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Glaciers, snow, and rain: Water source influences invertebrate community structure and secondary production across a hydrologically diverse subarctic landscape

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Abstract

The melting cryosphere adds heterogeneity to the abiotic and biotic characteristics of many high latitude and montane rivers. However, climate change threatens the cryosphere's persistence in many regions. While existing research has explored the impacts of cryospheric loss on the diversity and structure of freshwater communities, implications for functional traits of communities, such as production of aquatic invertebrates, remain unresolved. Here, we quantified aquatic invertebrate community structure and secondary production in southeast Alaska (USA) streams that represent a meltwater to non-meltwater gradient, including streams fed primarily by: (1) glacier-melt, (2) snowmelt, (3) rainfall, and (4) a combination of these sources. We found alpha diversity was highest in the snow-fed stream and lowest in the glacier-fed stream. Annual secondary production was also lowest in the glacier-fed stream (0.56 g ash-free dry mass m^{-2}), but 2–5 times higher in the other stream types primarily due to greater production of shared taxa that were found in all streams. However, despite low invertebrate diversity and productivity, the glacier-fed stream hosted distinct species assemblages associated with unique cycles of stream flow, water temperature, turbidity, and nutrient concentrations, which contributed to higher beta diversity between streams. Our findings suggest that the loss of glacier-melt contributions to rivers may result in increased freshwater invertebrate production but reduced beta diversity, which could have implications for community stability and the capacity of landscapes to support higher-level consumers, including fishes.

Climate change is driving the decline of the global cryosphere and reshaping abiotic regimes to which ecological communities have adapted (Elser et al. 2020). In high-altitude and -latitude freshwater ecosystems meltwaters from icefields, glaciers, and seasonal snowpack can exert major influences on stream flow, water temperature, and nutrient availability (Milner et al. 2017). Numerous studies provide evidence that loss of meltwater contributions will alter the biodiversity of downstream ecosystems through the loss of unique meltwater-adapted species, communities, and food webs (Jacobsen and Dangles 2012; Pitman et al. 2021). As meltwater streams become warmer and clearer it is also assumed that they will become more biologically productive; however, few studies have empirically examined how rates of productivity, such as the secondary production of aquatic insects may change as meltwater sources diminish (Pitman et al. 2020; Bellmore et al. 2022). Thus, the relationship between well-documented changes in freshwater invertebrate biodiversity and associated changes in secondary production remain unclear (Dolbeth et al. 2012, 2015).

As meltwater contributions diminish, secondary macroinvertebrate production is predicted to increase via two distinct, but not mutually exclusive mechanisms: (1) enhanced productivity of existing taxa as conditions become less harsh (Niedrist et al. 2018), and (2) the replacement of specialist taxa with a more diverse assemblage of productive generalist taxa (Brown et al. 2018). In the first mechanism, the productivity of existing aquatic communities increases due to more

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favorable conditions for aquatic invertebrates and production of primary food sources (e.g., algae). For instance, reduced glacial meltwater results in: warmer water temperatures which can accelerate consumer metabolism and growth, more stable stream beds for benthic organisms, and greater water clarity which facilitates primary production (Bernhardt et al. 2022; Cross et al. 2022). In the second mechanism, new species colonize, replacing cold-water specialist taxa that cannot adapt to or compete in changing conditions (Giersch et al. 2017). Colonizing invertebrates may also increase secondary production by expressing traits that allow for higher turnover, such as small bodies and short life cycles, which are typical of many high-production generalist taxa (Albrecht et al. 2021). Associated increases in local biodiversity through colonization could also enhance production, as assumed by biodiversity-to-ecosystem function relationships (Thébault and Loreau 2003; Wu et al. 2023), though these relationships are far from certain for freshwater invertebrate communities (e.g., Little and Altermatt 2018).

One approach for testing these mechanisms is to compare aquatic invertebrate community structure and production in a hydrologically diverse landscape that contains streams fed by a gradient of meltwater (glacial or snow) to non-meltwater (rain or groundwater) inputs. In southeast Alaska for instance, a single watershed can contain streams fed primarily by glacial-melt, snowmelt, and rainfall (groundwater spring-fed streams are uncommon in this region). These stream types have been conceptualized as representing a space-for-time gradient, whereby glacier-fed streams transition to snow-fed streams, and snow-fed streams transition to rain-fed streams (Bellmore et al. 2022). Such streams also encompass gradients in many stream physicochemical conditions known to influence aquatic macroinvertebrates, such as flow, water temperature, turbidity, and nutrient regimes (Brown et al. 2006). For instance, discharge in glacier fed streams are generally high and cold in the summer, whereas rain-fed streams are relatively low and warm, and snow-fed streams are intermediate between the two (Sergeant et al. 2020). Southeast Alaskan streams also provide important habitat for Pacific salmon species, which rear in streams for up to 2 yr feeding mainly on aquatic invertebrates (Johnson et al. 2019; Fellman et al. 2022). Thus, understanding changes in macroinvertebrate community structure and productivity with loss of glacier-melt and snowmelt is critical to predicting climate change impacts on salmon-bearing streams and the human communities that rely on salmon for their food security (O'Neel et al. 2015; Pitman et al. 2020).

Here, we examine aquatic macroinvertebrate community structure and secondary productivity across four streams that represent a meltwater to non-meltwater gradient near the Juneau Icefield, Alaska, USA (Sergeant et al. 2020; Giesbrecht et al. 2022). Selected streams reflected relative endmember (i.e., predominantly single-source) signatures of glacier-fed, snow-fed, and rain-fed streams, and one transitional stream that received runoff from all three sources. Previous research in the region suggests these streams would have substantial differences in abiotic conditions, nutrients, and periphyton and detrital biomass pools that influence invertebrate communities (Fellman et al. 2014; Bellmore et al. 2022). We measured streamflow and physicochemical conditions (water temperature, turbidity, and dissolved nutrients), and conducted year-around sampling for aquatic macroinvertebrates in each stream type to examine gradients of invertebrate community structure (richness, diversity, and species composition) and secondary production. Based on previous research, we expected (1) the glacier-fed stream would have the lowest invertebrate diversity, the most distinct community composition, and the lowest secondary production relative to the other streams due to high summer flows that are cold and turbid; (2) the rain-fed stream would have the highest macroinvertebrate richness, diversity, and production due to warmer water temperature and lower flows in the summer; and (3) the snow-fed and transitional streams would have intermediate values of diversity and productivity due to moderate water temperature and relatively stable flows in summer (Brittain et al. 2000; Gislason et al. 2000; Brown et al. 2018). To better understand the mechanisms controlling changes in secondary production across our study sites, we examined whether differences in invertebrate secondary production were better explained by differences in community composition (community turnover), or differences in production rates of shared taxa that occurred across sites. Our findings suggest that declining meltwaters may result in greater aquatic productivity, but—as previous studies have shown—this enhanced productivity is likely associated with the loss of distinct communities of organisms and more synchronized temporal dynamics of aquatic biodiversity (Hotaling et al. 2019; Leathers et al. 2023).

