

Article

Factors Influencing Carbon and Nitrogen Emissions Induced by Freeze–Thaw Collapse in Altai Mountain Peatlands

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Abstract

Permafrost peatlands in high-altitude regions store substantial amounts of organic carbon, yet the biogeochemical consequences of thermokarst collapse remain poorly understood. Using a space-for-time substitution approach, we selected four habitats representing a thermokarst development sequence in the Altai Mountains peatlands—slightly collapsed peat mounds (P1), severely collapsed peat mounds (P2), thawed herbaceous peat (PB1), and thermokarst ponds (PB2)—and conducted in situ greenhouse gas flux monitoring, soil physicochemical analysis, enzyme activity assays, and structural equation modeling. We found that thermokarst development fundamentally altered the greenhouse gas source–sink balance through three interconnected mechanisms. First, CO₂ fluxes shifted from net emission in P1 (684.1 mg m^{−2} h^{−1}) to net uptake in PB2 (−25.6 mg m^{−2} h^{−1}), driven primarily by the oxidative loss of mineral-associated organic carbon in the 40–60 cm layer (71.3% loss), whereas lateral dissolved organic carbon export accounted for only 12.3% of total carbon loss. Second, CH₄ fluxes in PB2 (3.8 ± 0.7 mg m^{−2} h^{−1}) reached approximately 43% of the theoretical maximum, with this suppression associated with phosphorus limitation (total phosphorus < 0.05 g kg^{−1}) and a marked reduction in alkaline phosphatase activity. Third, N₂O uptake increased along the thaw sequence to −28.6 μg m^{−2} h^{−1} in PB2, with the 40–80 cm layer contributing 42% more than the surface layer. This increase in N₂O uptake occurred when the soil C/N ratio exceeded 300, a threshold that reflects the substantial stoichiometric imbalance between carbon and nitrogen following thermokarst development. These findings demonstrate that the transition from peat mounds to thermokarst ponds alters the net greenhouse gas source–sink balance through changes in MAOC stability, phosphorus availability, and carbon-to-nitrogen stoichiometry. Our results provide empirical constraints for evaluating carbon–climate feedbacks in cold-region peatlands.

Keywords: alpine peatland; thermokarst succession; carbon and nitrogen transport; source–sink transformation



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1. Introduction

Peatlands in high-altitude permafrost regions store substantial amounts of soil organic carbon and have historically functioned as net carbon sinks [1]. Climate warming is accelerating permafrost degradation, which may shift these ecosystems from carbon sinks to carbon sources through enhanced microbial decomposition of previously frozen organic matter [2,3]. Thermokarst collapse, the abrupt subsidence of ice-rich permafrost terrain, represents a particularly widespread form of permafrost degradation in peatland

ecosystems [4,5]. As ice wedges melt and surface topography collapses, peat plateaus transition to thermokarst ponds and lakes, accompanied by changes in hydrology, vegetation, and soil thermal regimes [6]. Previous studies have documented substantial changes in greenhouse gas exchange following thermokarst collapse. In northern Norway, permafrost thaw slumping increased CO_2 release to $177.5 \text{ g CO}_2 \text{ m}^{-2}$, compared to $59.0 \text{ g CO}_2 \text{ m}^{-2}$ from intact peat plateau. Methane release also increased dramatically in thaw slumps, ranging from 9.7 to $36.1 \text{ g CH}_4 \text{ m}^{-2}$ [7]. In northwestern Canada, methane emissions from young thermokarst bogs reached $21 \text{ g C-CH}_4 \text{ m}^{-2} \text{ year}^{-1}$, whereas mature bogs emitted $7 \text{ g C-CH}_4 \text{ m}^{-2} \text{ year}^{-1}$ [6]. On the Qinghai–Tibet Plateau, alpine thermokarst lakes emitted $13.4 \pm 1.5 \text{ mmol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ during the ice-free period [8]. These observations indicate that thermokarst collapse generally enhances greenhouse gas emissions, though the magnitude of this enhancement varies substantially across regions and developmental stages.

The resistance of soil organic carbon to microbial decomposition—hereafter referred to as carbon stability, defined as the persistence of organic carbon against decomposition under current environmental conditions—in permafrost peatlands is largely determined by its physical and chemical protection mechanisms [9]. Mineral-associated organic carbon (MAOC), which is protected from rapid decomposition through association with soil minerals, may become vulnerable to oxidation when physical protection is disrupted by freeze–thaw disturbance [10]. We use the term MAOC (rather than MAOM, mineral-associated organic matter) to specifically quantify the carbon pool, consistent with recent studies on permafrost carbon dynamics [11]. Studies on the Tibetan Plateau have shown that upon permafrost thaw, particulate organic carbon (POC) content decreases substantially, while MAOC content remains relatively stable and iron-bound organic carbon accumulates [11]. At the same time, dissolved organic carbon (DOC) can be exported laterally through hydrological flow paths, representing an additional pathway of carbon loss [12]. In addition to carbon dynamics, nitrogen cycling is also affected by thermokarst collapse [13]. Undisturbed permafrost peat plateaus in western Canada acted as N_2O sinks ($-0.6 \text{ mg N}_2\text{O m}^{-2} \text{ h}^{-1}$), and N_2O uptake increased following permafrost thaw in thermokarst bogs ($-1.3 \text{ mg N}_2\text{O m}^{-2} \text{ h}^{-1}$) [14]. The thermokarst bogs had below-ambient N_2O soil gas concentrations, suggesting that denitrification consumed atmospheric N_2O during reduction to dinitrogen. Phosphorus availability further modulates these processes: phosphorus limitation has been shown to suppress methanogen activity, thereby influencing the partitioning of carbon flow between CO_2 and CH_4 emission pathways [15]. Despite these advances, previous studies have largely focused on individual carbon fractions (MAOC, POC, DOC) or single gas fluxes in isolation. The concurrent changes in multiple carbon fractions and their combined effects on CO_2 , CH_4 , and N_2O emissions during thermokarst succession have received less attention. In particular, the relative importance of MAOC oxidation versus DOC export in contributing to total carbon loss, and how these processes interact with nitrogen cycling and phosphorus availability, remain insufficiently quantified.

The Altai Mountains peatlands, located in a temperate alpine permafrost region, provide an ideal setting to examine these processes. Thermokarst collapse is widespread in this region, and the peatlands exhibit a clear succession sequence from intact peat mounds to thermokarst ponds. Previous studies have documented peat initiation ages and carbon accumulation rates in this region [16], but the effects of thermokarst succession on greenhouse gas fluxes and associated soil properties have not been systematically examined. In this study, we used a space-for-time substitution approach to select four habitats representing a thermokarst succession sequence: slightly collapsed peat mounds (P1), severely collapsed peat mounds (P2), thawed herbaceous peat (PB1), and thermokarst ponds (PB2). We measured CO_2 , CH_4 , and N_2O fluxes, soil physicochemical properties,

carbon fractions (MAOC, POC, DOC), and enzyme activities across these habitats. Our objective was to examine how thermokarst succession affects greenhouse gas fluxes and to explore the relationships between these fluxes and changes in soil carbon fractions, nutrient availability, and enzyme activities. We hypothesized that (1) the transition from peat mounds to thermokarst ponds would alter the magnitude and direction of CO₂ fluxes, with these changes potentially associated with shifts in MAOC stability and DOC export; (2) CH₄ fluxes would vary across the succession sequence, potentially influenced by changes in phosphorus availability and associated enzyme activities; and (3) N₂O fluxes would shift along the development sequence, with these changes possibly related to variations in carbon-to-nitrogen stoichiometry and denitrification substrate availability.

2. Materials and Methods

2.1. Study Area

The Altai Mountains constitute the second-largest mountain system within the Altai Mountain range. Positioned in the central region of Eurasia (83° E–104° E, 42° N–50° N), they extend from the western part of Mongolia in the east to Siberia in the west (Figure 1). The portion of the Altai Mountains within China's territory is part of the southern slopes of the middle section. Peatlands in the Altai Mountains have developed amidst extensive areas of seasonal permafrost and insular permafrost [17]. The total area of these peatlands reaches 38,301.8 hectares (hm²), and roughly half of the peatlands are concentrated in the permafrost zone [18]. These peatlands are predominantly distributed in the middle section of the Altai Mountains, as well as at the northwestern and southeastern extremities. They are situated on the sunny slopes at elevations ranging from 1600 m to 2500 m [19]. The Salahazi peatland is a herb–peat–mound peatland with a vegetation community predominantly composed of *Carex lasiocarpa* and *Carex pamirensis*. Along the thermokarst development sequence, vegetation composition shifts markedly among the four habitats. The slightly collapsed peat mounds (P1) are dominated by *Carex* spp. with scattered *Sphagnum* moss patches. The severely collapsed peat mounds (P2) show reduced *Carex* cover and increased bare peat exposure. The thawed herbaceous peat (PB1) is characterized by hygrophilous herbaceous species including *Eriophorum* spp. and *Juncus* spp. The thermokarst pond (PB2) supports aquatic macrophytes including *Potamogeton* spp. and submerged mosses. No woody vegetation is present at any of the study sites. The Salahazi peatland in the central Altai Mountains initiated its development approximately 10,600 years ago and accumulated at an average rate of 0.035 cm per annum. It has formed a herb–peat–mound peatland predominantly composed of *Carex lasiocarpa* and *Carex pamirensis*. The average thickness of the peat is 4 m, and the peat mounds can reach up to 6 m in height [19]. Under the protection of fenced enclosure, the Salahazi peatland has maintained its natural state. In the enclosed area at an altitude of 2400 m, a large expanse of giant peat mounds has emerged. These mounds are 3 to 4 m in height and 5 to 10 m in length, presenting a typical dome shape. At the outer edge of the severely collapsed peat mounds, a thermokarst pond lake with an area of 2.3 square meters has been formed. Driven by climate warming, the peatlands, along with the permafrost and seasonal permafrost in the Altai Mountains, have undergone persistent and intense thawing [2]. According to the research, during the period from 1970 to 2015, the Altai Mountains witnessed a rapid warming trend, with an average temperature increase of 0.4 °C per decade and a wetting trend of 4.8 mm per decade. The significant warming and insignificant humidification led to a substantial loss of permafrost [20]. As the activity layer of permafrost thickens, peat mounds experience thermal thawing and subsidence. The collapse of peat mounds and the thawing of peat bogs result in the formation of thermokarst ponds and lakes, which modify the chemical composition and colonization structure of the peat and boost greenhouse gas emissions [21].

