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Determinants of invertebrate community structure in glacial-melt streams of southeast Tibet

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Abstract

1. A widely examined predictive model of invertebrate community dynamics in glacial-melt streams describes longitudinal changes in community structure with changing water temperature and channel stability with increasing distance from glaciers. Previous studies conducted in Europe, Greenland, New Zealand, and South America have supported the predictions of the invertebrate model and contributed to its refinement. However, none has evaluated if the model fits invertebrate community dynamics over a full range of distances from the glacier and water temperature conditions within glacial-melt streams in southeast Tibet.
2. We sampled invertebrates and measured water temperature, specific conductivity, turbidity, and associated glacier-related variables within 14 sites in three subalpine glacial-melt catchments in southeastern Tibet's Three Parallel Rivers region during 2010, 2011, 2013, and 2015. Our sites encompassed a temperature gradient from the upstream metakryal sites (maximum summer water temperature <2°C) to the furthest downstream site (maximum summer temperature >10°C) near the Mekong River.
3. We evaluated the relationships of invertebrate community structure with in situ water temperature and channel stability which are the focal habitat variables in the invertebrate model. The additional habitat variables of distance from the glacier, glacier size, conductivity, and turbidity were evaluated to see if these were more important determinants of community structure than in situ water temperature and channel stability.
4. Minimum and in situ water temperatures were positively correlated with distance from the glacier but Pfankuch Channel Stability Index bottom scores were not. Thus, the physical template within our study area differed from the expected template of the invertebrate model.
5. Similar to the invertebrate model, in situ water temperature by itself or combined with Pfankuch index best explained five invertebrate response variables. In contrast with the invertebrate model, conductivity and turbidity best explained invertebrate taxa richness, density, and the site scores of the first and second detrended correspondence analysis axes of relative abundance.
6. The invertebrate model predicts that only Diamesinae will occur in metakryal sites. However, in our metakryal sites we frequently captured 13 taxa (two Nemouridae morphotypes, Diamesinae, Orthocladiinae, *Rhyacophila*, *Epeorus*,

Taeniopterygidae, *Baetis*, *Capnia*, Simuliidae, Limnephilidae, *Himalopsyche*, and Collembola).

7. Invertebrate-habitat relationships and taxa occurrence trends in glacial-melt catchments in southeast Tibet differed from the invertebrate model predictions. Our findings highlight the need to develop a regional version of the invertebrate model applicable to Asian glacial-melt streams with unstable stream channels throughout their catchments and that do not freeze in the winter.

KEYWORDS

Chironomidae, invertebrate–habitat relationships, Plecoptera, sub-alpine glacier streams, Three Parallel Rivers region

1 | INTRODUCTION

The Milner et al., (2001) conceptual model of invertebrate community dynamics within glacial-melt streams postulates that water temperature and channel stability are the main factors influencing the longitudinal trends in invertebrate community structure and taxa occurrence with increasing distance from glaciers during the summer melt season (Milner, 2016; Milner, Brittain, et al., 2001; Milner & Petts, 1994). This conceptual model predicts that invertebrate taxa richness and density (i.e. abundance) will increase as the maximum summer water temperature (T_{max}) increases and channel stability increases with increasing distance from the glacier (Milner, 2016; Milner, Brittain, et al., 2001; Milner & Petts, 1994). The model also predicts the following changes in taxa composition with increasing water temperatures and channel stability (Milner, Brittain, et al., 2001). Metakryal sites (T_{max} <2°C) with the lowest channel stability will be dominated by the chironomid subfamily Diamesinae. The chironomid subfamily Orthocladiinae will colonise hypokryal sites (T_{max} >2°C and <4°C) with the lowest channel stability. Oligochaeta and Tipulidae will colonise hypokryal sites having greater channel stability than the metakryal sites closest to the glacier. Perlodidae, Taeniopterygidae, Baetidae, Simuliidae, and Empididae will become characteristic members of the invertebrate community in stream reaches with greater channel stability than the hypokryal sites and T_{max} from 4 to 6°C. Limnephilidae then colonise T_{max} (>6 and <8°C) reaches with increased channel stability and Nemouridae, Leuctridae, Heptageniidae, Rhyacophilidae, and Chironominae colonise the warmest sites exhibiting T_{max} >8 and <10°C and the most stable channels.

In accordance with the Milner, Brittain, et al., (2001) model predictions, water temperature and channel stability were identified as the primary determinants of invertebrate community structure in glacial-melt streams in Europe (Brittain et al., 2001; Castella et al., 2001; Hieber et al., 2005; Milner, Brittain, et al., 2001), New Zealand (Cadbury et al., 2011), and Ecuador (Jacobsen et al., 2010; Kuhn et al., 2011) and the model predictions of increased invertebrate taxa richness and density with increasing water temperatures and increasing channel stability in glacial-melt streams were also confirmed (Cadbury et al., 2011; Castella et al., 2001; Friberg et al., 2001; Jacobsen & Dangles, 2012; Jacobsen et al., 2010; Kuhn et al., 2011; Milner et al., 2001). Modifications were made to the model to provide more accurate taxa composition predictions based on different species pools found in North America (Milner, Brittain, et al., 2001), South America (Jacobsen et al., 2010; Milner, Brittain, et al., 2001), New Zealand (Cadbury et al., 2011), and Svalbard (Blaen et al., 2014). However, environmental factors other than water temperature and channel stability have been found to influence invertebrate community structure in glacial-melt streams, including suspended sediments, turbidity, conductivity, hydrologic variables, substrate size, coarse particulate organic matter, bryophyte biomass, channel slope, altitude, percent glacier cover in the catchment, and glacier size (Blaen et al., 2014; Cadbury et al., 2011; Castella et al., 2001; Friberg et al., 2001; Gislason et al., 2001; Jacobsen & Dangles, 2012; Kuhn et al., 2011; Lods-Crozet, Castella, et al., 2001; Lods-Crozet, Lencioni, et al., 2001; Milner, Taylor, et al., 2001). These findings suggest that water temperature and channel stability may not always be the primary determinants of community structure in glacial-melt streams as predicted by the Milner, Brittain, et al., (2001) model.

Monsoonal temperate glaciers with subalpine termini are perhaps the rarest glacier habitat remaining in the shrinking cryosphere and are characterised by heavy melting and subsequent high glacier stream discharge during the summer (Ageta & Higuchi, 1984; Pan et al., 2012). Mountain ranges in southeast Tibet contain the headwaters of the Three Parallel Rivers (Yangtze, Mekong, and Salween) and have the highest tree lines in the world (Baker & Moseley, 2007). The topographic relief of the area is extreme with gorges at 1,500 m above sea level (a.s.l), found within 20 km of peaks topping 6,700 m a.s.l., resulting in arid valleys, and subtropical, temperate, and boreal ecosystems in one of the most biodiverse regions of the world (Mittermeier et al., 1998). Additionally, the Mekong–Salween divide separates the eastern Himalayas and the Hengduan mountains and serves as a biogeographic barrier that may drive substantial allopatric speciation of the flora and fauna

(Li et al., 2011; Ward, 1921). The Hengduan mountains represents only 4.1% of China's total land area yet contains 52% of China's vascular plant species and 73% of China's protected wild animal species (Yang et al., 2004) with aquatic invertebrate biodiversity in this mountain region largely unexplored.

