Tributary junction, what's your function? Linking catchment processes to habitat alteration and testing mechanisms for community responses at stream confluences

by

David Aaron Tavernini

B.Sc. (Hon.), University of Lethbridge, 2016

#### A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

#### THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Forestry)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

April 2019

©David Aaron Tavernini, 2019

The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, a thesis/dissertation entitled:

Tributary junction, what's your function? Linking catchment processes to habitat alteration and testing mechanisms for community responses at stream confluences

submitted by	David Aaron Tavernini	in partial fulfilment of the requirements for		
the degree of	Master of Science			
in	Forestry			
Examining Committee:				
John Richardson, Forestry				
Supervisor				
Brett Eaton, Geography				
Supervisory Committee Member				
Scott Hinch, Forestry				
Supervisory Committee Member				
R. Dan Moore,	Geography			
Additional Exa	miner			

### Abstract

Biotic communities are shaped by both regional and local processes. Locally, communities can be influenced by the quality, quantity, and arrangement of habitat structure and resources. At the same time, landscape processes act to arrange structural components and resources in space. In streams, catchment processes can strongly control habitat attributes. This relationship between catchment processes and resulting effects on in-stream communities has been studied extensively in the context of uninterrupted stream reaches. Many processes are influenced by the size of the stream, which has important consequences for river networks. Streams of differing size and characteristics join to form tributary junctions, which have received relatively little attention in stream ecology. Tributary junctions are hypothesized to be biological hotspots due to high habitat heterogeneity and possibly unique niche space. However, observational studies show mixed support suggesting the need for more of a mechanistic understanding.

In this thesis, I link physicochemical processes to habitat attributes and test two mechanisms for community responses at tributary junctions. I conducted an observational study to test whether stream size explains tributary exports of habitat structural components and resources and the resulting effects on mainstem habitat attributes. I found that tributaries do alter the habitat attributes in the mainstem, but tributary size was rarely an accurate predictor, except for the concentration of coarse particulate organic matter (CPOM) and nutrient supply from the tributary relative to the mainstem. Additionally, many attributes varied strongly over time. Using a field-based experiment, I tested whether CPOM addition and substrate coarsening were important mechanisms for macroinvertebrate community responses at tributary inflow. Experimental treatments and environmental covariates explained little variance, except for effects on taxa-specific abundances with the supply of CPOM. Overall, this thesis shows that tributaries are important agents for altering habitat structure and resources in mainstem channels, but effects on communities are highly site specific and may instead be driven by dispersal processes. The results of this work suggest the need to investigate other specific processes and mechanisms for community responses at tributary junctions.

# Lay Summary

Tributary junctions (the confluence of two streams) are suggested to be hotspots of heightened biological diversity due to the presence of unique habitat from two different, converging streams. However, previous studies have been conflicting and limited. Better understanding the underlying mechanisms for what causes tributary junctions to be hotspots of diversity would be valuable to identify ecologically important locations in the river network for management, conservation, and restoration interests. Here, I use tributary stream size to predict the magnitude and attributes of habitat alteration and experimentally test whether inputs of coarse sediment and organic matter from tributaries are mechanisms for macroinvertebrate community responses. I found that habitat and community responses were highly site specific; habitat structure did not strongly relate to relative size of tributaries and community responses to coarse substrate and organic matter did not consistently resemble downstream communities.

# Preface

David Tavernini was the primary author of this work and completed the majority of the field and laboratory work,data analysis, and thesis preparation. David Tavernini worked in collaboration with John Richardson, who provided guidance throughout the development of the ideas, experimental design, analyses, and thesis preparation. Field work and sample collection was aided by Mary Botkin, Yudel Huberman, and Sabine Sherrin. Laboratory analysis of nitrate and phosphorous presented in Chapter II was completed by Jeff Curtis' lab at the University of British Columbia, Okanagan Campus.

Chapters II and III will be edited for manuscript form to be submitted for publication under co-authorship of David Tavernini and John Richardson.

# Contents

Abstract	iii
Lay Summary	iv
Preface	v
Contents	vi
List of Tables	viii
List of Figures	xii
Acknowledgements	xvi
Dedication	xvii
Chapter 1: Introduction	1
Habitat and community structure in the ecological landscape	1
Process influences structure in stream ecosystems	2
The river as a network	3
	4
tions along two mainstem rivers	7 7
Materials and Methods	9
Study Area	9
Substrate size analysis	10
CPOM exports	11
Nutrient Exports	12
Modeling mainstem changes in nutrient and organic matter concentrations	13
Stream Temperature	13
Results	14
	14
	1/
	15
	15
	10
	10
	10
	18
	19
	21
Chapter 3: Responses of macroinvertebrate communities to patch-scale alterations to habitat	
structure and resources from tributary exports	34
Introduction	34
Materials and Methods	36
Experimental design	36

Sampling protocol	88
Statistical Methods	8
Results	1
Environmental characteristics of community samples	1
Community responses	2
Discussion	3
Environmental contrasts at tributary junctions	4
Effects of position on community responses	5
Effects of substrate and CPOM on community structure	7
Tributary junctions in a metacommunity context	7
Caveats and implications	8
Conclusion	9
Chapter 4: General Discussion	30
Findings and Caveats	60
Implications and future directions	62
References	<b>3</b> 5
Appendix	31
Appendix A: Supporting information for Chapter 2	31
Appendix B: Supporting information for Chapter 3	0
··· ·· ·	

# List of Tables

2.1	Basin morphology and hydrologic parameters in the tributary and mainstem of each site in-	
	cluded in the study. Note: modelled discharge is calculated from the specific discharge of	
	the nearest gauging station multiplied by the basin area. Values indicate range of modelled	
	discharge during the course of the study	22
2.2	Results from linear mixed models testing the effect of position relative to tributary inflow on	
	median grain size (D $_{50}$ ), 84th percentile grain size (D $_{84}$ ), sediment sorting, Warren skewness,	
	and spread of coarse fraction of distribution ( $\phi_{84}$ – $\phi_{50}$ ). Significance determined by type III	
	analysis of deviance.	22
2.3	Results from weighted least squares regression (weighting variance by basin area) with $\log_{10}$ -	
	transformed CPOM ratio between tributary and mainstem as a response to crossed factors	
	of $log_{10}$ -transformed basin area ratio (BAR) and time period. Shapiro-Wilk results (to test	
	for normality of residuals) are included. Significance determined using a type III analysis of	
	deviance.	22
2.4	Results from OLS regression (R $^2$ = 0.022) with log $_{10}$ -transformed nitrate concentration ratio	
	between tributary and mainstem as a response to crossed factors of $\log_{10}$ basin area ratio and	
	time period. Shapiro-Wilk results are included as a test for normality of residuals. Significance	
	determined using type III sum of squares.	23
2.5	Results from weighted least squares regression (weighting variance by basin area) with $\log_{10}$ -	
	transformed total dissolved phosphorus (TDP) ratio between tributary and mainstem as a	
	response to crossed factors of $\log_{10}$ -transformed basin area ratio (BAR) and time period.	
	Shapiro-Wilk results (to test for normality of residuals) are included. Significance determined	
	using a type III analysis of deviance	23
2.6	Results from OLS regression ( $R^2$ = 0.168) with log <sub>10</sub> -transformed total phosphorus (TP) ratio	
	between tributary and mainstem as a response to crossed factors of log10-transformed basin	
	area ratio (BAR) and time period. Shapiro-Wilk results (to test for normality of residuals) are	
	included. Significance determined using type III sum of squares	23
2.7	Mean temperature ( $\pm$ 1SD), and range of tributary relative to mainstem across six study sites	
	during the coolest inflow and warmest inflow points of the day, with corresponding mean main-	
	stem and tributary temperatures during cool and warm water inflow (± 1SD)	24
3.1	Mean (± 1 SE) of measured environmental variables upstream and downstream of tributary	
	inflow during two sampling time periods. Mean and standard error calculated from values	
	measured across the six study sites	51
3.2	Chi-square analysis of deviance test results on individual terms for fitted models predicting	
	environmental variables in Table 3.1 with treatment factors.	51
3.3	Redundancy analysis (RDA) results of environmental variables predicted by fully crossed pre-	
	dictor variables of position relative to tributary inflow, site, and time period	51

- 3.4 Top model results for rarefied taxonomic richness, total abundance, Shannon index, and Pielou's evenness. All metrics except total abundance fitted with linear mixed effects models and selected based on lowest AICc values. Significance tests were conducted with t-tests using Satterthwaite's estimated denominator degrees of freedom (Est. ddf). Total abundance was fitted with a generalized linear mixed model (negative binomial, log link). Note that T-tests could not be conducted on this model and significance was determined using z-distribution, which may lead to inflated type I error.
- 3.5 Results of Monte-Carlo permutational ANOVA tests using Bray-Curtis distances of fourth-root transformed community abundance data using a reduced model from stepwise elimination. 53
- 3.6 Results of distance based redundancy analysis (db-RDA) of fourth-root transformed taxa abundance data. Total variance explained by the included constraining variables and the residual displayed above the header. On the left, variance explained by site, treatments, and environmental variables (including all shared variance) were calculated using sequential partial db-RDA. The significance of each constraining axis are depicted on the right, determined by Monte-Carlo permutational pseudo-ANOVA, with their corresponding portion of community variance explained as well as the proportion of variance explained by the first two non-redundant axes.
- 3.7 Results from top generalized linear mixed model via AICc ranking (Poisson or negative binomial distribution with log link function) for taxa specific responses.
   54
- B1 Summary statistics of taxa included (black) and omitted (grey) from analysis. Mean represents mean number of individuals in samples (± 1 SD). Total abundance is total across all samples.
   Percent of samples present is the percentage of total samples that the taxa was identified and present in. "MS" represents morphospecies that were not positively identified. . . . . . . . 91

### **List of Figures**

1.1	Conceptual model of processes at tributary junctions. Various materials are exported from
	the tributary, which alter the habitat structure and resource supply of the mainstem. In turn,
	this alters the nature of the environmental filter that acts on the potential community consist-
	ing of organisms from upstream in the mainstem and tributary. This thesis will address: (1)
	the controls on tributary exports based on the tributary stream size and (2) the resulting re-
	sponses in benthic communities due to alterations to habitat structure and resource supply in
	the mainstem.

- 2.3 Hydrographs of the (A) Mission Creek catchment at East Kelowna and (B) West Kettle River at McCulloch. Dark black line indicates recorded discharge for 2017. Dotted line indicates the upper and lower bounds of the interquartile range for historical record (1949 2014 for Mission Creek, 1949 2015 for West Kettle). Dashed line indicates the mean for the above periods.
- 2.4 Cumulative grain size distributions (mm) upstream (light) and downstream (dark) of tributary junctions at each of the six study sites, in increasing order of basin area ratio (BAR) of tributary:mainstem. Horizontal lines depict D<sub>16</sub>, D<sub>50</sub>, and D<sub>84</sub>. Shaded regions indicate 95% confidence bounds of grain size, calculated from Eaton et al. (2019).
- 2.5 Change in D<sub>50</sub> from upstream to downstream of tributary junctions in relation to (A) basin area-slope product ratio (psi), (B) basin area ratio, (C) Melton's ruggedness ratio, (D) basin area slope product of tributary, and (E) basin area of tributary, and (F) Melton's ruggedness of tributary (n = 6). MS represents mainstem, TR represents tributary.

6

- 2.7 (A) Relative (tributary / mainstem) concentration of coarse particulate organic matter (CPOM) across a gradient of relative basin area (BA). Relative values >1 correspond to higher tributary values compared to mainstem, whereas values <1 mean tributary values are less than the mainstem. (B) Modelled change in coarse particulate organic matter concentration (downstream / upstream) in the mainstem due to tributary supply. Dotted line represents the TP concentration ratio = 1. Multiple points within the same basin area ratio are separate sampling events of the same tributary.</p>
- 2.8 (A) Relative (tributary / mainstem) concentration of nitrate across a gradient of relative basin area (BA). Relative values >1 correspond to higher tributary values compared to mainstem, whereas values <1 mean tributary values are less than the mainstem. (B) Modelled change in nitrate (downstream / upstream) in the mainstem due to tributary supply. Dotted line represents the nitrate concentration ratio = 1. Multiple points within the same basin area ratio are separate sampling events of the same tributary.</p>
- 2.9 (A) Relative (tributary / mainstem) concentration of total dissolved phosphorus (TDP) across a gradient of relative basin area (BA). Relative values >1 correspond to higher tributary values compared to mainstem, whereas values <1 mean tributary values are less than the mainstem.</li>
  (B) Modelled change in total dissolved phosphorus concentration (downstream / upstream) in the mainstem due to tributary supply. Dotted line represents the TDP concentration ratio = 1. Multiple points within the same basin area ratio are separate sampling events of the same tributary.
- 2.11 Hourly temperature difference (°C) between tributary and mainstem during study period. Values > 0 indicate a tributary warmer than mainstem and values < 0 indicate a tributary cooler than the mainstem. Horizontal dashed line indicates equivalent temperatures. Tributaries are arranged by increasing basin area ratio (BAR) from left to right, top to bottom. Missing data from Dave's Creek was due to the tributary losing surface flow and missing data from KLO Creek was due to temperature logger malfunction. For absolute temperature data in the tributary and mainstem, see Figure A7 and Figure A8.</li>
- 2.12 Diel patterns in stream temperature using hourly temperature data in the tributary (blue) and mainstem (red). Each line corresponds to one day of sampling.33

31

- 3.1 Redundancy analysis of measured environmental variables across six study sites. Variance was reduced to two RDA axes which explain 49.9 % of total variance. Points represent each basket observation with 95% confidence ellipses around the centroid of upstream (grey) and downstream (black) position in both August (solid line) and September (dashed line).
- 3.2 Estimated marginal means (95% confidence error bars) of (A) rarefied taxonomic richness, (B) Shannon index, (C) total macroinvertebrate abundance (no. per basket, 490 cm<sup>2</sup>), and (D) Pielou's evenness upstream and downstream of tributary inflow. Point shape indicates substrate size: small (circle), large (triangle); point colour indicates CPOM addition: none (dark), added (light). Raw observations are plotted in light gray points behind corresponding means. Error bars for abundance are symmetrical despite being on log axis due to back-transformation from log link function.
- 3.3 Location of treatment centroids visualized using partial distance-based redundancy analysis scores from all samples for each site with the effect of environmental variables left out of the db-RDA model and the site-by-site variability partialled out. Points represent centroid values with 95 % confidence ellipses of site location in ordination space for the position, upstream (grey) and downstream (black) relative to tributary inflow. Filled points represent centroids with CPOM added and open points represent no CPOM added. Shapes represent substrate treatment, small (circle) and large (square). Model explained 16.7% of total variance, visualized on two RDA axes (9.2 and 3.8%, respectively; p < 0.0001).</p>
- 3.4 Site-specific positional effects on community structure visualized using partial distance-based redundancy analysis scores from all samples for each site with the effect of environmental variables removed from the db-RDA model and the site-by-site variability partialled out of analysis. Ellipses represent 95% confidence ellipses around position treatments (color) at each of the two time periods (solid and dotted lines). Model explained 16.7% of total variance, visualized on two RDA axes (9.4% and 3.6%, respectively; p < 0.0001).</p>

55

A2	Validation of modeled downstream mainstem TDP concentration by comparing predicted and	
	observed values. Black line indicates 1:1 ratio between the two values, meaning no error in	
	modeled values.	83
A3	Validation of modeled downstream mainstem TP concentration by comparing predicted and	
	observed values. Black line indicates 1:1 ratio between the two values, meaning no error in	
	modeled values.	84
A4	Observed nitrate concentration across the three sampling periods (panels 1-3) in the main-	
	stem (red) and tributary (blue) with the corresponding basin area of the upstream catchment.	
		85
A5	Observed total dissolved phosphorus concentration across the three sampling periods (pan-	
	els 1-3) in the mainstem (red) and tributary (blue) with the corresponding basin area of the	
	upstream catchment.	86
A6	Observed total phosphorus concentration across the three sampling periods (panels 1-3) in	
	the mainstem (red) and tributary (blue) with the corresponding basin area of the upstream	
	catchment.	87
A7	Mainstem (black) and tributary (grey) hourly temperature at each of the six tributaries	88
A8	Mainstem (black) and tributary (grey) hourly temperature at each of the six tributaries across	
	first ten days of sampling. The shorter timespan compared to Figure A7 is to more clearly	
	display the tributary-mainstem comparison. Note that during this time period, there were no	
	data available for for the mainstem in KLO Creek.	89
B1	Probability of significant difference (p < 0.05) in rarefied taxonomic richness due to position	
	across 100 simulations using generated data based on variance derived from observed data.	98

### Acknowledgements

I would first like to extend gratitude to my advisor, John Richardson. Thank you for the immeasurable support from the beginning to the end of this research journey. Your encouragement and guidance through the most challenging times undoubtedly pushed my development as a student, researcher, and ecologist.

For the research development and professional guidance, I would like to thank my committee members, Scott Hinch and Brett Eaton.

For the unwavering support, though good times and bad, I would like to thank my family and friends. Each of you played a unique part in my life, from enduring my rambling of research ideas, to providing unwavering support during the times most needed. Mom, thank you for your continuous care and encouragement throughout my life and teaching me to truly appreciate those around me. Dad, thank you for teaching me the importance of thinking critically and cultivating curiosity. It is something I hope I can master during my life. I always knew that you two supported and trusted me regardless of the decisions I have made in my life; for that, I could not be more grateful.

For always making the office an enjoyable place to work (even after spending long, lonely, consecutive days at the microscope), I would like to thank the (many) members of the Stream and Riparian Research Lab and several other fellow students in forestry. To list all of you and everything that each you have done would take the majority of this document. Please know that you have each impacted my life and my research in your own unique way and I'll be sure to thank you personally.

For making every administrative task as quick and painless as possible, thank you Andrea, Christine, Natasha, and Rosemarie.

For field and laboratory assistance, I would like to thank Mary Botkin, Yudel Hubermann, Kasey Moran, and Sabine Sherrin. I would like to also thank Angie Nicolas for her amazing skills as a lab manager. Angie, you are a linchpin that keeps the lab functioning smoothly during the peak of the field season. Further, I would like to thank Jeff Curtis and Laura Hooker for lab space and equipment as well as Megan Ludwig for providing resources and instructional support for water nutrient analysis. Finally, I would like to provide my gratitude to the two employees of the Okanagan Basin Water Board – whom I did not gather names – for the emergency provision of a Swoffer meter, when ours no longer continued to work.

