

1 **C:N:P stoichiometry in six distinct habitats of a glacier terminus in the**
2 **Yangtze River Source Area**

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15

16 **Abstract**

17 Glaciers are among the least explored environments on Earth, especially from a perspective
18 of nutrient stoichiometry. In this study, we documented and compared the nutrient
19 availabilities (concentrations) and composition (stoichiometric ratios) of nutrients (C, N,
20 and P) in six distinct habitats of a glacier terminus in the Yangtze River Source area,
21 including surface ice (SI), basal ice (BI), basal sediment (BaS), newly exposed forefront
22 soil close to glacial terminus (TS), soil at increasing distances from glacier terminus (DS),
23 and forefront soil with well-developed vegetation (VS). The results showed that SI had
24 significantly higher DOC and N concentrations as well as higher C:P and N:P ratios than
25 BI. However, BI had significantly higher SRP than SI. In addition, both SI and BI had very
26 high C:P and N:P ratios, suggesting P-limitation. For sediment/soil in glacier terminus,
27 nitrogen and organic carbon concentrations were significantly lower in BaS, TS, and DS
28 than in VS. Moreover, TP and SRP concentrations were significantly higher in BaS and
29 VS than in TS and DS. These nutrient patterns could be explained by differences in biotic
30 influence in soil development or by changes in soil physical properties. With regard to
31 nutrient limitation, VS had a significantly higher C:N, C:P, and N:P ratios than BaS, TS,
32 and DS, supporting a long-held biogeochemical and ecological paradigm that ecosystem
33 processes during early successional stages are primarily organic C and N limited but are P-
34 limited in later successional stages. Considering that glaciers cover around 10% of the
35 terrestrial landmass and are experiencing severe retreat, documenting and comparing
36 nutrient contents and stoichiometry in glacier terminus can further our understanding of
37 global biogeochemical cycles under future climate change regimes.

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38 **Keywords:** Ecological stoichiometry, Glacier retreat, Nutrient limitation, Yangtze River

39 Source, Qinghai Tibet Plateau,

40

41 **Introduction**

42 Glaciers cover approximately 10% of land surface and hold about 75% of the freshwater
43 on Earth (Anesio et al, 2009; Stibal et al, 2012), comprising diverse and unique habitats
44 that host distinctive organisms and have distinct biogeochemical properties (Singer et al,
45 2012; Cauvy-Fraunié and Dangles, 2019; Stibal et al, 2020). However, glaciers are
46 retreating at accelerated rates globally as a result of climate change (Marzeion et al, 2014;
47 Zemp et al, 2019). Glacier retreat involves loss of surface and terminal ice masses, exposes
48 basal sediments to new soil habitats, and creates new aquatic environments, leading to
49 tremendous changes on structures and processes of glacial ecosystems (Fell et al, 2017;
50 Darcy et al, 2018). However, we had very limited knowledge of these distinct and rapidly
51 changing habitats, especially from a perspective of nutrient stoichiometry. Gaining such
52 knowledge could improve our understanding of glacial ecosystem functioning and global
53 biogeochemical cycles (Ren et al, 2019; Elser et al, 2020).

54 Glacial ecosystems provide diverse and dynamic habitats harboring extensive biological
55 diversity and supporting multiple trophic levels (Kohshima, 1984; Anesio and Laybourn-
56 Parry, 2012; Hotaling et al, 2019). Supraglacial environments, the surface ice layer, are
57 available habitats for primary productivity dominated by glacier and snow algae (Anesio
58 et al, 2017; Stibal et al, 2020). Autochthonous organic carbon is accumulated
59 photosynthetically by these photoautotrophs and sustains local heterotrophic biota as well
60 as downstream ecosystems (Williamson et al, 2019). Subglacial environments, including
61 the basal ice and basal sediments, also harbor taxonomically and functionally diverse
62 microorganisms, which are mainly prokaryotic and rely on chemical energy (Tranter et al,
63 2005; Stibal et al, 2020). Basal ice and basal sediments are directly contacted by

64 interactions between each other through basal processes, such as glaciohydraulic
65 supercooling (Lawson et al, 1998) and melt-refreezing (Knight, 1997), allowing exchanges
66 of nutrients and microorganisms (Doyle et al, 2013; Montross et al, 2014). Moreover,
67 subglacial environments are also connected with supraglacial environments through
68 fracture hydrological networks, which transport nutrients and microorganisms from the
69 surface to the base of glaciers, and eventually to the forefront soil and downstream aquatic
70 ecosystems (Fountain et al, 2005; Anesio et al, 2010; Milner et al, 2017; Ren et al, 2017).
71 During glacier retreat, the basal sediments in glacial terminus are exposed to barren soil
72 habitats which are colonized by pioneering organisms (Pessi et al, 2019). As the first biota
73 colonizing freshly exposed substrates, microorganisms play crucial roles in soil formation
74 and biogeochemical processes (Nemergut et al, 2007; Schmidt et al, 2008; Brankatschk et
75 al, 2011; Dresch et al, 2019), experiencing low temperature, aridity, and low nutrient
76 availability (Darcy et al, 2018). Over successional time, plant colonization promotes soil
77 formation by accumulating organic matter and secreting organic acids (Miniaci et al, 2007;
78 Li et al, 2020).