Habitat conditions and associated invertebrate relationships have been examined within high elevation glacial-melt streams (>4,000 m a.s.l.) on the Tibetan Plateau (Hamerlik & Jacobsen, 2012; Jiang et al., 2013; Laursen et al., 2015; Murakami et al., 2012; Xu et al., 2018). However, none of these studies examined the full range of water temperature, channel stability, and distance from the glacier as described in the Milner, Brittain, et al., (2001) model. Findings from Tibetan Plateau stream studies that are supportive of the Milner, Brittain, et al., (2001) model predictions include: (1) reduced taxa richness at sites with coldest water temperatures closest to the glacier (Murakami et al., 2012); (2) invertebrate taxa richness and Chironomidae taxa composition that differed longitudinally from the headwaters to the downstream reaches (Hamerlik & Jacobsen, 2012; Jiang et al., 2013); and (3) invertebrate taxa composition that was influenced by water temperature and substrate stability (Xu et al., 2018).

We hypothesised that longitudinal trends in invertebrate community structure and taxa composition within glacial-melt streams of the Hengduan Mountains during the ablation season would follow the trends predicted by the Milner, Brittain, et al., (2001) conceptual model. Our objectives were to determine if: (1) water temperature and channel stability were correlated with distance from the glacier; (2) invertebrate diversity, density, and taxa composition trends were influenced by water temperature and channel stability; and (3) water temperature and/or channel stability were better predictors of invertebrate community structure than other habitat factors (distance from glacier, glacier size, conductivity, turbidity).

2 | METHODS

2.1 | Study area

Sampling sites were located within three glacial-melt catchments in the Hengduan Mountain range of the Three Parallel Rivers region. The Mingyong and Sinong Glacier catchments are source headwaters of the Mekong River and the Hailuogou Glacier catchment is a source headwater of the Dadu and Yangtze Rivers. The Mingyong Glacier (12.55 km^2) on Mt. Kawagebo, Meilixueshan in Yunnan Province (28°26′14″N, 98°41′04″E) is one of the lowest elevation (2,750 m a.s.l.) and southernmost glaciers in China (He et al., 2003; Liu et al., 2015) that flows into the Mekong River. The neighbouring Sinong Glacier (10 km^2) terminates at 3,550 m a.s.l. and also drains into the Mekong. The Mingyong Glacier has been retreating at approximately 50 m per year since 2010 and the Sinong Glacier has been retreating, but at a slower rate (Fair, 2017). The Hailuogou Glacier catchment occurs in the Daxueshan mountain range in Sichuan province (29°35′48″N, 101°52′43″E) and contains the Hailuogou Glacier and Hailuogou Glacier #3. The Hailuogou Glacier originates on Mt. Gongga and has an area of 25 km^2 that has retreated 181 ± 23 m from 1994 to 2007 (Liu et al., 2010). Hailuogou Glacier #3 is a small glacier (2 km^2) above Hailuogou Glacier with a tributary that originates at 3,850 m a.s.l. and flows underneath the Hailuogou Glacier at approximately 3,200 m a.s.l. into the Hailuogou Glacier stream.

We sampled aquatic invertebrates, measured water temperature, specific conductivity, and turbidity, and evaluated channel stability from: (1) seven sites in the Mingyong catchment in 2010, 2011, 2013, and 2015; (2) three sites in the Hailuogou catchment in 2015; and (3) four sites in the Sinong catchment in 2015. Study sites were 10 times the length of the average bankfull width and ranged from 8.6 to 260 m long. Our sampling was conducted during the peak glacial melt season from June to August and during a 2-month window before (April–May) and a 3-month window after (October–December). Notably, samples collected outside of the peak glacial melt season were only included in the statistical analysis if the in situ water temperature was <10°C, turbidity values were >30 NTU, and we were unable to cross the stream channel due to torrential discharge. The number of times each site was sampled ranged from 1 to 9 over 4 years (Table S1). Sampling sites ranged from 0.02 to 8.7 km from the glacier snout (Table 1). All sites were located below the treeline and had canopy cover <1% (Table 1). In general, channel widths were the least in sites closest to the glaciers and the greatest in sites located the farthest from the glacier (Table 1).

2.2 | Measurements of water temperature, channel stability, and other habitat factors

In situ water temperature was measured with a multiparameter meter (YSI, 2009) at each site when invertebrate sampling occurred (Table S1). To verify that T_{max} values increase longitudinally with distance from the glacier as predicted by the Milner, Brittain, et al., (2001) model we installed water temperature data loggers (Onset Computer Corporation, Bourne, MA, U.S.A.) at different distances from the glaciers in the three glacier catchments. From August 2013 to February 2015, water temperature data loggers were in operation at five sites located at 0.2, 0.8, 2.5, 3.1, and 6.4 km from the Mingyong Glacier. In February 2015 only data from two water temperature data loggers (3.1 and 6.4 km) were retrievable due to loss of the logger or its burial within glacial flour. From May to August 2015 water temperature data loggers were operating at four sites located at 0.2, 0.8, 3.6, and 6.4 km from the Mingyong Glacier and the data were successfully retrieved at the end of August. From June to August 2015, two water temperature data loggers were compiling data at 0.8 and 2.4 km downstream of the Sinong Glacier. Only the logger located at 2.4 km downstream was retrievable in August due to burial of the upstream logger under boulders. From June to August 2015, three data loggers were in operation in the Hailuogou Glacier catchment at locations 0.5 km from the Hailuogou Glacier and 0.12 and 0.8 km from

TABLE 1 Selected physical characteristics of 14 sampling sites from five streams in the Hailuogou, Mingyong, and Sinong glacier-melt catchments in China

Site	Catchment	GPS coordinates	Distance from glacier (m)	Distance below tree line (m)	Channel width (m)	Slope (%)	Canopy cover (%)
HLG 3	Hailuogou	N29°32.42″ E101°57.54″	70	−350	3.1 (1.6)	4	0.0
HLG 3D	Hailuogou	N29°33.00″ E101°58.30″	800	−550	3.3 (0.3)	45	0.0
HLG 1	Hailuogou	N29°34.36″ E101°59.55″	25	−1,120	24.9 (7.1)	3	0.0
MYUV 1	Mingyong	N28°27.245″ E98°45.653″	15	−1439	1.9 (0.4)	30	0.0
MYUV 2	Mingyong	N28°27.245″ E98°45.653″	100	−1486	0.9 (0.5)	20	0.0
MY 1	Mingyong	N28°27.769″ E98°46.508″	95	−1647	8.6 (3.2)	4	0.0
MY 2	Mingyong	N28°27.436″ E98°46.286″	800	−1737	8.9 (3.7)	6	0.0
MY 3	Mingyong	N28°28.160″ E98°47.021″	2,500	−1,914	9.1 (2.6)	8	0.2
MY 4	Mingyong	N28°27.498″ E98°46.324″	3,000	−1,929	10.3 (6.9)	4	0.0
MY 5	Mingyong	N28°27.498″ E98°46.324″	5,500	−2,201	20.6 (6.5)	5	0.0
SN 1	Sinong	N28°29.090″ E98°43.744″	15	−616	5.0 (0.0)	3	0.0
SN 2	Sinong	N28°28.792″ E98°44.225″	1,000	−683	11.6 (6.7)	4	0.0
SN 3	Sinong	N28°28.741″ E98°44.939″	2,441	−981	5.5 (0)	5	0.0
SN 4	Sinong	N28°31.358″ E98°47.415″	8,700	−2120	7.65 (0.0)	3	0.0

Mean (*SD*) are reported for channel widths.

