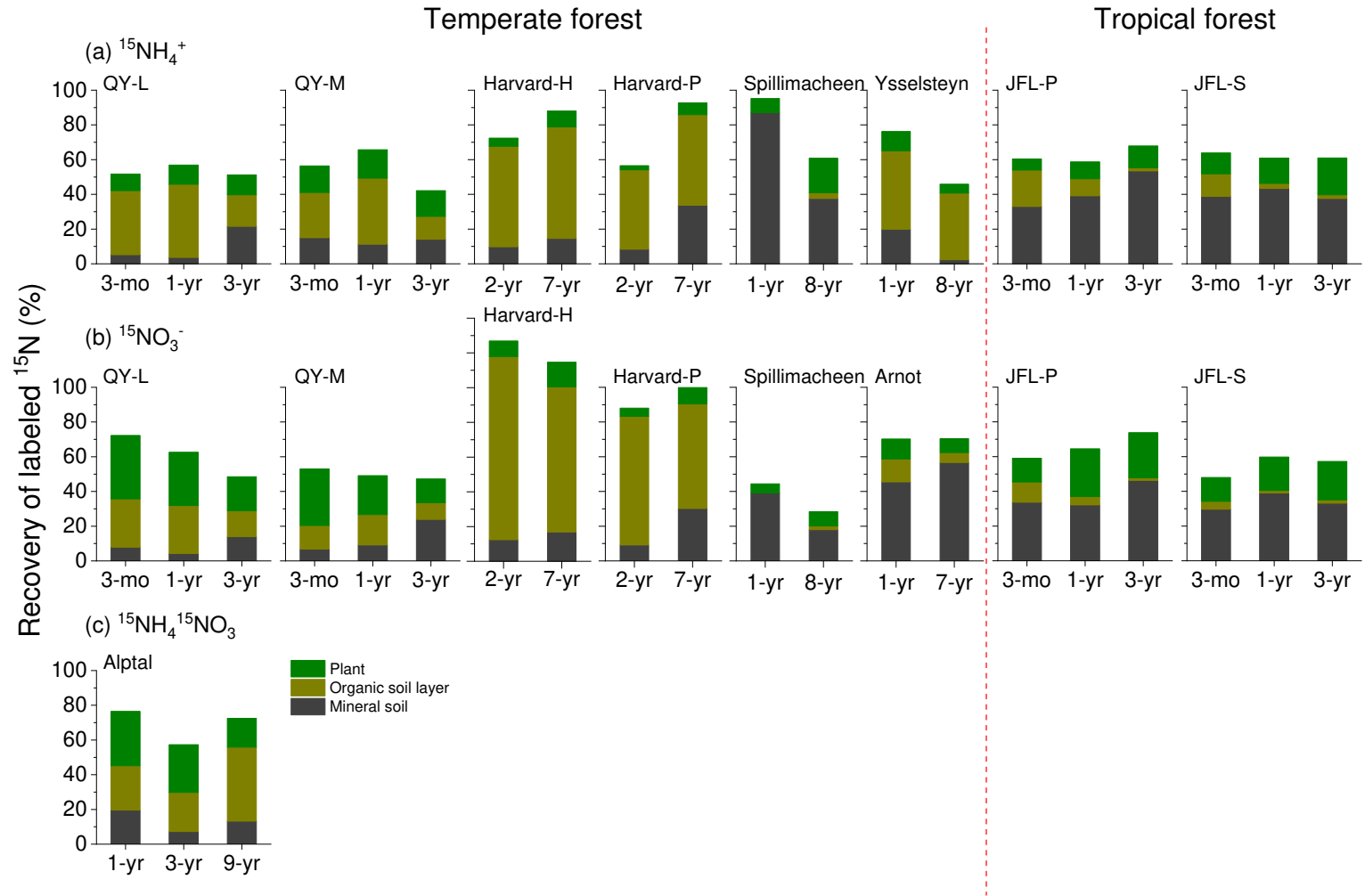


Figure 3



860 **Figure 4**



861