79 Nutrients are the key limiting factors for organismal growth and ecosystem productivity
80 (Elser et al, 2000; Sterner and Elser, 2002), especially in nutrient-scarce cryosphere
81 environments (Ren et al, 2019). The availability and composition of key chemical elements
82 (C, N, and P) are good indicators of ecosystem nutrient status and are critical in regulating
83 ecosystem structure and processes (Sterner and Elser, 2002; Elser et al, 2007), such as ice-
84 associated food webs and linkages among different habitats (Ren et al, 2019; Elser et al,
85 2020). C, N, and P concentrations in surface ice, snow, and cryoconite holes have been
86 widely reported in mountain glaciers, Greenland, and Antarctica (Ren et al, 2019).

87 However, C, N, and P are usually not studied simultaneously in the same area, which makes
88 it hard to assess the relative balance of different elements (C:N:P stoichiometry) as well as
89 stoichiometric relationships between different habitats (Ren et al, 2019). Specifically,
90 subglacial environments remain largely unknown due to difficulties in accessing and
91 sampling (Anesio et al, 2017; Kayani et al, 2018), resulting in scarce and patchy
92 information of C, N, and P (Ren et al, 2019). In the glacier forefield, C:N:P stoichiometry
93 is well-studied in glacier-fed streams and lakes (Hood and Scott, 2008; Slemmons and
94 Saros, 2012; Laspoumaderes et al, 2013; Milner et al, 2017) but is not well documented in
95 glacier forefront soils at different development stages. As glacier retreat continues, the
96 knowledge of C:N:P stoichiometry will assist in future predictions of changes in
97 biogeochemical processes and trophic interactions of mountain cryosphere (Ren et al,
98 2019). However, we lack a synthetic understanding of C:N:P stoichiometry of diverse
99 habitats in the same area or same glacier.

100 We conducted this study in the Dongkemadi Glacier in the Yangtze River Source Area in
101 the central Qinghai-Tibet Plateau (QTP). QTP is the largest reservoir of glaciers outside
102 the polar regions and regarded as the “Water Tower of Asia” (Yao et al, 2012).
103 Temperatures are rising three times faster on QTP than the global rate in the past 50 years
104 (Piao et al, 2011), resulting in rapid glacier retreat over the past decades (Xu et al, 2009).
105 In this study, we focused on six distinct habitats, including the surface ice, basal ice, basal
106 sediment, newly exposed forefront soil close to glacial terminus, soil at increasing
107 distances from glacier terminus, and forefront soil with well-developed vegetation. Our
108 aim is to provide the first comprehensive assessment of C:N:P stoichiometry in these
109 distinct habitats of a glacier terminus. Understanding nutrient stoichiometric properties of

110 these diverse, intimately connected, and rapidly changing habitats will help in gaining new
111 insights into glacial ecology and biogeochemistry.