Hailuogou Glacier #3. All loggers installed in the Hailuogou Glacier catchment were retrieved successfully in August 2015. However, the data logger at 0.5 km from the Hailuogou Glacier and the data logger 0.12 km from Hailuogou Glacier #3 did not compile data for the full time because of either removal by an unknown person or by changes in channel geomorphology. The data logger 0.5 km from the Hailuogou Glacier compiled data from June to 4 July 2015 and the Hailuogou Glacier #3 logger recorded data from 1 June to 24 June 2015. All water temperature data loggers were covered with TidbiT boots to protect them from sediment abrasion, tied securely with stainless steel cable to riparian boulders, and programmed to record water temperature every 15 min. T_{max} and T_{min} were determined by identifying maximum and minimum water temperatures recorded from the peak glacial melt season at each site for each year measured.

The bottom component of the Pfankuch Channel Stability Index was calculated based on visual assessments of rock angularity, substrate surface brightness, substrate consolidation/packing, percent of the streambed affected by scouring and deposition, and presence/absence of moss or vegetation growth (Pfankuch, 1975). Low bottom scores (0–20) represent stable channels and high bottom scores (40–60) represent unstable channels (Pfankuch, 1975). Pfankuch Channel Stability Index assessments were made prior to invertebrate sampling.

Distance from the glacier for each site was measured either with a hand-held laser rangefinder (Bushnell Corp., Overland Park, KS, U.S.A.) or Google Earth. During invertebrate sampling, specific conductivity was measured with the multiparameter meter (YSI, 2009) and four measurements of turbidity were made at each site with a turbidity tube (Science First, Yulee, FL, U.S.A.) and used to calculate mean turbidity from each site.

2.3 | Invertebrate collection and identification

Ten Surber (0.09 m^2, mesh size 250 μm) samples were taken from representative hydraulic habitats (riffles, runs, pools, rapids, step-rapids) in each site and composited into one sample. Specifically, in each site we sampled five riffles and runs, three rapids and step-rapids, one pool, and one additional hydraulic habitat type. All invertebrates except Chironomidae were enumerated and identified in the laboratory using a 0.7–3.0× dissecting microscope (American Optical Corp., Vernon Hills, IL). Chironomids were cleared, dehydrated, mounted in Euporal (Epler, 2001), and identified under a 40–400× compound microscope (Olympus Optical Company, Ltd., Tokyo, Japan). Invertebrates other than Ephemeroptera, Plecoptera, Trichoptera, Chironomidae, Hirudinea, Oligochaeta, Collembola, Hydrachnida, and Lepidoptera were identified to the family level. Ephemeroptera were identified to genus. Trichoptera and Plecoptera were identified to either family (Chloroperlidae, Glossasomatidae, Leuctridae, Limnephilidae, Taeniopterygidae), morphotypes (Nemouridae), or genus (*Amphinemura*, *Brachycentrus*, *Capnia*, *Rhyacophila*, *Himalopsyche*). Nemouridae morphotype identifications were based on gill structure and femur spine patterns (Baumann, 1975). Hirudinea, Oligochaeta, Collembola, and Hydrachnidia were identified at the subclass level and Lepidoptera and Isopoda were identified at the Order level. Chironomidae were identified to sub-family (Diamesinae, Orthocladiinae), tribe (Tanytarsini), or genus (*Boreoheptagyia*) (Epler, 2001; Merritt et al., 1996; Morse et al., 1994). Sub-sampling procedures were used only for Chironomidae identifications from two samples collected from the Hailuogou Glacier catchment in 2015 that had >600 Chironomidae specimens. From these samples, 125 Chironomidae individuals were identified.

2.4 | Statistical analysis

We conducted linear mixed effect model analysis to evaluate the relationships of water temperature, channel stability, and invertebrate response variables with selected fixed effect factors of interest. Linear mixed effect model analyses were used to address pseudoreplication that occurred as a result of repeatedly sampling the same sites over multiple years. Our first step in each analysis was to identify the best random effect for each response variable with the use of the Akaike's information criteria (AIC) to compare initial linear mixed effect models with the fixed effect factors of interest and having one of nine possible random effects (i.e. site, glacier catchment, site nested within glacier catchment, year and site, year and glacier catchment, year and site nested within glacier catchment, month and site, month and glacier catchment, month and site nested within glacier catchment). After identifying the best random effect, we then examined normality of the residuals with the Shapiro–Wilk test using the shapiro.test function (stats package, R Core Team, 2017) and the qqPlot function (car package, Fox & Weisberg, 2011) and examined the plots of the residuals and the fitted values to determine if the model residuals were homogenously distributed. The models of integer response variables that did not meet the residual assumptions were reanalyzed with generalised linear mixed effect model analyses. Models of non-integer response variables that did not meet the residual assumptions were reanalyzed using linear mixed effect model analyses with log(x + 1) or arcsine square root transformed response variables. Tables S2 and S3 summarise the statistical tests used, the data transformation used, and the best identified random effect for all linear mixed effect model analyses. AIC tests (AIC function), linear mixed effect model analyses (lmer function), and generalised linear mixed effect model analyses (glmer function with poisson family or glm.nb function) within the lme4 package (Bates et al., 2015) were conducted with R (R Core Team, 2017). The *p* values for the linear and generalised linear mixed effect model analyses were obtained with the lmerTest function from the lmerTest package (Kuznetsova et al., 2017). Linear mixed effect model analyses, generalised linear mixed effect model analyses, and the Shapiro–Wilk tests were conducted with a significance level of 0.05.

2.4.1 | Water temperature and channel stability analyses

We used linear mixed effect model analyses to evaluate the relationships of: (1) in situ water temperatures with distance from the glacier, T_{max} from May to October, and T_{min} from May to October with the distance from the glacier; (2) Pfankuch Channel Stability Index bottom score with distance from the glacier; (3) T_{max} from May to October with distance from the glacier; and (4) T_{min} from May to October with distance from the glacier (Table S2). Understanding these relationships was needed to examine if the longitudinal trends in water temperature and channel stability were consistent with the physical template stipulated by Milner, Brittain, et al., (2001) and the correspondence between our in situ water temperature measurements with T_{max} and T_{min}.

2.4.2 | Invertebrate relationships with water temperature, channel stability, and other habitat factors

We first conducted linear mixed effect model analysis to determine if invertebrate taxa richness, density, percent Diamesinae, Diamesinae abundance, Nemouridae abundance, and taxa composition trends (i.e. site scores from the first and second axes of the detrended correspondence analysis (DCA) of presence/absence and relative abundance) were influenced by the fixed effects of in situ water temperature and Pfankuch score (Table S3). Additionally, we used the AIC test to identify which of the three fixed effect models (in situ water temperature only, Pfankuch score only, or in situ water temperature and Pfankuch scores) was the best model for each of our nine invertebrate response variables. These initial AIC analyses reduced the redundancy in our final multimodel inference analyses described below by ensuring that only the best in situ water temperature and channel stability model was used in those analyses. Pearson correlation analysis between in situ water temperature and Pfankuch scores indicated that these two fixed effects were not correlated with each other ($r = 0.03$, p value $= 0.803$).