Last, but certainly not least, I would like to thank Jim and Debbie Basran, Black Mountain Irrigation District, and the Regional District of Central Okanagan for site access.

### Dedication

To Mom and Dad, for the sacrifices you have made – and the unwavering support you gave – to make this wonderful life possible.

> "Eventually, all things merge into one, and a river runs through it. The river was cut by the world's great flood and runs over rocks from the basement of time. On some of those rocks are timeless raindrops. Under the rocks are the words, and some of the words are theirs.

> > I am haunted by waters."

Norman Maclean, A River Runs Through it and Other Stories (2001, University of Chicago Press)

### **Chapter 1: Introduction**

#### Habitat and community structure in the ecological landscape

Organisms are in a constant interaction with the physical world. Physical processes both impose limits on the functioning of organisms and distribute the proper resources and habitat structure for one to survive (Vogel 2009). As each individual's habitat needs and life histories interact with the local abiotic conditions, natural variability in habitat structure and resources imposes limitations on the performance of some individuals and allowing the proliferation of others (Hutchinson 1957). Thus, the dynamic abiotic realm forms an amalgam of complex interacting processes in the natural landscape. To explain the structure and the underlying mechanisms for the spatial distribution of biota is a fundamental challenge for the community ecologist. This is a difficult task as communities are shaped by both local and regional processes that are difficult to decouple (Vellend and Agrawal 2010, Leibold and Chase 2017). On one hand, community assembly may be driven by relative differences in species' competitive abilities given local conditions, with coexistence enabled through resource and niche partitioning (Hutchinson 1957, Hardin 1960, Herder and Freyhof 2006, Crow et al. 2010). Another possibility is that community assembly is primarily dispersal-driven; either because organisms have similar competitive abilities (Hubbell 2001, Volkov et al. 2003, Muneepeerakul et al. 2008), or by the replenishment of poor competitors from a source population (Shmida and Wilson 1985, Pulliam 1988, Leibold and Chase 2017). The ways in which the physical environment shapes biotic communities has been a long-standing question for ecologists.

The physical realm of the ecological landscape consists of a hierarchical mosaic of patches of internallysimilar characteristics, delineated on boundaries of differences (Wiens 1976, Forman and Godron 1981). This mosaic consists of variation in habitat structure (i.e. the arrangement of material in space (Bell et al. 2012)) and resources across space. If variation among individuals' traits alters the relative fitness between individuals based on the habitat structure and resources present, then the attributes and arrangement of these patches are determinants of the spatial distribution of organisms across the landscape. This is further complicated, since context matters in the ecological landscape. Patches are linked through the flow of abiotic and biotic material that alter the habitat structure, resource supply, and quantity of organisms present (Polis et al. 1997, Poole 2002). This means that structural components and resources are dynamic over time. Recently, advances in spatial ecology, such as the meta-ecosystem concept (Loreau et al. 2003) have begun to explicitly incorporate the flow of material in conjunction with previous spatial community dynamics (Leibold and Chase 2017). Some of main objectives of these lines of research are to quantify the flux of abiotic and biotic material in order to explain community patterns over time.

#### Process influences structure in stream ecosystems

In stream ecology, the importance of the spatial arrangement and linkages of habitat patches and their resulting biotic implications are commonly highlighted across ecological paradigms (Frissell et al. 1986, Townsend 1989, Thorp and Delong 1994, Palmer and Poff 1997, Poole 2002, Winemiller et al. 2010). What distinguishes lotic ecosystems from other ecosystems is the predominantly downslope flow of water. The pervasive effects of flow make lotic systems a hydraulically stressful environment, especially for benthic organisms where flow can dislodge individuals in the water column or be subjected to damage from abrasive or saltating particles (Culp et al. 1986, Hart and Finelli 1999). Thus, habitat structure and resources can have important community implications as the spatial arrangement can provide stability in such disturbanceprone environments (Death 1996). Channel substrate, for instance, is an important structural component that provides refuge from the hydraulic forces on the surface, especially during peak flow periods (Lancaster and Hildrew 1993, Negishi and Richardson 2006). The retention and availability of particulate organic matter in the interstitial spaces of the channel bed allows for an energy source for detritivores and may minimize the exposure of organisms to the shear stresses present on the top surface of the substrate. The spatial and temporal distribution of such components (structure and resources) are the product of physicochemical processes that operate across scales. In streams, due to the predominantly downslope transport of material, processes upstream in the catchment can be highly influential for the characteristics and arrangement of habitat patches in the local channel (Hynes 1975).

Establishing the relationship between processes and resulting patterns in habitat and resource distribution is critical as anthropogenic effects are perturbing rates of processes beyond the range of natural variability and resilience of stream ecosystems. For example, land use conversion by agriculture and urbanization has removed riparian forests and changed soil permeability, altering nutrient cycling, hydrologic, and thermal regimes of streams (Paul and Meyer 2001, Moore et al. 2005a). Increased severity of wildfires due to climate change (Flannigan and Wagner 1991) remove large amounts of canopy foliage with extensive alterations to the nutrient regime via pyrolytic reactions (Hauer and Spencer 1998, Bladon et al. 2008, Smith et al. 2011). Intense wildfires can have hydrologic consequences from reduced canopy interception, decreased water uptake from the soil, and higher surface runoff through post-fire hydrophobic soils (Shakesby and Doerr 2006, Doerr et al. 2009). Alterations, such as these examples, have clear implications for the habitat structure and resource availability for in-stream organisms. Developing our understanding of the relationship between pattern and process in relatively natural systems can allow us to identify baseline conditions, provide insight into the response under future management scenarios or disturbances (Poff and Ward 1990), and provide indicators and goals for ecosystem restoration (Palmer et al. 1997a). This is particularly important for streams as they are highly connected systems with downstream effects.

Many processes that influence the quality and quantity of habitat structure and resources are directly or indirectly affected by the size of the stream. In mountainous environments, smaller streams are often supplied with poorly sorted material containing very coarse sediment delivered via mass-wasting from the steep

slopes surrounding (Benda 1990, Benda et al. 2005). Smaller streams in forested environments typically have a greater proportion of areal coverage from overhanging riparian canopy. This influences the thermal regime (Moore et al. 2005a, Gomi et al. 2006), increases the quantity of leaf litter inputs (Conners and Naiman 1984), and can limit primary productivity (Kiffney et al. 2004), decreasing nutrient uptake in the stream (Finlay et al. 2011). Due to the relationships between stream size and physicochemical processes, paradigms have emerged, such as the River Continuum Concept (Vannote et al. 1980), that attempt to generalize ecological characteristics based on stream size, with gradational changes to community composition and metabolic regime from headwater to delta. However, this linear view is challenged by the punctuated changes to habitat and community structure along the river through localized processes and the configuration of stream connectivity in the watershed (Ward and Stanford 1983, Bruns et al. 1984, Rice et al. 2001a, Benda et al. 2004).

#### The river as a network

In contrast to many terrestrial systems, the river functions as a dendritic network consisting of a series of branches (i.e. straight segments of stream, such as pools or riffles) and nodes, such as confluence points (Benda et al. 2004, Campbell Grant et al. 2007). The bulk of research in stream ecology focuses on understanding processes and patterns within the branches; at the time of writing, a crude search on the Web of Science for "ecology and (stream OR river) and (pool OR riffle OR reach)" revealed an order of magnitude more articles than one for "ecology (stream OR river OR tributary) AND (confluence OR junction)". These nodal points are unique in the river network as they are the connection of two distinct systems, whereby each stream is the product of the processes from the surrounding catchment and within the stream. However, despite their limited spatial extent (Kiffney et al. (2006) observed peaks in responses up to 12X the wetted width of the mainstem downstream), confluences are hypothesized to be critical disruptive points in the longitudinal gradient of the mainstem due to the influx of potentially novel biota, sediment, energy, and nutrients (Bruns et al. 1984, Rice et al. 2001a, Benda et al. 2004, Kiffney et al. 2006). As a result of this mixing, it is hypothesized that the combination of two characteristically distinct habitats yields a zone with increased habitat heterogeneity and "complementary reactants" (McClain et al. 2003). Therefore, tributary junctions are predicted to be hotspots of diversity and production (Rice et al. 2001b, 2008, Power and Dietrich 2002).

Many field studies have tested habitat and biological responses at tributary junctions in different contexts and at varying scales. For example, tributary junctions have been studied as points along a river continuum to delineate segments with consistent or predictable gradational patterns (Rice et al. 2001a, 2001b, Grenouillet et al. 2004, Jones and Schmidt 2016, 2018). They have also been recognized as supply locations to re-establish natural processes downstream of dams and impoundments (Katano et al. 2009, Sabo et al. 2012, 2018, Milner et al. 2019). Others have studied them intensively at the local scale to test hypotheses of community and habitat responses (Knispel and Castella 2003, Fernandes et al. 2004, Kiffney et al. 2006,

Wallis et al. 2009, Mac Nally et al. 2011, Milesi and Melo 2013, Wilson and McTammany 2014). However, despite the strong theoretical support for their ecological significance (Benda et al. 2004, Sabo and Hagen 2012, Jones and Schmidt 2016), empirical evidence focused on macroinvertebrate communities at tributary junctions has been inconclusive, with results ranging from no clear community response (Mac Nally et al. 2011, Milner et al. 2019) to increased diversity and altered community structure (Rice et al. 2001a, Kiffney et al. 2006, Katano et al. 2009, Wilson and McTammany 2014, Jones and Schmidt 2018). Moreover, few studies have measured both the magnitude and direction of macroinvertebrate community response in relation to the degree of change of specific habitat characteristics from upstream to downstream. By establishing relationships between river processes and habitat changes and experimentally testing their effects on macroinvertebrate communities, we will be able to disentangle some of the mechanisms driving the variability between previous descriptive studies. This could not only strengthen our understanding of river network structure and function, but could also improve the ability of ecosystem managers to identify ecologically significant locations in order to meet restoration and conservation goals.

Previously, there have been a few attempts to use tributary size to identify significant tributary junctions in the river network. However, these studies have focused on absolute and relative tributary size (i.e. relative to the mainstem) as being a discriminatory threshold for effects or used as a scaling factor for the magnitude of change and probability of ecological significance at tributary junctions (Rice 1998, Jones and Schmidt 2016). Since small streams are characteristically different from large streams in both structure and processes (see Gomi et al. (2002) for review), stream size may also be related to the qualitative changes at tributary junctions and may be a good predictor of both the magnitude and direction of alteration to resource supply, habitat structure, and community structure. In this thesis, I will use known physicochemical processes that typically vary with stream size to test specific hypotheses regarding alterations to the resource supply and habitat structure in a mainstem channel. I will further test whether these processes are driving mechanisms behind community assembly that may help inform the identification of ecologically significant points in the river network (Figure 1.1).

#### Thesis objectives and hypotheses

This thesis will describe the findings of an observational study and a field experiment that tests: (1) how tributary size controls the quantity and characteristics of material exports and the resulting effects on mainstem channel habitat and resource supply and (2) the mechanistic responses of invertebrates to subsidies and habitat structural change due to tributaries. In addition to the current introductory chapter, I will address these two objectives independently with concluding remarks in chapters 2 through 4.

Chapter 2 focuses on the comparison of tributary exports of sediment, contrasting water temperatures, CPOM, and nutrients (namely, nitrate and phosphorous) relative to the receiving, mainstem channel. I will use observational data across my study area to answer the following questions: (1) do small to mid-sized tributaries lead to the greatest changes in mainstem nutrient and CPOM concentration? (2) are smaller

tributaries sources of cold-water inputs for mainstem channels? and (3) do small, steep gradient tributaries cause the largest increase in substrate size in a receiving channel?

Chapter 3 details an experiment conducted to test the mechanistic responses of invertebrate communities to varying levels of substrate size, CPOM supply, and position relative to the tributary confluence. By manipulating the habitat structure and resource availability upstream of tributaries to mimic downstream locations, I will attempt to answer the following questions: (1) Does community structure of invertebrates shift between upstream and downstream of the tributary junction? and (2) To what extent does substrate coarsening and CPOM addition contribute to upstream-downstream community changes?

Finally, Chapter 4 concludes with a conceptual synthesis of the results from the above studies, directions for future research, and implications for researchers, practitioners, and ecosystem managers.



Figure 1.1: Conceptual model of processes at tributary junctions. Various materials are exported from the tributary, which alter the habitat structure and resource supply of the mainstem. In turn, this alters the nature of the environmental filter that acts on the potential community consisting of organisms from upstream in the mainstem and tributary. This thesis will address: (1) the controls on tributary exports based on the tributary stream size and (2) the resulting responses in benthic communities due to alterations to habitat structure and resource supply in the mainstem.

# Chapter 2: Effects of tributary size on the resource supply and physical habitat at tributary junctions along two mainstem rivers

#### Introduction

The ecological landscape consists of a network of patches linked by the fluxes of biotic and abiotic material which are foundational to the supply of resources and arrangement of habitat structure for local biota (Forman and Godron 1981). Resource subsidies can shape recipient communities by causing bottom-up food web effects (Polis et al. 1997, Sánchez-Piñero and Polis 2000, Marczak et al. 2007) or allow specialist consumers to persist with the presence of novel resource types (Sabo and Power 2002). The movement of abiotic material adds structural complexity to the environment, allowing for refuge from disturbance events (Lancaster and Hildrew 1993, Negishi and Richardson 2003) and harsh abiotic conditions, e.g., hydraulic stressors (Culp et al. 1986), thermal stress (Ebersole et al. 2001, Mathes et al. 2009). Structural components also add complex microtopography (Wetmore et al. 1990) and cover from predators (Brusven and Rose 1981). The local availability of habitat structure and resources form the habitat template (Southwood 1977), which imposes limitations on the persistence of individual species from the regional species pool based on their traits (Cottenie et al. 2003, Leibold and Chase 2017). Fluxes across contrasting ecosystem types can provide very unique sources of resources and habitat structure, leading to magnified responses in recipient food webs (Allen and Wesner 2016), opening of novel niche space and resource supply (Agostinho and Zalewski 1995, Baumgartner et al. 2018), and biotic interactions not present in either contributing system (Baxter et al. 2004, Carroll and Thorp 2014). By guantifying and describing material fluxes in a landscape, we can begin to understand the driving factors for the spatiotemporal distribution of resources and habitat structure and the consequent biological patterns.

Spatial fluxes of material are a ubiquitous feature of riverine ecosystems due to the flow of water. The strong upstream-downstream connectivity from the predominantly unidirectional flow has led to paradigms, such as the River Continuum Concept (Vannote et al. 1980), viewing rivers as gradational changes in biotic and abiotic structure and function due to the cumulative integration of upstream processes (Culp and Davies 1982, Naiman et al. 1987, Tomanova et al. 2007). However, physicochemical processes operate at all levels of scale that strongly influence the spatiotemporal distribution of habitat structure and resources important for biotic communities and ecosystem function (Frissell et al. 1986, Palmer and Poff 1997, Montgomery 1999, Thorp et al. 2006). These multi-scale processes can create localized patches of habitat structure and resource base that strongly contrasts areas immediately upstream, punctuating the downstream gradient (Ward and Stanford 1983, Rice et al. 2001a). For example, lateral supplies of sediment from mass-wasting events can lead to sudden changes in substrate size and character (Benda et al. 2003b), altering how resources are stored and the spatial distribution of biota (Rice et al. 2001a, Benda et al. 2004). Lake features can lead to sudden decreases in flow velocity and alter depositional patterns of organic matter, supplying the recipient lake fish populations with basal energy sources (Tanentzap et al. 2014, 2017). These sudden

changes in flow hydraulics (e.g. velocity, depth) at the inflows and outflows of lakes can be localized areas of unique combinations of suspended organic matter substrate characteristics (Richardson and Mackay 1991, Jones 2010). Groundwater discharge sites from preferential flow paths of subsurface water can lead to altered nutrient availability, organic carbon, and water temperature (Power et al. 1999, Hunt et al. 2006, Jansson et al. 2007, Kuglerová et al. 2014). All the above locations are examples of habitat interfaces that undergo a rapid change in habitat across a relatively small area. These locations are distinct as they have the potential to harbor unique processes and interactions which consequently add habitat and resource heterogeneity to the broader region (Naiman et al. 1988). The natural processes that act to form the spatial distribution of habitat and resources are becoming increasingly perturbed through land-use conversion (Paul and Meyer 2001), climate change (Merritt et al. 2006, Nelson and Palmer 2007, Boyer et al. 2010, Mantua et al. 2010), and resource extraction (Kiffney et al. 2004, Moore and Wondzell 2005). Understanding how processes and structure are connected would help inform practitioners and researchers on the anticipated ecological responses to these perturbations.

Tributary junctions are another location in the river network that make up a very small proportion of area, but are hypothesized to be ecologically significant areas. The sudden convergence of two distinct contributing streams form nodal points in the river (Campbell Grant et al. 2007) that are the product of their respective upstream catchments. Consequently, the downstream ecosystem may have unique combinations of materials leading to altered resource base and habitat structure. Numerous studies have found that tributary streams are important sources of drifting invertebrates (Wipfli 1997, Wipfli and Gregovich 2002, Pond et al. 2016), detritus (Wipfli and Gregovich 2002, Pond et al. 2016), detritus (Wipfli and Gregovich 2002, Pond et al. 2016), nutrients (Kiffney et al. 2006), thermal refugia (Sabo et al. 2012, Brewitt et al. 2017), sediment (Rice et al. 2001a, Benda et al. 2004, Rice 2016), and large wood (Kiffney et al. 2006). As such, tributary junctions have been regarded as zones of high habitat heterogeneity (Benda et al. 2004), heightened biological diversity (Fernandes et al. 2004, Kiffney et al. 2006, Thorp et al. 2006, Rice et al. 2008, Wilson and McTammany 2014), and have been hypothesized to be hotspots of increased nutrient cycling and reaction rates (McClain et al. 2003). However, the significance and magnitude of these changes are highly variable between tributary junctions. By incorporating our *a priori* understanding of the processes governing these stream exports, we can improve our predictions of where ecologically distinct areas occur in the river network.