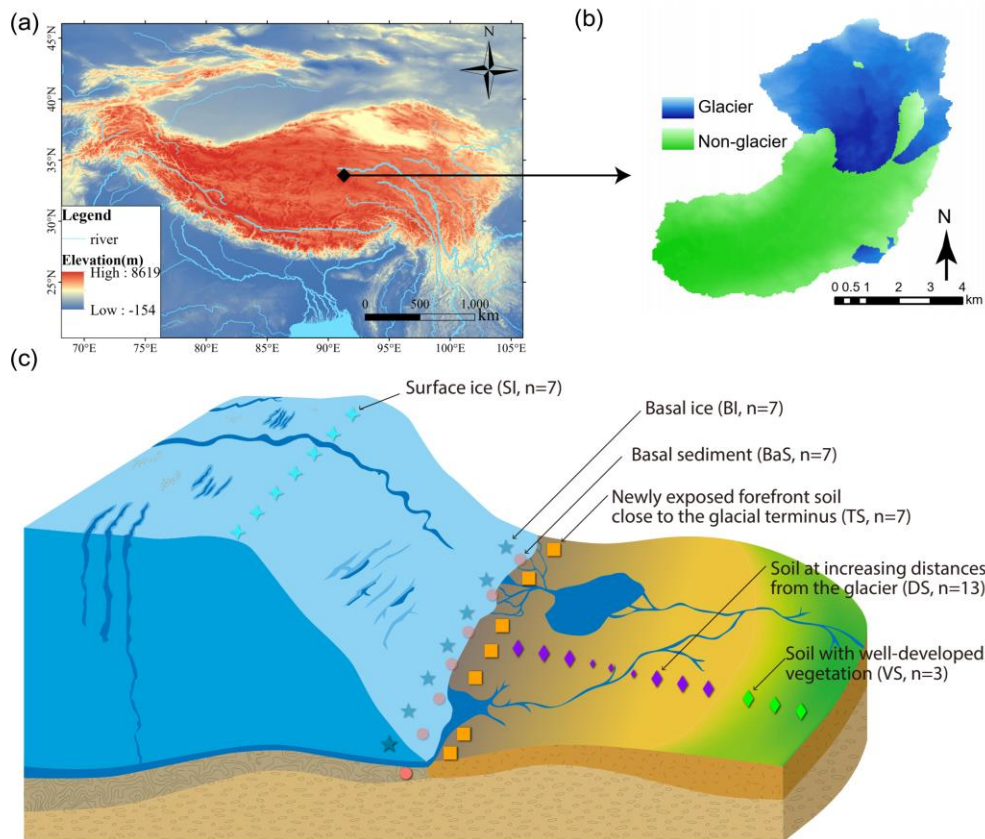
112 **Methods**

113 *Study area and field sampling*

114 Located in the Yangtze River Source in the central QTP, the Dongkemadi Glacier (33°04'N,
115 92°04'E) covers an area of 15.89 km² and has the altitude between 5420 to 5919 m (Figure
116 1). The annual precipitation of Dongkemadi Glacier is 680 mm and the annual air
117 temperature is -8.6°C. Since 1970, Dongkemadi Glacier has started to shrink rapidly and
118 provides an increasing amount of meltwater to the Yangtze River.

119 The field sampling was conducted in early July, 2019. In the terminus of Dongkemadi
120 Glacier (Figure 1), we set up sample sites to collect surface ice (SI, n=7), basal ice (BI,
121 n=7), basal sediment (BaS, n=7), newly exposed forefront soil close to glacial terminus
122 (TS, n=7), soil at increasing distances from the glacier (DS, n=13), and soil with well-
123 developed vegetation (VS, n=3). SI samples were collected at the depth of 0-10 cm on the
124 glacier surface. BI samples were collected at the bottom of the ice sheet with 10 cm above
125 the base. BaS samples were collected from the sediments under the ice for a depth of 0-10
126 cm. TS samples were collected in front of the glacier at a distance of 1 meter to the glacier
127 snout, representing the newly exposed soil. DS samples were collected from the foreland
128 soil with an increased distance from 5 to 450 meters to the glacier snout without vegetation
129 or with scarce vegetation. VS samples were collected with well-developed vegetation
130 (vegetation coverage >90%) at a distance beyond 665 meters. For each soil sample (TS,
131 DS, and VS), five representative points of the topsoil (0-10 cm in depth) were sampled by
132 a soil auger (10 cm inner diameter, cleaned between each sampling) and pooled into one

133 composite sample. All the ice, sediment, and soil samples were placed in sterile bags and
134 transported to the field laboratory for further processing in a cooler.



135

136 Figure 1 (a) The location of the study area in the Yangtze River Source in the central
137 Qinghai-Tibetan Plateau (QTP). (b) A schematic view of the Dongkemadi Glacier. (c) A
138 schematic view of the sampling sites from six different habitats.

139 *Chemical analyses*

140 For ice samples (SI and BI), nutrient concentrations were tested after the ice melted at room
141 temperature. Total nitrogen (TN) was measured by ion chromatography after persulfate
142 oxidation (EPA 300.0). Total phosphorus (TP) was measured using the ascorbic acid
143 colorimetric method after persulfate oxidation (EPA 365.3). The meltwater samples used
144 for analyzing nitrate (NO_3^- -N), ammonium (NH_4^+ -N), and soluble reactive phosphorus

145 (SRP) were filtered using glass fiber filters (GF/F, Whatman). After filtration, NO_3^- -N was
146 determined by ion chromatography (EPA 300.0). NH_4^+ -N was determined using the
147 indophenol colorimetric method (EPA 350.1). Soluble reactive phosphorus (SRP) was
148 quantified using the ascorbic acid colorimetric method (EPA 365.3). pH and conductivity
149 in meltwater were also measured using a multiparameter instrument (YSI ProPlus, Yellow
150 Springs, Ohio) (Figure S1).

151 Sediment and soil samples (BaS, TS, DS, and VS) were naturally dried and sieved through
152 100-mesh size to remove all visible roots, residues, and stones. Soil/sediment organic
153 carbon (SOC) was measured by oxidizing with potassium dichromate (HJ615-2011). Total
154 nitrogen (TN) was measured using the modified Kjeldahl Method (HJ717-2014). Total
155 phosphorus (TP) was measured using the ascorbic acid colorimetric method. Nitrate (NO_3^-
156 -N) and ammonium (NH_4^+ -N) were extracted using 2 M potassium chloride and percolated
157 through filters and measured by a spectrophotometer (HJ634-2012). Soluble reactive
158 phosphorus (SRP) were extracted using 0.5 M sodium bicarbonate and percolated through
159 filters and then measured using the ascorbic acid colorimetric method. pH was measured
160 in 1:2.5 soil to distilled water ratio using a pH and conductivity was measured in 1:5 soil
161 to distilled water ratio using a conductivity meter (Figure S2).

