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

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Abstract

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

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

Glacial ecosystems provide diverse and dynamic habitats harboring extensive biological diversity and supporting multiple trophic levels (Kohshima, 1984; Anesio and Laybourn-Parry, 2012; Hotaling et al., 2019). Supraglacial environments, the surface ice layer, are available habitats for primary productivity dominated by glacier and snow algae (Anesio et al., 2017; Stibal et al., 2020). Autochthonous organic carbon is accumulated photosynthetically by these photoautotrophs and sustains local heterotrophic biota as well as downstream ecosystems (Williamson et al., 2019). Subglacial environments, including the basal ice and basal sediments, also harbor taxonomically and functionally diverse microorganisms, which are mainly prokaryotic and rely on chemical energy (Tranter et al., 2005; Stibal et al., 2020). Basal ice and basal sediments are directly contacted by...
interactions between each other through basal processes, such as glaciohydraulic supercooling (Lawson et al, 1998) and melt-refreezing (Knight, 1997), allowing exchanges of nutrients and microorganisms (Doyle et al, 2013; Montross et al, 2014). Moreover, subglacial environments are also connected with supraglacial environments through fracture hydrological networks, which transport nutrients and microorganisms from the surface to the base of glaciers, and eventually to the forefront soil and downstream aquatic ecosystems (Fountain et al, 2005; Anesio et al, 2010; Milner et al, 2017; Ren et al, 2017). During glacier retreat, the basal sediments in glacial terminus are exposed to barren soil habitats which are colonized by pioneering organisms (Pessi et al, 2019). As the first biota colonizing freshly exposed substrates, microorganisms play crucial roles in soil formation and biogeochemical processes (Nemergut et al, 2007; Schmidt et al, 2008; Brankatschk et al, 2011; Dresch et al, 2019), experiencing low temperature, aridity, and low nutrient availability (Darcy et al, 2018). Over successional time, plant colonization promotes soil formation by accumulating organic matter and secreting organic acids (Miniaci et al, 2007; Li et al, 2020).

Nutrients are the key limiting factors for organismal growth and ecosystem productivity (Elser et al, 2000; Sterner and Elser, 2002), especially in nutrient-scarce cryosphere environments (Ren et al, 2019). The availability and composition of key chemical elements (C, N, and P) are good indicators of ecosystem nutrient status and are critical in regulating ecosystem structure and processes (Sterner and Elser, 2002; Elser et al, 2007), such as ice-associated food webs and linkages among different habitats (Ren et al, 2019; Elser et al, 2020). C, N, and P concentrations in surface ice, snow, and cryoconite holes have been widely reported in mountain glaciers, Greenland, and Antarctica (Ren et al, 2019).
However, C, N, and P are usually not studied simultaneously in the same area, which makes it hard to assess the relative balance of different elements (C:N:P stoichiometry) as well as stoichiometric relationships between different habitats (Ren et al, 2019). Specifically, subglacial environments remain largely unknown due to difficulties in accessing and sampling (Anesio et al, 2017; Kayani et al, 2018), resulting in scarce and patchy information of C, N, and P (Ren et al, 2019). In the glacier forefield, C:N:P stoichiometry is well-studied in glacier-fed streams and lakes (Hood and Scott, 2008; Slemmons and Saros, 2012; Laspoumaderes et al, 2013; Milner et al, 2017) but is not well documented in glacier forefront soils at different development stages. As glacier retreat continues, the knowledge of C:N:P stoichiometry will assist in future predictions of changes in biogeochemical processes and trophic interactions of mountain cryosphere (Ren et al, 2019). However, we lack a synthetic understanding of C:N:P stoichiometry of diverse habitats in the same area or same glacier.

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

Methods

Study area and field sampling

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

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

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

**Chemical analyses**

For ice samples (SI and BI), nutrient concentrations were tested after the ice melted at room temperature. Total nitrogen (TN) was measured by ion chromatography after persulfate oxidation (EPA 300.0). Total phosphorus (TP) was measured using the ascorbic acid colorimetric method after persulfate oxidation (EPA 365.3). The meltwater samples used for analyzing nitrate (NO$_3^-$-N), ammonium (NH$_4^+$-N), and soluble reactive phosphorus
(SRP) were filtered using glass fiber filters (GF/F, Whatman). After filtration, NO$_3^-$-N was determined by ion chromatography (EPA 300.0). NH$_4^+$-N was determined using the indophenol colorimetric method (EPA 350.1). Soluble reactive phosphorus (SRP) was quantified using the ascorbic acid colorimetric method (EPA 365.3). pH and conductivity in meltwater were also measured using a multiparameter instrument (YSI ProPlus, Yellow Springs, Ohio) (Figure S1).