These processes contribute to the loss of carbon and nitrogen from peatlands and the transformation between greenhouse gas sinks and sources, exerting a serious impact on climate warming under the positive feedback effect [22]. The soils in the study area are classified as Cryic Histosols according to the World Reference Base for Soil Resources (WRB), corresponding to Histels (Fibristels) in USDA Soil Taxonomy. The peat profiles consist of organic soil materials with organic carbon content exceeding 20% (by weight) throughout the 0–80 cm depth. The active layer thickness ranges from 40 to 125 cm depending on microtopographic position and permafrost conditions.

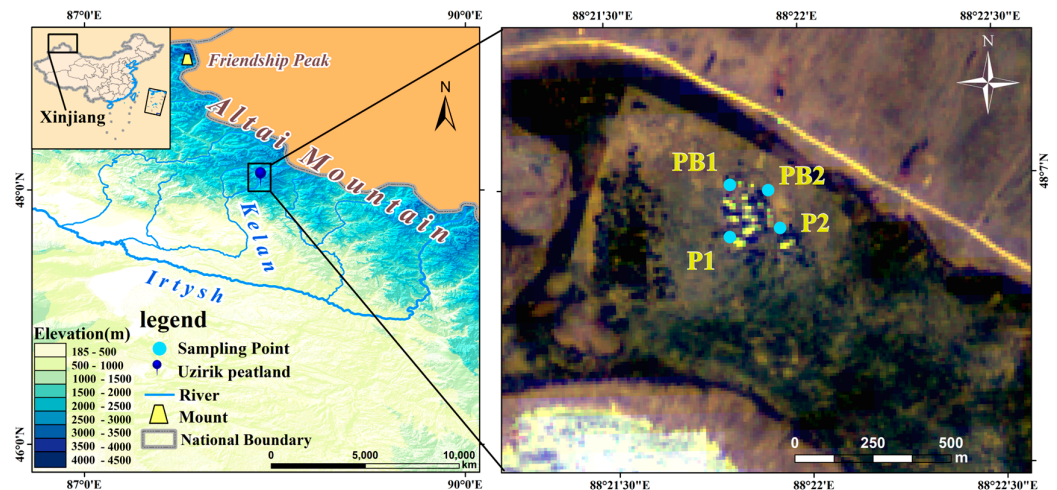


Figure 1. Geographical location of the study area. Four of them are slightly collapsed peat mound (P1), severely collapsed peat mound (P2), thawed herbaceous peat mound (PB1), and thermal melting pond lake (PB2).

2.2. Experimental Design and Data Collection

2.2.1. Sample Plot Setup and Gas Collection

In June 2023, we conducted a field experiment in the Salahazi Peatland using the static chamber-gas chromatography method. Vegetation cover and species composition were assessed in each 10 m × 10 m quadrat prior to gas sampling. Dominant species were identified and their relative cover estimated visually. Following the space-for-time substitution approach [23], we selected four habitats within the fenced enclosure at 2400 m a.s.l. based on measured environmental parameters (soil temperature, ST; soil moisture, SM; and bulk density, BD): slightly collapsed peat mounds (P1), severely collapsed peat mounds (P2), thawed herbaceous peat (PB1), and thermokarst pond (PB2) (Figure 2). These habitats represent a thermokarst development chronosequence verified by peat depth, vegetation succession, and long-term monitoring records [24]. In each habitat, we established one 10 m × 10 m quadrat for greenhouse gas sampling and soil property analysis.

For gas sampling from the peat mound profiles (P1 and P2), we used a soil profile gas in situ collection system adapted from previous studies. Vertical profiles were trimmed at collapsed sites, and boreholes were drilled at predetermined depths using a soil auger. The gas collectors were inserted vertically into the boreholes, and gaps between collectors and soil were sealed with polyurethane foam to prevent atmospheric contamination. The system consisted of five polytetrafluoroethylene (PTFE) gas collectors (20 cm length, 20 mm diameter), each connected via 1.6 mm diameter stainless steel tubes (1 m length) to three-way fittings on the ground surface. This design allowed simultaneous gas sampling from five soil layers: 0–10, 10–20, 20–40, 40–60, and 60–80 cm. For the thawed herbaceous peat (PB1) and thermokarst pond (PB2), we used opaque static chambers (opaque PVC cylinders) to measure ecosystem respiration exclusively [25]. Chambers were installed on stainless steel bases 24 h prior to sampling and sealed with water-filled grooves during sampling.

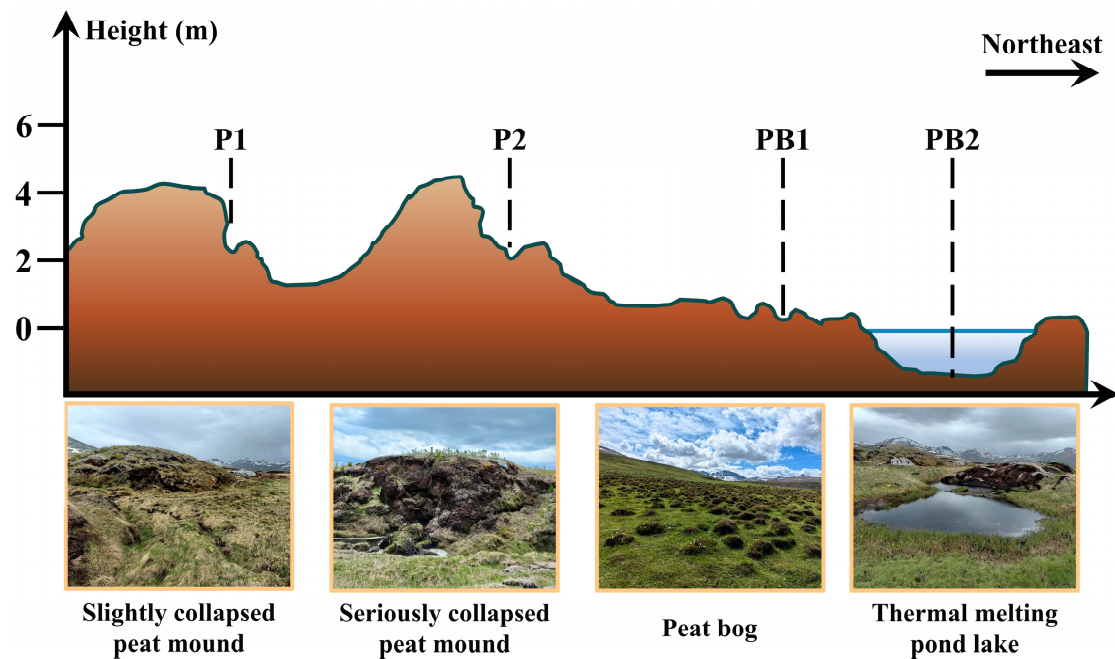


Figure 2. Schematic diagram of sampling sites across thermokarst succession habitats. Four of them are slightly collapsed peat mound (P1), severely collapsed peat mound (P2), thawed herbaceous peat mound (PB1), and thermal melting pond lake (PB2).

Gas samples were collected between 09:00 and 11:00 local time from 10 to 20 June 2023, under stable weather conditions (no precipitation for ≥ 3 days prior; air temperature 15–22 °C). At each sampling event, 50 mL gas samples were extracted using 100 mL plastic syringes at 0, 5, 10, and 15 min after chamber closure and transferred to pre-evacuated glass vials. For the five soil layers of the two peat mound profiles (P1 and P2), we conducted three replicate sampling rounds at 30 min intervals, yielding 120 samples (2 habitats $\times$ 5 layers $\times$ 4 time points $\times$ 3 replicates). For PB1 and PB2, we sampled from the surface (soil surface for PB1; water surface for PB2) following the same protocol, yielding 12 samples each (4 time points $\times$ 3 replicates). In total, 144 gas samples were collected across all habitats. All samples were transported to the Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, and analyzed using a gas chromatograph (Agilent 7890B-7000D, Agilent Technologies, Santa Clara, CA, USA) equipped with a flame ionization detector and an electron capture detector.