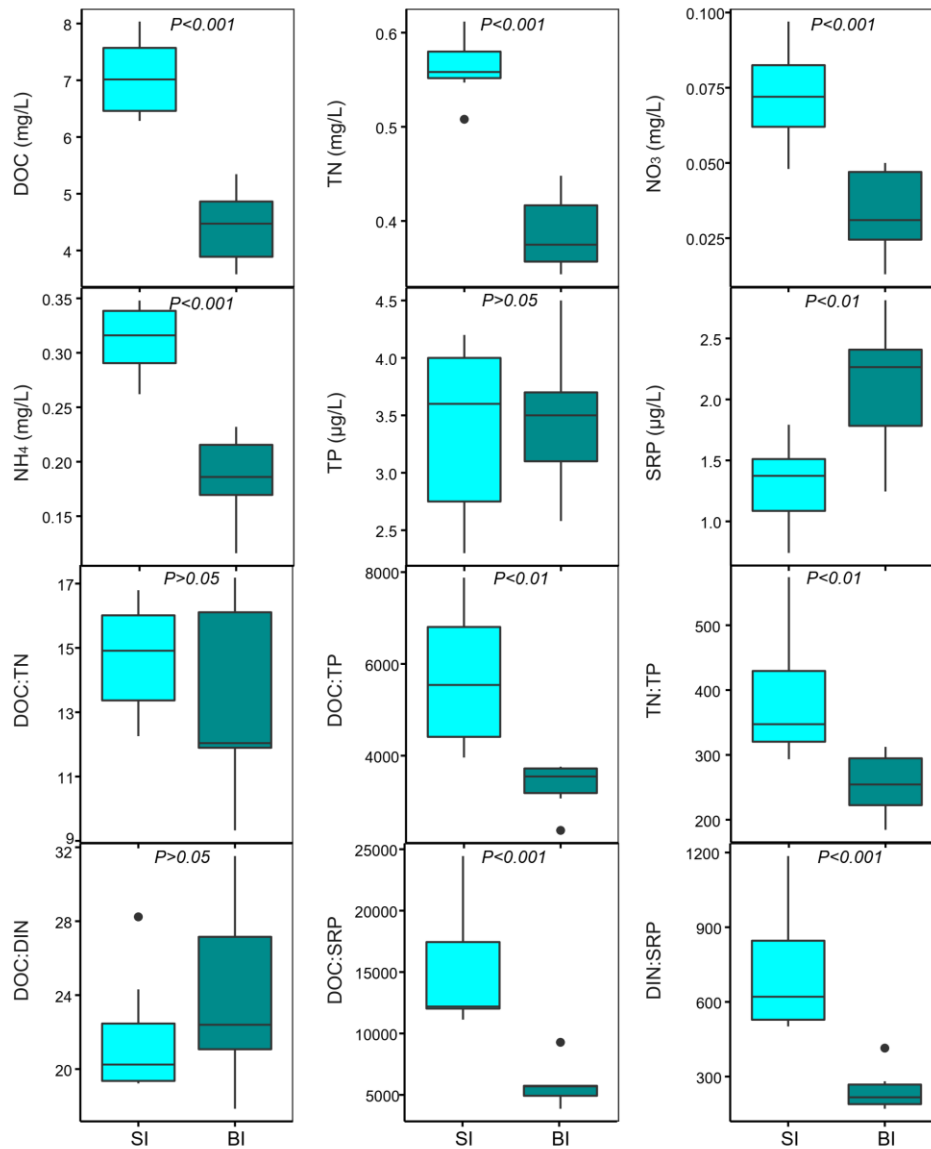
162 ***Analyses***

163 The statistical significance of differences of C, N, and P concentrations as well as their
164 stoichiometric ratios for different habitats were analyzed using ANOVA in R 3.4.4 (R Core
165 Team, 2017). All stoichiometric ratios are given as molar ratios. We plot the data using
166 ggplot2 package (Wickham, 2011) in R 3.4.4 (R Core Team, 2017).

167 **Results and Discussion**

168 *C, N, and P concentrations and stoichiometry ratios in ice*

169 At the glacier terminus, surface ice had a significantly higher DOC, TN, NO_3^- -N, and NH_4^+ -
170 N concentrations than basal ice (Figure 2). However, basal ice had a significantly higher
171 SRP than surface ice (Figure 2). TP was not significantly different between surface ice and
172 basal ice. In both surface ice and basal ice, NH_4^+ -N was 4.6 and 6.9 times higher than NO_3^- -
173 -N in surface and basal ice, respectively (Figure 2). DIN (estimated by NO_3^- -N and NH_4^+ -
174 N) accounted for 68% and 57% of TN in surface and basal ice on average, respectively.
175 SRP accounted for 38% and 62% of TP in surface and basal ice on average, respectively.
176 Surface ice had a significantly higher DOC:TP, TN:TP, DOC:SRP, and DIN:SRP than
177 basal ice (Figure 2). DOC:TN, and DOC:DIN were not significantly different between
178 surface ice and basal ice (Figure 2). The average value of DOC:TN was 15 and 14, DOC:TP
179 was 5,687 and 3,356, TN:TP was 388 and 255, DOC:DIN was 22 and 24, DOC:SRP was
180 15,244 and 5,739, and DIN:SRP was 722 and 245 in surface ice and basal ice, respectively.



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182 Figure 2 Nutrient concentrations and stoichiometry ratios in surface ice (SI) and basal ice
183 (BI). The differences were tested using ANOVA.