Sediment and soil samples (BaS, TS, DS, and VS) were naturally dried and sieved through 100-mesh size to remove all visible roots, residues, and stones. Soil/sediment organic carbon (SOC) was measured by oxidizing with potassium dichromate (HJ615-2011). Total nitrogen (TN) was measured using the modified Kjeldahl Method (HJ717-2014). Total phosphorus (TP) was measured using the ascorbic acid colorimetric method. Nitrate (NO$_3^-$-N) and ammonium (NH$_4^+$-N) were extracted using 2 M potassium chloride and percolated through filters and measured by a spectrophotometer (HJ634-2012). Soluble reactive phosphorus (SRP) were extracted using 0.5 M sodium bicarbonate and percolated through filters and then measured using the ascorbic acid colorimetric method. pH was measured in 1:2.5 soil to distilled water ratio using a pH and conductivity was measured in 1:5 soil to distilled water ratio using a conductivity meter (Figure S2).

Analyses

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

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

At the glacier terminus, surface ice had a significantly higher DOC, TN, NO$_3^-$-N, and NH$_4^+$-N concentrations than basal ice (Figure 2). However, basal ice had a significantly higher SRP than surface ice (Figure 2). TP was not significantly different between surface ice and basal ice. In both surface ice and basal ice, NH$_4^+$-N was 4.6 and 6.9 times higher than NO$_3^-$-N in surface and basal ice, respectively (Figure 2). DIN (estimated by NO$_3^-$-N and NH$_4^+$-N) accounted for 68% and 57% of TN in surface and basal ice on average, respectively. SRP accounted for 38% and 62% of TP in surface and basal ice on average, respectively.

Surface ice had a significantly higher DOC:TP, TN:TP, DOC:SRP, and DIN:SRP than basal ice (Figure 2). DOC:TN, and DOC:DIN were not significantly different between surface ice and basal ice (Figure 2). The average value of DOC:TN was 15 and 14, DOC:TP was 5,687 and 3,356, TN:TP was 388 and 255, DOC:DIN was 22 and 24, DOC:SRP was 15,244 and 5,739, and DIN:SRP was 722 and 245 in surface ice and basal ice, respectively.
Figure 2 Nutrient concentrations and stoichiometry ratios in surface ice (SI) and basal ice (BI). The differences were tested using ANOVA.

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

Basal sediment had significantly higher TN, NH₄⁺-N, and SRP concentrations than the newly exposed forefront soil close to glacial terminus (BaS vs. TS, Figure 3). The newly exposed forefront soil close to glacial terminus had organic carbon and nutrient
concentrations similar to the soil distant from the glacier (TS vs. DS, Figure 3). However, soil with well-developed vegetation had significantly higher SOC, TN, NO$_3^-$-N, and NH$_4^+$-N than BaS, TS, and DS (Figure 3). Meanwhile, TP and SRP concentrations were significantly higher in VS than in TS and DS (Figure 3). TP was also significantly higher in BaS than in TS, DS, and VS (Figure 3).

In these sediments and soils, DIN only accounted for a small proportion of TN with average values of 16%, 20%, 26%, and 7% in BaS, TS, DS, and VS, respectively (Figure 3). NH$_4^+$-N was much lower than NO$_3^-$-N especially in TS and DS (Figure 3). SRP accounted for a very small proportion of TP with average values of 0.45%, 0.20%, 0.17%, and 0.43% in BaS, TS, DS, and VS, respectively (Figure 3).

Basal sediment had significantly lower DIN:SRP ratio than newly exposed forefront soil close to glacial terminus (BaS vs. TS, Figure 3). Newly exposed forefront soil close to glacial terminus had significantly lower SOC:TN and DIN:SRP than the soil distant to the glacier (TS vs. DS, Figure 3). Vegetated soil had a significantly higher SOC:TN, SOC:TP, TN:TP, SOC:DIN, and SOC:SRP than BaS, TS, and DS (Figure 3). For BaS, TS, DS, and VS, the average values of SOC:TN were 4, 3, 5, and 16, SOC:TP was 9, 6, 8, and 305, TN:TP was 2.5, 2, 1.8, and 19, SOC:DIN was 24, 16, 19, and 37, SOC:SRP was 2606, 3008, 5488, and 68,937, and DIN:SRP was 109, 194, 300, and 191, respectively.
Figure 3 Nutrient concentrations and stoichiometric ratios of sediment and soil, including BaS (basal sediment), TS (newly exposed forefront soil close to glacial terminus), DS (soil at increasing distances from the glacier), and VS (soil with well-developed vegetation). Different lowercase letters indicate a significant difference between habitats while the same lowercase letter indicates a non-significant difference from ANOVA.
Discussion