Stream size is an important controlling factor for a wide range of physical and chemical processes in the stream and can alter the resource base and habitat structure of the stream (Gomi et al. 2002, Richardson et al. 2005). For instance, small channel widths have a greater proportion of riparian canopy cover and increase the area of water surface that is exposed to falling riparian leaf litter (Conners and Naiman 1984). Increased canopy cover also limits light availability, resulting in diminished primary productivity (Kiffney et al. 2004), increased nitrogen and phosphorous concentrations (Finlay et al. 2011), and reduced radiative heating of the stream (Brown 1969, Webb and Zhang 1997, 1999). Smaller tributaries, especially in mountainous terrain, are more tightly coupled to hillslope geomorphic processes that supply large quantities of poorly sorted sediment to the stream channel (Benda 1990, Benda et al. 2005) leading to large sedi-

ment loads moved downstream (Milliman and Syvitski 1992). These small tributaries are also associated with steep slopes, flashy hydrographs, and higher sediment transport capacity (Montgomery and Buffington 1997), often leading to inputs of coarse sediment into the receiving channel (Rice 1998). In the context of tributary junctions, the stream size of the tributary relative to the receiving channel has been identified for its geomorphic implications (Rhoads 1987, Rice 1998, Benda et al. 2004) and more broadly, the magnitude of ecological response (Jones and Schmidt 2016). However, there have been limited empirical efforts directed at understanding how the strength of the response in specific resource and habitat characteristics vary across tributary size, particularly in larger mainstem channels.

This study addressed this gap by describing how tributary size (relative to mainstem) influences the magnitude of response in nutrient and organic matter concentration, substrate size, and temperature in the mainstem of two medium-sized streams (mean basin area = 471 km<sup>2</sup>, range = 232 - 699 km<sup>2</sup>). We hypothesize that these parameters are controlled by processes that are strongly influenced by tributary size relative to mainstem. We have four main predictions in the following study. First, we predict that substrate size will increase downstream of tributary junctions and will show stronger contrasts from smaller, steep tributaries. Second, smaller tributaries will act as sources of cooler water to the mainstem channel. Third, tributaries export higher concentrations of nutrients and CPOM relative to the mainstem and that these differences will diminish as tributary size approaches that of the mainstem. Lastly, we expect that the tradeoff between the high concentration of nutrients and CPOM in small tributaries and the increased discharge of larger tributaries (Figure 2.1) will result in the greatest relative change in nutrient and CPOM concentration and in the mainstem will be greatest at mid-sized tributaries.

#### **Materials and Methods**

#### Study Area

Six study sites, three along each of the West Kettle River and Mission Creek, were selected in the Okanagan region of British Columbia, Canada (Figure 2.2; descriptions in Table 2.1). Selected sites were chosen across a gradient of relative tributary size (basin area ratio; BAR), with a range of BAR from 0.06 to 0.82. Mainstem channels varied in size from 232 km<sup>2</sup> to 699 km<sup>2</sup>.

All catchments are located on the western slopes of the Columbia Mountains in a warm climate with a 30year (1981 - 2010), mean daily temperature of 8.8 °C, ranging from -2.3 °C to 20.4 °C in December and July, respectively (Environment and Climate Change Canada 2018a). These regions are also characterized by a semi-arid climate, with an average of 414 mm of precipitation (30 yr mean, 1981 - 2010) in the lower elevations (491 masl). As a result, the hydrographs of these two catchments range considerably due to the snowpack storage in the source catchments, causing a large peak in the spring and declining to very low baseflow conditions due to little rain throughout the summer (Figure 2.3).

The Mission Creek catchment is an incised plateau with an underlying Paleozoic and Proterozoic gneiss and

schist geology (Schiarizza and Church 1996). Many of the far headwater reaches located atop the plateau are low gradient and frequently have small lakes and wetlands scattered in the upper reaches of the basin. During baseflow conditions, these lakes can maintain water volume providing a source of flow throughout the late summer in addition to groundwater. The topsoil in the region is comprised of well-drained sandy till and varies substantially in depth, often exposing underlying bedrock (Grainger and Associates Consulting Ltd. 2010). Historical evidence of landslides in the area suggests that mass-wasting may be an important source of sediment in the smaller tributaries (Dobson Engineering Ltd. 2003). The predominant forest types found in the catchment, according to the Biogeoclimatic Ecosystem Classification system is Interior Douglas-fir, Interior Cedar Hemlock, Montane Spruce, Engelmann Spruce Sub-alpine Fir (Hoy et al. 1994). However, small patches of *Populus trichocarpa* were observed in riparian zones on the downstream, low elevation reaches. Current and historical logging activity is common in the area, particularly in Dave's Creek catchment, along with some concentrated agricultural use in the floodplain of the Joe Rich region upstream of Belgo Creek. However, further upstream has limited logging and land use change due to the Greystokes Provincial Park boundary (Dobson Engineering Ltd. 2003).

Further to the east and at a higher elevation, the West Kettle catchment has a mixed bedrock geology, predominated by Early Cretaceous granite and granodiorite (Hoy et al. 1994). Riparian zones of the West Kettle River are mostly of Interior Douglas-fir BEC type with Montane Spruce dominating the upland and upstream areas of the catchment (Government of British Columbia 2018). Despite less pressure from human settlement and agricultural development as found in Mission Creek, there is extensive logging in the area. However, with the exception of some historical clearcut blocks adjacent to Trapping Creek (Molnar 1996), there does not appear to be much recent logging in the riparian zones of the river.

#### Substrate size analysis

Sediment size contrasts were based on field measurements by Wolman pebble count (Wolman 1954). At each tributary junction, a 100 m length plot was established upstream and downstream of the confluence (see Table A1 for description). The downstream plot was located as close to the mouth of the tributary where it was deemed safe to enter the stream and sufficiently downstream of the backwater created from the flow interference of the tributary confluence. The upstream plot was located at a randomly selected distance between 0 m and 100 m beyond the pooling effect caused by the alluvial fan of the tributary. This upstream criterion was selected to avoid the effects of fine sediment accumulation that would not be representative of the normal flow conditions of the mainstem channel, if the tributary had not been present. At each 100 m plot, transects were established from the bank to 5 m from the bank at 10 m intervals. In each transect, the stone located at each 1 m mark along the transect was measured for the longest b-axis for a total of 60 grain size measurements at each upstream and downstream plot.

Local grain size distributions were generated and median grain size ( $D_{50}$ ) and grain size of the 84th percentile ( $D_{84}$ ) were calculated. To describe the shape of the distribution and to test whether tributaries are associated

with increased sediment at the coarse end of the distribution, sorting, skewness, and the standard deviation of the coarse end ( $\phi_{84} - \phi_{50}$ , where  $\phi_x = \log_2(D_x)$ ; (Bunte and Abt 2001)). The two grain size metrics and distribution parameters for each plot were then contrasted upstream and downstream using a linear mixed model in R (R Core Team 2016), using site as a random effect. The magnitude of change in the two grain size metrics were then plotted against four basin morphological metrics of the tributary as well as their ratio between the tributary and the mainstem. These metrics included basin area (A), distal channel slope (S), basin-area slope product (Rice 1998), and Melton's ruggedness number. The basin area-slope product ( $\Psi$ ; Equation 1) has previously been used to discriminate significant confluences with regards to the tributary effects on substrate size (Rice 1998).

$$\Psi = AS \tag{1}$$

Melton's ruggedness number (R; Equation 2) is a measure of the relief of the basin relativized to the stream length or basin area (Melton 1958, 1965).

$$R = \frac{(Z_{max} - Z_{min})}{\sqrt{A}} \tag{2}$$

Ruggedness has previously been correlated with runoff intensity, as more rugged areas, such as steep valley side slopes in mountainous terrain, indicate high quantities of precipitation and runoff (Melton 1958) and can be used to discern the presence of a debris flow fan, characterized by poorly sorted material, often containing very large sediment, including boulders (Kostaschuk 1987). Although we were not interested in the presence of debris flows, these metrics were used as a proxy for coarse sediment supply through mass wasting and transport with steep channel slopes.

#### **CPOM** exports

To measure the quantity of organic matter exports from tributary streams, we installed drift nets upstream in the tributary and mainstem streams at each site location. Sampling took place on two occasions, once during the end of August, and once in mid-September. During each sampling event, 243 µm-mesh drift nets fixed to the channel using rebar posts and were mounted for 24 hours above the streambed surface to avoid inputs of walking and crawling macroinvertebrates (not used in this study). Each sample was stored in 70% ethanol until further laboratory analysis.

The coarse fraction (>1.0 mm) of each sample was sieved and separated from the remaining sample. All invertebrates from the coarse fraction were separated, leaving behind the coarse fraction of organic matter, which was dried for at least 24 h at 86 °C, weighed, pyrolized at 500 °C for 4 h, and weighed again to calculate dry mass and ash-free dry mass (AFDM).

The AFDM was converted to concentration then used to compute a ratio of CPOM concentration between tributary and mainstem. This concentration ratio was regressed against the basin area ratio between the tributary and mainstem to test the prediction that smaller tributaries will have a greater concentration of CPOM relative to the mainstem. A weighted least squares model (WLS) was fit using gls in the "nlme" package in R (R Core Team 2016, Pinheiro et al. 2018) with crossed time period and basin area ratio. Variance was weighted by basin area to account for the large spread in residuals at smaller BAR. Although catchment is not of interest in this study and would typically belong as a random effect to account for spatial dependence, only two catchments were sampled, making it difficult to obtain a measurement of variance across levels. The full model revealed that mainstem catchment had no effect and was eliminated from the final model. Effect significance was determined with an analysis of deviance using type III sum of squares to be compatible with the WLS model ( $\alpha = 0.05$ ).

#### **Nutrient Exports**

To compare the effects of tributary and mainstem exports of nutrients, 500 mL grab samples were taken upstream of the confluences in both the tributary and mainstem channel corresponding to the drift sampling (see above). Samples were stored in a cooler and either processed in the lab within 24 hr, or frozen until further analysis for nitrate (NO<sub>3</sub>-), total phosphorous (TP), and total dissolved phosphorous (TDP).

All chemical analyses were conducted by Jeff Curtis' lab at the University of British Columbia (Okanagan Campus). Total phosphorus was measured via colorimetric determination of phosphorus using ascorbic acid (Murphy and Riley 1962). Total dissolved phosphorus was determined in the same way but using filtrate from the sample passed through 45 µm reinforced membrane filters (Millipore®). Nitrate was measured through the Griess-Ilosvay reaction with vanadium(II)chloride as a reduction agent (Doane and Horwath 2003, Schnetger and Lehners 2014). Previous unpublished research in the region has shown that nitrite concentrations are negligible, and for the purpose of this study, were ignored (Megan Ludwig, University of British Columbia - Okanagan Campus, personal communication).

All three nutrient parameters were originally fitted with an OLS model in R (R Core Team 2016) to test whether nutrient concentration ratio between the tributary and mainstem are negatively related with tributary size. In the case of TDP, a WLS model was fitted to meet the assumption of homogeneity of residuals. In the case of nitrate, normality of residuals was not met (Shapiro-Wilk, p = 0.017) but was primarily driven by one outlier. Analysis was run with and without the outlier. In all models, time period was crossed with BAR as fixed factors. Like the CPOM analysis, mainstem catchment was included as a fixed factor but was not significant in all analyses and was omitted from all final models. Effect significance was determined with an analysis of variance using type III sums of squares, except for TDP where type III analysis of deviance was used for compatibility with the GLS model ( $\alpha = 0.05$ ).

#### Modeling mainstem changes in nutrient and organic matter concentrations

While small tributaries may contain a disproportionately high concentration of nutrients and CPOM, sufficiently large discharge from the tributary is necessary to make a signal detectable downstream, due to the dilution from the mainstem channel. To address this question, a basic model was constructed to mix the two resource contributions. Knowing the discharge of the mainstem and tributary, the concentration of CPOM and concentration of nutrients can be multiplied by the discharge of their respective basins to estimate flux rate. These flux rates can then be added and divided by the sum of the discharge of the contributing mainstem and tributary to determine concentration present downstream. Model results were validated with a partial dataset composed of samples taken downstream during the course of the study (see Appendix A) to confirm the assumption that specific discharge calculated from the gauging station is representative of the entire catchment. Samples were taken downstream of the flow interference of the tributary where flow appeared to reestablish.

Since site-specific discharge was not measured in the field, it was estimated through the specific discharge of the basin. Using field data collected from Environment and Climate Change Canada (2018b), discharge was gathered for the days of data collection and divided by the contributing basin area at that monitoring station. The basin areas of the mainstem and tributaries were then calculated using watersheds rendered from digital elevation data supplied by Natural Resources Canada and multiplied by the specific discharge to estimate discharge of each subcatchment. To generate the watersheds, the digital elevation model (DEM) was first processed to fill sinks using Fill in ArcGIS (v. 10.6 Esri (2017)). Catchment boundaries were then delineated by using the Watershed tool on a D8 flow direction raster generated in ArcGIS from the processed DEM.

The ratios of the downstream concentrations to the observed concentrations upstream in the mainstem were plotted against the basin area of the tributary to visually test whether the greatest changes in concentrations occur at mid-sized tributaries, according to our third hypothesis.

#### **Stream Temperature**

HOBO pendant temperature loggers (Onset®) were deployed in each of the upstream mainstem and tributary locations, and were programmed to record hourly mean temperature. Loggers were attached to rebar posts and mounted near the stream bed in a deep section of steadily flowing water. Data points one hour before and after logger installation, and during data downloads and removal, were removed. At each time point, the temperature of the mainstem was subtracted from the temperature of the tributary to calculate the difference at each site. These hourly differences were plotted against time to visually assess trends across increasing tributary size. Descriptive statistics, such as the maximum and minimum difference for each day were calculated to generate the average peak and low temperature differences at each tributary to compare these to the mainstem temperature at that same time point.

#### Results

#### Substrate contrasts

A total of 712 stones were measured across the twelve plots. Eight stones contained within the transects were not measured due to the inaccessibility (fast flowing or deep waters). Median substrate was 60% larger downstream of tributary confluences compared to upstream in the mainstem channel (mean  $D_{50}$  147.83 (95% CI: 124.6 - 171.1) mm vs. 92.25 (69.0 - 115.5) mm; Table 2.2). These results were significant (Linear Mixed Model; p < 0.001). This same general pattern was also identified in the  $D_{84}$  (mean  $D_{84}$  213.8 (151.4 - 302.0) mm vs. 323.6 (229.1 - 457.1) mm; p = 0.023; Table 2.2); however, there was much higher variability in the site-to-site observations and the influence of a strong outlier (Kallis Creek) leading to more uncertainty in the effects (Marginal  $R^2 = 0.25$  compared to Marginal  $R^2 = 0.60$  with  $D_{50}$ ). While there was a significant positional effect, there was no clear relationship with any of the basin morphology parameters for either median grain size (Figure 2.5) or  $D_{84}$  (Figure 2.6) as a response.

Sediment sorting between upstream (2.518 (1.93 - 3.24)) and downstream (2.587 (1.93 - 3.24)) were not significantly different (p = 0.797), both resulting in poorly sorted material. Substrate was skewed to the coarse side, indicating the presence of very coarse material in the distribution, but there was no difference between upstream (0.132 (-0.02 - 0.29)) and downstream (0.237 (0.08 - 0.39)) in Warren skewness (p = 0.114). We also found no differences in the spread of the coarse end of the distribution (i.e.  $\phi_{84} - \phi_{50}$ ) between upstream (1.24 (0.85 - 1.63)) and downstream (1.14 (0.75 - 1.53); p = 0.626)

#### **CPOM Subsidies**

Drift nets collected one sample in each the tributary and mainstem of each tributary junction for each date, except for Dave's Creek, where no surface flow was present during August and September and from Belgo Creek in August, where access was limited due to a wildfire in the area. As a result, a total of 18 samples were used in the analysis. The limited sampling effort made interpretation difficult, but some trends still emerged. As predicted, tributary CPOM concentration was higher than the mainstem and there was a significant decrease of CPOM ratio with BAR (WLS; p = 0.045, Table 2.3). However, this relationship was weak (Figure 2.7A) and may have been influenced by one outlier at the smallest BAR.

Kallis Creek (BAR = 0.3) showed a CPOM ratio <1, which is the opposite trend as compared to similarly sized tributaries. Wilkinson Creek (BAR = 0.82) showed very similar CPOM concentration to the mainstem channel, which is comparable in size. For the three tributaries that have both time periods sampled, the patterns were consistent but larger in August compared to September.

#### **Nutrient Subsidies**

Each location within the tributary junction sites were sampled at three time periods, except for the tributary of Dave's Creek, where the stream lacked surface flow in August and September. During the first sampling event, samples were only taken upstream in the tributary and mainstem channel. This resulted in a total of 38 samples for each of TP, TDP, and nitrate. Nitrate showed no clear relationship (OLS; p = 0.800; Table 2.4) between the relative (tributary / mainstem) concentration and the relative basin area (Figure 2.8A).

The relative concentration of TDP was negatively related with increasing basin area ratio (WLS; p < 0.0001; Table 2.5). Small tributaries showed disproportionately higher concentrations of TDP in relation to their corresponding mainstem channels compared to larger tributaries, which had TDP concentrations fairly similar to their mainstem (Figure 2.9A). TP also showed a similar relationship as TDP (Figure 2.10A). Although the relationship was significant (OLS; p = 0.045; Table 2.6), this relationship was weaker in comparison to TDP. To test for the possibility of observed trends driven by mainstem nutrient concentrations, all nutrient data were plotted as a response to basin area and no clear relationships between basin area and nutrient concentrations were observed in the mainstem channels (Appendix A). However, small tributaries had higher concentrations of nutrients compared to the larger mainstem channels.

After incorporating discharge and modeling for upstream-downstream contrasts, there were generally higher phosphorus concentrations upstream relative to downstream of the tributary junction, where downstream concentrations ranged from 86% to 188% of the upstream concentrations of TP (Figure 2.10B) and 92% to 142% of TDP (Figure 2.9B). However, nitrate concentrations varied substantially between time periods with no observable patterns. There was strong variability between sampling events and there was no visual relationship between the relative nutrient concentration and the size of the tributary relative to the mainstem for TDP, TP, and nitrate.