Materials and methods

Study area

The coastal watersheds on the western edge of the Juneau Icefield (~ 3800 km^2) in southeast Alaska, USA are influenced by glacial melt, seasonal snowpack, peatlands, and dense temperate rainforest (Shanley et al. 2015). These watersheds also support populations of Pacific salmon (*Oncorhynchus* spp.), Dolly Varden char (*Salvelinus malma*), and Coastrange Sculpin (*Cottus aleuticus*), which rely on production of aquatic invertebrates for growth during early freshwater rearing. The region has a cool maritime climate (mean annual air temperature = 2.17°C) with annual average precipitation of ~ 4068 mm (Long Lake SNOTEL Site #1001: 58.1833°–133.833°, Elevation 300 m, 30-yr mean). The region is also experiencing some of the fastest rates of glacier mass decline globally (Young et al. 2021), coincident with increasing winter snow-to-rain shifts (Shanley et al. 2015).

Our study sites included one study reach in each of four stream types: (1) a glacial meltwater stream (hereafter

"glacier-fed"), (2) a low-elevation stream sourced mainly from surface water (hereafter "rain-fed"), (3) a higher-elevation stream sourced mainly from alpine snowpack (hereafter "snow-fed"), and (4) a transitional stream with tributaries reflecting each of the above classifications (hereafter "transitional") (Fig. 1). Sites were selected in river basins that represent three relative endmember conditions (glacier-, snow-, rain-fed) classified based on previous studies (Fellman et al. 2014) and that have minimal inputs from smaller tributaries with different hydrologic influences. That said, most watersheds in the region integrate some level of hydrologic heterogeneity (Sergeant et al. 2020; Giesbrecht et al. 2022). For example, one major sub catchment of the glacier-fed river resembles a rain-fed system and contains a small lake which acts in a similar way to the adjacent rain-fed study stream, but we avoided glacial streams with pro-glacial lakes to avoid the potential confounding effects of lakes on stream physiochemistry (Hieber et al. 2002). We selected sampling reaches within each stream that were accessible to spawning salmon and that had similar gradient, though streams varied in size (Table 1).

Stream discharge and physico-chemistry

In each stream, we used an Exosonde (YSI Inc.) to record hourly measurements of water temperature. Discharge was measured differently at each site. At the rain-fed stream we measured discharge using a pressure transducer that collected hourly stage data, and a stage-discharge relationship constructed from manual discharge measurements taken over a wide range of flow conditions. For the glacier-fed river, we used a modeled relationship with a nearby gauged glacier-fed river (~ 15 km away) and supplemented with > 20 measurements using an acoustic doppler current profiler (RiverRay, Teledyne RD Instruments Inc.) at different flow levels. The snow-fed and transitional streams were gauged and managed by Alaska Hydroscience and the National Weather Service, Juneau Office, respectively. We converted flow data to runoff (i.e., discharge per unit watershed area per day) to allow for seasonal comparisons in flow dynamics between watersheds of different sizes. We summarized weekly mean runoff for statistical analyses and monthly mean discharge data for ordination analyses to correspond with biotic sampling.

We collected discrete grab samples for water chemistry once per month (April 2018–November 2018, January 2019, April 2019). Stream water was field filtered through a pre-combusted (4 h at 450°C) Whatman GF/F filter (0.7 μm pore size). We measured dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) using an elemental analyzer with a lower detection limit of ~ 0.3–0.5 mg/L (Shimadzu Model TOC/TN-V-CSH) and total dissolved phosphorus (TDP) was measured using the ascorbic acid method with a lower detection limit of 0.5–1.0 μg L^{-1} (Valderrama, 1981). Turbidity was measured in triplicate in the field using a handheld turbidity meter (Model 2100Q, Hatch Company). During biweekly sampling events, we measured pH using a handheld pH Meter (Orion Star A221, ThermoFisher Scientific) and conductivity using a handheld multiprobe unit (YSI Model 556, YSI Inc.).

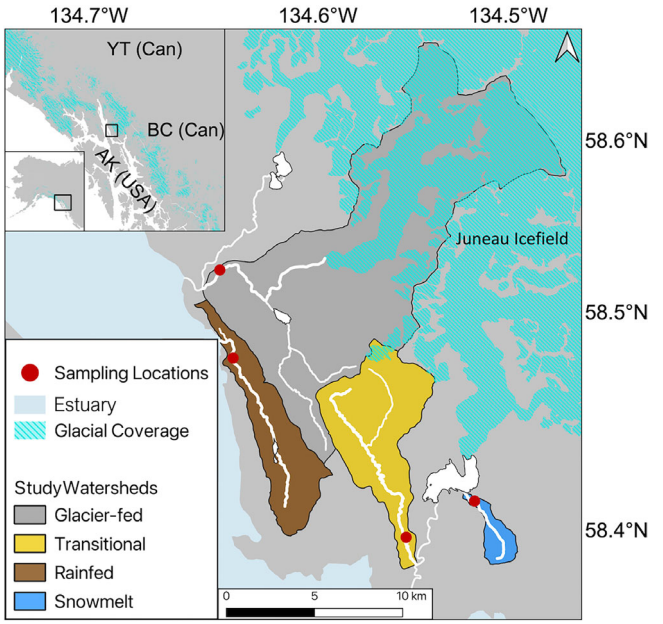

Fig. 1. Location of study watersheds and sampling sites (red dots) near the Juneau Icefield in southeast Alaska, with an overlay showing the distribution of glacier coverage (light blue) from the Randolph Glacier Inventory version 6.0 (RGI Consortium 2017).

Benthic invertebrate sampling

We sampled benthic invertebrates every 4 weeks (April 2018–November 2018) and every 8 weeks (December 2018–April 2019) resulting in 10 sampling events per site over 13 months. During each sampling event, we collected five replicate pooled samples of benthic invertebrates using a Surber sampler (0.25 m^2, 250-μm mesh, Aquatic Research Instruments). Each of the five samples was a composite of three subsamples collected in riffle habitats at the bottom, middle, and upper third of each reach, such that a total of 15 net placements were collected from throughout the reach. We elutriated each of the five replicates in the field using a 250-μm mesh sieve to separate organic material from stream gravel and preserved the former in 95% ethanol. In the lab, we used a two-phased invertebrate sample processing approach (Vinson and Hawkins 1996). First, we transferred the sample to a 125-μm sieve and visually identified and removed large and rare organisms (body length ≥ ~ 15 mm). We then extracted $1/8^{th}$ subsamples until a minimum of 500 individuals were present in the subsample fraction. If fewer than 500 individuals were present, the entire sample was processed. We removed macroinvertebrates from detritus using a dissecting microscope under 10× magnification, identified to the lowest practical taxonomic level (generally genus or lower for all taxa except Chironomidae, Oligochaeta, Gastropoda, and Mollusca) and

measured body length to the nearest 0.5 mm using either an ocular micrometer or grid paper.