Detrended correspondence analyses were conducted with presence/absence data from each taxa to obtain the site scores (i.e. an index) from the resulting axes that describes trends in taxa composition among samples based on taxa occurrence. We also conducted DCA with the relative abundance of each taxa to obtain the site scores that describes trends in taxa composition among samples based on the taxa relative abundance. The influence of rare taxa on DCA results was reduced by deleting taxa that occurred in <10% of all samples prior to analyses and selecting the PC-ORD option that downweights taxa that occurred < the frequency of the most common taxa/5. DCA was chosen to summarise our taxa composition trends because it a well-known approach that is effective in extracting species composition gradients (Ejrnaes, 2000; Larsen & Ormerod, 2010). Additionally, our initial inspection of the DCA plots confirmed that our DCA results were not influenced by the wedge-shaped distortion that can arise with some data sets. DCAs were conducted with PC-ORD version 6.17 (McCune & Mefford, 2011).

The second part of our invertebrate analysis was to determine if the best identified models from our initial analysis of in situ water temperature and/or Pfankuch scores described above were better predictors of our nine invertebrate response variables than models containing one of four other habitat variables. For this part of our analysis, we first conducted linear mixed effect model analysis or generalised linear mixed effect model analysis with a single fixed effect to determine if invertebrate taxa richness, density, percent Diamesinae, Diamesinae abundance, Nemouridae abundance, and taxa composition trends were influenced ($p < 0.05$)

by fixed effects of distance from the glacier, glacier size, conductivity, and turbidity (Table S3). This component of our analysis was necessary to ensure that the follow up multimodel inference analyses included only models having fixed effects that had a significant effect ($p < 0.05$) on the invertebrate response variables. Then we conducted multimodel inference analysis to determine if the best in situ water temperature and channel stability models were better than single fixed effect models developed with those additional fixed effects found to have a significant effect ($p < 0.05$) on the nine invertebrate response variables. Our multimodel inference analysis involved obtaining the small sample AIC (AICc) score, ΔAICc (the difference in AICc between each model and the model with the minimum AICc), and Akaike weight (Wi) from the best in situ water temperature and channel stability model and single fixed effect models containing those additional fixed effects that had a significant effect ($p < 0.05$) on an invertebrate response variable (Burnham & Anderson, 2002; Johnson & Omland, 2004). We based our multimodel inference analysis on the AICc because the ratio of n/K was <40 for all models (Burnham & Anderson, 2002; Johnson & Omland, 2004). AICc values were obtained with the AICc function within the AICcmodavg package (Mazerolle, 2016) in R.

2.4.3 | Invertebrate taxa percent occurrence trends among water temperature, conductivity, and turbidity categories

We evaluated the trends in the presence–absence of the 21 most frequently occurring taxa by calculating the percent occurrence of each taxa (number of samples with presence of an invertebrate taxa/total number of samples) within six in situ water temperature categories used by Milner, Brittain, et al., (2001) (<2°C, 2–4°C, 4–6°C, 6–8°C, 8–10°C, >10°C). We did not evaluate the trends in presence–absence of each taxa among Pfankuch score categories because 97% of all samples fell within one bottom score category. Additionally, taxa captured in <10% of all samples were not included in these analyses.

3 | RESULTS

3.1 | Water temperature and channel stability

In situ water temperatures obtained during invertebrate sampling ranged from 0.10 to 11.60°C with an overall mean of 3.14°C. Notably, only two of 57 samples had in situ water temperatures >8°C. Our water temperature data loggers documented that T_{max} ranged from 0.99 to 7.77°C and T_{min} ranged from 0.05 to 3.41°C. In general, our water temperature data confirm that the water temperatures we encountered during invertebrate sampling were well within the conditions that typify glacial-melt streams (Milner & Petts, 1994). Pfankuch scores ranged from 32 to 60 with an overall mean of 53.4, which indicated that the majority of invertebrate samples were collected from sites having unstable channels.

In situ water temperatures and T_{min} were positively correlated ($p < 0.05$) with distance from the glacier (Figure 1). T_{max} and Pfankuch scores were not correlated ($p > 0.05$) with distance from the glacier (Figure 1). Additionally, T_{max} and T_{min} obtained from the water temperature data loggers were positively correlated ($p < 0.05$) with in situ water temperatures obtained during invertebrate sampling (Figure 1).

3.2 | Invertebrate relationships with water temperature, channel stability, and other habitat factors

We documented 42 taxa from 6,618 individuals collected in the three catchments (Table S4). The five most abundant taxa overall were: (1) Nemouridae morphotype 1; (2) Diamesinae; (3) Orthocladiinae; (4) Nemouridae morphotype 2; and (5) *Epeorus* (Table S4). Within individual streams taxa richness ranged from 18 (Hailuogou) to 38 (Mingyong) and abundance ranged from 1,729 (Hailuogou) to 4,124 (Mingyong; Table S4).

The first two DCA axes with the invertebrate presence/absence data explained 22% of the variance in the data. The first presence/absence DCA (paDCA) axis was a gradient where increasing site scores along paDCA axis 1 corresponded with increasing Himalopsyche and Hydrachnidia occurrences and decreasing site scores corresponded with increasing Tipulidae occurrence (Figure 2). The second paDCA axis was a gradient where increasing site scores corresponded with increasing Tanytarsini occurrences and decreasing site scores corresponded with increasing Rhyacophila occurrences (Figure 2). The first two DCA axes with the invertebrate relative abundance data explained 35% of the variance in the data. The first relative abundance DCA (raDCA) axis consisted of a gradient where increasing site scores corresponded with increasing Diamesinae relative abundance and decreasing site scores corresponded with increasing Nemouridae morphotype 1 relative abundance (Figure 3). The second raDCA axis was a gradient where increasing site scores corresponded with increasing Capnia and Taeniopterygidae relative abundance and decreasing site scores corresponded with increasing Nemouridae morphotype 2 relative abundance (Figure 3).

Taxa richness, Diamesinae abundance, Nemouridae abundance, paDCA axis 1 scores, paDCA axis 2 scores, and raDCA axis 2 scores were correlated ($p < 0.05$) with in situ water temperature (Table 2). Taxa richness, Diamesinae abundance, Nemouridae abundance, and paDCA axis 2 scores increased and paDCA axis 1 scores and raDCA axis 2 scores decreased with increasing in situ water temperatures (Table 2). Nemouridae abundance and paDCA axis 2 scores were positively correlated ($p < 0.05$) with the Pfankuch scores (Table 2). The results of multivariate models containing in situ water temperature and Pfankuch scores were consistent with the results of univariate models, except for the multivariate model of Diamesinae abundance that indicated that water temperature and Pfankuch