#### **Stream Temperature**

Temperature was measured hourly across all tributaries, except for Dave's Creek which lost surface flow in early August, and KLO Creek which had logger malfunctions during the first half of the sampling period. Stream temperature of the tributary relative to the mainstem showed clear diel patterns and had no clear visual relationship of overall temperature differences or magnitude of temperature fluctuations with the basin area ratio (Figure 2.11). All tributaries had periods of relatively warm water and cooler water flowing into the mainstem channel (Figure 2.12); however, the minimum and maximum relative temperature was highly specific to the tributary (Table 2.7). The mainstem temperature at 20.5 °C and the average minimum at 12.9 °C (Figure A7 and Figure A8). Dave's Creek and Belgo Creek showed the coolest minimum relative temperatures, which were 2.8 °C and 2.6 °C cooler than the mainstem, respectively. During these times, the mainstem was usually around 21.2 °C and 18.9 °C at Dave's Creek and Belgo Creek. Tributaries also had

warm water inflow periods, especially in the case of Wilkinson Creek, which was generally warmer than the mainstem Figure 2.11, but was also apparent in Kallis Creek. At Wilkinson Creek, the warmest inflow periods were 2.1 °C warmer than the 19.5 °C mainstem water, and at Kallis Creek, the warm inflow periods were generally 2.2 °C warmer than the 17.3 °C mainstem water.

#### Discussion

Previous empirical research has identified tributary junctions as ecologically distinct areas in the river network (Rice et al. 2001a, McClain et al. 2003, Benda et al. 2004, Campbell Grant et al. 2007); however, our understanding of these locations is limited to quantifying changes in specific environmental characteristics of the mainstem channel with few quantitative links to processes that are present in either contributing catchment (but see Jones and Schmidt, 2016). This study attempted to address this gap by using established relationships between stream size and physicochemical processes to test whether increasing stream size leads to lower contrasts of nutrients, CPOM, substrate size, and temperature between the tributary and mainstem due to the increasing similarity between the tributary and mainstem. Our data agreed with previous research that observed coarsened substrate (Rice et al. 2001a, Benda et al. 2004, Rice 2016), higher nutrient concentration (Rice et al. 2008), higher organic matter supply (Bruns et al. 1984, Wallis et al. 2009), and contrasting water temperature (Brewitt et al. 2017) due to tributaries. However, we found that tributary size was a weak predictor of many parameters measured and was complicated by high spatial and temporal variability and the limited spatial extent of the study.

#### **Substrate Characteristics**

Channel substrate was shown to consistently coarsen downstream of tributaries, which confirms half of our first hypothesis. However, there was no clear relationship with BAR or tributary size, ruggedness, or basin area-slope ratio. Previous research has documented significant geomorphic shifts of sediment grain size at tributary junctions at basin area ratios as low as 0.015 in alluvial channels (Benda et al. 2003a, 2004). While there seems to be a threshold in tributary size relative to mainstem to show coarsening at tributary junctions (Benda et al. 2004), using stream size to predict geomorphic significance has been challenging (Rice 1998) and often requires the use of other basin parameters, such as slope to reduce false positive and false negative identification. Even the use of other basin parameters in our study showed no improvement for predicting magnitude of substrate coarsening at tributary junctions. Considering other processes may be necessary to elucidate the effects that tributaries have on the mainstem substrate since many of the tributaries were similar plane-bed morphologies despite varying in their channel size and slope.

Channel morphology characteristics can be strongly influenced by both the sediment supply and the transport capacity of the stream (Montgomery and Buffington 1997). Site-by-site variability in these controls may explain the deviance away from the expected relationship between the BAR and magnitude of change in substrate size in the mainstem. First and foremost, some reaches of the West Kettle and Mission Creek flowed adjacent to major highways or property that was reinforced by rip-rap to minimize bank undercutting. This was observed at Belgo Creek and Kallis Creek sites. While the anthropogenic inputs of sediment could alter the substrate characteristics, we did not encounter any stones in our measurements that were unusually angular, which is typical for rip-rap. However, legacy effects of sediment modification from historical construction in the mainstem or tributaries may have confounded our findings. Another important element to consider is the severity and time since last disturbance or geomorphic event. Historical records show mass wasting events, including landslides and rockslides, are highly frequent in the region (Westrek Geotechnical Services 2000). These landslides varied substantially in the volume and timing, many consisting of very poorly sorted material containing large clasts. If some catchments experienced a relatively recent geomorphic event, there may not have been enough time for fluvial processes to act on this sediment to make it comparable to catchments that have had less recent or severe events.

There are a few caveats regarding our substrate results. First, substrate size was not measured in the tributary, so we are unable to decouple the effects of sediment export versus the additional discharge contributions at peak flow increasing the capacity of the receiving channel (Rice et al. 2001a). For example, Milner et al. (2019) found that substrate downstream is coarser than upstream, but substrate in the tributaries was generally smaller than downstream suggesting that large substrate exports are not a primary driver of grain size change. Second, we also attempted to overcome upstream effects from tributary inflows by sampling upstream of clear visual morphological indicators, such as pooling and reduced slope due to tributary inflow (Benda et al. 2004). We used this sampling scheme to isolate the effects of the tributary to obtain a measure of effect size. However, the limitation of this approach is that localized deposition patterns may confound results and does not provide an estimate of the mean substrate size of the mainstem that is not disrupted by lateral sediment sources (Rice and Church 1998).

Tributary sources of coarse sediment may have particularly interesting ecological implications for tributary junctions. Since stream power (a measure of stream competence) is proportional to the product of discharge and channel slope, tributaries that are proportionately greater in slope (i.e. greater than how much more discharge the mainstem supplies), may be important sources of sediment that act as refugia (Negishi and Richardson 2003), even during peak flows. For example, a tributary that is four times as steep compared to the mainstem that only has twice the discharge could input sediment that exceeds the competence of the mainstem by two-fold. These coarse sediment inputs are also important as they could play an important role in the formation of resource patches by creating retention structures from increased stone protrusion (Hoover et al. 2006), particularly in low-flow conditions during autumnal litterfall. Little research has been done to describe how sediment coarsening interacts with other physical and biological processes in mainstem channels. Future research looking at the functional role of sediment coarsening in stream processes and ecological responses could yield interesting insights regarding ecological processes at tributary junctions.

#### **Stream Temperature**

Our study did not confirm our second hypothesis regarding stream temperatures. Relative stream temperatures were highly variable throughout the day and were catchment specific. While cold water inputs occurred during certain time periods in most tributaries, we had one site that consistently delivered warmer water to the mainstem. Stream temperature is fundamentally driven by radiative inputs and outputs from the stream, sensible heat transfer with the atmosphere, and conduction with the stream banks and channel bed (Webb et al. 2008). Stream size relative to canopy enclosure can greatly affect the amount of solar radiation via shading (Brown 1969, Webb and Zhang 1997, 1999, Johnson 2004), which was a driving reason for our initial hypotheses. Without an intact riparian forest or effect of shading, streams can show increased temperature maxima and greater diel variation (Moore et al. 2005a). This could explain the patterns in relative temperature we observed. Open canopies over the mainstem channels meant a high fluctuation in temperatures through the day, where tributaries had a more stable temperature profile leading to the alternation between the relatively warm and relatively cold water inputs from the tributary. KLO Creek is one of the smallest tributaries with a very dense riparian canopy with a high degree of canopy closure. KLO Creek showed the lowest degree of diel variability (Figure A7). However, small streams without an intact riparian canopy are sensitive to radiative heating, which can remove the stabilizing effects on stream temperature (Moore et al. 2005b, Gomi et al. 2006). Kallis Creek, also a small tributary, had a sizable length of stream that flowed through an open meadow and bog that had very little surrounding riparian vegetation that would act to shade the stream, allowing for large inputs of solar radiation. This might explain the large fluctuations in tributary temperature, due to the combination of high variability in radiative inputs in combination with the low thermal mass of the small stream making it more sensitive to temperature alteration.

Localized morphological and catchment characteristics can strongly alter stream temperature, more so than the catchment area (Leach et al. 2017). For instance, wider, shallower channels not only reduce the degree to which the riparian canopy reduces incoming solar radiation, but also increases the surface area for energy inputs from the relatively warmer air above the stream (McSwain 1987). Wilkinson Creek, the largest tributary, is only a bit smaller than the mainstem, with a BAR of 0.82. However, satellite imagery shows that the distal reaches of Wilkinson Creek show a much wider bankfull width and a greater degree of historical meandering from the relatively wide gravel bars. This potentially greater width to depth ratio of the channel might explain why it is the only tributary in this study that supplied relatively warmer water throughout the course of the study. In addition to the above processes, other catchment characteristics need to be considered, such as discharge sources (e.g. groundwater, lake-fed, snowmelt (Smith and Lavis 1975, Moore et al. 2013)), hyporheic exchange (Leach and Moore 2011), and topographical factors, such as channel slope (Hawkins et al. 1997, Mayer 2012) We are not able to parse out the specific processes that resulted in the observed data. These catchment-specific characteristics can lead to a great deal of network temperature heterogeneity (Brown et al. 2005, Leach et al. 2017). Future research considering these other processes could help explain the temperature dynamics at tributary junctions throughout the river network.

Tributary supply of water of contrasting temperature to the mainstem has been regarded as sources of thermal refugia, both for cold-water and warm-water inputs (Knispel and Castella 2003, Sabo et al. 2012, Brewitt et al. 2017). However, we know that processes can alter not only the mean state, but the magnitude, frequency, duration, timing, and rate of change in mean and peak temperatures (Chu et al. 2010). On top of the niche preferences of organisms, which has direct consequences for community structure (Wehrly et al. 2003), stream temperature is closely coupled with the metabolic processes of in-stream biota and processing rates of energy and nutrients (Demars et al. 2011). Temporal variability is an important factor to consider as the indirect effects on energy and nutrient consumption can alter the cycling and downstream export of these materials. Temperature variability may also have important implications for highly motile organisms. Fish use tributary junctions as temperature refugia for cold water inputs as the mainstem channel reaches peak temperatures (Welsh Jr et al. 2001, Brewitt et al. 2017). While steady inflows of cold water may be a stable refugia, alternation between relatively cold water and warm water inputs may have important implications for patch occupancy for highly motile organisms such as fish, opening an avenue of research for small-scale temporal dynamics throughout the river network.

#### Nutrient and CPOM Supply

With regards to phosphorus, we confirmed our third hypothesis that smaller tributaries contained relatively higher concentrations compared to the mainstem, and that the tributary:mainstem concentration ratio decreased with tributary size. This trend was not consistent in the nitrate data; however similar results were observed in Finlay et al. (2011). In their study, there was a threshold increase in N:P ratios when the water-shed area reached ca. 100 km<sup>2</sup>. They associated these increases to the relaxation of light limitation allowing increased uptake of dissolved phosphorus alongside an increase in nitrogen fixing algae. This could be a possible explanation of our data, which would further support our second hypothesis.

According to our modelled downstream nutrient concentrations, we did not find the predicted peak in relative change upstream and downstream of the tributary in the mainstem at mid-sized tributaries (our fourth hypothesis). It is possible that the relationship between BAR and nutrient concentration ratio could be driven by mainstem catchment area (denominator driven rather than numerator driven). However, no relationship between TP, TDP, and nitrate concentration and mainstem catchment area was found, making this an unlikely cause (Figures A4 - A6). Other studies have found that nutrient concentrations peak downstream of tributaries and at groundwater inflow sites (Kiffney et al. 2006, Kuglerová et al. 2014). Although our results aligned with previous research, this results of this study highlighted that tributary exports of nutrients can be highly variable in time and site dependent.

We also confirmed our hypothesis that smaller tributaries supply relatively higher concentrations of CPOM than the upstream mainstem channel. However, the weak relationship between stream size and concentration ratio suggested other processes that influenced the final delivery to the mainstem channel. CPOM dynamics are driven by the supply, retention, and breakdown of organic matter, all of which can be strongly
driven by localized effects. Catchment-specific processes that are highly variable in time, such as wind events that increase leaf release quantity, can cause pulses of leaf litter inputs into the stream channel (Stone 1977, Staelens et al. 2003, Bilby and Heffner 2016). Once in the stream, leaf litter is highly sensitive to localized hydraulics (e.g. near-bed velocity or turbulence) and retention features, such as protruding boulders, large wood, and pool segments, can alter the probability that leaf litter inputs are retained within the channel or exported downstream (Negishi and Richardson 2003, Hoover et al. 2006, de Brouwer et al. 2017). We suspect this may partly explain the lack of trend in the CPOM data. Kallis Creek, a small tributary in our study that showed CPOM exports lower than that of the mainstem has a very gentle slope in the distal reaches of the tributary. The low gradient resulted in a very slow-moving pool along the final ~50 m before reaching the tributary junction. Upstream reaches of Kallis Creek also flowed through a meadow and low gradient bog. Both of these processes may have decreased the riparian contributions of leaf litter with a high proportion of inputs retained prior to entering the mainstem channel.

CPOM has long been regarded as important energy sources in fluvial systems (Wallace et al. 1999). CPOM and leaf litter can alter the structure and abundance of benthic communities (Dobson and Hildrew 1992). However, CPOM and leaf litter resources are regarded as less important basal resources in larger rivers, due to the predominance of exports of FPOM from upstream and autochthonous production (Naiman et al. 1987, Benfield 1997). In systems where coarse organic fractions are less predominant, such as downstream of dams in regulated streams, tributaries have been shown to reestablish the organic matter supply leading to altered resource uptake and change in macroinvertebrate community structure (Negishi and Richardson 2003, Sabo et al. 2018). With added supply of CPOM from tributary exports as well as coarser substrate that may encourage leaf litter retention, it would be useful to reexamine the role that CPOM has as a basal resource and the implications for biological community structuring in larger rivers at tributary junctions.

Although there is a legacy of timber harvesting and agricultural development in many parts of the study area, riparian buffers have mostly remained intact (pers. obs.) and harvesting had been dispersed throughout the study area, rather than concentrated in specific catchments. Much of the data also showed substantial variability across the time periods of interest. This temporal variability could be due to sampling error, but considering that the downstream nutrient model validation aligned with observed data (Figures A1 - A3) suggests that this was not the case, at least for the phosphorus analysis. However, one caveat for this data validation is that the downstream nutrient samples assumes complete lateral mixing of the tributary any mainstem. While we did sample nutrients downstream of flow interference (ca. 50 - 100 m downstream) to try and meet this assumption, it is possible that the sampling location did not represent complete mixing from the confluence. In a field study at the Bayonne-Berthier confluence in Québec, Canada, complete mixing occurred approximately 200 m downstream of the confluence at low flow conditions (Biron et al. 2004). However, this distance in relatively short compared to other research that the authors cited, where mixing could occur nearly 100 - 300 times the channel width downstream of the confluence. Most of our study sites approximated the size of the channel in Biron et al. (2004), but morphological differences in width, depth, and tributary junction angle may have led to complete mixing or mixing zones that extend further

downstream.

# Conclusion

Overall, this study attempted to generalize many known physical and chemical processes using stream size as a predictor for responses in habitat structure and resource supply. Tributaries were still observed to be linked with alterations to habitat structure and resource supply; however, using stream size may have been too much of a generalization and overlooked the effects of multiple interacting processes that cause more idiosyncratic effects of tributaries, many of which are temporally variable. Future research that explicitly considers specific processes and the variability over time may improve our understanding of the magnitude and direction of alteration to habitat structure and resources at tributary junctions. Table 2.1: Basin morphology and hydrologic parameters in the tributary and mainstem of each site included in the study. Note: modelled discharge is calculated from the specific discharge of the nearest gauging station multiplied by the basin area. Values indicate range of modelled discharge during the course of the study.

			Tributary Parameters	
Mainstem	Tributary	Basin Area (km <sup>2</sup> )	Modeled Discharge (m $^3$ s $^{-1}$ )	Channel Slope (cm m $^{-1}$ )
Mission Creek	Belgo Creek	179	0.233 - 0.314	1.4
	Dave's Creek	34.6	0.061 - 0.061	7.4
	KLO Creek	75.2	0.098 - 0.127	5.5
West Kettle River	Kallis Creek	69.7	0.028 - 0.066	0.6
	Trapping Creek	143	0.059 - 0.135	4.2
	Wilkinson Creek	509	0.209 - 0.481	1.9
			Mainstem Parameters	
Mainstem	Tributary	Basin Area (km <sup>2</sup> )	Modeled Discharge (m $^3$ s $^{-1}$ )	Channel Slope (cm m $^{-1}$ )
Mission Creek	Belgo Creek	328	0.428 - 0.577	1.3
	Dave's Creek	568	0.703 - 0.998	0.6
	KLO Creek	699	0.911 - 1.180	0.4
West Kettle River	Kallis Creek	232	0.094 - 0.219	1.1
	Trapping Creek	380	0.156 - 0.359	0.7
	Wilkinson Creek	621	0.255 - 0.587	0.1

Table 2.2: Results from linear mixed models testing the effect of position relative to tributary inflow on median grain size (D<sub>50</sub>), 84th percentile grain size (D<sub>84</sub>), sediment sorting, Warren skewness, and spread of coarse fraction of distribution ( $\phi_{84} - \phi_{50}$ ). Significance determined by type III analysis of deviance.

	Factor	eta	SE	$X^2$	df	р
<b>D</b> <sub>50</sub>	Intercept	147.833	9.708	231.89	1	<0.0001
	Upstream	-55.583	7.194	59.69	1	<0.0001
$\log_{10}(D_{84})$	Intercept	2.50701	0.6607	1439.8	1	<0.0001
	Upstream	-0.17949	0.07905	5.16	1	0.0232
Sorting	Intercept	2.587	0.272	90.18	1	<0.0001
	Upstream	-0.069	0.266	0.07	1	0.797
Skewness	Intercept	0.237	0.065	13.46	1	0.0002
	Upstream	-0.105	0.066	2.49	1	0.114
$\phi_{84}$ – $\phi_{50}$	Intercept	2.587	0.272	47.68	1	<0.0001
	Upstream	-0.068	0.266	0.63	1	0.626

Table 2.3: Results from weighted least squares regression (weighting variance by basin area) with  $log_{10}$ -transformed CPOM ratio between tributary and mainstem as a response to crossed factors of  $log_{10}$ -transformed basin area ratio (BAR) and time period. Shapiro-Wilk results (to test for normality of residuals) are included. Significance determined using a type III analysis of deviance.

Factor	Estimate	SE	df	$X^2$	р
Intercept	-0.317	0.345	1	0.84	0.358
$\log_{10}(BAR)$	-0.885	0.441	1	4.03	0.045
Period	0.256	0.454	1	0.32	0.572
$\log_{10}(BAR)$ x Period	0.725	0.592	1	1.5	0.221
Residuals		0.393	5		
Shapiro Wilk					0.195

Table 2.4: Results from OLS regression ( $R^2 = 0.022$ ) with  $log_{10}$ -transformed nitrate concentration ratio between tributary and mainstem as a response to crossed factors of  $log_{10}$  basin area ratio and time period. Shapiro-Wilk results are included as a test for normality of residuals. Significance determined using type III sum of squares.