Invertebrate community metrics

The density (individuals m^{-2}) and richness (distinct taxa per sample) of benthic invertebrates from each sample were used to calculate invertebrate within-stream diversity (Shannon–Weaver S'), evenness (Pielou's J), and between-stream beta diversity (Sorensen's index). We calculated beta diversity as the between stream pairwise Sorensen's similarity index (the inverse of beta diversity) for each sampling event. We then conducted pairwise comparisons of mean values for each diversity metric using a Wilcoxon test. Redundancy analysis (RDA) was used to identify community composition associations with eight stream properties (mean monthly water temperature, discharge, TDP, TDN, DOC, turbidity, pH, and conductivity). In addition, we used these data to evaluate the role of individual taxa driving community functional separation. Prior to analysis, we standardized data using a Hellinger transformation to account for substantially different abundances between sites and used mean invertebrate abundances per sampling event at each site (Legendre and Gallagher 2001). We tested the significance of our predictor variables on ordinations using ANOVA with 999 permutations. We then used forward selection from a null model with no environmental predictors to our full model, which confirmed that 80% of the total variance was explained by our constrained model. Because all environmental variables were found to be significant predictors of variation, all were included in our plots. Families with an $r > 0.333$ were included in our plots. All ordination analyses were done in R using the package "vegan" (Oksanen et al. 2007).

Biomass and secondary production

The biomass of individual macroinvertebrates was calculated using literature-based length-dry mass relationships (Benke et al. 1999; Sabo et al. 2002; Robert W. Wisseman, Aquatic Biology Associates Inc., unpublished data) and scaled by abundance to estimate standing stock biomass for each taxon. Estimating variance in secondary production estimates remains a challenge and is typically addressed via bootstrapping (Bellmore et al. 2013; Benke and Huryn 2017). Using this approach, we resampled size-specific abundances of each taxon from each site by date with replacement 1000 times to create an array of size distribution estimates. We then used each resampled array to estimate secondary production using the size–frequency approach to generate a vector of biomass, abundance, and production estimates along with their variance (Cross et al. 2013; Scholl et al. 2023). We estimated production for most taxa at the family-level using the size–frequency method corrected for cohort production interval (Benke and Huryn 2017). For rare or unevenly sampled taxa where it was not possible to estimate local-site production, we converted biomass estimates to production using literature-based P : B ratios (Supporting Information Table S2). We then calculated total annual production as the sum of the mean annual production estimate of each taxon.

Results

Stream physicochemistry and runoff

Mean daily runoff and physicochemistry varied between streams on an annual scale (Fig. 2). Annual mean daily water temperature was lowest in the glacier-fed river (2.3°C), but similar at other sites (5–7°C; Fig. 2A). Although annual mean discharge was substantially higher in the glacier-fed river than other sites, when scaled to watershed area, annual mean daily runoff was similar between the glacier-fed and transitional stream (Fig. 2B). All streams differed in mean annual turbidity with the glacier-fed stream being the highest (104 NTU) and the snow-fed stream being the lowest (0.66 NTU; Fig. 2C). Water chemistry also varied between streams, with significantly higher DOC concentrations in the rain-fed stream (mean annual 6.43 mg L^{-1}) compared to all other sites (Wicoxon $p < 0.0001$; Fig. 2D). Concentrations of TDN were significantly higher in the rain-fed (0.15 mg L^{-1}) and transitional streams (1.35 mg L^{-1}) compared to the glacier-fed and snow-fed streams (Wicoxon $p < 0.0001$; Fig. 2E). Annual mean concentrations of TDP were lowest in the snow-fed stream (5.43 μg L^{-1}, Wicoxon $p < 0.05$) and higher in the glacier-fed stream (67.5 μg L^{-1}), but similar in the rain-fed and transitional streams (16.5–19.6 μg L^{-1}; Fig. 2F). Seasonal variability in environmental conditions (e.g., runoff, conductivity, TDN, TDP) was generally higher in the glacier-fed stream than snow-fed and transitional

Table 1. Physical characteristics of study reaches from the Netmap database (Benda et al. 2007) and field measurements and assumed salmon spawning densities from site observations.

Stream	Gradient (%)	Average wetted width (m)	Average depth (m)	Measured flow range (m^3 s^{-1})	Distance from ocean (km)	Watershed size (m^2)	Salmon spawning density
Glacier-fed	2.1	24.8	0.73	2.2–152.4	3.8	1286	Low
Transitional	1.9	16.9	0.63	0.9–27.2	6.8	954	Moderate
Snow-fed	2.3	7.4	0.52	0.04–2.1	12.3	485	High
Rain-fed	1.6	17.3	0.61	0.02–16.9	2.4	600	High

streams with runoff, turbidity, and TDP increasing during the meltwater season. Conversely, concentrations of DOC and TDN decreased in the glacier-fed site during the meltwater season while water temperature remained similar

Macroinvertebrate community structure, and diversity

Mean invertebrate density varied among sites, with the highest density in the rain-fed stream and lowest in the glacier-fed stream (Fig. 3A). Taxon richness (*S*) and Shannon–Weaver diversity (*H′*) at the family-level were both highest in the snow-fed stream and lowest in the glacier-fed stream (Fig. 3B,C). Patterns of family-level Shannon diversity largely mirrored patterns in taxon richness because evenness (*J*) across streams was similar except for lower values in the rain-fed stream. Overall, the snow-fed stream had relatively high density, richness, and evenness; the rain-fed stream had the highest density but lower richness and low evenness; and the transitional stream was intermediate (Fig. 3). The glacier-fed stream was characterized by 10-fold lower density, richness and relatively high, but variable, evenness (Fig. 3). We found the lowest beta diversity (inverse Sorensen's index) on average between rain-fed and transitional streams followed by rain-fed and snow-fed streams and the least similarity between the glacier-fed stream and either the rain-fed or snow-fed streams (Fig. 4A). Beta-diversity was highest between the glacier-fed stream and the other stream types during midsummer (Fig. 4B), but this divergence diminished outside the glacial melt season (September through April).

Contrary to our predictions, the invertebrate community found in the glacier-fed stream appeared to be a subset of a larger species pool present at all sites. Redundancy analyses revealed somewhat distinct communities by taxonomic groupings between the three disparate stream types and an intermediate community in the transitional stream (Fig. 5A), but this was due to differences in relative abundance of shared taxa and the absence of taxa in the families Chloroperlidae and Limnephilidae in the glacier-fed stream rather than the presence of glacier-fed specialist species. The dominant taxa in determining community dispersion in the RDA were the mayflies in the families Baetidae and Heptageniidae (snow-fed), stoneflies in the Chloroperlidae (transitional), and segmented worms (rain-fed). Although weaker, the glacier-fed community showed moderate associations with midges in the family Chironomidae and stoneflies in the family Nemouridae. Dominant physicochemical drivers explained 15.6% (Axis 1) and 10.2% (Axis 2) of the variation in average monthly community taxonomic structure (Supporting Information Table S1). The glacier-fed community had the largest community variation as determined by the size of standard ellipses and was positively associated with total dissolved phosphorous, turbidity, and discharge. The snow-fed stream had the smallest standard ellipse and was positively associated with pH and conductivity. The rain-fed and transitional streams had similar ellipse sizes and were positively associated with water temperature, TDN, and DOC. Community positions in ordination space also showed a temporal dynamic (Fig. 5B) with the communities from the four streams occupying a more similar position in the fall and winter months and diverging during the summer meltwater season.