2.2.2. Collection of Soil Samples

Concurrent with gas sampling, we collected soil and sediment samples from each plot for determination of soil physicochemical properties and carbon fractions. Soil profiles were described following WRB guidelines prior to sampling. In the peat mound profiles (P1 and P2), the 0–10, 10–20, and 20–40 cm layers corresponded to the Oi, Oe, and lower Oe horizons, respectively, while the 40–60 and 60–80 cm layers corresponded to the Oa horizon, with the lower boundary of the Oa horizon coinciding with the permafrost table. In the thawed herbaceous peat (PB1) and thermokarst pond (PB2), only the surface organic layer (0–10 cm) was sampled; this layer consisted of highly decomposed organic material (Oa horizon material) in PB1 and unconsolidated organic-rich sediment in PB2, reflecting the partial disruption of the original soil horization by thaw subsidence. Soil sampling was conducted at fixed depth intervals rather than exclusively by genetic horizons for three reasons. First, greenhouse gas fluxes are primarily controlled by depth-dependent physical processes—gas diffusion, temperature gradients, and moisture distribution—rather than by pedological horizon boundaries. Second, fixed-depth sampling ensures

consistent comparison across habitats where genetic horizon boundaries differ due to differential thaw histories; for instance, the Oi-Oe-Oa boundaries in P2 were shifted relative to P1, making horizon-based comparisons less straightforward. Third, this approach is standard in permafrost greenhouse gas flux studies, facilitating comparability with published datasets. Genetic horizon information was nevertheless recorded for each profile to provide pedological context. Soil bulk density (BD) was determined using the core cutter method (standard core cutter volume: 100 cm³). Fresh soil samples were oven-dried at 105 °C to constant weight, and BD was calculated as the ratio of dry soil mass to core cutter volume. We collected fresh soil samples in sealed bags, with three replicates per plot, yielding a total of 108 samples. All samples were air-dried and sieved through a 2 mm mesh (for general properties) and a 100-mesh sieve (for carbon fraction analysis). Soil temperature (ST) and moisture content (SM) were measured in situ using a soil three-parameter sensor (Acclima SOI-12 Sensor Reader) at three positions adjacent to each gas collection point across the surface plots and soil profiles.

2.3. Sample Analysis

Soil pH was determined potentiometrically using a pH meter (Microprocessor pH Meter). Soil organic carbon (SOC) was determined using the potassium dichromate oxidation-external heating method [26]. Total phosphorus (TP) was measured using the molybdenum-antimony colorimetric method with a UV spectrophotometer (Model UV1200) [27]. Total nitrogen (TN) was analyzed via the Kjeldahl method. Ammonium nitrogen (NH₄⁺-N) and nitrate nitrogen (NO₃⁻-N) were extracted with 2 M KCl solution (soil:solution = 1:10, *w/v*) and determined using a continuous flow analyzer (SEAL AutoAnalyzer AA3) [28]. Total carbon (TC) and total organic carbon (TOC) were determined using a CN analyzer (multi N/C 2100S, Jena, Germany). Dissolved organic carbon (DOC) was extracted from fresh soil with deionized water (soil:water = 1:5, *w/v*), filtered through 0.45 µm glass fiber filters, and measured using the same CN analyzer [29]. Particulate organic carbon (POC) was determined following the wet-sieving method [30]. Mineral-associated organic carbon (MAOC) was calculated as MAOC = SOC – POC [31]. Total inorganic carbon (TIC) was calculated as TIC = TC – TOC [32]. Activities of α-glucosidase, β-glucosidase, leucine aminopeptidase, alkaline phosphatase, and cellulase were determined using a Tecan Spark multifunctional microplate reader (Model: Spark) following standard fluorometric protocols [33]. To ensure analytical accuracy, all SOC and TN measurements were performed in triplicate. The relative standard deviation for replicate measurements was <5% for SOC and <8% for TN, confirming the reliability of the reported data.

2.3.1. Greenhouse Gas Flux Calculation

Gas fluxes were calculated using the following equation:

$$F = \frac{60}{100p} \times \frac{P}{101.3} \times \frac{273}{273 + T} \times \frac{dC}{dt}$$

where *F* is the gas flux (CO₂: mg m⁻² h⁻¹; CH₄: mg m⁻² h⁻¹; N₂O: mg m⁻² h⁻¹), *p* is the gas density at standard conditions (CO₂: 1.98 g L⁻¹; CH₄: 0.717 g L⁻¹; N₂O: 1.98 g L⁻¹), *P* is atmospheric pressure (kPa), *T* is the average chamber temperature during sampling (°C), and *dC/dt* is the rate of change in gas concentration in the chamber (µL L⁻¹ min⁻¹). Concentrations of CH₄ and CO₂ were determined using a gas chromatograph (Agilent 7890B-7000D) equipped with a flame ionization detector (FID) and a methanizer, while N₂O was measured using an electron capture detector (ECD).

2.3.2. Calculation of DOC Lateral Export

Lateral DOC flux (P , g C m⁻² d⁻¹) was estimated using the following equation:

$$P = \frac{DOC \times BD \times D \times k}{1000}$$

where DOC is the dissolved organic carbon concentration (mg kg⁻¹), BD is bulk density (kg m⁻³), D is the sampling depth (m), and k is the lateral export coefficient (d⁻¹). We adopted $k = 0.005$ d⁻¹ based on long-term hydrological monitoring in the Altai Mountains (mean daily runoff depth: 0.5 cm d⁻¹) [34]. This value falls within the range reported for similar permafrost-affected peatlands (0.003–0.007 d⁻¹) [35]. To assess the sensitivity of our estimates to the choice of k, we calculated DOC lateral fluxes using k values across this reported range and found variations of <15% in the estimated fluxes [36]. The denominator “1000” converts the units from mg to g.

2.4. Statistical Analysis

We used Pearson correlation analysis, one-way analysis of variance (ANOVA), and two-way ANOVA to examine the relationships and variability among soil greenhouse gas (GHG) fluxes, carbon fractions, physicochemical properties, environmental factors, and enzyme activities. All statistical analyses were performed using SPSS 26.0 and Python 3.12.0, with figures generated using Python 3.12.0.

To explore the pathways through which environmental factors influence GHG fluxes, we constructed a partial least squares structural equation model (PLS-SEM) using SmartPLS 4.0. The model was specified based on established theoretical frameworks of carbon cycling in cold-region ecosystems [2]. The model included three hierarchical blocks: environmental factors (eight indicators: soil temperature, soil moisture, C/N ratio, total phosphorus, total nitrogen, pH, ammonium nitrogen, and nitrate nitrogen), enzyme activities (β -glucosidase, leucine aminopeptidase, cellulase, α -glucosidase, and alkaline phosphatase), and carbon fractions (MAOC, POC, DOC, and TOC), with GHG fluxes (CO₂, CH₄, and N₂O) as the final dependent variables.

Model data were derived from four habitats (P1, P2, PB1, and PB2) with three independent sampling points per habitat, yielding a total of 12 samples. PLS-SEM was selected over covariance-based SEM (CB-SEM) due to its suitability for exploratory modeling and its greater tolerance for smaller sample sizes. Although the sample size is modest, PLS-SEM with Bootstrap resampling (5000 iterations) can provide stable parameter estimates under such conditions [37]. Model fit was assessed using the standardized root mean square residual (SRMR = 0.056), with supplementary indices including the Bollen-Stine Bootstrap goodness-of-fit ($p = 0.142$), root mean square error of approximation (RMSEA = 0.062), and comparative fit index (CFI = 0.93) [38]. Measurement model quality was evaluated via composite reliability (CR), average variance extracted (AVE), and the heterotrait-monotrait ratio (HTMT) [39]. Path significance was tested using Bootstrap with 5000 iterations, with $p < 0.05$ considered statistically significant [40].

3. Results

3.1. Greenhouse Gas Emission Fluxes

Net CO₂ and CH₄ emissions decreased significantly with thaw progression ($p < 0.05$), while N₂O uptake increased progressively, indicating a systematic shift in the GHG source-sink balance along the development sequence (Figure 3). In the collapse phases (P1 and P2), CO₂ was consistently emitted. In P1, the maximum net CO₂ emission reached 684.1 mg m⁻² h⁻¹ (Figure 3a). Vertically, CO₂ flux decreased by 69.7% from the surface layer (0–10 cm: 509.9 mg m⁻² h⁻¹) to the deepest layer (60–80 cm: 154.3 mg m⁻² h⁻¹) (Figure 3a).

In the P1 profile, the 0–10, 10–20, 20–40, and 40–60/60–80 cm layers correspond to the Oi, Oe (upper), Oe (lower), and Oa horizons, respectively; the observed decrease in CO₂ flux with depth thus reflects the transition from slightly decomposed surface peat to highly decomposed deeper peat. This depth-dependent pattern indicated that CO₂ emissions were strongly concentrated near the surface. In the fully thawed stages (PB1 and PB2), CO₂ shifted to net uptake. In PB2, the uptake intensity was $-25.6 \text{ mg m}^{-2} \text{ h}^{-1}$ (Figure 3h), with deeper layers (40–80 cm) showing 32% greater uptake than the surface layer, suggesting that carbon uptake shifted from surface-dominated to depth-dominated patterns following complete thaw. CH₄ emissions in P1 were primarily from the shallow layer (0–20 cm: $45.4 \text{ mg m}^{-2} \text{ h}^{-1}$), reflecting a surface-concentrated emission pattern (Figure 3b). In P2, CH₄ uptake ($-4.2 \text{ mg m}^{-2} \text{ h}^{-1}$) was observed in the 20–40 cm layer (Figure 3e). In PB1 and PB2, all CH₄ fluxes were below $5 \text{ mg m}^{-2} \text{ h}^{-1}$ with no significant vertical heterogeneity ($p > 0.05$), indicating that methanogenic activity was largely suppressed in the fully thawed aquatic habitats. N₂O uptake increased progressively along the thaw sequence, reaching $-28.6 \text{ mg m}^{-2} \text{ h}^{-1}$ in PB2 (Figure 3i). The contribution of the deeper layer (40–80 cm) was 42% higher than that of the surface layer, suggesting that N₂O consumption (via denitrification) was more active in deeper soils following thermokarst formation. Overall, the transition from P1 to PB2 was accompanied by a progressive decrease in CO₂ and CH₄ emissions, a shift from emission-dominated to uptake-dominated CO₂ dynamics, and a sustained increase in N₂O uptake capacity.