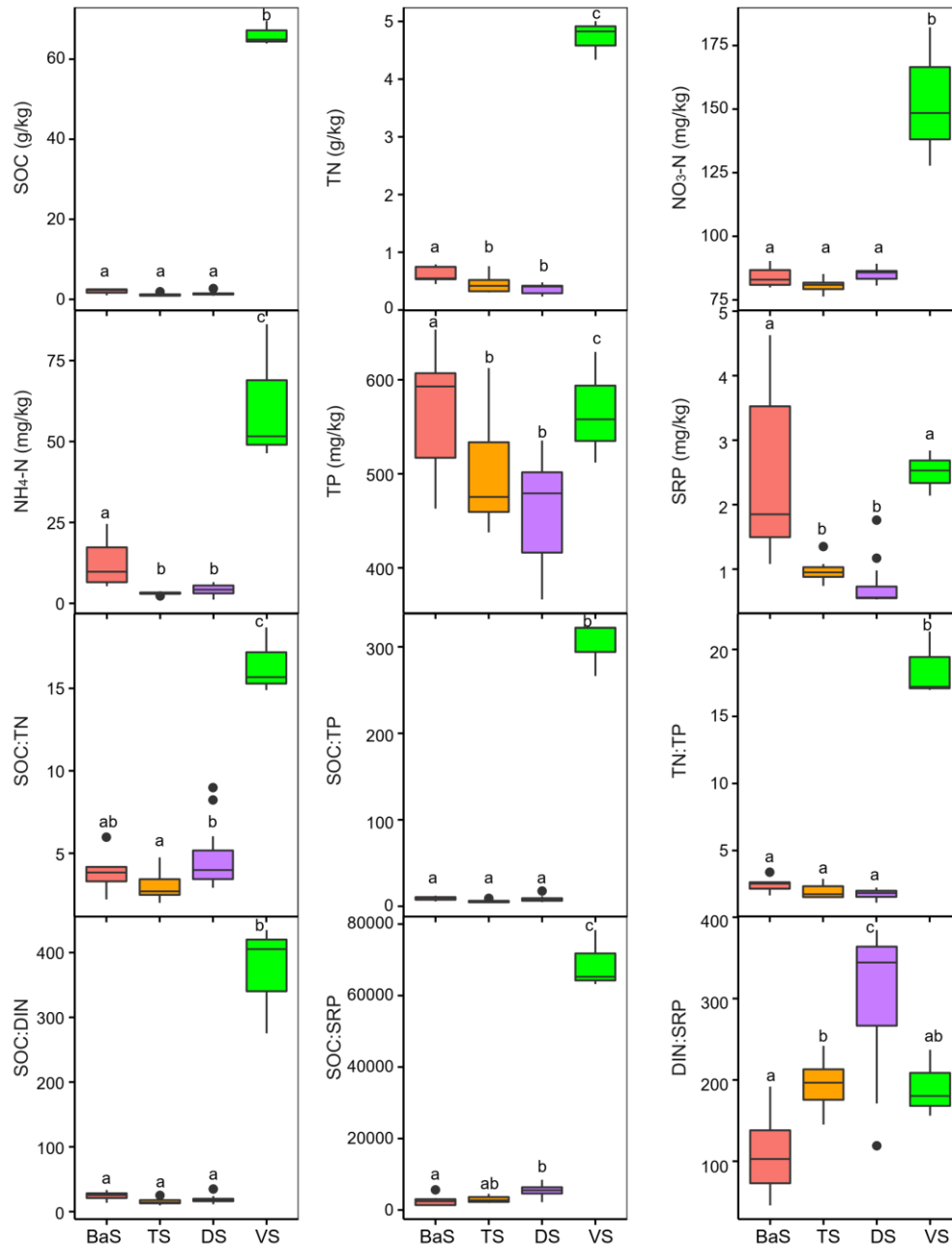
184 ***C, N, and P concentrations and stoichiometry ratios in sediment and soil***

185 Basal sediment had significantly higher TN, NH₄⁺-N, and SRP concentrations than the
186 newly exposed forefront soil close to glacial terminus (BaS vs. TS, Figure 3). The newly
187 exposed forefront soil close to glacial terminus had organic carbon and nutrient

188 concentrations similar to the soil distant from the glacier (TS vs. DS, Figure 3). However,
189 soil with well-developed vegetation had significantly higher SOC, TN, NO_3^- -N, and NH_4^+ -
190 N than BaS, TS, and DS (Figure 3). Meanwhile, TP and SRP concentrations were
191 significantly higher in VS than in TS and DS (Figure 3). TP was also significantly higher
192 in BaS than in TS, DS, and VS (Figure 3).

193 In these sediments and soils, DIN only accounted for a small proportion of TN with average
194 values of 16%, 20%, 26%, and 7% in BaS, TS, DS, and VS, respectively (Figure 3). NH_4^+ -
195 N was much lower than NO_3^- -N especially in TS and DS (Figure 3). SRP accounted for a
196 very small proportion of TP with average values of 0.45%, 0.20%, 0.17%, and 0.43% in
197 BaS, TS, DS, and VS, respectively (Figure 3).