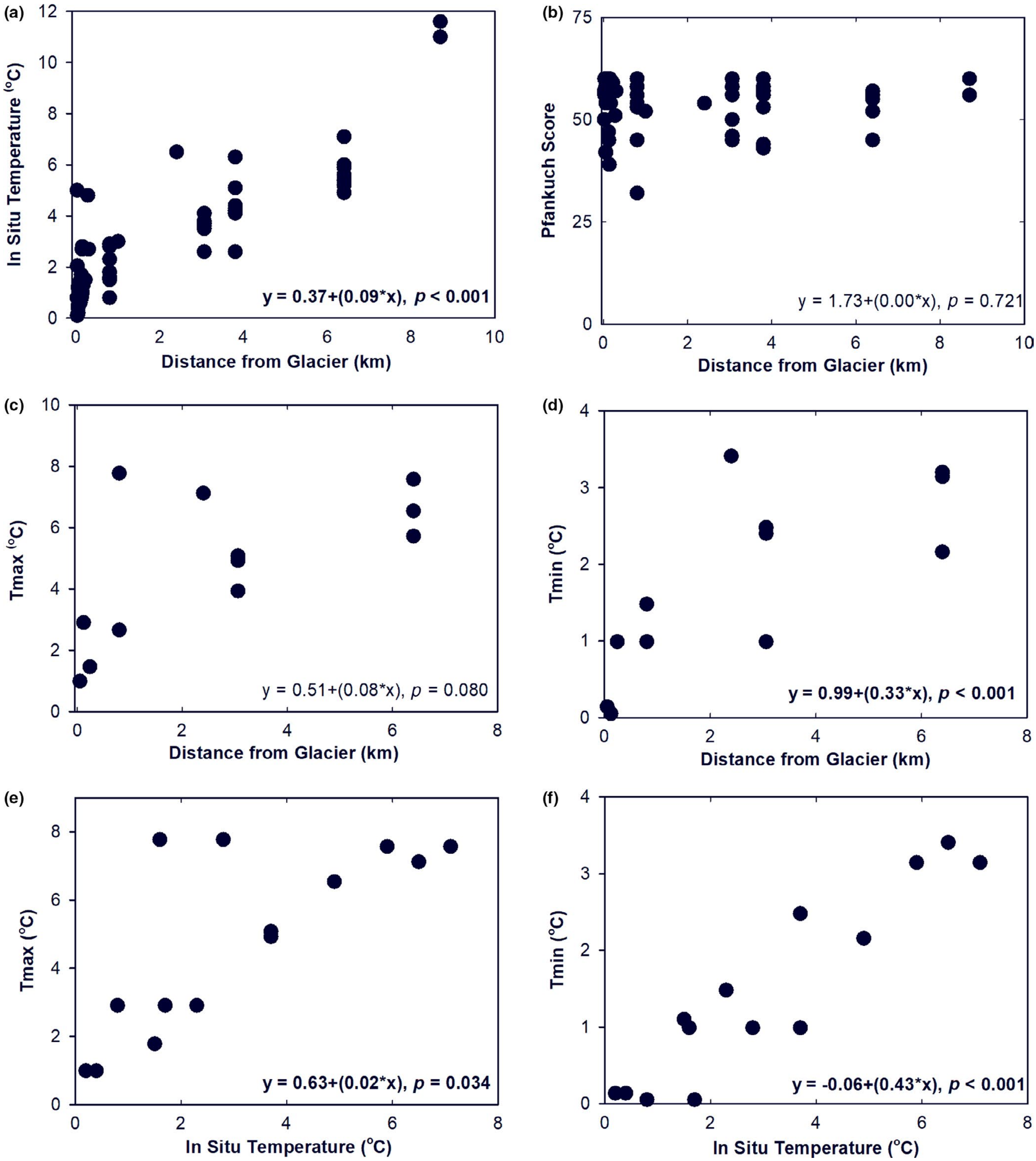

FIGURE 1 Relationships of in situ water temperature (a), Pfankuch Channel Stability bottom scores (b), T_{max} (c), and T_{min} (d) with distance from the glacier within three glacial-melt catchments in China, 2010 to 2015. Depicted also is the relationship of T_{max} (e) and T_{min} (f) with in situ water temperatures. The linear mixed effect model analysis equation and their associated *p* values are presented within each sub-figure

scores were positively correlated ($p < 0.05$) with Diamesinae abundance (Table 2). Additionally, AIC scores indicated that the univariate model of in situ water temperature was the best model for five response variables (taxa richness, density, percent Diamesinae, paDCA 1, raDCA2) and the multivariate model was the best model for four response variables (Diamesinae abundance, Nemouridae abundance, paDCA2, raDCA1; Table 2).

Taxa richness, density, Diamesinae abundance, Nemouridae abundance, paDCA axis 2 scores, and raDCA axis 2 scores were correlated ($p < 0.05$) with distance from the glacier (Table 3). Taxa

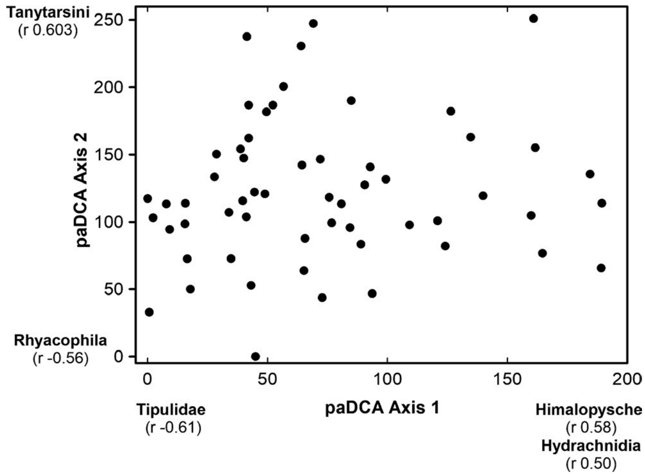

FIGURE 2 Detrended correspondence analysis (DCA) results based on the presence/absence of 21 common invertebrate taxa captured within three glacial-melt catchments in China, 2010 to 2015. The Pearson correlation coefficient (*r*) describes the correlation between the presence of each taxa and the site scores of the associated DCA axis

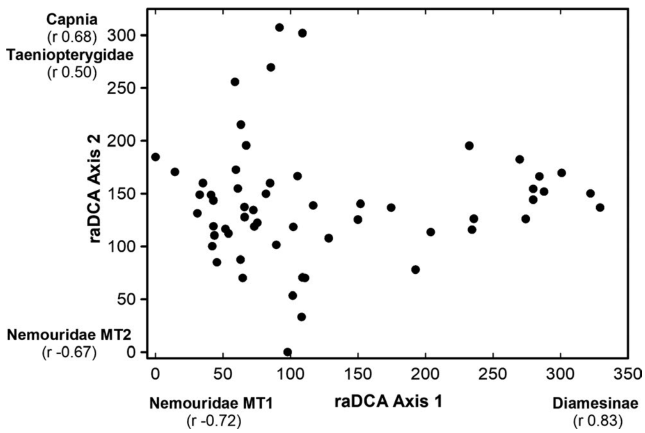

FIGURE 3 Detrended correspondence analysis (DCA) results based on the relative abundance of 21 common invertebrate taxa captured within three glacial-melt catchments in China, 2010 to 2015. The Pearson correlation coefficient (*r*) describes the correlation between the relative abundance of each taxa and the site scores of the associated DCA axis. MT1, morphotype 1; MT2: morphotype 2

richness, density, Diamesinae abundance, Nemouridae abundance and paDCA axis 2 scores increased and raDCA axis 2 scores decreased with increasing distance from the glacier (Table 3). Diamesinae abundance increased ($p < 0.05$) with glacier size (Table 3). Taxa richness, density, Diamesinae abundance, and raDCA axis 2 scores were correlated ($p < 0.05$) with conductivity (Table 3). Taxa richness, density, and Diamesinae abundance increased and raDCA axis 2 scores decreased with increasing conductivity (Table 3). Density, percent Diamesinae, and raDCA axis 1 scores were negatively correlated with turbidity (Table 3).