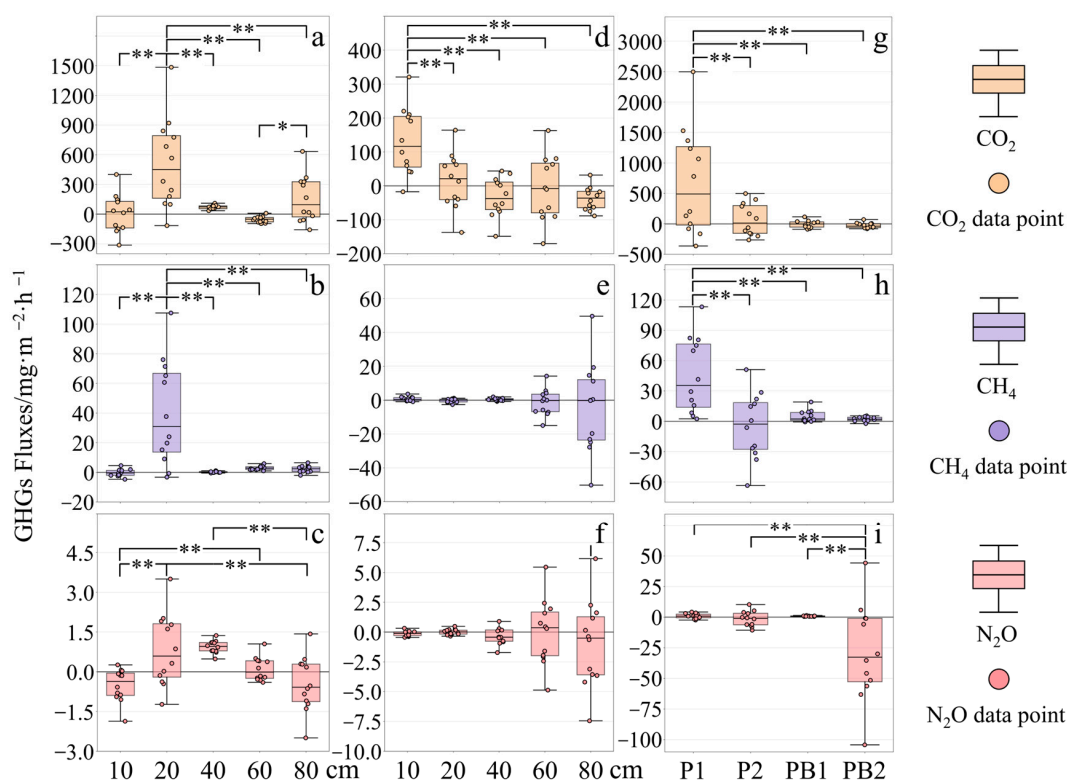


Figure 3. Greenhouse gas (GHG) emission fluxes from the four habitats. (a–c) CO₂, CH₄, and N₂O fluxes in the soil profile of slightly collapsed peat mound (P1). (d–f) CO₂, CH₄, and N₂O fluxes in the soil profile of severely collapsed peat mound (P2) and in the thawed herbaceous peat (PB1) and thermokarst pond (PB2). (g–i) Mean net fluxes of CO₂, CH₄, and N₂O across the four habitats. In panels (a–f), circles represent the measured flux values at each depth, and lines connect the mean values across depths to illustrate vertical trends. In boxplots, the central line indicates the median, box boundaries represent the 25th and 75th percentiles, and whiskers extend to the 5th and 95th percentiles ($n = 12$ per habitat). Asterisks denote significant differences among habitats or depths (ANOVA with Tukey's HSD post hoc test): * $p < 0.05$, ** $p < 0.01$.

3.2. Soil Organic Carbon and Carbon Fractions

Soil organic carbon and its fractions—particulate organic carbon (POC), mineral-associated organic carbon (MAOC), and dissolved organic carbon (DOC)—showed distinct responses to thermokarst development (Figure 4). SOC content peaked at 488.9 g kg^{-1} in PB1, which was 6.9% higher than in P1, and decreased to 453.8 g kg^{-1} in PB2 (Figure 4a). Vertically, the proportion of SOC in the 0–20 cm layer increased by 12.7%, while SOC decreased substantially in the 40–80 cm layer, suggesting that carbon loss during thaw was primarily localized to deeper soil layers. POC dominated the SOC pool, accounting for 62.2% of total SOC across all habitats (Figure 4a), indicating that particulate organic matter—rather than mineral-bound organic matter—constituted the majority of the carbon pool. POC reached 324.9 g kg^{-1} in PB1 (4.6% higher than P1) and decreased to 286.3 g kg^{-1} in P2 (7.8% lower than P1) (Figure 4a). In P1, POC content in the surface layer (0–10 cm) was 18.5% higher than in the deep layer (60–80 cm) (Figure 4c), suggesting that POC was preferentially concentrated near the surface. MAOC decreased to 34.2 g kg^{-1} in PB2, a 65.8% reduction from P1. In P1, the decrease in the 40–60 cm layer was 71.3% greater than that in the surface layer (Figure 4c), indicating that MAOC loss was disproportionately severe in deeper soils. DOC reached its minimum of 318.8 mg kg^{-1} in PB1, a 24.3% decrease from P1 (Figure 4b), while no clear vertical distribution pattern was observed for DOC across any habitat. Across all samples, SOC was positively correlated with POC (slope: 0.75, $p < 0.01$) and MAOC (slope: 0.33, $p < 0.01$), but not with DOC (slope: 0.30, $p > 0.05$) (Figure 4d,f), suggesting that SOC dynamics were more closely tied to particulate and mineral-associated fractions than to the dissolved fraction.

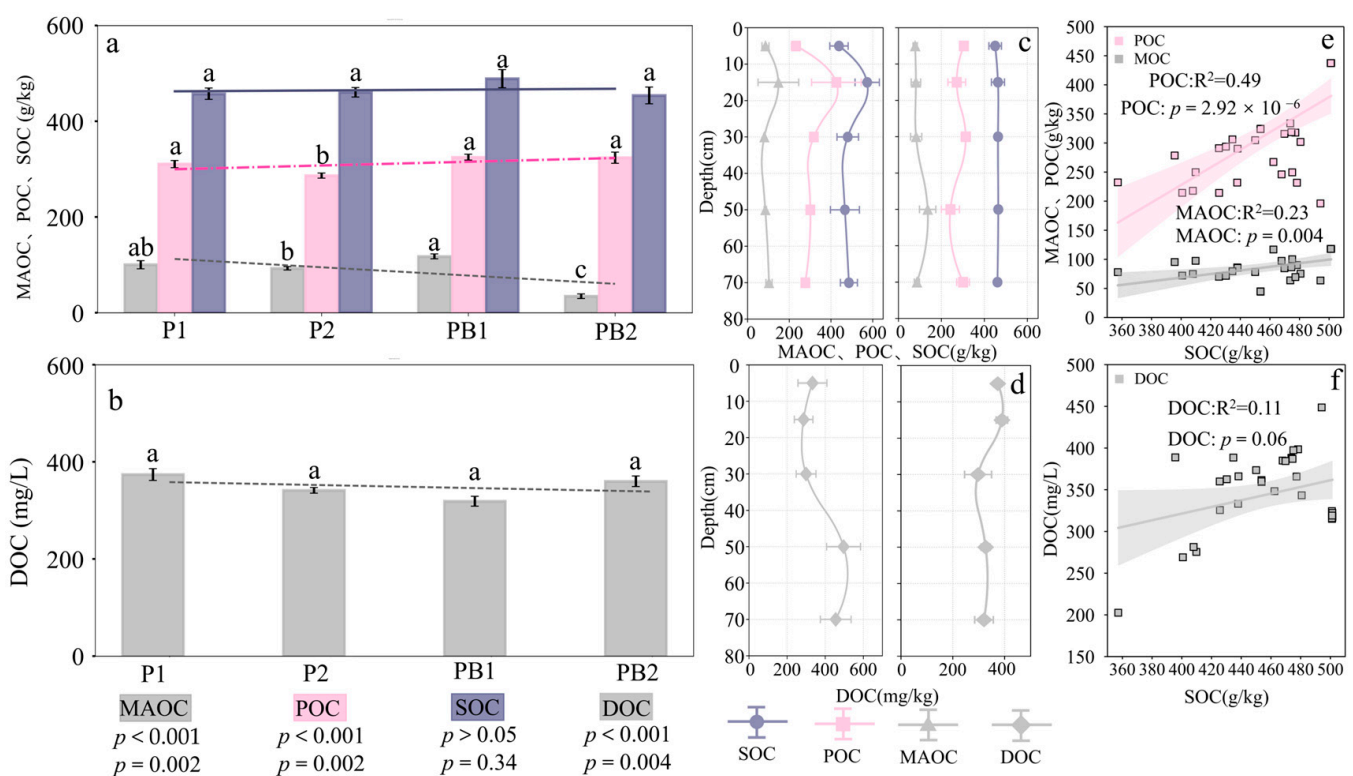


Figure 4. Soil organic carbon fractions in the four habitats. (a) SOC, POC, and MAOC contents in P1, P2, PB1, and PB2. Bars represent means $\pm$ SD ($n = 10$ per depth per habitat). Different lowercase letters above bars indicate significant differences among habitats for each fraction (one-way ANOVA).

with Tukey's HSD post hoc test, $p < 0.05$). (b) DOC contents in the four habitats; statistical annotations as in (a). (c) Vertical profiles of SOC, POC, MAOC, and DOC in the P1 soil profile. Symbols represent means $\pm$ SD at each depth ($n = 10$). (d) Relationships between SOC and POC, MAOC, and DOC across all P1 samples; solid lines are linear regression fits with 95% confidence bands (shaded areas). (e,f) Same as (c,d) but for P2.