Nutrient concentrations and stoichiometry ratios in ice

At the Dongkemadi Glacier, surface ice had significantly higher DOC and N concentrations as well as higher C:P and N:P ratios than basal ice. However, basal ice had significantly higher SRP concentrations than surface ice. In addition, both surface and basal ice had very high C:P and N:P ratios. These differences might result from distinct biogeochemical processes occurring in surface ice and basal ice. In surface ice, organic matter originates from autochthonous and allochthonous sources, including in situ primary producers (glacier and snow algae) as well as wet and dry deposition of terrigenous and anthropogenic materials (Hood et al, 2009; Stibal et al, 2012; Anesio et al, 2017). This organic matter can be accumulated in surface ice and transformed by microorganisms through anabolic and catabolic metabolism (Antony et al, 2017). Moreover, this organic matter, especially the primary productivity occurring in the supraglacial habitat, has critical implications for glacier albedo and for other hydrologically connected habitats, such as the basal portion of glaciers and proglacial land and water (Hodson et al, 2015; Ganey et al, 2017; Milner et al, 2017). However, surface ice habitats are typically poor in nutrients (especially for P) and microbial communities are severely P-limited (Mindl et al, 2007; Stibal et al, 2008; Grzesiak et al, 2015). Thus, only a small proportion of organic carbon is used by heterotrophic microorganisms in supraglacial environments (Anesio et al, 2010), resulting in high organic carbon concentrations in surface ice. The remaining organic carbon in surface ice but is not consumed by microorganisms is delivered by meltwater to subglacial and downstream environments (Milner et al, 2017; Ren et al, 2019).
In addition to C, microorganisms in supraglacial habitats also exert a major influence on nitrogen and phosphorus cycling (Hodson et al, 2005; Stibal et al, 2012; Havig and Hamilton, 2019). Supraglacial microbial communities drive N cycle through nitrification, nitrate reduction, and N-fixation (Hodson et al, 2005; Wynn et al, 2007; Telling et al, 2011). Wet and dry nitrogen deposition is an additional significant source of N to the supraglacial zone (Anderson et al, 2017; Havig and Hamilton, 2019), increasing supraglacial nitrogen concentration (Tranter et al, 1993; Hodson et al, 2005). Thus, surface ice showed significantly higher N concentrations than basal ice (Figure 2). However, P concentrations are typically very low in supraglacial environments (Ren et al, 2019). Due to lack of a gaseous source and segregation from bedrock, P-deficiency cannot be ameliorated by biotic and abiotic P generation (Stibal et al, 2009; Modenutti et al, 2018). Thus, P demand likely exceeds supply, suggesting that supraglacial microorganisms are generally P-limited and thus P limitation constrains overall biogeochemical processes (Grzesiak et al, 2015; Wadham et al, 2016; Ren et al, 2019). These data also suggest that melting of surface ice will provide high C:P and N:P ratio water to downstream environments (Ren et al, 2019).

Compared to supraglacial habitats, our understanding on basal glacier environments remains limited for many aspects, such as biodiversity, trophic interactions, as well as nutrient availability and stoichiometry, due to the challenges of accessing these environments (Boetius et al, 2015; Kayani et al, 2018; Ren et al, 2019). In our study, we sampled basal ice in a glacier terminus. The results showed that basal ice had lower nitrogen and organic carbon but higher SRP concentrations than surface ice. In the deepest portion of a glacier, the subglacial ecosystem provides habitats for a wide range of microorganisms, including lithotrophs and heterotrophs but not phototrophs due to the
absence of light (Kayani et al, 2018). These diverse microorganisms play an important part in global biogeochemical cycles (Sułowicz et al, 2020). For example, heterotrophs consume organic carbon and acquire nutrients for biosynthesis and metabolism (Boetius et al, 2015). Nitrate can also be reduced as the terminal electron acceptor in anaerobic respiration (Boyd et al, 2011), resulting in low NO$_3^-$-N concentration in basal ice. Subglacial environments do not exist in isolation but play important roles in biogeochemical processes in a glacier terminus. Subglacial ecosystems are associated with supraglacial environments via hydrological networks that transport water and other materials from the surface to the basal environment (Tranter et al, 2005), fueling microorganisms. Moreover, basal ice directly interacts with underlying bedrock/sediments (Montross et al, 2014), where diverse assemblages of microorganisms drive various biogeochemical processes, such as pyrite oxidation, nitrification, and apatite weathering (Boyd et al, 2011; Mitchell et al, 2013). The possibility of nutrient limitations, especially P limitation, in subglacial habitats is supported by our data showing that basal ice had very low nitrogen and organic carbon concentrations as well as very high C:P and N:P ratios.