198 Basal sediment had significantly lower DIN:SRP ratio than newly exposed forefront soil
199 close to glacial terminus (BaS vs. TS, Figure 3). Newly exposed forefront soil close to
200 glacial terminus had significantly lower SOC:TN and DIN:SRP than the soil distant to the
201 glacier (TS vs. DS, Figure 3). Vegetated soil had a significantly higher SOC:TN, SOC:TP,
202 TN:TP, SOC:DIN, and SOC:SRP than BaS, TS, and DS (Figure 3). For BaS, TS, DS, and
203 VS, the average values of SOC:TN were 4, 3, 5, and 16, SOC:TP was 9, 6, 8, and 305,
204 TN:TP was 2.5, 2, 1.8, and 19, SOC:DIN was 24, 16, 19, and 37, SOC:SRP was 2606,
205 3008, 5488, and 68,937, and DIN:SRP was 109, 194, 300, and 191, respectively.



206

207 Figure 3 Nutrient concentrations and stoichiometric ratios of sediment and soil, including
 208 BaS (basal sediment), TS (newly exposed forefront soil close to glacial terminus), DS (soil
 209 at increasing distances from the glacier), and VS (soil with well-developed vegetation).
 210 Different lowercase letters indicate a significant difference between habitats while the same
 211 lowercase letter indicates a non-significant difference from ANOVA.

212 **Discussion**

213 *Nutrient concentrations and stoichiometry ratios in ice*

214 At the Dongkemadi Glacier, surface ice had significantly higher DOC and N concentrations
215 as well as higher C:P and N:P ratios than basal ice. However, basal ice had significantly
216 higher SRP concentrations than surface ice. In addition, both surface and basal ice had very
217 high C:P and N:P ratios. These differences might result from distinct biogeochemical
218 processes occurring in surface ice and basal ice. In surface ice, organic matter originates
219 from autochthonous and allochthonous sources, including *in situ* primary producers
220 (glacier and snow algae) as well as wet and dry deposition of terrigenous and anthropogenic
221 materials (Hood et al, 2009; Stibal et al, 2012; Anesio et al, 2017). This organic matter can
222 be accumulated in surface ice and transformed by microorganisms through anabolic and
223 catabolic metabolism (Antony et al, 2017). Moreover, this organic matter, especially the
224 primary productivity occurring in the supraglacial habitat, has critical implications for
225 glacier albedo and for other hydrologically connected habitats, such as the basal portion of
226 glaciers and proglacial land and water (Hodson et al, 2015; Ganey et al, 2017; Milner et al,
227 2017). However, surface ice habitats are typically poor in nutrients (especially for P) and
228 microbial communities are severely P-limited (Mindl et al, 2007; Stibal et al, 2008;
229 Grzesiak et al, 2015). Thus, only a small proportion of organic carbon is used by
230 heterotrophic microorganisms in supraglacial environments (Anesio et al, 2010), resulting
231 in high organic carbon concentrations in surface ice. The remaining organic carbon in
232 surface ice but is not consumed by microorganisms is delivered by meltwater to subglacial
233 and downstream environments (Milner et al, 2017; Ren et al, 2019).

234 In addition to C, microorganisms in supraglacial habitats also exert a major influence on
235 nitrogen and phosphorus cycling (Hodson et al, 2005; Stibal et al, 2012; Havig and
236 Hamilton, 2019). Supraglacial microbial communities drive N cycle through nitrification,
237 nitrate reduction, and N-fixation (Hodson et al, 2005; Wynn et al, 2007; Telling et al, 2011).
238 Wet and dry nitrogen deposition is an additional significant source of N to the supraglacial
239 zone (Anderson et al, 2017; Havig and Hamilton, 2019), increasing supraglacial nitrogen
240 concentration (Tranter et al, 1993; Hodson et al, 2005). Thus, surface ice showed
241 significantly higher N concentrations than basal ice (Figure 2). However, P concentrations
242 are typically very low in supraglacial environments (Ren et al, 2019). Due to lack of a
243 gaseous source and segregation from bedrock, P-deficiency cannot be ameliorated by biotic
244 and abiotic P generation (Stibal et al, 2009; Modenutti et al, 2018). Thus, P demand likely
245 exceeds supply, suggesting that supraglacial microorganisms are generally P-limited and
246 thus P limitation constrains overall biogeochemical processes (Grzesiak et al, 2015;
247 Wadham et al, 2016; Ren et al, 2019). These data also suggest that melting of surface ice
248 will provide high C:P and N:P ratio water to downstream environments (Ren et al, 2019).

249 Compared to supraglacial habitats, our understanding on basal glacier environments
250 remains limited for many aspects, such as biodiversity, trophic interactions, as well as
251 nutrient availability and stoichiometry, due to the challenges of accessing these
252 environments (Boetius et al, 2015; Kayani et al, 2018; Ren et al, 2019). In our study, we
253 sampled basal ice in a glacier terminus. The results showed that basal ice had lower
254 nitrogen and organic carbon but higher SRP concentrations than surface ice. In the deepest
255 portion of a glacier, the subglacial ecosystem provides habitats for a wide range of
256 microorganisms, including lithotrophs and heterotrophs but not phototrophs due to the