3.3. Soil Environmental Factors

Soil nutrients (total nitrogen and total phosphorus), carbon-to-nitrogen ratios, inorganic nitrogen forms (NH_4^+ -N and NO_3^- -N), soil moisture, temperature, and pH all varied systematically across the four habitats (Figure 5). In the collapse zone (P1/P2), TN and TP showed subsurface enrichment (Figure 5). In P1, TN peaked at 14.5 g kg^{-1} in the 40–60 cm layer (14.9% higher than the surface), and TP peaked at 0.93 g kg^{-1} in the 20–40 cm layer (34.4% higher than the surface), indicating that nutrients were preferentially retained in subsurface layers during early collapse. In P2, both TN and TP decreased relative to P1, with TP loss accelerating in the 60–80 cm layer, suggesting that deeper nutrient pools became vulnerable to loss as collapse intensified. In the fully thawed stages (PB1/PB2), nutrient pools were substantially depleted. TP decreased from 0.23 g kg^{-1} in PB1 to 0.04 g kg^{-1} in PB2 (82.6% reduction), and TN decreased from 1.9 g kg^{-1} to 1.3 g kg^{-1} (29.2% reduction), indicating that complete thaw led to near-exhaustion of phosphorus and significant nitrogen loss. The C/N ratio remained low in the collapse zone (P1: 25.6–46.8; P2: 28.2–44.4), with vertical variation less than 20%. In the thawed stages, C/N increased sharply to 303.9 in PB1 and 360.0 in PB2, representing an 810% increase relative to P1. These values are substantially higher than those typically reported for mineral soils, but are within the range of stoichiometric ratios documented for peat soils in high-altitude permafrost regions. NH_4^+ -N fluctuated strongly in the collapse zone, reaching a maximum of $1181.2 \text{ mg kg}^{-1}$ in the 10–20 cm layer of P1 (Figure 5). NO_3^- -N decreased with depth in P1, from $284.95 \text{ mg kg}^{-1}$ at the surface to 267.4 mg kg^{-1} at depth. In PB2, NH_4^+ -N stabilized at 716.3 mg kg^{-1} , while mean NO_3^- -N increased to 435.5 mg kg^{-1} , suggesting a shift in nitrogen speciation from ammonium-dominated in collapse zones to nitrate-dominated in thawed aquatic habitats. Soil moisture (SM) in the collapse zone decreased from 27.6 to 28.1% in P1 to 19.2–20.0% in P2. In PB2, SM increased sharply to 62.1–78.2% (mean: 69.6%), with TP content negatively correlated with SM (when $\text{SM} > 60\%$, TP decreased by 82.6%), indicating that waterlogging was associated with phosphorus depletion. Soil temperature (ST) in PB2 was stable, ranging from 1.2 to 1.7 °C ($\Delta T \leq 0.5$ °C), compared to up to 8.9 °C in P2, suggesting that thermal variability was greatly suppressed in the aquatic habitat. Soil pH was lower in the collapse zone (P1: 4.1–4.8) than in PB2 (5.3–5.4) (Figure 5), indicating that complete thaw was associated with a shift toward less acidic conditions.

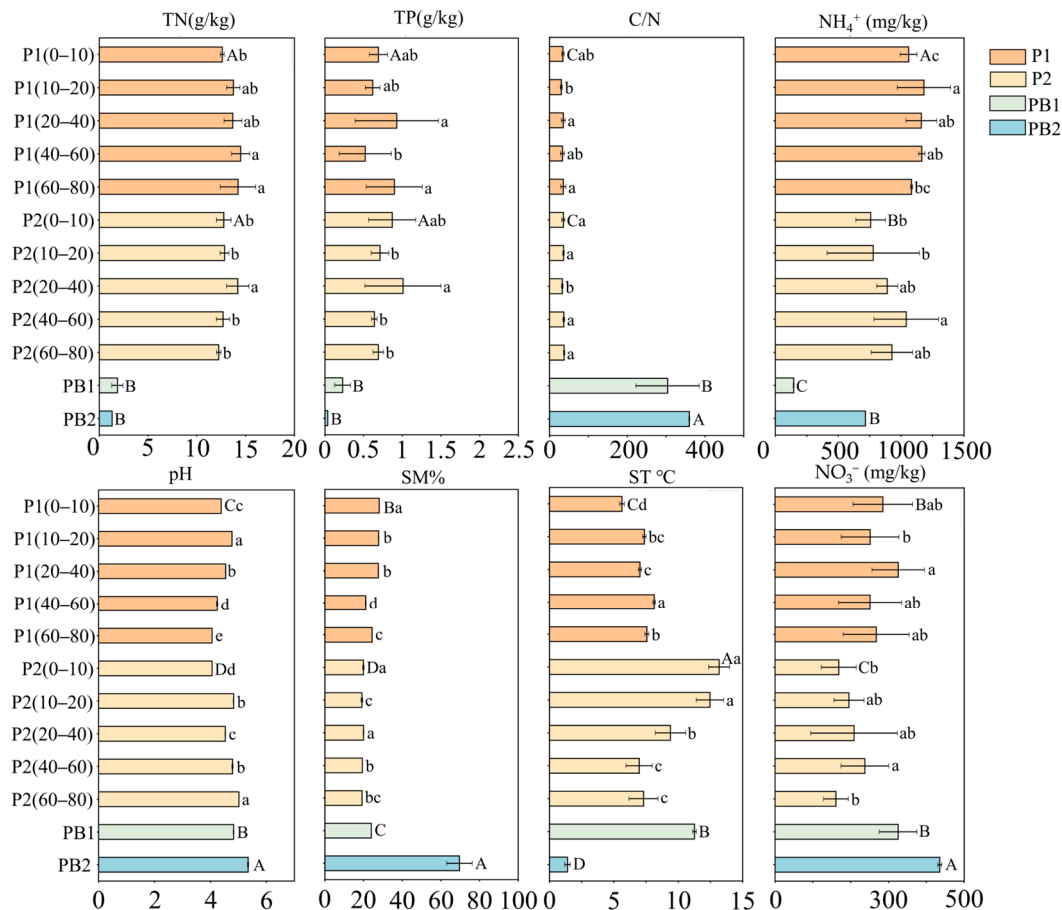


Figure 5. Soil nutrients and environmental factors across the four habitats. Bar charts show the values of each indicator, and area charts show vertical variation trends. Lowercase letters (a, b, c, d, e) denote significant differences among soil layers within each profile; uppercase letters (A, B, C, D) denote significant differences among habitats (ANOVA with Tukey's HSD post hoc test, $p < 0.05$).

3.4. Soil Enzyme Activities

Activities of five extracellular enzymes— α -glucosidase, cellulase, β -glucosidase, alkaline phosphatase, and leucine aminopeptidase—showed divergent responses to thermokarst development across the four habitats (Figure 6). α -Glucosidase and cellulase activities increased under mechanical disturbance (Figure 6). α -Glucosidase activity in the surface layer of P2 reached $349.5 \text{ nmol h}^{-1} \text{ g}^{-1}$, which was 194.6% higher than in P1 ($118.6 \text{ nmol h}^{-1} \text{ g}^{-1}$), suggesting that collapse disturbance stimulated the activity of carbon-acquiring enzymes. Its activity varied with depth, with the lowest value ($173.7 \text{ nmol h}^{-1} \text{ g}^{-1}$) at the 10–20 cm layer. In PB2, α -glucosidase activity was $583.4 \text{ nmol h}^{-1} \text{ g}^{-1}$, 8.9% higher than in PB1. Cellulase activity in the 20–40 cm layer of P2 reached $1180.2 \text{ nmol h}^{-1} \text{ g}^{-1}$, with a profile mean of $1211.9 \text{ nmol h}^{-1} \text{ g}^{-1}$ (194% higher than in P1), suggesting that cellulose-degrading enzymes were particularly responsive to mechanical disturbance. Its activity also varied with depth, with the lowest value at the 10–20 cm layer. In PB2, cellulase activity in the surface layer ($1250.7 \text{ nmol h}^{-1} \text{ g}^{-1}$) was 171.4% higher than in P1 ($460.8 \text{ nmol h}^{-1} \text{ g}^{-1}$), indicating that elevated cellulase activity persisted even after complete thaw. In contrast, β -glucosidase, alkaline phosphatase, and leucine aminopeptidase activities decreased along the thaw sequence, suggesting that prolonged carbon–nitrogen–phosphorus imbalance led to suppression of enzymes involved in polysaccharide metabolism, phosphorus mineralization, and nitrogen mineralization. β -Glucosidase activity in the 20–40 cm layer of P2 was $1543.2 \text{ nmol h}^{-1} \text{ g}^{-1}$ (higher than the same layer in P1), but in PB2 it decreased to $458.3 \text{ nmol h}^{-1} \text{ g}^{-1}$ —a 62.1% reduction from

PB1, indicating that the initial stimulation in deeper layers did not persist into the fully thawed stage. Alkaline phosphatase decreased vertically in P1 from 3976.3 nmol h⁻¹ g⁻¹ in the surface layer to 998.3 nmol h⁻¹ g⁻¹ in the deep layer (74.9% reduction), with a further 52.6% decrease in the corresponding layer of P2. In PB2, alkaline phosphatase activity was 1706.6 nmol h⁻¹ g⁻¹, suggesting that phosphorus-mineralizing capacity was maintained at moderate levels in the aquatic habitat. Leucine aminopeptidase in the deep layer of P2 (2455 nmol h⁻¹ g⁻¹) was 9.8% higher than in the corresponding layer of P1 (2235.7 nmol h⁻¹ g⁻¹). In the surface layer of PB2 (1485.1 nmol h⁻¹ g⁻¹), it was 21.6% lower than in P1 (1893.4 nmol h⁻¹ g⁻¹), suggesting that nitrogen-mineralizing capacity declined following complete thaw. Overall, the enzyme activity patterns revealed a divergence between carbon-acquiring enzymes (α -glucosidase and cellulase), which were stimulated by collapse disturbance, and enzymes involved in nutrient mineralization (β -glucosidase, alkaline phosphatase, and leucine aminopeptidase), which declined along the thaw sequence. This divergence suggests that mechanical disturbance and carbon–nitrogen–phosphorus imbalance exerted contrasting effects on different components of the soil enzyme system.