			With outlie	ər				Wi	thout Outlie	ər		
Factor	Estimate	SE	SS	df	F	р	Estimate	SE	SS	df	F	р
Intercept	-0.0873	0.0917	0.01436	1	0.9054	0.37	-0.01242	0.09175	0.000232	1	0.0183	0.89
log <sub>10</sub> (BAR)	-0.1773	0.1309	0.02909	1	1.8335	0.21	0.04468	0.16943	0.00088	1	0.0695	0.80
Period			0.01456	2	0.4587	0.65			0.015306	2	0.6045	0.57
Period 2	0.1135	0.759					0.0386	0.1399				
Period 3	-0.0309	-0.224					-0.1057	0.1298				
log <sub>10</sub> (BAR) x Period			0.00172	2	0.0543	0.95			0.007609	2	0.3005	0.75
Period 2	0.0723	0.302					-0.1497	0.2463				
Period 3	0.0504	0.219					-0.1716	0.2396				
Residuals			0.14279	9					0.101273	8		
Shapiro-Wilk						0.017						0.25

Table 2.5: Results from weighted least squares regression (weighting variance by basin area) with  $log_{10}$ -transformed total dissolved phosphorus (TDP) ratio between tributary and mainstem as a response to crossed factors of  $log_{10}$ -transformed basin area ratio (BAR) and time period. Shapiro-Wilk results (to test for normality of residuals) are included. Significance determined using a type III analysis of deviance.

Factor	Estimate	SE	df	$X^2$	р
Intercept	-0.987	0.17258	1	0.33	0.567
$\log_{10}(BAR)$	-0.6805	0.17326	1	15.4	<0.0001
Period			2	0.69	0.709
Period 2	0.21101	0.29122			
Period 3	-0.02464	0.26458			
$\log_{10}(BAR)$ x Period			2	3.15	0.207
Period 2	0.58956	0.3462			
Period 3	-0.00506	0.3195			
Residuals		0.35786	9		
Shapiro Wilk					0.519

Table 2.6: Results from OLS regression ( $R^2 = 0.168$ ) with  $log_{10}$ -transformed total phosphorus (TP) ratio between tributary and mainstem as a response to crossed factors of log10-transformed basin area ratio (BAR) and time period. Shapiro-Wilk results (to test for normality of residuals) are included. Significance determined using type III sum of squares.

Factor	Estimate	SE	SS	df	F	р
Intercept	-0.13231	-0.18412	0.033	1	0.5165	0.491
$\log_{10}(BAR)$	-0.61233	0.26288	0.347	1	5.4258	0.045
Period			0.0252	2	0.1973	0.824
Period 2	0.18808	0.30037				
Period 3	0.05781	0.27645				
$\log_{10}(BAR)$ x Period			0.1031	2	0.8064	0.476
Period 2	0.60958	0.48001				
Period 3	0.17804	0.46272				
Residuals			0.5755	9		
Shapiro Wilk						0.1662

Table 2.7: Mean temperature ( $\pm$  1SD), and range of tributary relative to mainstem across six study sites during the coolest inflow and warmest inflow points of the day, with corresponding mean mainstem and tributary temperatures during cool and warm water inflow ( $\pm$  1SD).

Coolest Inflow											
Tributary	TR - M	IS (°C; ± SD)	Ran	ge	MS Ter	mperature (°C)	TR Ten	nperature (°C)	n days		
Dave's Creek	-2.77	± 1.02	-0.70,	-3.90	21.16	± 6.07	18.39	± 6.76	15		
KLO Creek	-1.72	± 1.42	0.04,	-4.39	18.03	± 2.97	16.31	± 2.38	28		
Kallis Creek	-1.33	± 0.85	0.19,	-3.99	19.39	± 4.98	18.07	± 4.95	71		
Trapping Creek	-1.58	± 0.72	-0.40 ,	-4.47	19.30	± 4.27	17.72	± 4.11	66		
Belgo Creek	-2.56	± 1.06	-0.48 ,	-4.67	18.87	± 4.95	16.32	± 5.05	78		
Wilkinson Creek	-0.55	± 1.08	0.57,	-5.42	18.93	± 6.39	18.38	± 5.78	71		
Warmest Inflow											
Tributary	TR - M	IS (°C; ± SD)	Ran	ge	MS Ter	mperature (°C)	TR Ten	nperature (°C)	n days		
Dave's Creek	1.86	± 1.46	0.38,	5.26	18.29	± 6.30	20.15	± 7.15	15		
KLO Creek	0.69	± 0.55	-0.25 ,	2.02	13.96	± 2.65	14.64	± 2.40	28		
Kallis Creek	2.23	± 1.66	-0.29,	5.43	17.31	± 3.32	19.55	± 3.42	71		
Trapping Creek	1.64	± 0.86	0.04,	4.73	14.09	± 5.64	15.73	± 5.85	66		
Belgo Creek	0.32	± 0.65	-0.48 ,	4.19	14.59	± 5.20	14.91	± 5.57	78		
Wilkinson Creek	2.11	± 0.86	0.10,	3.91	19.53	± 6.01	21.64	± 6.01	71		



Figure 2.1: Conceptual model of tributary size-concentration tradeoff. As size (basin area) of the tributary (TR) relative to the mainstem (MS) increases, the degree to which the tributary influences the mainstem channel environmental characteristics increases (red line). However, at the same time, tributaries of similar size to the mainstem increase in similarity due to the watershed characteristics, making a less pronounced effect on the mainstem channel (blue line). Therefore, the greatest effect size (dashed line) is at some intermediate level where tributaries are sufficiently different, but also large enough to create an enhanced signal.



Figure 2.2: Map of study area in the Okanagan Region of British Columbia, Canada. Tributary subcatchments shaded in gray with study sites established at the confluence of each tributary with the mainstem river (grey bold line and capitalized text)



Figure 2.3: Hydrographs of the (A) Mission Creek catchment at East Kelowna and (B) West Kettle River at McCulloch. Dark black line indicates recorded discharge for 2017. Dotted line indicates the upper and lower bounds of the interquartile range for historical record (1949 - 2014 for Mission Creek, 1949 - 2015 for West Kettle). Dashed line indicates the mean for the above periods.



Figure 2.4: Cumulative grain size distributions (mm) upstream (light) and downstream (dark) of tributary junctions at each of the six study sites, in increasing order of basin area ratio (BAR) of tributary:mainstem. Horizontal lines depict  $D_{16}$ ,  $D_{50}$ , and  $D_{84}$ . Shaded regions indicate 95% confidence bounds of grain size, calculated from Eaton et al. (2019).



Figure 2.5: Change in  $D_{50}$  from upstream to downstream of tributary junctions in relation to (A) basin areaslope product ratio (psi), (B) basin area ratio, (C) Melton's ruggedness ratio, (D) basin area slope product of tributary, and (E) basin area of tributary, and (F) Melton's ruggedness of tributary (n = 6). MS represents mainstem, TR represents tributary.



Figure 2.6: Change in  $D_{84}$  from upstream to downstream of tributary junctions in relation to (A) basin areaslope product ratio (psi), (B) basin area ratio, (C) Melton's ruggedness ratio, (D) basin area slope product of tributary, and (E) basin area of tributary, and (F) Melton's ruggedness of tributary (n = 6). MS represents mainstem, TR represents tributary.



Figure 2.7: (A) Relative (tributary / mainstem) concentration of coarse particulate organic matter (CPOM) across a gradient of relative basin area (BA). Relative values >1 correspond to higher tributary values compared to mainstem, whereas values <1 mean tributary values are less than the mainstem. (B) Modelled change in coarse particulate organic matter concentration (downstream / upstream) in the mainstem due to tributary supply. Dotted line represents the TP concentration ratio = 1. Multiple points within the same basin area ratio are separate sampling events of the same tributary.



Figure 2.8: (A) Relative (tributary / mainstem) concentration of nitrate across a gradient of relative basin area (BA). Relative values >1 correspond to higher tributary values compared to mainstem, whereas values <1 mean tributary values are less than the mainstem. (B) Modelled change in nitrate (downstream / upstream) in the mainstem due to tributary supply. Dotted line represents the nitrate concentration ratio = 1. Multiple points within the same basin area ratio are separate sampling events of the same tributary.



Figure 2.9: (A) Relative (tributary / mainstem) concentration of total dissolved phosphorus (TDP) across a gradient of relative basin area (BA). Relative values >1 correspond to higher tributary values compared to mainstem, whereas values <1 mean tributary values are less than the mainstem. (B) Modelled change in total dissolved phosphorus concentration (downstream / upstream) in the mainstem due to tributary supply. Dotted line represents the TDP concentration ratio = 1. Multiple points within the same basin area ratio are separate sampling events of the same tributary.



Figure 2.10: (A) Relative (tributary / mainstem) concentration of total phosphorus (TP) across a gradient of relative basin area (BA). Relative values >1 correspond to higher tributary values compared to mainstem, whereas values <1 mean tributary values are less than the mainstem. (B) Modelled change in total phosphorus concentration (downstream / upstream) in the mainstem due to tributary supply. Dotted line represents the TP concentration ratio = 1. Multiple points within the same basin area ratio are separate sampling events of the same tributary.



Figure 2.11: Hourly temperature difference (°C) between tributary and mainstem during study period. Values > 0 indicate a tributary warmer than mainstem and values < 0 indicate a tributary cooler than the mainstem. Horizontal dashed line indicates equivalent temperatures. Tributaries are arranged by increasing basin area ratio (BAR) from left to right, top to bottom. Missing data from Dave's Creek was due to the tributary losing surface flow and missing data from KLO Creek was due to temperature logger malfunction. For absolute temperature data in the tributary and mainstem, see Figure A7 and Figure A8.



Figure 2.12: Diel patterns in stream temperature using hourly temperature data in the tributary (blue) and mainstem (red). Each line corresponds to one day of sampling.

# Chapter 3: Responses of macroinvertebrate communities to patchscale alterations to habitat structure and resources from tributary exports

# Introduction

The primary concern of community ecology is to explain the structure and functioning of species assemblages across space and time. Although there are clearly observed patterns in community assembly, understanding the underlying drivers of these patterns is challenging as they are driven by both regional and local processes, which can be difficult to decouple (Vellend and Agrawal 2010, Leibold and Chase 2017). On one hand, community assembly may be driven by relative differences in species' competitive abilities given local conditions, with coexistence enabled through niche partitioning (Hardin 1960, Herder and Freyhof 2006, Crow et al. 2010). Another possibility is that community assembly is primarily dispersal-driven; either because organisms have similar competitive abilities (Hubbell 2001), or by the replenishment of poor competitors from a source population (Shmida and Wilson 1985, Leibold and Chase 2017).

The advective nature of lotic ecosystems is a distinguishing feature that is highly influential for the spatial arrangement of habitats (Church 2006) and resources (de Brouwer et al. 2017) at the patch scale. Retained sediment and particulate organic matter from incoming fluxes form the habitat patch template and may impose environmental filters on the community. Channel substrate, being an important structural component for benthic organisms, is eroded and deposited based on the spatial and temporal variability in local hydrodynamics, providing benthic organisms hydraulic refugia (Negishi and Richardson 2006) and cover from predators (Brusven and Rose 1981). Similarly, passive transport of particulate organic matter, from fine particulates to coarse leaf and woody inputs is strongly governed by interactions of localized hydraulics (Hoover et al. 2006) and the intrinsic qualities of the organic matter (Hoover et al. 2009). When retained, this organic matter becomes an accessible energy resource for benthic organisms and can increase secondary production (Wallace et al. 1999, Walther and Whiles 2011) and alter community structure based on differing resource preferences (Leroy and Marks 2006).

Hydraulic forces also have important implications for benthic invertebrates. Hydraulic forces are an important dispersal mechanism for not only downstream transport, but also entry and exit into the water column with prolonged suspension there (Elliott 2002, Naman et al. 2016). Density of drift from upstream and local dispersal has been shown to predict local patch colonization density, particularly during base flow conditions (Downes and Lancaster 2010). However, Downes and Lancaster (2010) have also shown that for a given density of incoming drift, colonization density is highly variable, suggesting that there is unsuccessful exit from the drift or patches are only temporarily occupied before exiting for further movement. Consequently, drift processes cause involuntary or non-ideal patch selection and residence (Wooster and Sih 1995, Hoover and Richardson 2009). Because of the continual and influential effects of flow on the arrangement of habitat

structure, resources, as well as biota, it is difficult to determine the relative contribution of the multitude of interacting processes driving local community assembly in stream ecosystems (Townsend 1989, Thompson and Townsend 2006, Winemiller et al. 2010).

In lotic ecosystems, patch-scale characteristics integrate upslope catchment and in-stream processes as a result of downslope transport and the predominantly unidirectional flow (Hynes 1975). As a result, the cumulative effects of the upstream processes influence or constrain the local patch habitat structure, resource supply, and migrant biota, displaying characteristics that scale with the size of the stream in a gradational pattern (Vannote et al. 1980, Culp and Davies 1982, Tomanova et al. 2007). Substrate, especially in mountainous environments, derived from surrounding mass wasting of hill slopes (Benda 1990, Benda et al. 2005), undergoes a downstream fining due to in-stream erosional processes and size selective transport (Paola et al. 1992, Ferguson et al. 1996). The quality and quantity of nutrients and energy supplies are a product of the characteristics of the surrounding catchment, such as geology and vegetation, but are heavily influenced by the cycling within upstream reaches (Finlay et al. 2011). Organic matter undergoes extensive fragmentation through biotic and physical processing (Gessner and Chauvet 1994, Heard et al. 1999, Graca et al. 2015). Large quantities of highly fragmented fine particulate organic matter are exported to larger reaches (Wallace et al. 1991), while direct inputs of coarse forms, such as leaf litter, are limited in these downstream reaches (Naiman et al. 1987, Benfield 1997) due to riparian canopy being restricted to the margins of the wider channel (Conners and Naiman 1984). Thus, downstream patches are predominantly characterized by substrate that is smaller and homogeneous (Knighton 1980, Powell 1998), and have an energy base of FPOM and primary production (Naiman et al. 1987).

We know that this linear view is not entirely accurate as rivers operate as a dendritic network consisting of links (uninterrupted reaches or river lengths) connected by nodes (tributary junctions (Campbell Grant et al. 2007)). The linear gradient is disrupted by the supply of abiotic and biotic material from tributaries which can lead to punctuated changes in substrate size (Rice et al. 2001a), nutrient availability (Kiffney et al. 2006), detritus (Bruns et al. 1984), and water chemistry (Knispel and Castella 2003) over small distances. Often these exports are characteristically distinct from the mainstem, leading to altered patch structure and resource availability within the reach, suggesting tributary junctions as biological hot-spots in the river network (Rice et al. 2001b, 2008, Power and Dietrich 2002). Empirical evidence exists both in support of (Rice et al. 2001a, Kiffney et al. 2006, Katano et al. 2009, Wilson and McTammany 2014, Jones and Schmidt 2018) and in opposition to (Mac Nally et al. 2011, Milner et al. 2019) the notion that tributary junctions are associated with high productivity, increased biological diversity, and altered community structure. So far, there have been few attempts at testing specific mechanisms for community-level patterns.

Previous attempts at identifying tributary junctions that are ecologically significant in terms of their habitat and community structure have incorporated tributary size, but mostly as a scaling factor on the strength of signal (Jones and Schmidt 2016). Although this is an important factor, this approach only considers the magnitude of the effect without regards to biological, physical, and chemical processes that often relate with stream size, which result in contrasting contributions of the two converging streams (but see Kiffney et al. (2006) for some hypotheses linking process to response). Since smaller streams are typically associated with coarse sediment and an allochthonous resource base (primarily leaf litter), which arrive at the tributary junction without having undergone much sorting or fragmentation. This is in contrast to the larger mainstem river, which is associated with smaller, homogeneous substrates (Knighton 1980, Powell 1998), highly fragmented organic matter, and an autochthonous resource base (Naiman et al. 1987, Benfield 1997). Thus, we hypothesize that altered habitat patches due to inputs of coarse substrate and coarse particulate organic matter (leaf litter) may contribute to observed differences in community structure at tributary junctions in a larger receiving channel. However, larger mainstem channels are also the common link between peripheral and headwater streams, acting as important dispersal corridors in the dendritic network (Parker 1989, Brown et al. 2011, Altermatt 2013). As such, local communities may be driven by higher-scale dispersal dynamics, overwhelming the effects of local habitat.

In this study, we attempt to develop a mechanistic understanding of community shifts at tributary junctions based on predicted changes in habitat structure (channel substrate) and resource availability (leaf litter). We tested these mechanisms in the context of a mid-sized mainstem river system (mean basin area = 471 km<sup>2</sup>, range = 232 - 699 km<sup>2</sup>), which have received even less attention with regards to the role of tributaries in the assembly of benthic macroinvertebrates at tributary junctions (but see Milesi and Melo, 2013 and Kiffney et al. 2006 for a few examples). We tested the following two hypotheses: (1) tributaries will increase community diversity and show consistent shifts in community structure from upstream to downstream, (2) experimental addition of organic matter and coarse substrate upstream of the tributary junction will result in similar communities as downstream of the tributary. We also asked the question how much do treatment effects and other environmental characteristics influence the community assembly relative to higher-level spatial structuring? In doing so, we may develop a more nuanced understanding of the complex interactions between organisms, resources, and the structural components of streams, allowing managers and restoration practitioners to identify some of the most ecologically distinct locations in the river network.

# **Materials and Methods**

### **Experimental design**

To test the relative effects of microhabitat structure and resource availability in relation to other tributary effects, a 2 x 2 x 2 factorial split-plot experiment was conducted across six tributaries: three along Mission Creek and three along the West Kettle River in British Columbia, Canada (See Chapter 2 for description). Using 25 cm diameter cylindrical sediment baskets, we measured responses of community structure to increased substrate size, presence of organic matter, and position relative to tributary inflow (details of each treatment are explained below). The cylindrical baskets were constructed with 1.5 cm square hole mesh with a bottom consisting of landscaping fabric. The porous sides of the basket allowed for the continuation of hyporheic flow and movement of invertebrates and organic matter. The bottom restricted the loss of sample

upon removal, while maintaining a degree of vertical hyporheic connectivity. While this construction does allow for the inputs of organic matter from outside the experimental manipulation, this design was required to allow unrestricted colonization of invertebrates to occur. Once filled with sediment and organic matter according to treatment specifications, baskets were placed in their randomly assigned position upstream or downstream of the tributary and were embedded into the streambed at sufficient depth to make the top of the basket, and sediment within, flush with the streambed surface.