257 absence of light (Kayani et al, 2018). These diverse microorganisms play an important part
258 in global biogeochemical cycles (Sułowicz et al, 2020). For example, heterotrophs
259 consume organic carbon and acquire nutrients for biosynthesis and metabolism (Boetius et
260 al, 2015). Nitrate can also be reduced as the terminal electron acceptor in anaerobic
261 respiration (Boyd et al, 2011), resulting in low NO_3^- -N concentration in basal ice.
262 Subglacial environments do not exist in isolation but play important roles in
263 biogeochemical processes in a glacier terminus. Subglacial ecosystems are associated with
264 supraglacial environments via hydrological networks that transport water and other
265 materials from the surface to the basal environment (Tranter et al, 2005), fueling
266 microorganisms. Moreover, basal ice directly interacts with underlying bedrock/sediments
267 (Montross et al, 2014), where diverse assemblages of microorganisms drive various
268 biogeochemical processes, such as pyrite oxidation, nitrification, and apatite weathering
269 (Boyd et al, 2011; Mitchell et al, 2013). The possibility of nutrient limitations, especially
270 P limitation, in subglacial habitats is supported by our data showing that basal ice had very
271 low nitrogen and organic carbon concentrations as well as very high C:P and N:P ratios.

272 ***Nutrient concentrations and stoichiometry ratios in sediment and soil***

273 At a glacier's terminus, basal sediments are exposed when the ice melts, forming barren
274 soil habitats. These newly exposed landscapes of glacier forefields are unique and sensitive
275 environments for studying ecosystem succession (Pessi et al, 2019). In our study, we
276 documented the nutrient concentrations and ratios in sediments/soils along successional
277 gradients, including BaS (basal sediment), TS (newly exposed forefront soil close to glacial
278 terminus), DS (soil with distances to glacier), and VS (soil with well-developed vegetation).
279 In our study, nitrogen and organic carbon concentrations were significantly lower in BaS,

280 TS, and DS than in VS. Moreover, TP and SRP concentrations were significantly higher in
281 BaS and VS than in TS and DS (Figure 3). These nutrient patterns could be explained by
282 the influence of organisms in soil development and by changes in soil physical properties.
283 Proglacial soils close to the glacier terminus usually have low nutrient content but high
284 levels of disturbance (Matthews, 1992; Bradley et al, 2014). This harsh environment is first
285 colonized by pioneering microorganisms that precede the establishment of plant
286 communities (Matthews, 1992; Dresch et al, 2019; Pessi et al, 2019). Microorganisms,
287 including bacteria, algae, fungi, and lichens, form complex communities and play
288 important roles in initial biogeochemical processes and soil development (Kastovska et al,
289 2005; Zumsteg et al, 2012; Pushkareva et al, 2016). For example, microbial excreted
290 organic acids can mine phosphorus from glacial till (Brunner et al, 2014). Because of
291 absent (or low) vegetation coverage, the mined phosphorus will runoff easily, leading to
292 decreased P from BaS to DS. Beyond the limitations of low nutrient availability, the rate
293 of ecosystem succession in glacier forefields might be further limited by low temperature
294 and aridity (Darcy et al, 2018). The intensified drought from BaS to DS (as indicated by
295 the decreased moisture, Figure S2) might also impede microbial activities, resulting in low
296 soil phosphorus in the soil of preplant stage of ecosystem succession.

297 During ecosystem succession, microorganisms promote the accumulation of organic matter
298 and availability of nutrients in the glacier forefield and form the trophic foundation for
299 other biological communities, such as plants in latter successional stages (Hodkinson et al,
300 2003; Breen and Levesque, 2006; Yoshitake et al, 2010). Our results showed notable high
301 SOC, TN, NO_3^- -N, and NH_4^+ -N concentrations in soils with well-developed vegetation
302 relative to unvegetated soils (BaS, TS, and DS). These results are generally in accordance

303 with many previous studies that soil organic carbon and total nitrogen increase along the
304 exposure time gradient (Liu et al, 2012; Zumsteg et al, 2012; Wu et al, 2018). In our study,
305 however, nitrogen and organic carbon were generally not changed until the vegetation was
306 well-developed. Because of sparse biological communities, especially a lack of plants,
307 nitrogen and organic carbon are low in the glacier forefield (Wu et al, 2018). During soil
308 formation, an important step is plant colonization. With growth of vegetation, dead organic
309 matter and root exudates accumulate in soil (Walker and Del Moral, 2003; Zhou et al, 2013;
310 Wietrzyk et al, 2018), resulting in a dramatic increase of organic carbon and nitrogen in
311 soil with well-developed vegetation. Furthermore, direct interactions between plants and
312 soil microorganisms facilitate symbiotic nitrogen fixation, which is particularly important
313 in nutrient-poor soil during early soil development and is greater in well-vegetated soils
314 (Knelman et al, 2012). Thus, in the glacier forefield, soil with well-developed vegetation
315 also had dramatically higher nitrogen content compared to barren soil. Moreover, organic
316 acids supplied by plant litter, root secretion, and microorganisms can promote phosphorus
317 weathering, with phosphorus captured and retained in soil by well-developed vegetation.