Our AICc analyses resulted in the comparisons of subsets of two to four models for each invertebrate response variable from seven possible models (Table 4). The univariate model of conductivity had the least AICc and the greatest Wi for taxa richness and raDCA axis 2 site scores (Table 4). None of the other taxa richness and raDCA axis 2 site score models exhibited a ΔAICc <2 that would indicate substantial support for another model (Burnham & Anderson, 2002). The univariate model of turbidity had the least AICc and the greatest Wi for invertebrate density, but the univariate model of conductivity had substantial support because its ΔAICc value was <2 from that of the turbidity model (Table 4). The univariate model of turbidity had the least AICc and the greatest Wi for raDCA axis 1 site scores and the multivariate model of water temperature and Pfankuch scores did not exhibit a ΔAICc <2 (Table 4). The univariate model of water temperature had the least AICc and the greatest Wi for percent Diamesinae, but the univariate model of turbidity had substantial support because its ΔAICc value was <2 from that of the water temperature model (Table 4). Additionally, percent Diamesinae was correlated ($p < 0.05$) with turbidity, but not water temperature, which provides additional support for the univariate model of turbidity. The multivariate model of in situ water temperature and Pfankuch scores exhibited the least AICc and the greatest Wi for Diamesinae abundance, Nemouridae abundance and paDCA axis 2 site scores (Table 4).

3.3 | Invertebrate taxa percent occurrence trends among water temperature categories

Nemouridae morphotype 1 exhibited >70% occurrence in all water temperature categories (Table 5). Diamesinae exhibited at least 70% occurrence in <2°C, 4–6°C, 6–8°C, and >10°C water temperature categories (Table 5). Orthocladiinae had >70% occurrence within the 4–6°C, 6–8°C, and >10°C water temperature categories (Table 5). *Epeorus*, *Baetis*, Tipulidae, Nemouridae morphotype 2, *Rithrogena*, Tanytarsini, Oligochaeta, and Hydrachnidia occurred with 100% of the samples in the 6–8°C and/or >10°C water temperature categories (Table 5). Notably, 13 taxa (Nemouridae morphotype 1, Diamesinae, Orthocladiinae, *Rhyacophila*, *Epeorus*, Taeniopterygidae, *Baetis*, *Capnia*, Nemouridae morphotype 2, Simuliidae, Limnephilidae, *Himalopsyche*, and Collembola) occurred in >20% of all of samples having the coldest water temperatures (Table 5).

4 | DISCUSSION

Our results indicated that the physical habitat template and invertebrate–habitat relationships within glacial-melt streams in southeastern Tibet differed from the predictions of the Milner, Brittain, et al., (2001) model. The most pronounced difference between the physical habitat template of our catchments and those on which the Milner, Brittain, et al., (2001) model is based is that the Pfankuch bottom scores in our sites did not vary with distance from the glacier snout and remained consistently high throughout the catchments. Accordingly, our finding that water temperature was

TABLE 2 Fixed effect estimates (FEE), *p* values, and Akaike's Information Criteria (AIC) values from linear and generalised linear mixed effect models evaluating the influence of water temperature (WT) and Pfankuch Channel Stability bottom scores (PS) on macroinvertebrate community response variables within the Hailuogou, Mingyong, and Sinong glacial-melt catchments in China, 2010 to 2015

Response variable	Model	WT FEE (*p* value)	PS FEE (*p* value)	AIC
Taxa Richness	WT	**0.855 (<0.001)**	–	**591.21**
Taxa Richness	PS	–	0.021 (0.699)	612.78
Taxa Richness	WT & PS	**0.855 (<0.001)**	0.003 (0.955)	591.34
Density	WT	0.050 (0.147)	–	**117.60**
Density	PS	–	−0.007 (0.570)	121.39
Density	WT & PS	0.051 (0.144)	−0.008 (0.531)	126.15
Percent Diamesinae	WT	−0.024 (0.102)	–	**−4.08**
Percent Diamesinae	PS	–	0.001 (0.841)	1.11
Percent Diamesinae	WT & PS	−0.024 (0.100)	0.001 (0.749)	6.95
Diamesinae Abundance	WT	**0.189 (<0.001)**	–	2,569.47
Diamesinae Abundance	PS	–	0.046 (0.171)	2,644.23
Diamesinae Abundance	WT & PS	**0.216 (<0.001)**	**0.019 (<0.001)**	**2,558.85**
Nemouridae Abundance	WT	**0.304 (<0.001)**	–	1745.60
Nemouridae Abundance	PS	–	**0.039 (<0.001)**	1701.30
Nemouridae Abundance	WT & PS	**0.205(<0.001)**	**0.032 (<0.001)**	**1667.10**
paDCA 1	WT	**−7.092 (0.023)**	–	**578.32**
paDCA 1	PS	–	0.110 (0.894)	586.17
paDCA 1	WT & PS	**−7.155 (0.023)**	0.250 (0.759)	578.82
paDCA 2	WT	**8.382 (0.003)**	–	603.81
paDCA 2	PS	–	**2.661 (0.014)**	608.46
paDCA 2	WT & PS	**9.312 (0.001)**	**2.781 (0.006)**	**596.77**
raDCA 1	WT	2.244 (0.678)	–	647.39
raDCA 1	PS	–	−0.031 (0.983)	650.15
raDCA 1	WT & PS	2.246 (0.681)	−0.078 (0.958)	**646.79**
raDCA 2	WT	**−11.951 (<0.001)**	–	**591.21**
raDCA 2	PS	–	−0.595 (0.607)	612.78
raDCA 2	WT & PS	**−11.928 (<0.001)**	−0.365 (0.703)	591.34

Bolded *p* values are those that are <0.05 and bolded AIC values are the smallest values from among three models for each invertebrate response variable

positively correlated with distance from the glacier and Pfankuch bottom scores was not contradicted the Milner, Brittain, et al., (2001) conceptual model that postulates both will increase with distance from the glacier. Our invertebrate–habitat relationship findings indicated that water temperature, conductivity, and turbidity were the most important determinants of invertebrate community structure rather than water temperature and channel stability, as predicted by the Milner, Brittain, et al., (2001) model. We also observed the frequent occurrence of 13 taxa in sites with water temperatures <2°C, which contradicted the Milner, Brittain, et al., (2001) model prediction that only Diamesinae will occur in sites with water temperatures <2°C.

Other studies conducted on the Tibetan Plateau within glacial melt streams (Hamerlik & Jacobsen, 2012; Laursen et al., 2015; Murakami et al., 2012) also found that water temperature increased with distance from the glacier but channel stability did not during the summer ablation season, suggesting that the physical template within Tibetan glacial melt-streams differs from that used to develop the Milner, Brittain, et al., (2001) conceptual model. Torrential discharge conditions along entire catchments during the combined summer glacier ablation and monsoon season in the region probably resulted in high Pfankuch bottom scores (i.e. low channel stability) throughout the catchments.