# Substrate

Microhabitat structure was manipulated using contrasting substrate size at the sub-plot level. Substrate was sourced from upstream in the mainstem from nearby gravel bars to represent the ambient mainstem gravel size (ca. 5 - 7 cm). Gravel was thoroughly cleaned by hand and brushed and randomly assigned to each experimental unit. Large cobbles 10 - 12 cm were sourced from nearby gravel bars and were washed and measured after being randomly assigned to cobble addition treatments. Sourcing sediment from gravel bars was to ensure that any biota had been desiccated to minimize any previous colonization by invertebrates or algal communities. While this thorough cleaning can extend the time of proper colonization to match the actual communities present in the stream, previous studies have shown that mainly shredders are affected and that other functional groups match the actual density after 1 - 2 weeks, especially when stones were sourced from the previously wetted channel (Mackay 1992). The size of the substrate did not correspond to site-specific characteristics, but were chosen to approximate the observed substrate sizes across all sites.

## **Organic matter**

Organic matter availability was tested using the addition of leaf litter packs at the sub-plot level. To account for the potential treatment effects of the litter packs, all treatments were provided litter packs containing leaf litter, for the addition of organic matter, or empty litter packs, to control for treatment effects. Leaf packs contained  $4.0 \pm 0.5$  g of dried red alder leaves (*Alnus rubra*) sourced from the Malcolm Knapp Research Forest (near Maple Ridge, British Columbia) in 2013, which amounted to approximately five full-sized leaves for each litter pack. Although this litter is not necessarily representative of local riparian vegetation, we believe it is still an appropriate treatment as it eliminates the possible "home-advantage" from using a localized detrital source across the two study catchments. (Ayres et al. 2009). In the controls (i.e. lacking organic matter), empty mesh bags were placed in the basket to isolate the effects of leaf litter. Both the filled and empty litter packs were placed under the top layer of sediment to ensure that they would not be suspended from the basket due to flow and to minimize the effects of physical fragmentation on measured mass loss.

## **Position in confluence**

In order to compare the responses to CPOM addition and substrate coarsening to other effects of the tributary (e.g. nutrient availability, changing water depth and velocity, drift inputs from tributary), baskets were placed

both upstream and downstream of each tributary junction (whole-plot). Upstream plots were selected at a random distance between 0 and 100 m in a straight segment upstream of identified pooling due to the alluvial fan from the tributary. Downstream plots were selected in a similar fashion downstream of flow convergence (i.e. avoiding any pooling or eddies due to tributary inflow). For more detail regarding site location and plot selection, see Table A1.

# Sampling protocol

Baskets were first installed in mid-July during baseflow conditions. Upon installation, each basket was measured for several covariates including: water depth, velocity, dissolved oxygen (DO), electrical conductivity (EC), and pH. Water temperature was measured continuously at each location (upstream and downstream at each site) and was used to calculate a minimum, mean, and maximum water temperature. After a three week colonization period, covariates were measured and baskets were removed. Baskets were removed by placing a 243  $\mu$ m D-net immediately downstream of the basket to catch any invertebrates that released into the water column during sampling. Baskets were placed into the D-net, removed from the stream, and then placed into a bucket of stream water filtered at 243  $\mu$ m. Substrate was gently agitated and manually washed to remove any clinging organic matter and invertebrates and placed back into the basket. The water containing invertebrates and organic matter was then sieved at 63  $\mu$ m and placed into jars with 75% ethanol until further analysis. Baskets containing the rinsed sediment was placed back into the stream and covariates were measured again. This procedure was repeated again for another three weeks, resulting in another set of samples in mid-September, except for one site where access was only permitted for one sampling period. In total, 89 samples were collected and analyzed.

Back in the laboratory, samples were sieved at 1 mm and subsequently separated for coarse particulate organic matter (CPOM) and invertebrate fractions. Invertebrates were identified to the lowest practical taxonomic level (typically genus in EPT taxa, higher for others) using established taxonomic keys (Merritt et al. 2008). Organic matter was dried at 86 °C, weighed for dry mass, ashed at 500 °C, and weighed to calculate benthic CPOM ash-free dry mass (AFDM).

# **Statistical Methods**

All of the statistical analyses were completed in R (R Core Team 2016). The following statistical approaches were used to test the effects of tributary inflow on the community structure and whether the addition of organic matter and coarse sediment upstream of tributaries shapes the community to mimic that of downstream of tributaries to isolate these specific mechanisms. First, to better understand the trends in environmental characteristics with respect to site and position relative to tributary, velocity, water depth, pH, dissolved oxygen, mean and minimum temperature, and accumulated organic matter were individually run as response variables in a linear mixed-effects model (package "Ime4" (Bates et al. 2015)). These responses were fitted

with all treatment factors as well as time period and mainstem as predictor variables. Additionally, the interaction between position and time was included to account for asynchronous changes between tributary and mainstem. Random intercepts by site were included to account for site-to-site variability. The random error term of position nested within site (whole-plot) was included in the model to test positional effects to account for the split-plot design. To identify idiosyncratic tributary characteristics, a redundancy analysis on all environmental variables was run with a full cross of position, site, and time period as predictor variables.

Univariate analyses of rarefied taxonomic richness, Shannon diversity, abundance, and Pielou's evenness were measured using linear mixed models from the packages "Ime4" (Bates et al. 2015), or "gImmADMB" (Skaug et al. 2016) in the case of total abundance to account for the non-normally distributed count data. Rarefied taxonomic richness was used instead of raw taxonomic richness to estimate the asymptote by which taxonomic richness does not increase with numbers of individuals sampled. While this study involves equal sampling effort across all sampling events, sampling conditions cannot be guaranteed to be the same for each event. This measure will attempt to estimate the "true" taxonomic richness in each sample to make them comparable (Gotelli and Colwell 2001). Prior to model fitting, covariates were first checked for multicollinearity using a variance inflation factor (VIF) threshold of 10 (Borcard et al. 2011).

First, the following global model (Equation 3) was constructed prior to model selection to include the following terms:

$$\hat{y} = \beta_0 + \beta_1 \text{Position} + \beta_2 \text{CPOM} + \beta_3 \text{Substrate} + \beta_4 \text{Position} \times \text{Substrate} + \beta_5 \text{Position} \times \text{CPOM} + \beta_5 \text{Period} + \beta_6 \text{Mainstem} + \beta_7 \text{Velocity} + \beta_8 \text{Depth} + \beta_9 \text{CPOMAccum} + \text{Site} + \tau_{\text{Position} \times \text{Site}} + \epsilon$$
(3)

All factors were included as fixed effects, except for site, which was a random effect to account for the spatial variability among sampling sites. Due to the split-plot design, a whole-plot error term,  $\tau_{\text{Position}\times\text{Site}}$ , was included in all models to test the positional treatment with the correct degrees of freedom. Due to the number of terms in the global model, interactions were limited to only those pertaining to specific hypotheses being tested.

This global model was decomposed into alternative models of all combinations of environmental covariates as well as models without interaction terms of fixed effects, resulting in a total of 32 possible models for model selection. Visual inspection of the coefficients of fitted models revealed that there was stability in coefficient estimates for included covariates, suggesting that top ranked models did not appear to be over-fitted since inclusion and exclusion of other variables did not drastically affect the predicted coefficients for other variables. For each of the diversity, abundance, evenness, and richness metrics as response variables, candidate model selection was completed based on the information theoretic (IT) approach using Akaike's Information Criterion (AIC). AICc was used as a selection metric, due to small sample sizes relative to the number of included terms (Burnham and Anderson 2003). Despite applying controlled experimental

treatments, this study was field-based and likely had many external interacting factors that influenced the observations, making AIC a more appropriate index for model ranking over other information criteria (2014). The top model was selected to test for term significance (See Table B2 - B5 for model rankings). Linear mixed-effects models had terms tested for significance by t-tests using Satterthwaite estimations of the denominator degrees of freedom. This was to account for the small sample size at the whole plot level. However, there was no clear way to apply this method to models fitted as generalized linear mixed models, thus significance was determined by assuming z-distributed errors of model coefficients.

Prior to testing the effects of treatments on basket community structure, community data were trimmed and transformed to remove bias from dominant and rare taxa. All taxa identified in pupal or adult stages were omitted alongside all taxa that did not appear in at least 10% of samples (see Table B1). All abundances were transformed to the fourth root to minimize the skew in the data due to highly dominant taxa, such as *Lepidostoma* sp. (Lepidostomatidae), which comprised 37.1% of all individuals. Overall community structure effects were tested for significance using a Monte-Carlo Permutational ANOVA (10,000 permutations; adonis in "vegan" (Oksanen et al. 2018)). Due to the inability to specify random error structure in this function, analyses were conducted in two parts to account for the split-plot design. First, the subplot effects and the subplot treatment interactions with position were tested using the transformed community data with all fixed factors in Equation 3. Permutations were restricted (stratified) to within plot. Non-significant interactions (p > 0.05) were removed using backwards elimination until a final model was achieved. To test the positional effect with the correct error term, centroid values from Bray-Curtis dissimilarity matrix were determined for each site x position grouping. The same permutational ANOVA was run with the response variables against site and position to determine significance of position.

For understanding the multivariate effects on community structure, a distance-based redundancy analysis (db-RDA), was constructed with all environmental covariates, treatment combinations, period, and site. However, a VIF analysis of the global model revealed high collinearity between mean and minimum temperature, so mean temperature was kept in the analysis. This model structure was used to predict the trimmed and transformed community abundance data via db-RDA from the capscale function in the "vegan" package (Oksanen et al. 2018). The db-RDA is a constrained ordination technique that reduces fitted values derived from linear modeling of a distance-based response matrix (in this case, using Bray-Curtis distances) to a set of canonical axes, based on a predetermined set of predictor variables (Borcard et al. 2011). The db-RDA was selected over similar analyses, such as CCA, as the environmental gradient length is sufficiently short enough to miss a unimodal response in taxa abundance. This was confirmed using a detrended correspondence analysis (Borcard et al. 2011). Through a two-way stepwise selection procedure using the function ordistep in "vegan", non-significant interaction terms and environmental variables were removed.

The degree to which treatments vs. environment vs. site contribute to the structuring of communities was determined through variance partitioning (Cottenie et al. 2003, Heino and Myrkä 2008, Heino et al. 2012, Wilson and McTammany 2016). These three groupings of variables were each fitted to the above db-RDA individually to determine the total variance explained by that variable group. The total variance explained by

all groups were fitted using the full dbRDA, explained above. Each combination of variable groupings were then partialled out using a partial-dbRDA to calculate the fraction of variance explained by: all groups, each group individually, and the variance shared by each combination of groups.

Lastly, to test the hypothesis that coarse substrate and addition of CPOM resemble communities downstream, a partial db-RDA was run, only including treatment effects and time period, while partialling out the variance due to site-to-site variability. We predicted that community centroids with CPOM and coarse substrate added would resemble the downstream centroid in comparison to those without CPOM and smaller substrate. Using this same model, we made post-hoc interpretations of trends in taxa between upstream and downstream of the tributary.

Individual models were fitted using the above specification and selection procedure to the abundance of five commonly found taxa: *Lepidostoma* sp. (Lepidostomatidae), *Pteronarcys* sp. (Pteronarcyidae), Heptageniidae spp., *Brachycentrus* sp. (Brachycentridae), Hydropsychidae spp., and *Baetis* sp. (Baetidae). Since the response variable was count data (abundance), generalized linear mixed models were fitted with a Poisson distribution (log link function), or in the case of overdispersion, a negative binomial distribution (log link function) using glmmadmb from the glmmADMB package (Skaug et al. 2016). Models were ranked by AICc and the top model was used for testing of significance (See Table B6 - B11 for model rankings).

# Results

## Environmental characteristics of community samples

First, an analysis of measured environmental covariates across treatments and sites were conducted to test if characteristics are similar across treatment groups and if these values shift downstream of tributaries. In particular, we predicted that organic matter accumulation, dissolved oxygen, water depth and velocity would have been higher alongside lower water temperature downstream of tributary junctions. As expected, substrate size and organic matter addition had no effect on the measured environmental characteristics, except for stream velocity, where localized velocity measures were dependent on the substrate treatment applied ( $X^2$  = 6.09; *p* = 0.014; Table 3.1). Accumulation of organic matter was lower in the second time period ( $X^2$  = 18.21, *p* < 0.0001), but there was no significant difference between upstream and downstream baskets ( $X^2$  = 0.01, *p* = 0.919. Water chemistry parameters (EC and DO) were highly dependent on the period and position, many of which showed interactions between position and time period, summarized in Table 3.1. DO was generally higher downstream ( $X^2$  = 7.88, *p* = 0.005), but mostly during sampling in August. Temperature was unaffected by position relative to tributary, but a more detailed analysis in Chapter 2 revealed the importance of diel and site to site variability on temperature.

When analyzed with an RDA, environmental characteristics revealed that position, time period, and site explained 85.1% of the variance in environmental characteristics and there was a significant three-way interaction between tributary position, site, and time period ( $F^* = 3.57$ , p < 0.001; Table 3.3). The top two RDA

axes explained 51.5% of the variance and revealed the clear interaction effects between site and position, with no consistent observable pattern in environmental characteristics due to position (Figure 3.1). Belgo Creek showed little difference in environmental characteristics across time periods and position relative to tributary, illustrated by the large degree of overlap of samples in ordination space (Figure 3.1). Other tributaries showed differences in depth, temperature, pH, EC, and dissolved oxygen across time periods and position and position. However, the magnitude and direction of change varied based on the site.

## **Community responses**

A total of 27,277 invertebrates across 88 taxa were identified and counted. All data were used for univariate metrics, such as evenness, diversity, richness, and abundance. After paring down community data for multivariate analysis, 44 rare taxa were removed, resulting in the decrease of 247 individuals, with a total of 27,030 individuals included in the multivariate community structure analysis.

Candidate models for rarefied taxonomic richness, Shannon index, abundance, and Pielou's evenness were selected from all models and are presented in Appendix B (Tables B1 - B4). Statistical summaries are presented in Table 3.4. Most top models did not include any significant environmental covariates, except for stream velocity. Downstream relative to tributary inflow, although showing little to no effects on taxonomic richness (upstream: 11.93 (95% CI: 10.03 - 13.83) vs. downstream: 12.39 (10.49 - 14.28); p = 0.595; Figure 3.2A), diversity (upstream: 2.03 (1.67 - 2.39) vs. downstream: 2.15 (1.79 - 2.50); p = 0.387; Figure 3.2B), or evenness (upstream: 0.67 (0.55 - 0.79) vs. downstream: 0.71 (0.59 - 0.82); p = 0.226; Figure 3.2D) compared to upstream, showed lower total abundance (upstream: 250.7 (146.7 - 428.5) vs. downstream: 209.6 (113.8 - 386.1); p = 0.03; Figure 3.2C).

Coarsened substrate had no clear effect on structure metrics of diversity (small: 2.03 (1.67 - 2.39) vs. large: 2.14 (1.78 - 2.50); p = 0.087; Figure 3.2B), richness (small: 11.93 (10.06 - 13.80) vs. coarse: 12.38 (10.51 - 14.25); p = 0.197; Figure 3.2A) or evenness (small: 0.67 (0.55 - 0.79) vs. coarse: 0.71 (0.59 - 0.82); p = 0.055; Figure 3.2D); however, abundance was observed to be lower compared to small substrate (small: 246.8 (143.4 - 424.9) vs. coarse: 212.9 (117.9 - 384.7); p = 0.007: Figure 3.2C). Addition of organic matter seemed to have the strongest effect on all four metrics. Most results were marginally non-significant, except for total abundance. There was no significant difference in taxa richness (none: 12.5 (10.6 - 14.3) vs. added: 11.8 (10.0 - 13.7) ; p = 0.062; Figure 3.2A) or diversity (none: 2.13 (1.78 - 2.49) vs. added: 2.04 (1.68 - 2.40); p = 0.149; Figure 3.2B), but communities were less even (none: 0.71 (0.59 - 0.82) vs. added: 0.67 (0.55 - 0.78); p = 0.040; Figure 3.2D) and more abundant (none: 200.7 (115.7 - 348.2) vs. added: 261.6 (148.3 - 462.1); p < 0.001; Figure 3.2C) with the addition of organic matter.

The lack of effects due to treatments were also observed in the permutational ANOVA of community abundance data (Table 3.5). Addition of coarse substrate ( $F^* = 0.59$ , p = 0.491) and CPOM ( $F^* = 1.03$ , p = 0.127) had no clear effect on community structure. Position across the six tributaries had no consistent effect ( $F^* = 0.731$ , p = 0.693). Water depth ( $F^* = 6.98$ , p = <0.001) and velocity ( $F^* = 13.77$ , p = <0.001) had much

stronger effects on community structure.

The final db-RDA model included stream velocity, dissolved oxygen, and electrical conductivity in addition to the treatment factors, time period, and site. All these factors combined explained only 42.1% of the variation in community structure (Table 3.6). Most of the community variability was captured by site-to-site variability (21.1%), 5.3% of which was shared with environmental characteristics. An additional 5.3% was explained by environmental characteristics alone. Treatments explained only 3.1% of variability in community data, none of which was shared by other measured variables. Most of the variance went unexplained (57.9%) in the model.

The variability explained by treatment effects alone, without environmental characteristics and site-to-site effects, were visualized on two main axes of a partial db-RDA that explained a total of only 13% of the variance. Variance in community structure explained by position was mostly represented on the second axis (3.8% explained). Upstream, the addition of organic matter and coarse substrate had communities that more closely resembled overall upstream community structure (Figure 3.3) during both time periods. Downstream the addition of CPOM more closely resembled upstream communities, whereas the coarse substrate without CPOM resembled downstream communities. In the second period, there was no clear trend in the downstream treatments. Further visual assessment of the partial db-RDA partitioned by site revealed the strong site x positional effects (Figure 3.4). The three tributaries in Mission Creek showed a high degree of overlap between the upstream and downstream sites, except some separation during the second time period in Dave's Creek. The downstream locations of Trapping Creek and Wilkinson Creek showed a general trend towards *Haploperla* spp. (Chloroperlidae) and *Ameletus* spp. (Ameletidae), whereas Kallis Creek's downstream location trended toward multiple taxa, such as *Simulium* spp. (Simuliidae), *Arctopsyche* spp. (Hydropsychidae) and *Brachycentrus* spp. (Brachycentridae).