Invertebrate biomass and secondary production

Annual mean standing stock biomass (ash-free dry mass, AFDM) was lowest in the glacier-fed stream at 0.15 g AFDM m^{-2}, moderate in the transitional stream at 0.38 g AFDM m^{-2}, and highest in the snow- and rain-fed streams at 0.75 and 0.67 g AFDM m^{-2}, respectively (Fig. 6A; Supporting Information Table S2). Although we expected the glacial stream to contain glacial specialist taxa absent at other sites, we found that the community at this location several kilometers downstream of the glacial terminus was instead a subset of a larger species pool found at other sites. That said, some taxa such as stoneflies in the families Perlodidae and Nemouridae (e.g., *Zapada* spp., *Nemoura* sp., and *Visoka* sp.) were much more common in the glacial stream than at other sites and contributed to biomass and production. Shared taxa found across the three limited-to-no glacial influence sites comprised the majority of standing stock biomass (81–82%; Fig. 6C). Taxa not found in the glacier-fed system contributed to the remainder of the biomass in the other three streams. Biomass in the glacier-fed stream was dominated by large-bodied stoneflies in the family Perlodidae, namely *Isoperla* spp. The snow-fed stream shared a large biomass of Perlodidae, but also had moderately large biomasses of mayflies in the Heptageniidae and stoneflies in the Chloroperlidae. The transitional and rain-fed streams had larger proportional biomass of Chloroperlidae than other sites, but also had substantial biomasses of Oligochaeta and Heptageniidae. Caddisflies in the Limnephilidae were commonly found in the rain-fed stream but were rare and did not constitute a large proportional biomass in other sites. Predatory caddisflies in the family Rhyacophilidae were present and contributed to substantial biomass in the glacier-fed and snow-fed streams but were uncommon at other sites. In addition, small-bodied stoneflies in the family Capniidae contributed substantial biomass in the glacier-fed and transitional streams but contributed minimal biomass at other sites.

We found a fivefold difference in secondary production among streams. As predicted, the glacier-fed stream had the lowest annual production at 0.56 g AFDM m^{-2} yr^{-1} (Fig. 6B). The transitional stream had over twice the annual production of the glacier-fed stream at 1.22 g AFDM m^{-2} yr^{-1} and the rain-fed stream had an additional 36% greater production than the transitional stream at 1.22 g AFDM m^{-2} yr^{-1}. The greatest production was observed in the snow-fed stream at 2.9 g AFDM m^{-2} yr^{-1}. The most productive taxa varied considerably between streams (Fig. 6D). Production in the glacier-fed stream was shared across many families, whereas the snow-fed stream experienced high production in

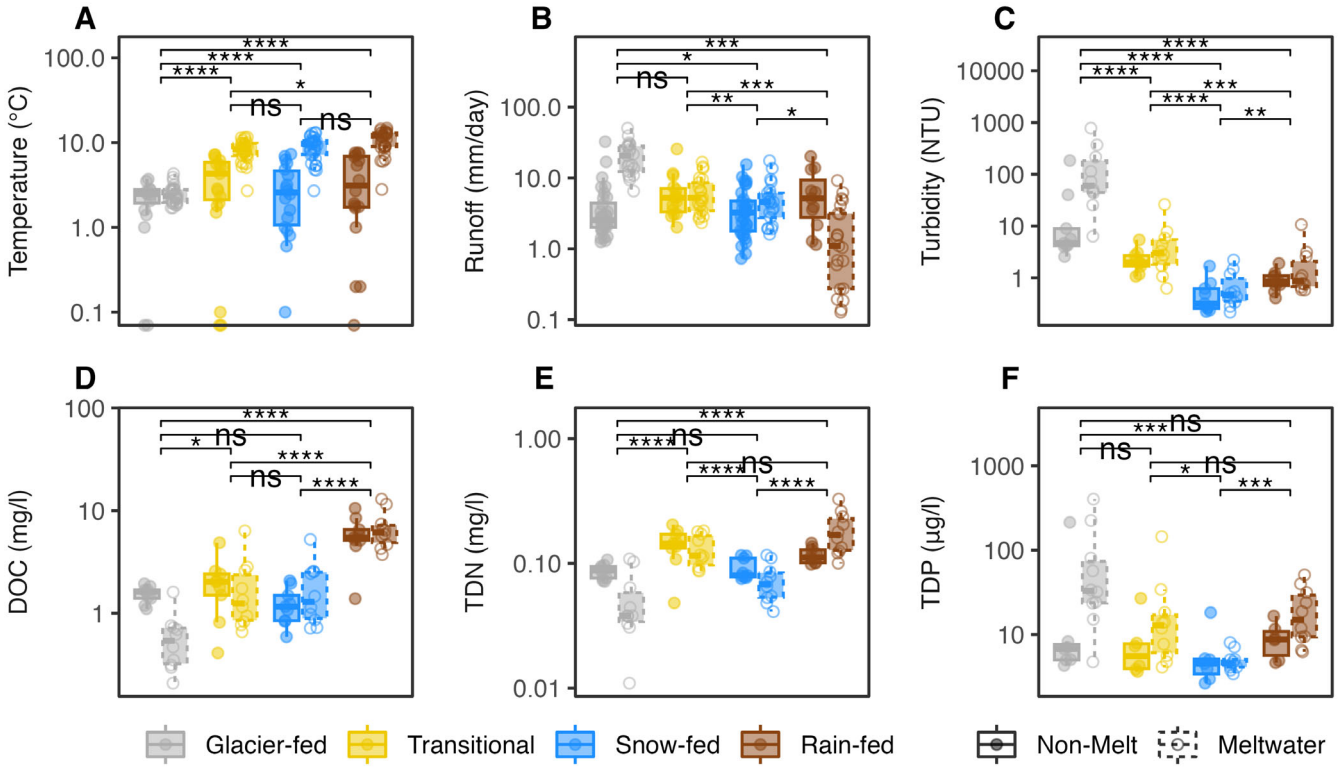

Fig. 2. Box and whisker plots of (**A**) weekly mean water temperature, (**B**) weekly mean discharge corrected for watershed area per day (runoff), and biweekly samples of (**C**) turbidity, (**D**) DOC, (**E**) TDN, and (**F**) TDP for each site plotted on a log scale. Plots show distributions for the summer meltwater period (open points, dashed boxplots: May–September) and non-meltwater period (solid points, solid boxplots: October–April). Pairwise comparisons of annual aggregated values are noted above (Wilcoxon p values: ns: $p > 0.05$, *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, ****$p \leq 0.0001$). Line with each box is the median, box boundaries represent the 25th and 75th percentiles, whiskers are the maximum and minimum.

mayflies (e.g., Heptageniidae, Baetidae). Both the rain-fed and transitional streams had substantial production of functional shredders or collector-gatherers (e.g., Chloroperlidae, Oligochaeta). Generally, most productive taxa were also high in biomass across the stream types, except in the glacier-fed stream, where several families had proportionally high production but low standing biomass. To estimate the drivers of increased production in the rain-fed, snow-fed, and transitional streams relative to the glacier-fed stream, we calculated production of taxa found across all streams (aka "Shared Taxa") and the production of taxa not found in the glacier-fed stream (aka "Turnover") (Fig. 6B). Increased production in the non-glacier fed streams relative to the glacier-fed stream was primarily due to increased production of shared taxa (76–88%) with the greatest production from species turnover in the rain-fed stream (24%). This increase was largely due to high production in stoneflies in the family Chloroperlidae and in the case-building caddisflies in the family Limnephilidae.