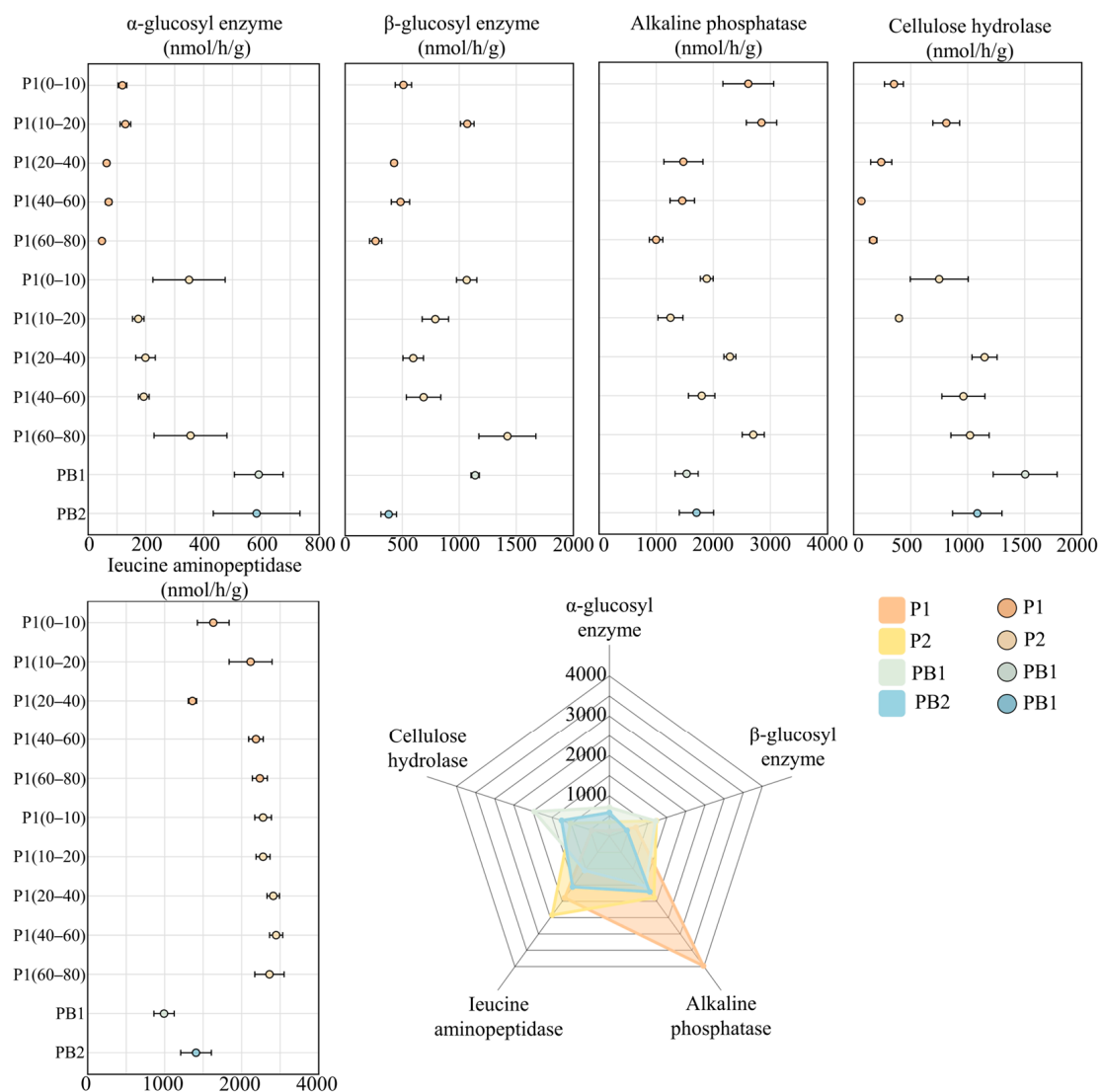


Figure 6. Soil enzyme activities in the four habitats. Bar charts (left panels) show mean activities of α -glucosidase, cellulase, β -glucosidase, alkaline phosphatase, and leucine aminopeptidase for each soil layer (0–10, 10–20, 20–40, 40–60, and 60–80 cm) in P1, P2, PB1, and PB2. Error bars represent standard deviations ($n = 3$ per layer). Area charts (right panels) show vertical variation trends of each enzyme activity across the soil profile for P1 and P2.

3.5. Structural Equation Modeling Results

A partial least squares structural equation model was constructed to examine the direct and indirect pathways through which environmental factors, enzyme activities, and carbon fractions influenced greenhouse gas fluxes (Figure 7). The structural equation model (SEM) explained a substantial portion of the variance in enzyme activity ($R^2 = 0.36$), carbon fractions ($R^2 = 0.78$), and GHG fluxes ($R^2 = 0.71$) across the four habitats. The model fit was acceptable (SRMR = 0.056), and the path coefficient patterns differed notably among the three successional stages (P1, P2, and PB). In the P1 stage (slightly collapsed peat mounds), enzyme activity was negatively associated with α -glucosidase (path coefficient = -0.51) and cellulase (path coefficient = -0.85), indicating that higher activities of these carbon-acquiring enzymes corresponded to lower overall enzyme activity. Carbon fractions were strongly positively associated with MAOC (path coefficient = 0.95) and POC (path coefficient = 0.85), suggesting that mineral-associated and particulate organic carbon were the dominant components of the soil carbon pool at this early collapse stage. GHG fluxes were positively associated with carbon fractions (path coefficient = 0.44, $p < 0.05$), indicating that carbon release was coupled with the availability of labile carbon substrates. Environmental factors, particularly soil moisture, showed a strong positive association with the environmental factor node (path coefficient = 0.93), reflecting the dominant role of hydrological conditions in structuring the early-stage collapse environment. In the P2 stage (severely collapsed peat mounds), the pathway from environmental factors to enzyme activity (path coefficient = 0.39) suggested that soil environmental conditions began to exert a stronger direct influence on microbial metabolic potential. Leucine aminopeptidase showed a strong positive association with nitrogen metabolism (path coefficient = 0.83), but its pathway to GHG fluxes was not significant ($p > 0.05$), indicating a decoupling between nitrogen mineralization and greenhouse gas emissions at this stage. POC (path coefficient = 0.86) and MAOC (path coefficient = 0.80) both showed strong positive associations with GHG fluxes (path coefficient = 0.47), suggesting that carbon release was primarily driven by the decomposition of both particulate and mineral-associated fractions. Soil acidification (pH path coefficient = 0.77) and waterlogging (soil moisture path coefficient = 0.86) showed positive associations with enzyme activity, and enzyme activity in turn showed a strong positive association with SOC decomposition (path coefficient = 0.96). This pattern indicates that as collapse intensified, environmental stressors directly stimulated microbial activity and accelerated organic matter decomposition. In the PB stage (thawed herbaceous peat and thermokarst pond), the pathway structure shifted markedly. In PB1 (thawed herbaceous peat), MAOC remained strongly associated with carbon dynamics (path coefficient = 0.95), while environmental factors showed a moderate association with carbon dynamics (path coefficient = 0.71). Cellulase activity showed a positive association with N_2O emissions (path coefficient = 0.47), suggesting a potential link between carbon decomposition and nitrogen gas losses under the anaerobic conditions of the thawed peat. In PB2 (thermokarst pond), the pathway from environmental factors to SOC decomposition (path coefficient = 0.47) indicated that environmental conditions became the primary driver of carbon dynamics, whereas the pathway from SOC to GHG fluxes was negative (path coefficient = -0.22), consistent with the observed shift from net CO_2 emission to net uptake in this stage (Figure 3).