Numeric responses of commonly found taxa (Figure 3.5) were most strongly noticed in shredder taxa, *Lepidostoma* sp. (Lepidostomatidae) and *Pteronarcys* sp. (Pteronarcyidae), summarized in Table 3.7. Abundance of *Lepidostoma* sp. was observed to be 58.7% lower (95% CI: 42.0% - 70.7%, p = 0.009) downstream of tributary junctions. *Pteronarcys* sp. also showed similar responses downstream of the tributary junctions where abundance was observed to be 39.3% lower (95% CI: 27.5% - 49.2%, p = 0.005). No other taxa showed responses that were significant in either direction; however, all coefficients were estimated to be negative, generally indicating lower abundances downstream of the tributary. Treatment addition of organic matter showed significantly higher abundance of both shredder taxa with 2.13X (95% CI: 1.80X - 2.53X) the abundance of *Lepidostoma* sp. and 1.40X (95% CI: 1.24X - 1.58X) the abundance of *Pteronarcys* sp. with the addition of leaf litter. Other taxa showed little response to the addition of CPOM. Substrate, overall had weak effects with generally lower abundance present with coarse substrate. This was apparent with *Lepidostoma* sp., net-spinning caddisflies (Hydropsychidae spp.), and *Baetis* sp.

# Discussion

Overall, we found that tributary junctions were important punctuations in environmental characteristics, consistent with much of the current literature. The specific changes that occurred were highly context dependent in space and time. Position relative to tributary inflow had effects on total taxa abundance and had significant effects on the abundance of a couple of taxa, in particular. However, there was no significant effect on overall multivariate community structure. With added organic matter, total abundance increased with a very large increase of a couple of shredder taxa. Communities with added organic matter tended to shift towards a less diverse and less even community. Coarse substrate had no effect on multivariate community structure or diversity, but had a decrease in total abundance, particularly for a few taxa. Overall, the results of this study were contrary to hypothesized increases in community diversity and structural shifts at tributary junctions. In fact, it appeared that tributary junctions led to an overall decrease of abundance among most taxa. We also did not find any clear relationship between the experimental treatments and the tributary effects, suggesting that these were not consistently strong mechanisms across sites within the study system. Variation in effect size and direction among sites suggest that tributary effects may not be consistently found, rather, these effects are highly context depndent.

#### Environmental contrasts at tributary junctions

Generally, environmental characteristics showed a strong site x time x position interaction. While the strength of the effects varied from site to site, the most prominent changes due to tributary inflow were water chemistry (DO, EC, and temperature) and water depth. One of the striking results was that despite tributaries supplying high concentrations of CPOM (see Chapter 2; (Pond et al. 2016)), we found no differences in CPOM accumulation due to tributary position. The sites that had higher CPOM accumulation downstream were also sites with high water velocity downstream, making it difficult to disentangle positional effects due to the high degree of variability of patch scale hydraulics. One possibility for the observed lower CPOM accumulation might have been due to the water depth observed. Depth across sites - both upstream and downstream - was typically around 15 cm, which would diminish most stone protrusion and minimize retention barriers for litter that is buoyant at the water surface (Hoover et al. 2006). McTammany and Wilson (2014) found that in a large river (mean Q = 310 m<sup>3</sup> s<sup>-1</sup>), benthic organic matter showed little difference upstream and downstream in the mid-channel, but higher concentrations near-bank downstream of tributaries, suggesting that retention of organic matter in larger mainstems may be constrained to retention features in the channel margins. Furthermore, drift samples taken (see Chapter 2) often contained large quantities of leaf litter (personal observation), which requires sufficient exposure to wetting to become negatively buoyant (Hoover et al. 2009). This is especially the case of *Populus* spp. (which are located in these catchments), where it can take upwards of 24 h for most leaves to begin sinking, depending on taxon and leaf condition (Tavernini and Hoover, unpublished data). More research regarding the fate of organic matter exports, such as the necessary conditions for retention and the distance that these exports travel until they are consumed

would yield insight into the role that tributary exports play in network resource dynamics.

### Effects of position on community responses

Our first hypothesis predicted that there would be higher diversity and shifts in community structure downstream of tributaries due to the convergence of contrasting abiotic material and supply of biota from the mainstem and tributary. We found that there was no significant effect of position on diversity, taxonomic richness, evenness, or overall community structure. Idiosyncratic effects of the tributaries resulted in only tributaries located along the West Kettle River showing effects on community structure, with trends in opposing directions between sites. At tributary junctions further downstream in the mainstem, such as Trapping Creek and Wilkinson Creek, communities shifted away from most taxa, many of which are filter feeders, and towards two taxa that are characterized as a gatherer and predator (Merritt et al. 2008). Upstream in the catchment at Kallis Creek, we noticed the opposite pattern, despite showing similar environmental characteristics at the three sites from the environmental RDA.

We found that position did significantly decrease abundance, particularly in a few taxa. Trapping Creek and Wilkinson Creek are two sites that have relatively large BAR and showed a general trend away from most taxa. Trapping Creek increased from 11.2 to 18.7 cm depth and Wilkinson Creek increased from 8.3 to 16.3 cm depth. These marked increases in depth in addition to the potential turbulent water column from converging flowpaths of two large streams may have reduced organic matter retention. Organic matter accumulation reduced from 0.196 g to 0.154 g at Trapping Creek and 0.436 g to 0.210 g at Wilkinson Creek. This may have indirect consequences for total abundance, especially for the two shredder taxa, *Pteronarcys* sp. and *Lepidostoma* sp. which showed strong decreases in abundance. At Kallis Creek, there was little change in depth (12.5 cm to 13.7 cm) and an increase in accumulated organic matter (0.125 g to 0.287 g). Furthermore, Kallis Creek supplied the mainstem with high concentrations of phosphorus (Chapter 2) and was observed to have large quantities of benthic algae in contrast to upstream (pers. obs.). Bottom-up effects could explain the patterns we saw across these three sites. However, this is speculative as we did not observe major differences in community structure at the three sites along Mission Creek despite having differences in nutrient and CPOM availability upstream and downstream.

The mounting evidence for community responses at tributary junctions has revealed the high variability in the types and strengths of responses. In the case of larger mainstem rivers, Rice et al. (2001a) found that increases in benthic diversity can co-occur with increases in sediment size. Among these community responses were the general increases in abundance of *Brachycentrus americanus* (Brachycentridae) and *Arctopsyche* sp. (Hydropsychidae), which they attributed to the preference of coarse substrate due to stable mounting surface for filter feeding Rice et al. (2001b). Our investigations of responses in *Brachycentrus* sp. and Hydropsychidae spp. revealed no effect due to position. In fact, coarsening of substrate showed decreased abundance of Hydropsychidae spp., which is contrary to what was hypothesized. This could be due to the low flow conditions during the study, which may have reduced the contrasting effects that coarse

substrate has on stability. This is further outlined below in the discussion regarding the coarse substate treatments. Rice et al (2001b) also tested the response of *Leucrocuta* sp., a heptageniid scraper. This was under the assumption that tributary junctions are locations of increased primary productivity, hypothesizing bottom-up effects on taxa abundance. However, they found decreased abundances and hypothesized that despite being in a typically rheophilic family, *Leucrocuta* sp. is generally averse to fast-flowing waters. In our study, we found no significant response in total heptageniid abundance, which may be due to no responses in primary productivity.

Community responses appear to be fairly apparent in smaller catchments. Kiffney et al. (2006) sampled various habitat and community metrics across thirteen tributary junctions with mainstems ranging from 15.78 - 301 km<sup>2</sup> (mean: 133 km<sup>2</sup>). Many phyiscal and bioloigcal characteristics peaked downstream of the tributary junction, including fish diversity and abundance of large-cased caddisflies. The biotic effects seemed to be less clear in the Cedar River, which is a larger receiving stream showing smaller effect sizes on fish density around tributary junctions. However, community assembly at tributary junctions along larger mainstem rivers can still be affected by tributaries but these processes may be constrained to the channel margins (Wilson and McTammany 2014).

Tributary effects can be particularly apparent when the tributary and mainstem are highly contrasted habitat types, such as the case with Knispel and Castella's (2003) work, where the confluence of two glacially-fed tributaries (Upper Rhône and Mutt River), differing in their distance (1 km vs. 3.6 km) from their source, converge. The longer distance of the Mutt River exposed the stream to more solar radiation, groundwater inflow, and a less pronounced kryal signature present in the Upper Rhône. These contrasting conditions harbour highly contrasted communities in both tributaries. Downstream of the confluence, many communities contained taxa and resembled those found in the Mutt River, despite still showing more unfavorable glacial habitat. In contrast to these studies, Mac Nally et al. (2011) found little change to benthic diversity or functional feeding group composition downstream of tributaries. In this study, the tributaries and mainstem showed very weak differences in community composition. They proposed that null effects on diversity observed were the product of the catchment having very uniform slope and substrate characteristics, which have an immediate effect on the habitat structure upon entering the mainstem.

The extensive efforts directed towards understanding community patterns at tributary junctions have focused strongly on univariate characteristics, such as diversity, abundance, or dissimilarity indices. There have been a few studies that incorporate multivariate analyses to test for differences in both direction and magnitude (Rice et al. 2001a, Milesi and Melo 2013, Wilson and McTammany 2014, Milner et al. 2019). However, this area is still relatively unexplored, especially regarding explicitly linking habitat alterations to community response magnitude and direction. Milesi and Melo (2013) attempted to address this issue by sampling microhabitat that is as similar as possible in terms of substrate size, depth, and velocity upstream and downstream. We approached this gap by experimentally treating baskets and standardizing the habtat structure to isolate mechanisms. Our results aligned with Milesi and Melo's (2013), who found little change at tributary junctions in medium-sized receiving streams.

#### Effects of substrate and CPOM on community structure

With regards to our second hypothesis that additions of CPOM and coarse substrate would mimic trends observed due to position, we found that diversity metrics were altered due to treatments, but in general, no significant effect was observed regarding multivariate community structure. Site-specific positional effects made it difficult to establish a link between observed upstream-downstream trends and alterations to habitat structure and resource supply. In general, the addition of organic matter trended towards very small differences, but lower taxa richness, diversity, and evenness, alongside an increase in total abundance. A surplus of one specific resource, like in the case of the CPOM additions, might have resulted in the significantly higher abundance of shredder taxa, *Lepidostoma* sp. or *Pteronarcys* sp., via intraspecific aggregation (Presa Abos et al. 2006). The use of detrital exports from tributaries is still relatively unexplored. However, in systems that are CPOM limited, such as reaches downstream of dams, tributaries act as an important supply point, which restocks benthic CPOM supplies and reestablishes it as a basal food source for invertebrates (Katano et al. 2009, Sabo et al. 2018).

The present study showed very little effect of the coarse substrate treatment. Channel substrate is regarded as an important structural component for habitat for macroinvertebrates. Substrate plays a key role as cover from consumers at higher trophic levels and a mounting surface for filter feeders. The size of the small substrate (similar to grain sizes found upstream of tributaries in this study area) was still sufficiently large to maintain sizable interstitial space for invertebrates and may have been large enough to resist hydraulic disturbance of substrate. Given the below-average baseflow conditions during the course of the study, hydraulic stresses may have been too low to cause instability in sediment, making the two substrate sizes equivalent in their role as habitat refugia for macroinvertebrates. As substrate becomes coarser, surface area is reduced and in productive streams such as Mission Creek and the West Kettle River, exploitable surface area from invertebrates may have found no such relationship (Culp et al. 1983, Parker 1989). Further research into the role that coarse substrate plays as habitat refugia during periods of high flows may yield interesting insights into the effects of tributary sediment exports in mainstem rivers.

## Tributary junctions in a metacommunity context

Due to the influential effects of flow on the movement of organisms in streams, local environmental filtering versus dispersal processes can vary greatly in their relative contributions toward community assembly between and within streams (Thompson and Townsend 2006, Brown and Swan 2010, Heino et al. 2012). In this study, we found that the applied treatments showed very small effects on the community and these are much smaller than environmental factors (velocity, EC, DO) and site-to-site variability. This is important to consider in the context of larger streams as this study focused on community assembly at the patch scale. Previous research has shown that regional vs. local processes can differ depending on the location and degree of connectivity in the network (Tonkin et al. 2018). Small stream communities are primarily driven by local factors (e.g. environmental filtering and biological interactions), mainstem communities are largely driven by both local factors and regional factors, such as in-stream dispersal (Brown and Swan 2010). Headwaters are isolated, allowing environmental filtering to take place, whereas mainstems are dispersal corridors and can integrate community composition from contributing branches (Parker 1989, Fagan 2002, Campbell Grant et al. 2007, Meyer et al. 2007). Thus, the minimal effects due to tributary position, as well as microhabitat treatments in the present study may be overwhelmed by dispersal processes present in larger streams (Milesi and Melo 2013), especially with the possibility of strong passive dispersion from post-flood effects (Wilson and McTammany 2016).

Another consideration is the effects of upstream dispersal. Although dispersal is predominantly a process acting in the downstream direction, movement of terrestrial adults upstream for oviposition as well as upstream swimming or walking of larvae can lead to a flux of organisms in the upstream direction (Williams and Hynes 1976, Elizabeth Graham et al. 2017). This has important consequences at tributary junctions since the effect of tributary drift may show gradational changes in community structure upstream of the junction (Wilson and McTammany 2014), which were not captured in our study design.

#### **Caveats and implications**

Some of the main caveats to this study pertain to the issue of scale of sampling and treatment application. While site selection attempted to incorporate random selection of plot location upstream and downstream of the tributary, the spatial extent of all baskets were limited to, at most, 5 m x 10 m and may not accurately capture the overall trends in water depth or velocity, which are highly localized and may not be generalizable to tributary junctions overall. These localized conditions may have also indirectly affected the measurement of CPOM retention. To develop a better idea of the CPOM accumulation, a more extensive survey of CPOM standing stocks upstream and downstream would be beneficial to incorporate into future research, especially when paired with CPOM flux data from tributaries. The biotic implications for this can lead to high patch-to-patch variability. For instance, Kiffney et al. (2006) highly localized quadrat sampling (0.25 m<sup>2</sup>) revealed large variability in *Dicosmoecus gilvipes* density requiring in numerous samples within a small area to reveal general patterns due to tributary inflow. This study used baskets that were ca. 20% of the area and may have contained too much noise to detect more subtle responses. This noise is particularly evident as the quantity of variation in our observed taxonomic richness values requires an effect size that is approximately 10% of the mean value to consistently detect significant results (Figure B1).

The limited extent of plot boundaries may have caused a loss of signal of basket treatments due to local dispersal between experimental units. The experimental design attempted to reduce the environmental variability between baskets to control for the treatment effects and reduce other sources of variability while capturing patch preferences. However, benthic macroinvertebrates can disperse several m/d (Elliott 2003), far exceeding the distance between the substrate baskets. This necessitates further investigation regarding the mechanisms of interest at the reach or larger scale. This does not negate the role that tributaries play

in the alteration of habitat and environmental characteristics, nor their effect on benthic communities in larger rivers. However, it does suggest that tributary catchment characteristics and exports of biota may not be generalizable across tributaries at the patch scale. It could be possible that tributary junctions are important for unique habitat that is exploited by adjacent communities (Power and Dietrich 2002) and may not show a clear boundary of community change within the scale of our study. Since tributaries can show both gradational and abrupt changes to communities (Jones and Schmidt 2018), future studies attempting to test specific mechanisms regarding habitat structure and resource supply may need to incorporate larger-scale sampling of communities.

Another consideration is the anomalous hydrograph present for the year of study. During the spring freshet, rapid snowmelt and rain-on-snow events caused extremely high peak flows. Mission Creek experienced a 110 year flood, resulting in devastating flooding effects for nearby human settlements. This led to an episodic morphological change to many areas of the channel, according to several nearby residents. Even though the experiment took place after flows subsided, legacy effects of the channel disturbance may have led to altered distribution of biota through the channel. High passive dispersal can lead to patterns more dependent on spatial distance rather than environmental similarity (Milesi and Melo 2013, Wilson and McTammany 2016), which may have been triggered from the high flow event through catastrophic drift (Gibbins et al. 2007). The effects of flow on dispersal processes are challenging. Intuitively, higher flow would be expected to cause higher rates of drift through involuntary entry and transport in the water column. However, previous research suggests that drift is much higher during low flow, suggesting active departure from occupied patches and entry into drift (Fonseca and Hart 1996), hypothetically showing stronger environmental filtering via preferential selection.

Lastly, we did not examine the role of interacting environmental variables and only measured a subset of biologically relevant variables. Though we found spatial structuring of communities not explained by environmental characteristics, these interacting and unmeasured effects may play a role in the filtering of community assembly not explained by dispersal-driven dynamics. For example, we tried to incorporate the effects of local hydraulics by including depth and velocity as covariates, but other hydraulic metrics such as turbulence and shear stress are important factors to consider reagarding habitat preferences for organisms (Hart and Finelli 1999).

## Conclusion

This research, through a manipulative experiment, tested some of the commonly suggested mechanisms for community shifts at tributary junctions. Despite tributaries being important agents of structural alterations and resource supply, community responses to these changes appears to be highly context-dependent based on the tributary. Generally, we did not see any effect on diversity and communities decreased in abundance downstream of tributaries. Coarsened substrate showed similar decreases in total abundance, but both coarse substrate and added CPOM did not have communities that resembled downstream. This suggests

that these mechanisms did not have a strong effect on community assembly. However, this study highlights the opportunities to disentangle mechanisms behind not only the magnitude of change in communities at tributary junctions, but the direction as well. In doing so, this would allow ecologists and practitioners to better understand how upstream catchments can control the dynamics of communities at tributary junctions.

Table 3.1: Mean ( $\pm$  1 SE) of measured environmental variables upstream and downstream of tributary inflow during two sampling time periods. Mean and standard error calculated from values measured across the six study sites.