Discussion

Climate change is shrinking the global cryosphere with implications for the diversity and productivity of freshwater communities which receive meltwaters (Milner et al. 2017; Elser et al. 2020). To date, most aquatic invertebrate studies have focused on the effects of cryosphere loss on stream invertebrate diversity (Brown et al. 2007; Niedrist and Füreder 2018; Brighenti et al. 2021) or species persistence (Giersch et al. 2017; Birrell et al. 2020). However, much less research has explored how a melting cryosphere may affect the functional traits of stream invertebrate communities such as rates of secondary production of biomass (Benke 2018). We illustrate that landscapes such as those in the Pacific coastal temperate rainforest contain streams that differ in fundamental physical and chemical properties (Fellman et al. 2014; Bellmore et al. 2022), setting the stage for dramatically different rates of invertebrate secondary production.

We predicted that secondary production should increase from glacier-fed to rain-fed signatures as a function of either (1) increased rates of production of shared taxa or (2) addition of more productive generalist taxa. Contrary to expectations, secondary production was 54% higher in the snow-fed stream than the rainfed stream. We found support for both hypotheses, with 76–88% the production in the transitional, snow-, and rain-fed streams was attributed to taxa that were also found in the glacier-fed stream. As glacier meltwater inputs to

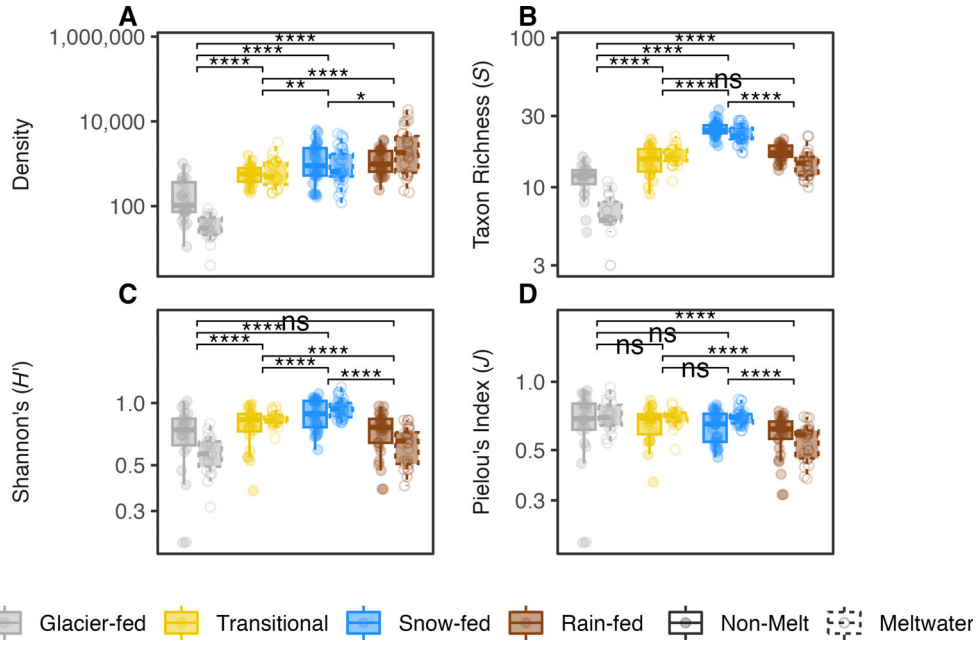

Fig. 3. Box and whisker plots of (**A**) invertebrate density (individuals m^{-2}), (**B**) taxon richness (*S*, taxa per sample), (**C**) Shannon's diversity index (*H'*), and (**D**) Pielou's evenness index (*J*) of individual invertebrate samples collected in non-melt (solid points and lines) and meltwater (open points and dashed lines) seasons. Pairwise comparisons of annual mean values are noted above (Wilcoxon *p* values: ns: $p > 0.05$, *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$, ****$p \leq 0.0001$). Line with each box is the median, box boundaries represent the 25th and 75th percentiles, whiskers are the maximum and minimum.

streams decrease and, eventually, disappear our findings suggest that rates of freshwater secondary invertebrate production will increase with a possible peak in invertebrate production in streams receiving seasonal snowmelt. These changes to invertebrate production will also likely coincide with a loss of the distinct community structures and landscape beta diversity contributed by glacier- and snow-fed streams relative to those driven by surface runoff of rainfall.

Physicochemical drivers of invertebrate biomass and secondary production

Community structure across the four study streams reflected differences in physical and chemical conditions. Specifically, the community structure in the glacier-fed river was associated with water temperature, discharge, and turbidity, supporting the view that physical harshness may control secondary production in this stream (Jacobsen and Dangles 2012). Conversely, other streams were more associated with water chemistry (e.g., DOC), nutrient availability (e.g., TDN), and water temperature. Together, these analyses support the landscape filtering hypothesis (Poff 1997), whereby differing environmental conditions act as filters through which individual taxa from a regional pool must pass to be present in a location, assuming all sampled locations were within the dispersal and colonization range of invertebrate taxa. As abiotically harsh reaches of the stream network become more benign, community structure (e.g., assemblage composition) and traits, like the rate of biomass production, may homogenize.

Our results supported the expectation that cold and physically harsh conditions found in the glacial-fed stream result in low aquatic invertebrate secondary production. We also predicted the rain-fed stream to be the most productive stream in our study due to warm conditions and higher DOC, TDN, and TDP concentrations. However, we found that the snow-fed stream had slightly higher aquatic invertebrate biomass, and much higher production, and diversity despite colder conditions. More stochastic flow regimes along with higher DOC and low pH may limit invertebrate diversity and productivity in rain-fed systems in the Gulf of Alaska, relative to the clear and stable post-spring-runoff conditions frequently found snow-fed streams (Seekell et al. 2015). The transitional stream, which reflected intermediate water sources relative to the three endmember streams, had roughly twice the production of the glacier-fed stream, but 26.5% less production than the rainfed stream and 58% less than the snow-fed stream. These transitional conditions may become more common in the region as glaciers are lost and winter snow is replaced by winter rain (Lader et al. 2020; Sergeant et al. 2020). Together, these findings support the assertion that invertebrate production may be constrained by flow and water temperature stability (Chadwick and Huryn 2007; Mehler et al. 2015), and that production may increase into the future as glacial meltwater inputs to streams are lost, but decrease if snow meltwaters are lost.