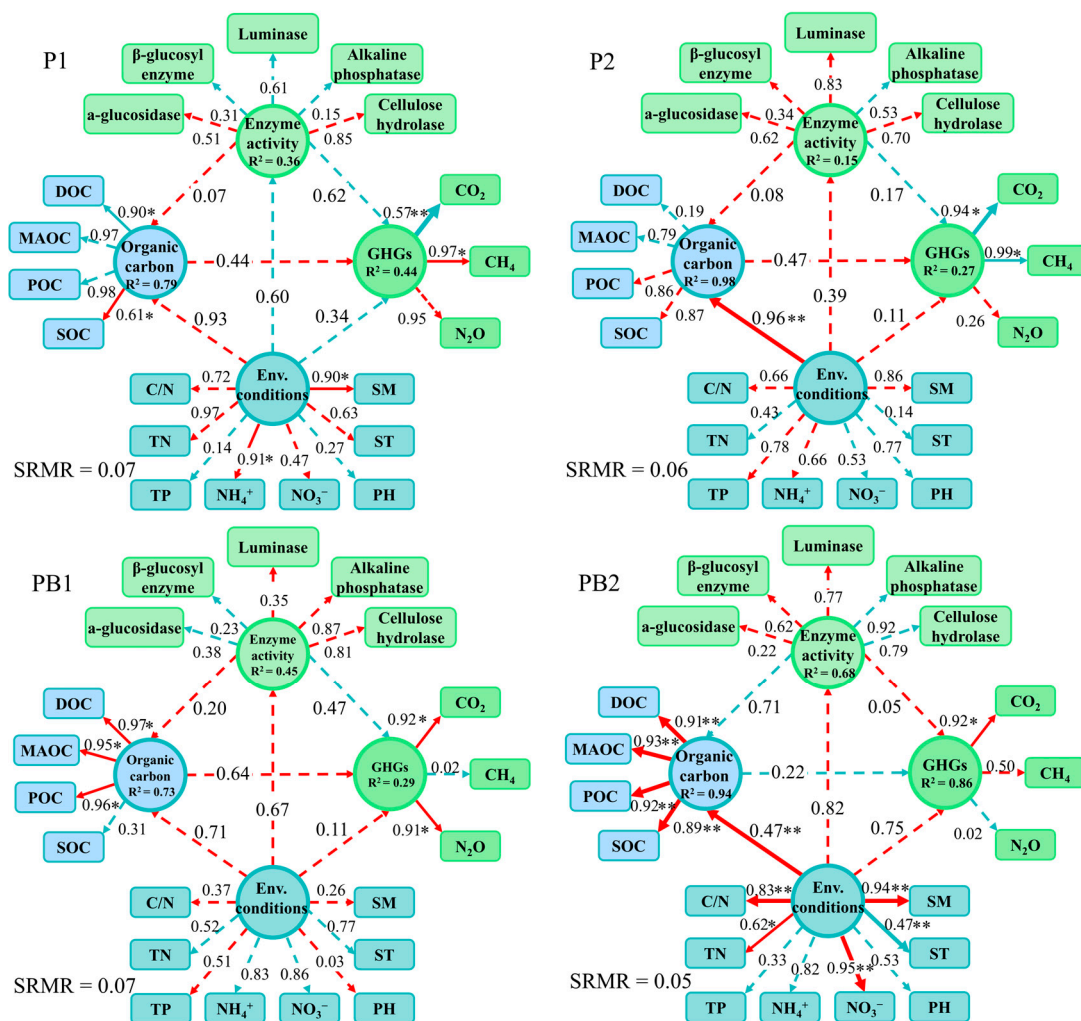


Figure 7. SEM illustrating the cascade mechanisms of thermokarst succession on carbon and nitrogen cycling and greenhouse gas emissions. Red and blue arrows represent positive and negative relationships, respectively. Arrow styles indicate significance levels: thick solid arrows denote highly significant paths ($p < 0.01$), solid arrows denote significant paths ($p < 0.05$), and dashed arrows denote non-significant paths ($p \geq 0.05$). Asterisks on arrows further specify significance: * $p < 0.05$, ** $p < 0.01$. Standardized path coefficients are shown adjacent to each arrow. Numbers within boxes (R²) represent the proportion of variance explained for endogenous variables. Environmental factors are collectively represented as “Env. conditions”.

Overall, the SEM results revealed a progressive shift in the dominant pathways controlling GHG fluxes across the thermokarst development. In the early collapse stage, carbon fractions and enzyme activities were the primary drivers of carbon release. With intensified collapse, environmental factors—particularly soil moisture and pH—exerted increasing control over enzyme activity and decomposition. In the final thawed stage, environmental conditions became the dominant regulator of carbon dynamics, coinciding with the transition of the system from a carbon source to a carbon sink.

4. Discussion

4.1. MAOC Oxidation and DOC Export in Carbon Loss

The physical disruption of mineral-associated organic carbon (MAOC) during thermokarst collapse has been identified as a key mechanism driving carbon loss in permafrost peatlands [41]. Studies in Arctic peatlands have reported MAOC oxidation losses of 20–35% during freeze–thaw processes, accompanied by a 1.5- to 2-fold increase in CO₂

emissions [42]. In the Altai Mountains, we observed a MAOC loss of 71.3% in the 40–60 cm layer at the P1 stage (Figure 4), substantially exceeding the rates reported for Arctic sites. The peak CO₂ emission (684.1 mg m⁻² h⁻¹; Figure 3) coincided with this MAOC loss, suggesting that oxidative loss of MAOC was the primary contributor to carbon release. In contrast, lateral DOC export (0.08 g C m⁻² d⁻¹) accounted for only 12.3% of total carbon loss. This contrasts with findings from Arctic peatlands, where hydrological export of DOC has been emphasized as a dominant carbon loss pathway [35]. The relatively minor role of DOC export in our study may reflect the low bulk density of collapsed peat (P1: 25.01 kg m⁻³), which limits water retention and flow connectivity, and the high bulk density of thermokarst ponds (PB2: 53.8 kg m⁻³), which physically impedes lateral water movement. This pattern differs from that observed in tropical peatlands, where drainage-induced DOC export dominates carbon loss [43]. Together, these observations suggest that carbon loss in temperate alpine peatlands may follow a pathway in which MAOC oxidation plays a more prominent role than DOC export. Hydrological conditions are known to regulate CH₄ emissions in northern peatlands [12]. In contrast to studies showing that water level fluctuations suppress CH₄ emissions following freeze–thaw [44], we found that CH₄ flux increased to 3.8 mg m⁻² h⁻¹ in the PB2 stage—4.3 times higher than under dry conditions. This increase was associated with the development of anaerobic conditions following thermokarst pond formation, which may have enhanced methanogenic activity [45]. However, phosphorus limitation (mean TP: 0.04 g kg⁻¹) appeared to constrain this process. The SEM results (Figure 7) showed that the path coefficient from MAOC to CH₄ in PB2 was 0.32 ($p > 0.05$), suggesting that the substrate supply from MAOC oxidation did not translate into a significant increase in CH₄ emissions. This may be attributable to phosphorus limitation suppressing methanogen activity, as has been observed in other peatland systems [46]. Thus, CH₄ emissions in alpine peatlands appear to be regulated by an interaction between substrate availability and phosphorus limitation.

The C/N ratio plays an important role in regulating the nitrogen cycle [47]. Studies on the Zoige peatland on the Tibetan Plateau have shown that when C/N exceeds 18, denitrifying enzyme activity is suppressed and N₂O emissions decline [48]. In our study, we observed a more pronounced pattern: when C/N exceeded 300, N₂O uptake increased by 42% relative to the collapsed areas, reaching −28.6 mg m⁻² h⁻¹ (Figure 3). This threshold is substantially higher than that reported for tropical peatlands [49], suggesting that the nitrogen cycle in alpine peatlands may be more sensitive to C–N imbalance. The lateral DOC loss (0.08 g C m⁻² d⁻¹) may further limit denitrification substrate availability by reducing the carbon supply to microorganisms [50], contributing to the elevated NO₃[−] content (435.5 mg kg⁻¹) and reduced TN (1.3 g kg⁻¹) observed in PB2. Deep soils (40–80 cm) contributed 42% more to N₂O uptake than surface layers, a pattern that differs from Amazonian peatlands where denitrification is surface-concentrated [51]. The SEM results (Figure 7) suggested that collapse-induced soil structure disruption may facilitate oxygen diffusion to deeper layers, potentially activating deep denitrifying communities. The correlation between leucine aminopeptidase activity and NO₃[−] content ($r = 0.83$) was consistent with the view that nitrogen-mineralizing enzymes participate in regulating N₂O emissions. When C/N exceeded 300, leucine aminopeptidase activity decreased, which may have reduced the nitrogen mineralization rate and, together with phosphorus limitation, limited nitrification. These observations point to a regulatory pathway in which enzyme activity and resource availability jointly influence N₂O dynamics in alpine peatlands.

The C/N ratios exceeding 300 observed in the fully thawed stages warrant further consideration. In mineral soils, C/N ratios typically range from 10 to 30, and values above 40 are uncommon [52]. However, peat soils in permafrost regions can exhibit substantially different stoichiometric characteristics due to the distinct accumulation histories of carbon

and nitrogen. In the Altai Mountains, the long-term peat carbon accumulation rate has been estimated at $25.4 \pm 7.7 \text{ g C m}^{-2} \text{ yr}^{-1}$, whereas the nitrogen accumulation rate is substantially lower at $1.5 \pm 0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$, and notably, the nitrogen accumulation rate does not covary with the carbon accumulation rate [53]. This asynchronous accumulation of carbon and nitrogen over millennial timescales contributes to a progressive widening of the C/N ratio in the peat profile. Following thermokarst collapse, nitrogen loss from the system is accelerated: total nitrogen declined from 14.5 g kg^{-1} in intact peat mounds to 1.3 g kg^{-1} in thermokarst ponds [2]. A pan-Arctic synthesis has shown that nitrogen content in boreal permafrost peatlands is significantly lower than in permafrost-free bogs despite similar vegetation types (0.9% versus 1.5% N), suggesting that permafrost conditions generally constrain nitrogen availability [54]. The values reported here (303.9–360.0) represent the upper end of the range documented for permafrost-affected peatlands, reflecting the combination of high organic carbon content and advanced nitrogen depletion in this study system.

4.2. Enzyme Activity Patterns and Their Implications

The response of enzyme activities to thermokarst collapse showed divergent patterns among different enzyme groups. α -Glucosidase and cellulase activities increased substantially following collapse disturbance (Figure 6). Cellulase activity in the 20–40 cm layer of P2 reached $1180.2 \text{ nmol h}^{-1} \text{ g}^{-1}$, nearly three times the level in P1. This stimulation may reflect the physical fragmentation of organic matter during collapse, which increases the surface area available for enzymatic attack. A similar increase in cellulase activity has been observed following drainage in tropical peatlands [55]. However, the persistence of elevated cellulase activity in PB2 ($1250.7 \text{ nmol h}^{-1} \text{ g}^{-1}$) suggests that the disturbance effect may extend beyond the initial collapse phase.