318 With regard to nutrient limitation, our results are consistent with previous studies indicating
319 that nitrogen and carbon are usually the limiting resources for microbial activities during
320 early ecosystem succession state following deglaciation (Bernasconi et al, 2011; Hodson
321 et al, 2015; Jiang et al, 2019; Li et al, 2020). Moreover, due to low nutrient concentration,
322 phosphorus is also reported as a limiting nutrient during the earliest successional stages
323 along glacial chronosequences (Darcy et al, 2018). Our study showed that soil with well-
324 developed vegetation had a significantly higher C:N, C:P, and N:P ratios than other soils
325 (except that DS had a higher DIN:SRP than VS). These results also support a long-held

326 biogeochemical and ecological paradigm in primary succession that early successional
327 stage is primarily nitrogen limited, while later successional stages are primarily phosphorus
328 limited (Selmants and Hart, 2010; Menge et al, 2012).

329 **Conclusions**

330 Glaciers provide diverse and unique habitats, harboring extensive biological diversity and
331 playing important roles in global biogeochemical cycles. However, accelerating global
332 climate change places glaciers at risk of a permanent disappearance. Our study focused on
333 six distinct habitats in one glacier terminus in the Yangtze River Source area. This study
334 provided a comprehensive assessment of nutrient concentrations and stoichiometry in
335 distinct habitats in a glacier terminus. Our data showed that surface ice had significantly
336 higher DOC and N concentrations as well as higher C:P and N:P ratios than basal ice.
337 Moreover, both surface ice and basal ice had very high C:P and N:P ratios, suggesting the
338 possibility of strong P-limitation, especially for surface ice. For sediment/soil in glacier
339 terminus, the change patterns of nutrient concentrations and stoichiometric ratios support
340 that early successional stage is primarily nitrogen limited, while later successional stages
341 are primarily phosphorus limited. The results provide integrated understanding of the
342 ecological and biogeochemical differences and relationships between these dynamically
343 linked habitats, adding to our knowledge of the consequences of ongoing global change for
344 glacier ecosystems.

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349 laboratory work.

350 **Conflict of Interest Statement**

351 The authors declare no competing interests.

352 **Author Contributions**

353 Ze Ren designed the study, collected the samples, did the analyses, and prepared the
354 manuscript. Hongkai Gao designed the study and prepared the manuscript. Wei Luo and
355 James J. Elser prepared the manuscript.

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360

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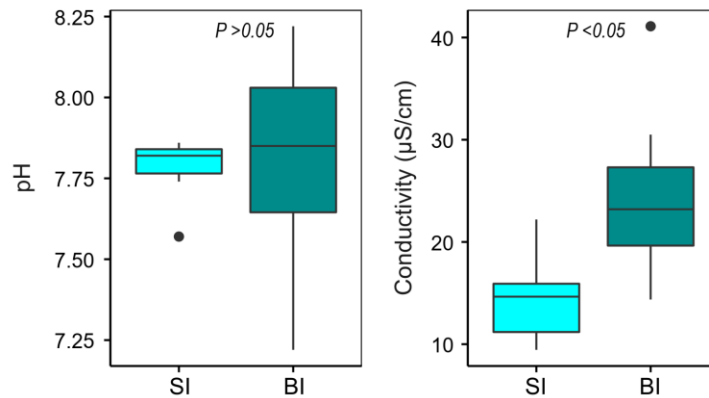
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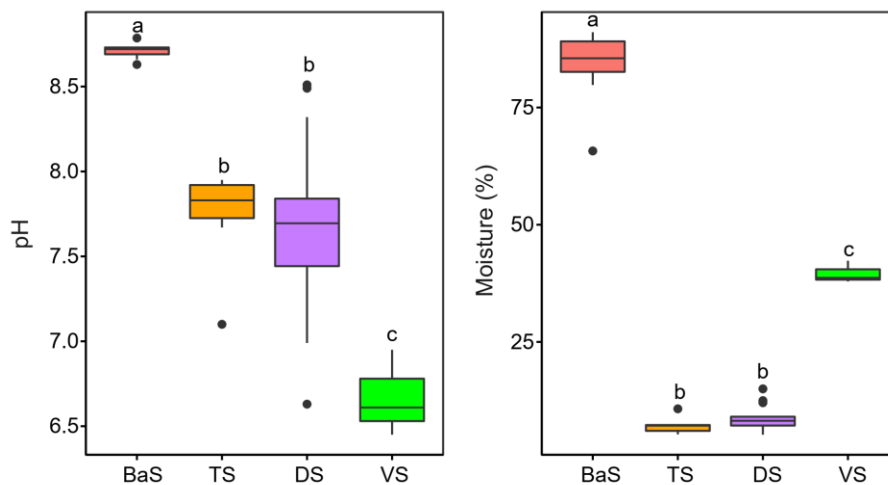
581 **Supplementary Information**

582 Figure S1 pH and conductivity of surface ice (SI) and basal ice (IB). The differences were
583 tested using ANOVA.



584

585 Figure S2 pH and conductivity of sediment and soil, including BaS (basal sediment), TS
586 (newly exposed forefront soil close to glacial terminus), DS (soil at increasing distances
587 from the glacier), and VS (soil with well-developed vegetation). The different lowercase
588 letter indicates a significant difference between habitats and the same lowercase letter
589 indicates a non-significant difference tested using ANOVA.



590