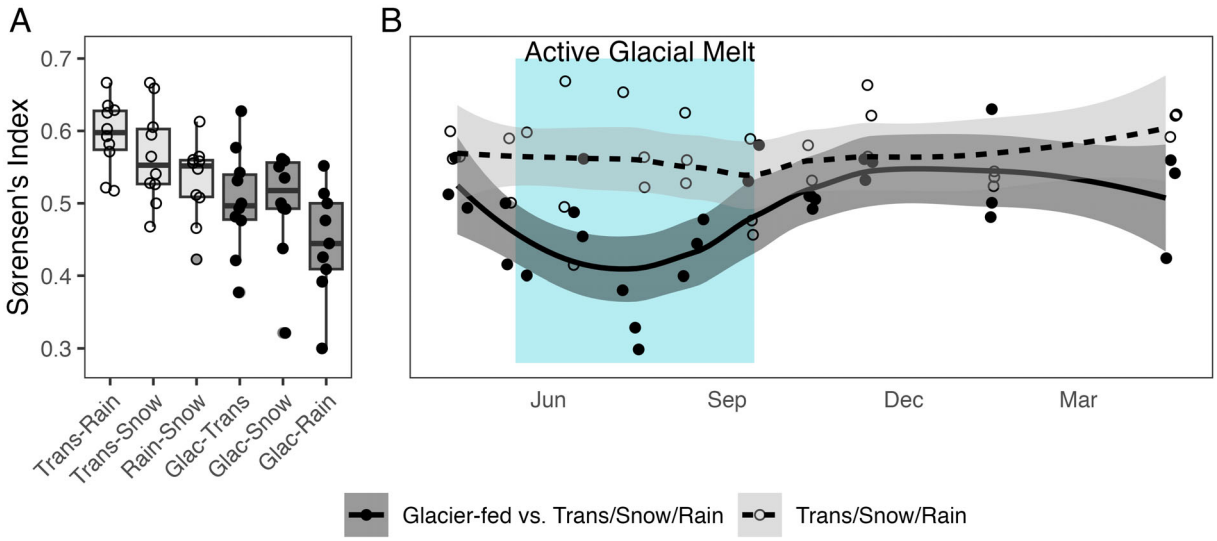

Fig. 4. (Inverse) beta diversity between glacier-fed and other streams calculated using Sorensen's index for each sampling window (**A**) and the same data shown for temporal patterns of Sorensen's index for beta diversity across the landscape (**B**) between the glacier-fed stream and other streams together. Points have been jittered to show overlap. Season of active glacier-fed melt (June–August) shaded in light blue. Values closer to 1 are more similar; values closer to 0 are less similar.

The increase in secondary production we observed between glacier-, transitional-, and rain/snow-fed streams was driven mostly (86–355% increase) by higher production of taxa shared across all locations. Turnover of taxa which were not found in the glacier-fed stream constituted a further 32–62% of increased secondary production. The production and biomass in the glacier-fed streams were dominated by stoneflies—namely large-bodied predators in the family Perlodidae. Contrary to studies conducted closer to glacial termini (Lods-Crozet et al. 2001; Robinson et al. 2007; Niedrist et al. 2018), we observed only marginal biomass and production in the family Chironomidae (though we anecdotally observed dense populations above our study reach just below the glacial terminus). We did not observe significant densities of glacier-fed river specialist taxa at this lower point in the watershed, but rather a distinct seasonal sub-assemblage of the landscape taxa pool found at other sites. Although differences between watersheds may have been greater if we had sampled at the glacier terminus, most aquatic habitats in glacier-fed streams in southeast Alaska do not resemble conditions at the glacier termini, and thus, our sampling is more likely to represent the vast the majority of glacier–river habitat available to support invertebrate production. The snow-fed, transitional, and rain-fed streams also had substantial stonefly production in the family Chloroperlidae as well as mayflies in Heptageniidae and Baetidae. Notably, segmented worms in Oligochaeta contributed substantially to production in the transitional and rain-fed streams but were uncommon in the glacier-fed river. While our approach estimated marginal Oligochaeta production in the glacier-fed stream, we expect that their presence was related to bank erosion or drift from tributaries rather than in situ production within the glacier-fed stream reach. Overall, these patterns imply that as stream warm and clear with loss of glacial inputs, it will likely increase local taxa richness as additional species from the regional pool are able to colonize, which would likely increase secondary production.

The rates of total secondary production we observed were low relative to those from other systems conducted in warmer and lower latitude ecosystems (e.g., Washington State, Bellmore et al. 2013; Minnesota, Krueger and Waters 1983; Illinois, Walther and Whiles 2011; Appalachia, Johnson et al. 2013). Our values were, however, in the range of those reported from northern Michigan, USA, where low water temperatures, flow intermittency, and substrate instability constrained invertebrate secondary production (Entrekin et al. 2007, 2009)—factors which are similar in coastal southeast Alaska. To our knowledge, we know of no other study which has reported the annual secondary production for an entire invertebrate community in a glacial stream or in comparison to nearby stream types. However, we are aware of only one other study of invertebrate secondary production conducted of invertebrates in a glacier-fed stream, which found that a single genus of large-bodied mayfly in New Zealand had annual secondary production ranging from 0.48 to 3.07 g dry mass m^{-2} yr^{-1} ($\sim$ 0.1–0.25 g AFDM m^{-2} yr^{-1}; Winterbourn et al. 2008) possibly due to a combination of low predation pressure and limited resource competition from other invertebrate taxa.

Invertebrate community diversity varies among stream types

This study supports previous research showing that glacier meltwaters contribute to landscape beta diversity relative to streams fed by other sources (Elser et al. 2020; Bellmore