In contrast, β -glucosidase, alkaline phosphatase, and leucine aminopeptidase activities generally decreased along the thaw sequence (Figure 6). β -Glucosidase activity in PB2 ($458.3 \text{ nmol h}^{-1} \text{ g}^{-1}$) was 62.1% lower than in PB1, and leucine aminopeptidase in the PB2 surface layer was 21.6% lower than in P1. This decline is consistent with observations from Arctic peatlands, where polysaccharide metabolism deteriorates under prolonged freeze–thaw conditions [56]. The decrease in alkaline phosphatase activity (from $3976.3 \text{ nmol h}^{-1} \text{ g}^{-1}$ in P1 surface to $1706.6 \text{ nmol h}^{-1} \text{ g}^{-1}$ in PB2) coincided with the depletion of TP (from 0.93 to 0.04 g kg^{-1}), suggesting that phosphorus mineralization capacity may have been constrained by substrate limitation. Phosphorus limitation has been shown to influence both CH_4 oxidation and CO_2 emissions in peatland systems [57,58]. The strong correlation between leucine aminopeptidase activity and NO_3^- content ($r = 0.83$) further suggests a potential role of nitrogen-mineralizing enzymes in regulating denitrification pathways [59]. The divergence between carbon-acquiring enzymes (stimulated) and nutrient-mineralizing enzymes (suppressed) indicates that different components of the soil enzyme system responded differently to thermokarst collapse and the associated changes in carbon, nitrogen, and phosphorus availability.

4.3. Regional Comparison and Broader Implications

The patterns observed in the Altai Mountains differ from those reported for other permafrost regions in several respects. The MAOC oxidation rate in our study (71.3% in the 40–60 cm layer) exceeded the range reported for Arctic permafrost (20–35%) [60]. The carbon loss rate (217%) was approximately twice that reported for Arctic sites [61]. Several factors may contribute to this difference. First, the frequency of freeze–thaw cycles in temperate alpine regions (approximately 120 cycles per year) is higher than in the Arctic (approximately 60 cycles per year), which may enhance the physical disruption of mineral–

organic associations [62]. Second, Altai peatland soils have lower clay content (8–12%) than Arctic sites (15–25%), potentially resulting in weaker mineral protection [41]. Third, water table fluctuations during the growing season may be more pronounced in the Altai Mountains, promoting oxygen penetration and oxidative decomposition [63].

The shift from net CO₂ emission in collapsed peat mounds to net uptake in thermokarst ponds ($-25.6 \text{ mg m}^{-2} \text{ h}^{-1}$ in PB2) contrasts with the persistent CO₂ emission pattern reported for Arctic peatlands [64]. However, the net loss characteristic of the carbon pool remains consistent: the deep-layer carbon release induced by MAOC loss (71.3%) far exceeds the CO₂ sequestration capacity (only 0.2 g C m^{-2} at the interannual scale), thereby maintaining the net carbon source attribute of the system. Methane (CH₄) emissions from Arctic peatlands only offset 50% of CO₂ uptake [64]. However, in both systems, the carbon pool remained a net source at the annual scale: the deep-layer carbon release induced by MAOC loss far exceeded the CO₂ sequestration capacity observed at the interannual scale. In the Altai Mountains, phosphorus limitation ($\text{TP} \leq 0.04 \text{ g kg}^{-1}$) appeared to truncate the carbon flow by reducing alkaline phosphatase activity (98.1% decrease), resulting in CH₄ fluxes that reached only 43% of the theoretical maximum. This may weaken the potential offsetting effect of CH₄ emissions on MAOC-induced carbon loss.

Compared with tropical peatlands, where CO₂ emissions are primarily driven by drainage-induced processes [65], the Altai peatlands exhibited a pattern in which MAOC oxidation played a more dominant role. The lateral DOC loss in tropical peatlands dominates carbon release, whereas in the Altai Mountains the oxidative loss of MAOC appeared to be the primary carbon loss pathway. The peak CO₂ emission in our study ($684.1 \text{ mg m}^{-2} \text{ h}^{-1}$) was higher than that reported for some tropical peatlands, possibly reflecting the more aerobic conditions associated with the aridification trend in the Altai region [66].

Compared with peatlands on the Tibetan Plateau, the post-thaw C/N ratio in the Altai Mountains (303.9–360.0) was substantially higher than that reported for the Zoige area (18) [67,68], suggesting more pronounced carbon–nitrogen decoupling. Deep soils (40–80 cm) contributed 42% to N₂O uptake, a pattern that differs from the surface-dominated denitrification reported for Amazonian peatlands [51]. This difference may be related to collapse-induced oxygen diffusion to deeper layers, which could activate denitrifying communities. The N₂O uptake capacity in the fully thawed stage ($-28.6 \text{ } \mu\text{g m}^{-2} \text{ h}^{-1}$) was stronger than that reported for the Hongyuan peatland [69], possibly reflecting substrate limitation for denitrification under high C/N conditions. These regional differences highlight the sensitivity of carbon and nitrogen cycling in alpine peatlands to thermokarst collapse and suggest that the mechanisms governing greenhouse gas emissions may vary substantially across permafrost regions.

5. Conclusions

This study integrated in situ greenhouse gas flux monitoring with soil physicochemical analysis and enzyme activity assays to examine carbon and nitrogen dynamics during thermokarst succession in the Altai Mountains peatlands. Our main findings are summarized below.

- (1) Carbon dioxide (CO₂) fluxes shifted from net emission in the collapsed peat mounds ($684.1 \text{ mg m}^{-2} \text{ h}^{-1}$ in P1) to net uptake in the fully thawed thermokarst ponds ($-25.6 \text{ mg m}^{-2} \text{ h}^{-1}$ in PB2). The oxidative loss of mineral-associated organic carbon (MAOC) in the 40–60 cm layer (71.3%) was the dominant contributor to carbon release, whereas lateral dissolved organic carbon (DOC) export accounted for only 12.3% of total carbon loss ($0.08 \pm 0.02 \text{ g C m}^{-2} \text{ d}^{-1}$). Methane (CH₄) fluxes in the thermokarst ponds ($3.8 \pm 0.7 \text{ mg m}^{-2} \text{ h}^{-1}$) reached only 43% of the theoretical maximum; this suppression was associated with phosphorus limitation (total phosphorus $< 0.05 \text{ g kg}^{-1}$)

and a marked reduction in alkaline phosphatase activity. Nitrous oxide (N₂O) uptake increased along the thaw sequence, reaching $-28.6 \mu\text{g m}^{-2} \text{h}^{-1}$ in PB2, with the 40–80 cm layer contributing 42% more than the surface layer.

- (2) Soil carbon pool dynamics showed that MAOC decreased by 65.8% (to 34.2 g kg^{-1}) in the PB2 stage, while DOC export remained a minor pathway (12.3% of total carbon loss). The C/N ratio increased from below 50 in the collapse zones to 303.9–360.0 in the fully thawed stages, accompanied by nitrogen retention (TN: 1.3 g kg^{-1}) and elevated NO₃[−] content (435.5 mg kg^{-1}). These patterns suggest that carbon–nitrogen decoupling intensified along the development sequence.
- (3) Enzyme activities showed divergent responses to thermokarst collapse. α -Glucosidase and cellulase activities increased under mechanical disturbance, whereas β -glucosidase, alkaline phosphatase, and leucine aminopeptidase activities generally decreased along the thaw sequence. The decline in β -glucosidase activity (59.5% reduction in PB2 relative to P1) was associated with the progression of thaw. CH₄ emission peaks occurred in habitats with soil moisture > 60% and total phosphorus > 0.05 g kg^{-1} , whereas under phosphorus-limited conditions (TP $\leq 0.04 \text{ g kg}^{-1}$), CH₄ fluxes were substantially lower despite high soil moisture. N₂O uptake was enhanced when C/N ratios exceeded 300, particularly in deeper soil layers (>40 cm), where leucine aminopeptidase activity was suppressed.

Together, these findings indicate that the transition from peat mounds to thermokarst ponds in the Altai Mountains alters the net greenhouse gas source–sink balance through changes in MAOC stability, phosphorus availability, and carbon-to-nitrogen stoichiometry. These results provide empirical constraints for evaluating carbon–climate feedbacks in cold-region peatlands and highlight the importance of considering multiple interacting factors—including mineral protection, nutrient limitation, and enzyme activity—in assessing the biogeochemical consequences of permafrost thaw.

6. Research Limitations and Future Directions

This study, based on the space-for-time substitution approach, examined thermokarst succession in alpine peatlands. Several limitations should be acknowledged. First, sampling was confined to a single growing season (June 2023), which may not capture interannual variability or seasonal extremes such as spring thaw pulses and autumn freeze-in events. Second, the space-for-time approach inherently assumes that spatial gradients represent temporal trajectories, but it cannot account for interannual climate variability or extreme events. Third, winter processes, which can contribute substantially to annual greenhouse gas budgets in cold regions, were not measured.

To address these limitations, future research could include the following: (1) establishing long-term eddy covariance towers across all habitat types to capture continuous, multi-year flux dynamics; (2) conducting paired monitoring across three or more complete freeze–thaw cycles using automated chambers to quantify seasonal transition contributions; (3) integrating UAV-based hyperspectral imaging with in situ sensor networks to resolve the spatial and temporal heterogeneity of DOC export pathways; and (4) deploying year-round automated sampling systems to capture winter emissions, particularly during snowmelt and freeze-in periods.

Such efforts may help reduce uncertainties in permafrost carbon loss projections and improve the parameterization of carbon–climate feedback models.

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