Our study confirmed the importance of water temperature as a determinant of invertebrate community structure and is consistent with the Milner, Brittain, et al., (2001) model predictions and findings from glacial-melt streams in Europe, New Zealand, and Ecuador (Milner, 2016). However, in our Asian catchments, channel stability was not identified as an important determinant of invertebrate community structure, which contradicts the Milner, Brittain, et al., (2001) model predictions and findings from glacial-melt streams from other parts of the world (Milner, 2016). Instead, we found that conductivity and turbidity were important determinants of invertebrate community structure. We are not the first to document deviations in the predicted invertebrate–habitat relationships from the Milner, Brittain, et al., (2001) model. Distance to the glacier and conductivity were the most important determinants of invertebrate community structure within glacial-melt streams in Iceland (Gislason

TABLE 3 Fixed effect estimate (FEE) and *p* values from linear and generalised linear mixed effect models evaluating the influence of distance from the glacier, glacier size, conductivity, and turbidity on macroinvertebrate community response variables within the Hailuogou, Mingyong, and Sinong glacial-melt catchments in China, 2010 to 2015

Response variable	Model	FEE	*p* value
Taxa Richness	Distance from Glacier	1.114	**0.003**
Taxa Richness	Glacier Size	−0.075	0.699
Taxa Richness	Conductivity	0.043	**<0.001**
Taxa Richness	Turbidity	−0.001	0.065
Density	Distance from Glacier	0.075	**0.019**
Density	Glacier Size	−0.001	0.962
Density	Conductivity	0.010	**<0.001**
Density	Turbidity	−0.001	**<0.001**
Percent Diamesinae	Distance from Glacier	−0.023	0.196
Percent Diamesinae	Glacier Size	0.009	0.302
Percent Diamesinae	Conductivity	0.000	0.700
Percent Diamesinae	Turbidity	−0.0002	**0.002**
Diamesinae Abundance	Distance from Glacier	0.086	**<0.001**
Diamesinae Abundance	Glacier Size	0.021	**<0.001**
Diamesinae Abundance	Conductivity	0.005	**<0.001**
Diamesinae Abundance	Turbidity	–	dnc
Nemouridae Abundance	Distance from Glacier	0.618	**0.012**
Nemouridae Abundance	Glacier Size	0.073	0.470
Nemouridae Abundance	Conductivity	–	dnc
Nemouridae Abundance	Turbidity	–	dnc
paDCA 1	Distance from Glacier	−7.329	0.082
paDCA 1	Glacier Size	−1.576	0.427
paDCA 1	Conductivity	−0.165	0.280
paDCA 1	Turbidity	0.002	0.845
paDCA 2	Distance from Glacier	5.930	**0.035**
paDCA 2	Glacier Size	1.398	0.389
paDCA 2	Conductivity	0.079	0.688
paDCA 2	Turbidity	−0.001	0.948
raDCA 1	Distance from Glacier	−0.496	0.938
raDCA 1	Glacier Size	1.571	0.624
raDCA 1	Conductivity	0.123	0.625
raDCA 1	Turbidity	−0.049	**0.006**
raDCA 2	Distance from Glacier	−10.934	**<0.001**
raDCA 2	Glacier Size	−1.141	0.517
raDCA 2	Conductivity	−0.430	**0.023**
raDCA 2	Turbidity	0.023	0.110

Bolded *p* values are those that are < 0.05. dnc, model did not converge; paDCA, presence/absence detrended correspondence analysis; raDCA, relative abundance detrended correspondence analysis

et al., 2001). Distance to the glacier was the most important determinant of community structure in Italian glacial-melt streams (Maiolini & Lencioni, 2001) and channel slope and distance to the glacier were the most influential variables on Chironomidae communities in six European glacial-melt streams (Lods-Crozet, Lencioni, et al., 2001). Jacobsen and Dangles (2012) documented that a glacial index based on distance from the glacier and glacier size was the best predictor of invertebrate taxa richness in glacial-melt streams in Europe and Ecuador. Although we did not identify distance from the glacier as an important determinant of invertebrate community structure, we observed that in situ water temperature and conductivity were correlated ($p < 0.05$) with distance from the glacier (in situ water temperature $r = 0.86$; conductivity $r = 0.49$). Thus, even though our statistical analyses were based on simple models containing only one or two uncorrelated fixed effects our water temperature and conductivity results probably reflect the underlying influence of distance from the glacier, which is consistent with the predictions of the original Milner and Petts (1994) model that postulated a combined effect of water temperature and distance from the glacier. In contrast the Milner, Brittain, et al., (2001) model omits distance from the glacier. We suspect that water temperature, conductivity, and turbidity accounted for more variation in the invertebrate response variables than distance from the glacier because the majority of our sites were repeatedly sampled throughout the study and probably exhibited different levels of water temperature, conductivity, and/or turbidity.

We observed a positive correlation of invertebrate taxa richness with water temperature, which is consistent with the Milner, Brittain, et al., (2001) model predictions and research findings from glacial-melt streams in other parts of the world (Milner, 2016). In contrast, invertebrate density was not correlated with water temperature, which differs from the Milner, Brittain, et al., (2001) model predictions. Invertebrate taxa richness and density were not correlated with Pfankuch scores, which also differs from the Milner, Brittain, et al., (2001) model predictions and findings of others who documented positive correlations between taxa richness and density with increasing channel stability (Milner, 2016). Diamesinae abundance increased with increasing water temperature and decreasing channel stability, which is only partially concordant with the Milner, Brittain, et al., (2001) model predictions that postulate positive correlations of Diamesinae abundance with both water temperature and channel stability. Additionally, our Diamesinae abundance findings are consistent with those of Castella et al., (2001) who documented that Diamesinae density was correlated with water temperature, but not channel stability in European glacial-melt streams.

Our study catchments were numerically dominated by Nemouridae and subsequently we incorporated Nemouridae abundance as part of our statistical analysis. The Milner, Brittain, et al., (2001) model suggests that Nemouridae abundance and density will exhibit a positive correlation with water temperatures and channel stability. However, we observed that Nemouridae abundance was positively correlated with both water temperature and Pfankuch scores, which is similar to findings by Castella et al., (2001) who observed positive correlations of Nemouridae density with water temperature and Pfankuch scores in seven European

TABLE 4 Summary of the number of parameters (k), small-sample Akaike information criterion (AICc), difference in AICc between each model and the model with the minimum AICc (ΔAICc), and Akaike weight (Wi) from linear and generalised linear mixed effect models with different independent variables to determine which independent variable had the greatest influence on invertebrate community response variables within the Hailuogou, Mingyong, and Sinong glacial-melt catchments in China, 2010–2015

Response variable	Model	k	AICc	ΔAICc	Wi
Taxa Richness	Water Temperature	5	286.60	16.09	0.00
Taxa Richness	Distance from Glacier	5	287.92	17.41	0.00
Taxa Richness	**Conductivity**	**5**	**270.51**	**0.00**	**1.00**
Density	Water Temperature	4	111.57	23.49	0.00
Density	Distance from Glacier	4	108.42	20.34	0.00
Density	Conductivity	4	88.14	0.06	0.49
Density	**Turbidity**	**4**	**88.08**	**0.00**	**0.51**
Percent Diamesinae	**Water Temperature**	**5**	**−13.14**	**0.00**	**0.53**
Percent Diamesinae	Turbidity	5	−13.37	0.23	0.47
Diamesinae Abundance	**Water Temperature & Pfankuch**	**4**	**2,559.62**	**0.00**	**1.00**
Diamesinae Abundance	Distance from Glacier	3	2,631.45	71.83	0.00
Diamesinae Abundance	Glacier Size	3	2,576.5	16.86	0.00
Diamesinae Abundance	Conductivity	3	2,616.42	56.80	0.00
Nemouridae Abundance	**Water Temperature & Pfankuch**	**4**	**1667.83**	**0.00**	**1.00**
Nemouridae Abundance	Distance from Glacier	3	1832.34	164.51	0.00
paDCA 2	**Water Temperature & Pfankuch**	**5**	**609.54**	**0.00**	**0.99**
paDCA 2	Distance from Glacier	4	618.45	8.91	0.01
raDCA 1	Water Temperature & Pfankuch	7	666.62	42.64	0.00
raDCA 1	**Turbidity**	**6**	**623.98**	**0.00**	**1.00**
raDCA 2	Water Temperature	5	605.13	5.70	0.05
raDCA 2	Distance from Glacier	5	604.72	5.29	0.06
raDCA 2	**Conductivity**	**5**	**599.43**	**0.00**	**0.80**