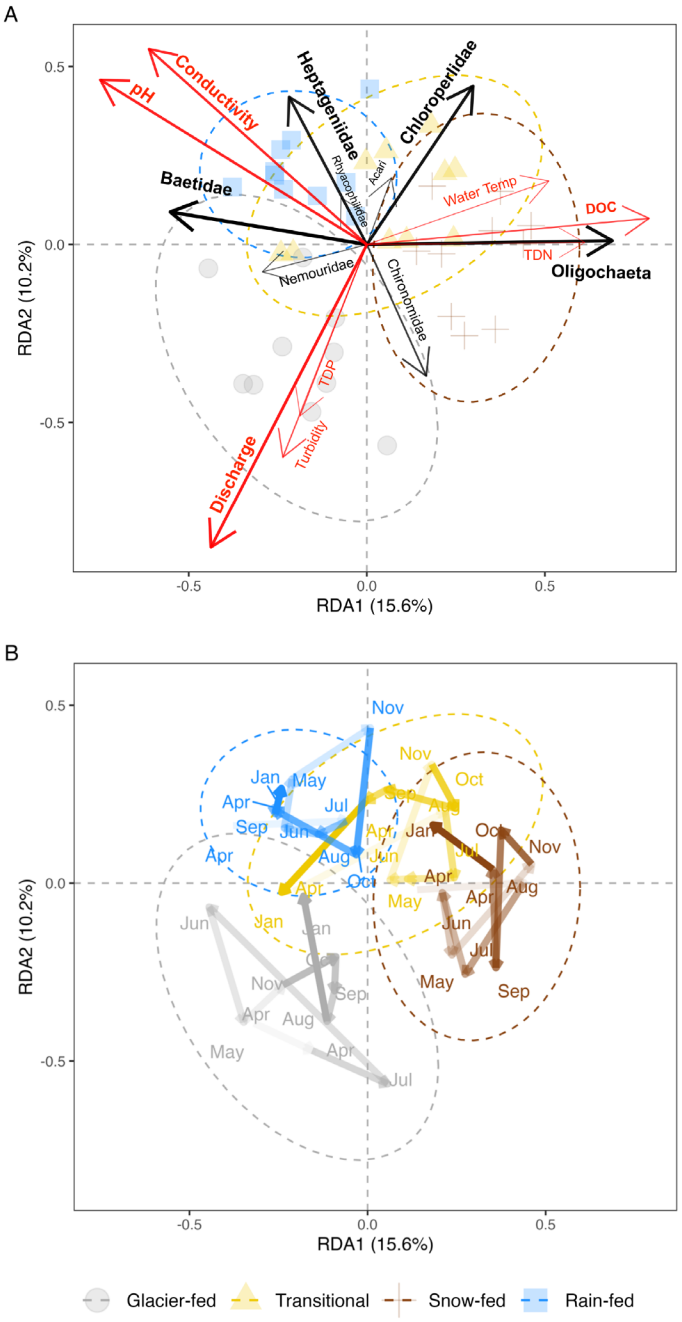

Fig. 5. (**A**) Redundancy analysis (RDA) of invertebrate community data shows dominant environmental (red arrows) and family (black arrows) associations with average monthly community composition (points) and (**B**) temporal dynamics of average monthly community composition. Standard ellipses in both panels reflect 95% normal confidence intervals based on multivariate *t*-distributions.

et al. 2022). However, unlike studies conducted closer to glacial termini (Brown et al. 2018; Füreder and Niedrist 2020), and in support of studies showing an increase in taxonomic richness downstream of glacier termini (Malard et al. 2003; Finn et al. 2010; Tronstad et al. 2016), we found that the community in our glacier-fed stream reflected a subset of the larger species pool with certain, presumably cold-, flow-, or turbidity- intolerant species filtered out. Differences in community structure and diversity between southeast Alaskan streams and those in other regions, such as the European Alps, could be related to recent landscape glaciation and shorter invertebrate colonization history (Milner et al. 2000, 2008). In addition, due to the steep mountains and relatively low-elevation icefields, glacier-fed rivers in this region often flow through dense temperate rainforests, rather than alpine zones with limited vegetation inputs (O'Neel et al. 2015) contributing to differences in detritus inputs and invertebrate food sources in this region vs. others. Regardless, the differences in the relative abundance of taxa in the glacier-fed community contributed to distinct seasonal invertebrate community structures and higher beta diversity relative to other stream types during peak glacial melt. Beta diversity between streams decreased during winter months as physical and chemical properties, and invertebrate communities became more similar. We note, however, that cryptic diversity may exist below the resolution of our identifications (Marten et al. 2006) and may be particularly relevant for midges in the family Chironomidae which are often the most diverse family in glacier-fed rivers (Lods-Crozet et al. 2001; Robinson et al. 2016).

Our work also generally supports the assertion that alpha diversity may increase in glacier-fed streams as they become less harsh with respect to flow, water temperature, bed stability, and/or light (Milner et al. 2009; Slemmons et al. 2013), but that communities across the landscape may become dominated by generalist taxa, reducing beta and gamma diversity (Niedrist and Füreder 2018; Füreder and Niedrist 2020). As with some other mountain stream invertebrate research, we found that snow-fed streams may be particularly diverse relative to other stream types (Tronstad et al. 2020; Brighenti et al. 2021). This could be due to somewhat predictable and less stochastic spring runoff hydrology in snow-fed streams relative to rain-fed streams, which are prone to both periodic drought and rain-driven freshets (Ledger et al. 2011; Shanley et al. 2015). Furthermore, if summer drought becomes more frequent in this region and in other mountainous regions, snow-fed streams may provide refugia for invertebrate diversity and production. However, the stabilizing benefits of snow-meltwater streams may be diminishing with future climate change as winter precipitation patterns and forms shift away from lasting snowpack, with implications for the diversity and production of invertebrates in these streams (Docherty et al. 2018). More broadly, the pattern of invertebrate diversity and production reinforce the need to better understand the relationship between alpha vs. beta diversity in shaping patterns of secondary production in space and time (Dolbeth et al. 2015; Mehler et al. 2015).

Although this study represents one of the most comprehensive comparative analyses of invertebrate community