Nutrient concentrations and stoichiometry ratios in sediment and soil

At a glacier’s terminus, basal sediments are exposed when the ice melts, forming barren soil habitats. These newly exposed landscapes of glacier forefields are unique and sensitive environments for studying ecosystem succession (Pessi et al, 2019). In our study, we documented the nutrient concentrations and ratios in sediments/soils along successional gradients, including BaS (basal sediment), TS (newly exposed forefront soil close to glacial terminus), DS (soil with distances to glacier), and VS (soil with well-developed vegetation). In our study, nitrogen and organic carbon concentrations were significantly lower in BaS,
TS, and DS than in VS. Moreover, TP and SRP concentrations were significantly higher in 
BaS and VS than in TS and DS (Figure 3). These nutrient patterns could be explained by 
the influence of organisms in soil development and by changes in soil physical properties. 
Proglacial soils close to the glacier terminus usually have low nutrient content but high 
levels of disturbance (Matthews, 1992; Bradley et al, 2014). This harsh environment is first 
colonized by pioneering microorganisms that precede the establishment of plant 
communities (Matthews, 1992; Dresch et al, 2019; Pessi et al, 2019). Microorganisms, 
including bacteria, algae, fungi, and lichens, form complex communities and play 
important roles in initial biogeochemical processes and soil development (Kastovska et al, 
2005; Zumsteg et al, 2012; Pushkareva et al, 2016). For example, microbial excreted 
organic acids can mine phosphorus from glacial till (Brunner et al, 2014). Because of 
absent (or low) vegetation coverage, the mined phosphorus will runoff easily, leading to 
decreased P from BaS to DS. Beyond the limitations of low nutrient availability, the rate 
of ecosystem succession in glacier forefields might be further limited by low temperature 
and aridity (Darcy et al, 2018). The intensified drought from BaS to DS (as indicated by 
the decreased moisture, Figure S2) might also impede microbial activities, resulting in low 
soil phosphorus in the soil of preplant stage of ecosystem succession.

During ecosystem succession, microorganisms promote the accumulation of organic matter 
and availability of nutrients in the glacier forefield and form the trophic foundation for 
other biological communities, such as plants in latter successional stages (Hodkinson et al, 
2003; Breen and Levesque, 2006; Yoshitake et al, 2010). Our results showed notable high 
SOC, TN, NO₃⁻-N, and NH₄⁺-N concentrations in soils with well-developed vegetation 
relative to unvegetated soils (BaS, TS, and DS). These results are generally in accordance
with many previous studies that soil organic carbon and total nitrogen increase along the exposure time gradient (Liu et al, 2012; Zumsteg et al, 2012; Wu et al, 2018). In our study, however, nitrogen and organic carbon were generally not changed until the vegetation was well-developed. Because of sparse biological communities, especially a lack of plants, nitrogen and organic carbon are low in the glacier forefield (Wu et al, 2018). During soil formation, an important step is plant colonization. With growth of vegetation, dead organic matter and root exudates accumulate in soil (Walker and Del Moral, 2003; Zhou et al, 2013; Wietrzyk et al, 2018), resulting in a dramatic increase of organic carbon and nitrogen in soil with well-developed vegetation. Furthermore, direct interactions between plants and soil microorganisms facilitate symbiotic nitrogen fixation, which is particularly important in nutrient-poor soil during early soil development and is greater in well-vegetated soils (Kneman et al, 2012). Thus, in the glacier forefield, soil with well-developed vegetation also had dramatically higher nitrogen content compared to barren soil. Moreover, organic acids supplied by plant litter, root secretion, and microorganisms can promote phosphorus weathering, with phosphorus captured and retained in soil by well-developed vegetation.

With regard to nutrient limitation, our results are consistent with previous studies indicating that nitrogen and carbon are usually the limiting resources for microbial activities during early ecosystem succession state following deglaciation (Bernasconi et al, 2011; Hodson et al, 2015; Jiang et al, 2019; Li et al, 2020). Moreover, due to low nutrient concentration, phosphorus is also reported as a limiting nutrient during the earliest successional stages along glacial chronosequences (Darcy et al, 2018). Our study showed that soil with well-developed vegetation had a significantly higher C:N, C:P, and N:P ratios than other soils (except that DS had a higher DIN:SRP than VS). These results also support a long-held
biogeochemical and ecological paradigm in primary succession that early successional
stage is primarily nitrogen limited, while later successional stages are primarily phosphorus
limited (Selmants and Hart, 2010; Menge et al, 2012).

**Conclusions**

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

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Conflict of Interest Statement

The authors declare no competing interests.

Author Contributions

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

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**Supplementary Information**

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

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