Bolded text and values indicate those models having the lowest AICc and the greatest Wi values for each invertebrate response variable. paDCA, presence/absence detrended correspondence analysis; raDCA, relative abundance detrended correspondence analysis

glacial-melt streams. Our findings and those of Castella et al., (2001) suggest that future research should identify the morphological, physiological, and behavioural adaptations that enable Nemouridae to persist in harsh unstable conditions.

Our results that indicated presence–absence taxa composition gradients were best predicted by water temperature or a combination of water temperature and Pfankuch scores is consistent with the predictions of the Milner, Brittain, et al., (2001) model and with the relationships documented by others working in glacial-melt streams in Tibet (Xu et al., 2018), Ecuador (Jacobsen et al., 2010), and Norway (Brittain et al., 2001). However, our finding that relative abundance taxa composition gradients were more strongly correlated with habitat variables other than water temperature and Pfankuch scores were inconsistent with the Milner, Brittain, et al., (2001) model, but were similar to the results of others working in Ecuador (Kuhn et al., 2011), Svalbard (Blaen et al.,2014), and Iceland (Gislason et al., 2001).

Our taxa percent occurrence trends differed substantially from those predicted by the Milner, Brittain, et al., (2001) model. In addition to Diamesinae, 12 taxa (Nemouridae morphotype 1, Orthocladiinae, *Rhyacophila*, *Epeorus*, Taeniopterygidae, *Baetis*, *Capnia*, Nemouridae morphotype 2, Simuliidae, Limnephilidae, *Himalopsyche*, and Collembola) were frequently captured in the metakryal zone (<2°C), which is colder than their first predicted occurrence in the Milner, Brittain, et al., (2001) model. Notable among these deviations is the frequent occurrence of Nemouridae, Heptageniidae, and Rhyacophilidae in the metakryal zone, because these taxa are only predicted to occur in sites with water temperatures >8°C. Additionally, Capniidae and Collembola were captured frequently within the metakryal zone, but they are not listed as focal taxa in the Milner, Brittain, et al., (2001) model. Future glacial-melt stream research in other parts of Asia need to document if the taxa occurrence trends we observed are representative of the entire region.

TABLE 5 Overall percent occurrence and percent occurrence of invertebrate taxa within six in situ water temperature (°C) categories within the Hailuogou, Mingyong, and Sinong glacial-melt catchments in China, 2010–2015. Percent occurrences ≥70 are denoted by white text and black cell shading

Taxa (overall % occurrence)	Water temperature categories <2 (*n* = 23)	2–4 (*n* = 15)	4–6 (*n* = 14)	6–8 (*n* = 3)	8–10 (*n* = 0)	>10 (*n* = 2)
Nemouridae morphotype 1 (82)	83	80	79	100	–	100
Diamesinae (74)	70	67	71	100	–	100
Orthocladiinae (61)	39	67	71	100	–	100
Rhyacophila (54)	57	53	43	67	–	50
Epeorus (53)	35	60	64	67	–	100
Taeniopterygidae (49)	57	60	43	0	–	0
Baetis (47)	39	40	57	67	–	100
Capnia (46)	43	53	43	67	–	0
Tipulidae (37)	4	20	57	100	–	50
Nemouridae morphotype 2 (35)	22	27	50	67	–	100
Simuliidae (32)	22	27	43	67	–	50
Rithrogena (32)	13	40	29	33	–	100
Limnephilidae (28)	35	20	14	0	–	050
Tanytarsini (26)	9	7	50	100	–	100
Oligochaeta (26)	17	13	29	100	–	100
Himalopsyche (19)	26	13	7	33	–	0
Collembola (16)	22	13	7	0	–	0
Hydrachnidia (14)	13	7	7	0	–	100
Boreoheptagyia (12)	13	0	14	0	–	0
Empididae (12)	13	0	7	33	–	50
Stratiomyidae (11)	4	7	14	33	–	0

Physical habitat trends and invertebrate species pools of glacial-melt streams are expected to differ among different geographic regions of the world (Milner, 2016). Thus, it is not a surprise that our results differ from the Milner, Brittain, et al., (2001) model predictions. We suspect our results are driven by a combination of the following factors: (1) our Asian catchments exhibit a unique physical habitat template characterised by increasing water temperatures with increasing distance from the glacier and unstable channels throughout the entire catchment during the ablation season; (2) our catchments contain a species pool that differs from European, Ecuadorian, and New Zealand glacial-melt streams; and (3) the glacier termini are located below the zero-degree isotherm altitude. Therefore, these streams, the melt-streams do not freeze solid and remained mostly snow-free during the winter. We strongly suspect our taxa occurrence trends were influenced by the lack of freezing in the metakryal sites during the winter, which would enable invertebrate taxa other than Diamesinae to colonise. In contrast, glacial-melt streams with glacier termini above the zero-degree isotherm altitude will be more likely to freeze in the winter, resulting in harsh habitat conditions (Danks, 2007) that limit community composition to Diamesinae and other taxa having physiological freeze tolerance mechanisms (Oswood et al., 1991).

In conclusion, we have presented the first evaluation of the applicability of the Milner, Brittain, et al., (2001) conceptual model of invertebrate community dynamics to monsoonal temperate glacial-melt streams within the Three Parallel Rivers Region, China. Our results represent the first documentation of the following for glacial-melt streams in southeast Tibet: (1) the importance of water temperature, conductivity, and turbidity as determinants of invertebrate community structure; (2) the relationships of invertebrate taxa richness with water temperature and conductivity; (3) the relationships of invertebrate abundance, Diamesinae abundance, Nemouridae abundance, and taxa composition with water temperature and Pfankuch scores; and (4) taxa percent occurrence trends across a full spectrum of water temperatures and distances from the glacier. Our novel results differ from the Milner, Brittain, et al., (2001) conceptual model predictions that were derived primarily from glacial-melt streams located outside of the Himalayan region. Our findings indicate a need for the development of a regional version of the Milner, Brittain, et al., (2001) model applicable to glacial-melt streams in Asia that possess unstable stream channels throughout their catchments and that do not freeze during the winter. We also suggest that future research in monsoonal glacial melt streams in Asia evaluate the relationships of invertebrate functional traits (functional feeding groups, life history traits, freeze tolerance adaptations, and morphological groups) diversity, abundance, and composition with physical habitat variables (water chemistry, stream discharge, and other glacial-melt driven variables) to improve our understanding of invertebrate–habitat relationships within these dynamic streams and contribute to future refinements of the Milner, Brittain, et al., (2001) model.

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DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

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

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