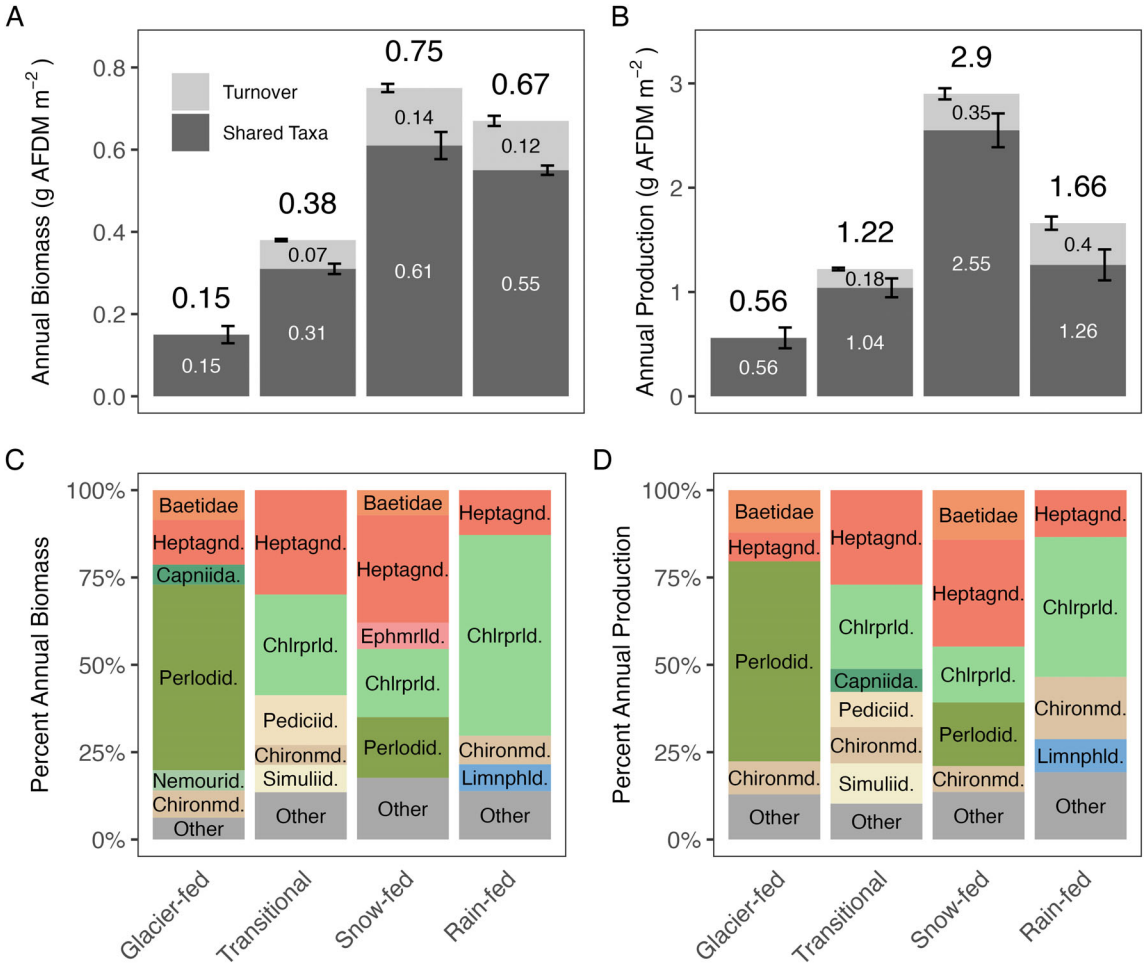

Fig. 6. Bootstrapped aquatic invertebrate (**A**) average annual standing stock biomass (ash-free dry mass, g m^{-2}) and (**B**) secondary production of taxa found across all four streams ("shared taxa") and taxa not found in the glacier-fed river ("non-glacier-fed taxa") ± SE. Proportional mean (**C**) standing biomass and (**D**) annual production by taxon; taxa with less than 2.5% of annual production combined as "Other." Colors reflect the following orders: Diptera (tan shades), Ephemeroptera (red shades), Plecoptera (green shades), and Trichoptera (blue shades). Abbreviations are as follows: Heptageniidae (Heptagnd.), Capniidae (Capniida.), Perlodidae (Perlodid.), Nemouridae (Nemourid.), Chironomidae (Chironmd.), Chloroperlidae (Chlrprld.), Pediciidae (Pediciid.), Simuliidae (Simuliid.), Ephemerellidae (Ephmrlld.), and Limnephilidae (Limnphld.).

secondary production among streams reflecting different hydrochemical regimes (Birrell et al. 2020; Leathers et al. 2023), this level of detail reflects a trade off in single site-level understanding vs. spatial replication over multiple representative streams. Interannual variation in secondary production is high in many streams, particularly in response to variation in discharge, ambient air temperatures, or marine-derived nutrient subsidies from spawning salmon. Across the landscape, differences in watershed hydrology, proportional water sources, and seasonal meteorology will all affect the hydrochemical conditions among glacier-, snow-, and rain-fed streams as well as those experiencing rapid water source transitions. In addition, because we focused our sampling on riffle microhabitats, the sites typically have the highest production within streams (Buffagni and Comin 2000), we were unable to represent variation in community structure or production between different microhabitats within a study reach. Regardless, the results highlight the need to better understand spatial and seasonal heterogeneity in secondary production at the landscape scale (Cross et al. 2013; Scholl et al. 2023).

Impacts of climate change on secondary production

Climate change is poised to restructure and potentially homogenize the structure and function of stream ecosystems as contributions of ice and snowmelt diminish and disappear (Hock et al. 2019; Elser et al. 2020). However, the cryosphere is shrinking unevenly. In some regions of the world (e.g., European Alps), meltwater contributions have already passed their projected maximum (i.e., "peak meltwater") whereas contributions from glaciers in Alaska are projected to peak in latter part of the 21st century (Huss and Hock 2018).

This suggests that the short-term implications of climate-driven shrinking of the cryosphere on downstream ecosystems will differ regionally with some regions seeing a gradual decline in glacier meltwater contributions as remnant glaciers are lost and others seeing a short-term increase in glacier meltwater contributions due to a large volume of ice remaining in rapidly melting icefields. In addition, regional differences in weather patterns will impact the way stream networks change. In the southeast Alaska region, warmer and more variable winters are projected to be accompanied by increased rain instead of snow and rain-on-snow events (Young et al. 2021). This will lead to more frequent high-flow events in winter and low flow events in summer due to the loss of snowpack in coastal watersheds (Lader et al. 2020). These changes may promote the colonization of generalist taxa and increased biological productivity, but there remains a paucity of knowledge on higher-level trophic level and/or "multitrophic" implications of melting ice reserves on freshwater ecosystems (Fell et al. 2017).

The capacity of stream ecosystems to produce secondary invertebrate biomass will influence the ability to support the growth of higher-level consumers, such a regionally important salmon populations in the Gulf of Alaska. It is critical to link robust secondary production estimates with dietary and energetic demands of consumers to elucidate the trophic basis of fish growth and the potential implications of climate change-driven homogenization on the functional capacity and diversity of stream invertebrate communities (Fell et al. 2017). As meltwater streams transition to other sources in southeast Alaska, we may see an overall increase in the capacity of the landscape to produce higher-level consumers (Pitman et al. 2020, 2021), but this may come at the cost of the biodiversity and heterogeneity on these landscapes. Specifically, warmer, and more productive streams on an annual scale may also be more synchronous, resulting in seasonal bottlenecks constraining tertiary production (Kennedy et al., 2008; Bellmore et al. 2022).

As the cryosphere shrinks, the distinct communities we have observed may become more similar and the energetic pathways that support higher level consumers may be simplified or synchronized (Fellman et al. 2022). Future studies should place invertebrate production in the context of consumption by higher consumers, such as riparian songbirds or juvenile fish. In addition, modeling efforts could reveal emergent phenomena caused by physicochemical homogenization on interacting meta-food webs with diminishing meltwater influence (Bellmore et al. 2022). Lastly, climate change is impacting the diversity and functioning of stream ecosystems across the globe (Sabater et al. 2018; Tiegs et al. 2019). Despite glacier-fed streams being cold, harsh, and having relatively low annual production, they contain communities with distinct functional traits and contribute to landscape beta diversity. As climate change decreases heterogeneity provided by the cryosphere on the landscape, our results suggest that we may see an increase in secondary production. However, this may coincide with a decrease in biological diversity (Brown et al. 2007; Brown et al. 2018) across the landscape, which could be important to the maintenance of ecosystem stability and resilience (McCann and Rooney 2009; Rooney and McCann 2012).

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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