		Period 1	(August	)	Period 2 (September)			
	Upstre	Upstream		Downstream		Upstream		tream
CPOM Accumulation (g)	0.48	± 0.11	0.47	± 0.14	0.25	± 0.10	0.24	± 0.05
Water Depth (cm)	14.58	± 1.70	18.76	± 1.37	12.69	± 2.62	16.78	± 2.21
Water Velocity (cm s $^{-1}$ )	21.00	± 2.92	26.10	± 6.21	38.63	± 8.26	32.18	± 5.53
рН	7.69	± 0.08	7.63	± 0.10	7.81	± 0.08	7.59	± 0.05
Dissolved Oxygen (mg $L^{-1}$ )	6.92	± 1.17	8.55	± 1.43	5.36	± 1.18	5.94	± 0.39
EC (mS cm $^{-1}$ )	0.082	± 0.008	0.076	± 0.006	0.079	± 0.006	0.076	± 0.007
Mean Temperature (°C)	15.74	± 0.17	16.19	± 0.37	15.21	± 0.32	15.14	± 0.38
Minimum Temperature (°C)	12.94	± 0.20	13.33	± 0.45	12.57	± 0.61	12.65	± 0.64

Table 3.2: Chi-square analysis of deviance test results on individual terms for fitted models predicting environmental variables in Table 3.1 with treatment factors.

	Position CPOM		РОМ	Substrate		Period		Position x Period		
	$X^2$	р	$X^2$	р	$X^2$	р	$X^2$	р	$X^2$	р
CPOM Accumulation (g)	0.01	0.919	0.08	0.775	0.00	0.957	18.21	<0.0001	0.01	0.91
Water Depth (cm)	14.17	0.0002	0.06	0.81	0.07	0.797	6.71	0.010	0.05	0.829
Water Velocity (cm s $^{-1}$ )	0.01	0.942	0.64	0.423	6.09	0.014	0.03	0.860	10.18	0.001
рН	2.81	0.094	0.00	0.984	0.31	0.580	4.58	0.032	49.04	<0.0001
Dissolved Oxygen (mg L $^{-1}$ )	7.88	0.005	0.00	0.945	0.03	0.864	21.77	<0.0001	2.55	0.11
EC (mS cm $^{-1}$ )	5.61	0.018	0.00	1.000	0.02	0.875	23.39	<0.0001	0.14	0.713
Mean Temperature (°C)	0.61	0.434	0.00	0.990	0.00	0.996	101.18	<0.0001	13.4	<0.0001
Minimum Temperature (°C)	1.41	0.236	0.00	0.983	0.00	0.978	44.55	<0.0001	5.39	0.02

Table 3.3: Redundancy analysis (RDA) results of environmental variables predicted by fully crossed predictor variables of position relative to tributary inflow, site, and time period.

Variance Explained	Constrained	85.1						
	Residual	14.9						
	Terms					Axes		
Variable:	df	Variance	F*	р	Axis	% Var. Explained	F*	р
Position	1	0.329	18.5	<0.001	RDA1	30.9	165.55	<0.001
Site	5	4.303	48.4	<0.001	RDA2	20.6	110.41	<0.001
Period	1	0.502	28.2	<0.001	RDA3	15.3	82.3	<0.001
Position x Site	5	0.666	7.5	<0.001				
Position x Period	1	0.168	9.4	<0.001	RDA8	4	2.44	1
Site x Period	4	0.585	8.2	<0.001	Residual	14.9		
Position x Site x Period	4	0.254	3.6	<0.001	PC1	6.1		
Residual	66	1.193			PC2	5		

Table 3.4: Top model results for rarefied taxonomic richness, total abundance, Shannon index, and Pielou's evenness. All metrics except total abundance fitted with linear mixed effects models and selected based on lowest AICc values. Significance tests were conducted with t-tests using Satterthwaite's estimated denominator degrees of freedom (Est. ddf). Total abundance was fitted with a generalized linear mixed model (negative binomial, log link). Note that T-tests could not be conducted on this model and significance was determined using z-distribution, which may lead to inflated type I error.

Rarefied Taxonomic Richness											
Term	$\beta$	SE	Est. ddf	t	р						
(Intercept)	10.902	1.086	6.2	10.044	<0.001						
Position - Downstream	0.455	0.803	5.1	0.566	0.595						
Substrate - Coarse	0.451	0.347	73.3	1.301	0.197						
CPOM - Added	-0.639	0.337	73.1	-1.897	0.062						
Mainstem - WK	3.800	1.414	4.6	2.686	0.048						
Period - 2	-1.556	0.350	74.1	-4.439	<0.001						
Velocity	0.505	0.263	76.4	1.919	0.059						
Marginal R2	0.382										
Conditional R2	0.738										
	Shanı	non Inde	X								
Term	β	SE	Est. ddf	t	р						
(Intercept)	1.885	0.202	5.7	9.327	<0.001						
Position - Downstream	0.118	0.125	5.2	0.944	0.387						
Substrate - Coarse	0.111	0.064	74.4	1.733	0.087						
CPOM - Added	-0.094	0.064	74.4	-1.458	0.149						
Mainstem - WK	0.499	0.262	4.1	1.907	0.128						
Period - 2	-0.230	0.067	75.3	-3.431	0.001						
Marginal R2	0.309										
Conditional R2	0.690										
	Total A	bundan	се								
Term	$\beta$	SE	Z	р							
(Intercept)	5.868	0.230	25.496	<0.001							
Position - Downstream	-0.298	0.134	-2.229	0.026							
Substrate - Coarse	-0.266	0.099	-2.701	0.007							
CPOM - Added	0.266	0.070	3.786	<0.001							
Substrate x Position	0.237	0.140	1.686	0.092							
Mainstem - WK	-1.171	0.301	-3.884	<0.001							
Period - 2	0.484	0.074	6.572	<0.001							
	Pielou's	s Evenn	ess								
Term	$\beta$	SE	Est. ddf	t	р						
(Intercept)	0.613	0.063	5.0	9.714	<0.001						
Position - Downstream	0.035	0.025	5.2	1.371	0.226						
Substrate - Coarse	0.037	0.019	74.5	1.951	0.055						
CPOM - Added	-0.040	0.019	74.5	-2.085	0.040						
Mainstem - WK	0.205	0.085	4.0	2.426	0.072						
Period - 2	-0.087	0.020	75.3	-4.337	<0.001						
Marginal R2	0.437										
Conditional R2	0.753										

Source		df	SS	MS	F*	$\mathbb{R}^2$	p (>F)
Whole Plot	Position	1	0.052	0.052	0.731	0.07	0.693
	Site	5	0.323	0.065	0.917	0.44	0.602
	Whole Plot Error	5	0.352	0.070	NA	0.48	NA
	Total	11	0.727	NA	NA	1.00	NA
Sub-plot	Period	1	1.488	1.488	19.057	0.15	<0.001
	Substrate	1	0.046	0.046	0.588	0.00	0.491
	CPOM	1	0.081	0.081	1.031	0.01	0.127
	Velocity	1	1.075	1.075	13.769	0.11	<0.001
	Depth	1	0.545	0.545	6.978	0.06	<0.001
	Sub-plot Error	83	6.483	0.078	NA	0.67	NA
	Total	88	9.718	NA	NA	1.00	NA

Table 3.5: Results of Monte-Carlo permutational ANOVA tests using Bray-Curtis distances of fourth-root transformed community abundance data using a reduced model from stepwise elimination.

Table 3.6: Results of distance based redundancy analysis (db-RDA) of fourth-root transformed taxa abundance data. Total variance explained by the included constraining variables and the residual displayed above the header. On the left, variance explained by site, treatments, and environmental variables (including all shared variance) were calculated using sequential partial db-RDA. The significance of each constraining axis are depicted on the right, determined by Monte-Carlo permutational pseudo-ANOVA, with their corresponding portion of community variance explained as well as the proportion of variance explained by the first two non-redundant axes.

Variance Explained	Constrained	42.07%			
	Residual	57.93%			
Variance Partitionir	ng		Axes		
Source	% Explained	Axis	% Var. Explained	<b>F</b> *	р
Treatment	3.08	RDA1	10.8	13.3	<0.001
Environment	5.3	RDA2	6.6	8.1	<0.001
Site	15.84	RDA3	5.7	7	<0.001
Treatment & Environment	0	RDA4	3.6	4.4	<0.001
Treatment & Site	0.01	RDA5	2.1	2.5	<0.001
Environment & Site	5.29	RDA6	2	2.5	<0.001
Treatment & Environment & Site	0	RDA7	1.8	2.2	<0.001
Residual + Time Period	70.48	RDA8	1.5	1.9	0.031
Time Period	7.43				
		RDA17	0.4	0.6	1
		Residual	57.9	-	
		PC1	2.7		
		PC2	2.5		

Table 3.7: Results from top generalized linear mixed model via AICc ranking (Poisson or negative binomial distribution with log link function) for taxa specific responses.

	Shredders										Scraper					
	Lepidostoma sp.					Pteronarcys sp.					Heptageniidae spp.					
	β	SE	df	Z	р	$\beta$	SE	df	Z	р	β	SE	df	Z	р	
(Intercept)	2.218	0.525	1	4.228	<0.001	1.927	0.973	1	1.980	0.048	1.275	0.442	1	2.886	0.004	
Position	-0.885	0.341	1	-2.594	0.009	-0.500	0.178	1	-2.806	0.005	-0.179	0.141	1	-1.271	0.204	
CPOM	0.759	0.169	1	4.498	<0.001	0.336	0.119	1	2.812	0.005	-0.069	0.140	1	-0.492	0.623	
Substrate	-0.433	0.168	1	-2.572	0.010	-0.161	0.117	1	-1.376	0.169	0.079	0.140	1	0.565	0.572	
Pos x Substr																
Mainstem	-1.514	0.498	1	-3.042	0.002	-1.656	1.386	1	-1.195	0.232	0.474	0.592	1	0.801	0.423	
Period	2.496	0.191	1	13.094	<0.001	-0.767	0.147	1	-5.201	<0.001	0.953	0.150	1	6.355	<0.001	
CPOM Accum.						-0.376	0.234	1	-1.608	0.108						
Water Depth	0.053	0.020	1	2.713	0.007											
Water Velocity						0.013	0.005	1	2.364	0.018						

	Filterers									Gatherer						
	Brachycentrus sp.					Hydropsychidae spp.					Baetis sp.					
	β	SE	df	Z	р	β	SE	df	Z	р	β	SE	df	Z	р	
(Intercept)	1.579	0.626	1	2.522	0.012	1.215	1.472	1	0.825	0.409	2.757	0.559	1	4.929	<0.001	
Position	-0.445	0.566	1	-0.787	0.431	-0.937	0.673	1	-1.392	0.164	-0.396	0.290	1	-1.365	0.172	
CPOM	0.164	0.190	1	0.864	0.388	-0.937	0.673	1	0.736	0.462	-0.037	0.130	1	-0.284	0.776	
Substrate	0.213	0.194	1	1.101	0.271	-0.975	0.316	1	-3.089	0.002	-0.446	0.132	1	-3.382	0.001	
Pos x Substr						0.858	0.455	1	1.887	0.059						
Mainstem	-1.214	0.735	1	-1.651	0.099	0.570	1.781	1	0.320	0.749	-0.899	0.595	1	-1.510	0.131	
Period	-0.419	0.222	1	-1.891	0.059	-1.250	0.279	1	-4.482	<0.001	0.359	0.151	1	2.380	0.017	
CPOM Accum.	0.507	0.296	1	1.712	0.087						-0.555	0.238	1	-2.333	0.020	
Water Depth						-0.107	0.030	1	-3.517	<0.001	-0.030	0.016	1	-1.925	0.054	
Water Velocity						0.041	0.011	1	3.736	<0.001	0.015	0.006	1	2.537	0.011	



Figure 3.1: Redundancy analysis of measured environmental variables across six study sites. Variance was reduced to two RDA axes which explain 49.9 % of total variance. Points represent each basket observation with 95% confidence ellipses around the centroid of upstream (grey) and downstream (black) position in both August (solid line) and September (dashed line).


Figure 3.2: Estimated marginal means (95% confidence error bars) of (A) rarefied taxonomic richness, (B) Shannon index, (C) total macroinvertebrate abundance (no. per basket, 490 cm<sup>2</sup>), and (D) Pielou's evenness upstream and downstream of tributary inflow. Point shape indicates substrate size: small (circle), large (triangle); point colour indicates CPOM addition: none (dark), added (light). Raw observations are plotted in light gray points behind corresponding means. Error bars for abundance are symmetrical despite being on log axis due to back-transformation from log link function.



Figure 3.3: Location of treatment centroids visualized using partial distance-based redundancy analysis scores from all samples for each site with the effect of environmental variables left out of the db-RDA model and the site-by-site variability partialled out. Points represent centroid values with 95 % confidence ellipses of site location in ordination space for the position, upstream (grey) and downstream (black) relative to tributary inflow. Filled points represent centroids with CPOM added and open points represent no CPOM added. Shapes represent substrate treatment, small (circle) and large (square). Model explained 16.7% of total variance, visualized on two RDA axes (9.2 and 3.8%, respectively; p < 0.0001).



Figure 3.4: Site-specific positional effects on community structure visualized using partial distance-based redundancy analysis scores from all samples for each site with the effect of environmental variables removed from the db-RDA model and the site-by-site variability partialled out of analysis. Ellipses represent 95% confidence ellipses around position treatments (color) at each of the two time periods (solid and dotted lines). Model explained 16.7% of total variance, visualized on two RDA axes (9.4% and 3.6%, respectively; p < 0.0001).



Figure 3.5: Estimated marginal mean (95% CI) abundances (no. per basket, 490 cm<sup>2</sup>) of six different common taxa found in the West Kettle and Mission Creek catchments derived from Poisson or negative binomial distributed (log link function) generalized linear mixed models. Factors include: upstream and downstream, with (light) and without (dark) CPOM, and small (circle) and large (triange) substrate. Individual observations for each treatment are light points in the background. A and B representative of shredder taxa, C and D representative of filter feeders, E representing scrapers, and F representing gatherers. Note that y-axis is log-transformed and points residing on the x-axis are observations of zero. Error bars are symmetrical despite being on log axis due to back-transformation from log link function.

## **Chapter 4: General Discussion**

#### **Findings and Caveats**

The field of community ecology has provided valuable contributions toward our current understanding of the structure and function of the ecological landscape. The substantial culmination of rigorous theoretical and empirical research has developed our understanding of community dynamics in the context of a patchy habitat landscape (Leibold et al. 2004, Holyoak et al. 2005, Loreau et al. 2005, Vellend and Agrawal 2010). It is well recognized that this landscape is not static and that the spatio-temporal arrangement of habitat structure and resources is mediated by various processes across scales (Forman and Godron 1981, Polis et al. 1997, Poole 2002). Our current understanding of the processes that give rise to this arrangement of habitat components and consequent effects of community structure and function is still at its infancy (Massol et al. 2011, Kovalenko et al. 2012). However, future work in this area is promising for both basic understanding and applied problems in restoration and conservation.

Restoration and conservation efforts are faced with challenges due to the linked, patchy structure of ecosystems (Palmer et al. 1997a). Localized objectives and actions without a thorough understanding of the surrounding context and processes and unfortunately has led to under-delivered results with very little improvement of target variables (Palmer et al. 2014). For example, under the "Field of Dreams" approach to restoration (Palmer et al. 1997a), habitat structure is manually manipulated to provide ideal habitat for desired organisms and function. However, without carefully considering the external context, higher-scale processes may be overlooked (e.g. regional dispersal) that are important for achieving the desired outcomes (Swan and Brown 2017). Therefore, not considering larger scale processes and interactions have unfortunately led to many examples of costly, ineffective projects, particularly in stream ecosystems (Roni et al. 2008, Nilsson et al. 2015). Further research in community ecology shows promising results that can help understand priority objectives and appropriate ongoing monitoring schemes to evaluate the performance of projects.

Current efforts in stream ecology have been geared towards understanding the importance of the spatial arrangement and connectivity of streams in the river network. While there has been a vast amount of research efforts at scale of the reach or linear features of the river, more recently researchers have turned towards understanding the role of tributary junctions in community assembly in mainstem channels from both a theoretical (Benda et al. 2004) and empirical perspective (Rice et al. 2001a). Tributaries are important supply points of sediment (Milner et al. 2019), detritus (Sabo et al. 2018), biota, contrasting water temperature (Sabo et al. 2012) and nutrients, and have been hypothesized to be critical disruptive points of community structure along the mainstem channel. While previous empirical research has supported this, often showing increases in biological diversity (Rice et al. 2001a, Knispel and Castella 2003, Kiffney et al. 2006, Katano et al. 2009, Wilson and McTammany 2014, Jones and Schmidt 2018), many studies have observed no effect of tributaries on community assembly or diversity (Mac Nally et al. 2011, Milesi and Melo 2013, Milner et al. 2019). Despite the extensive investment of research regarding our understanding of these locations, much of the current research to this point has been observational. While informative of pattern, we are left with a limited understanding of specific mechanisms and processes that occur. My research addressed this gap by testing hypotheses that relate processes to habitat structure and resource supply and used an experimental approach to test two specific mechanisms for community responses. In Chapter 1, I had set out the following two main objectives of the thesis: (1) to determine how tributary size controls the quantity and characteristics of material exports and the resulting effects on mainstem channel habitat and resource supply and (2) to test the mechanistic responses of invertebrates to subsidies and habitat structural change due to tributaries.

With regards to the first objective, I had hypothesized that tributary size – being a proxy for several physicochemical processes – would be a good predictor for alterations to the nutrient and CPOM availability, substrate size, and water temperature in the receiving channel. In Chapter 2, I had found that tributaries do cause the predicted increase in nutrient and CPOM concentration, substrate size, and the predicted decrease in stream temperature. However, my original hypothesis regarding the relationship of the magnitude with tributary size was rejected. There was no clear relationship for most variables with a lot of residual variance unaccounted for. I also found that many of these variables strongly varied across sampling intervals in non-systematic ways. I concluded that there are numerous other potential processes unaccounted for, which vary across time.

For the second objective, I had hypothesized that two mechanisms, the export of CPOM and coarse substrate from tributaries, would be driving factors for the assembly of communities at tributaries. I had predicted that addition of CPOM and coarse substrate would lead to increased diversity and altered community structure, which would trend in the direction of the effects due to position. In Chapter 3 I had found that generally, tributary junctions showed no significant, systematic effects on community assembly. The direction of response for community assembly was highly site-specific, suggesting idiosyncratic effects of tributaries on community assembly. I also found that treatments of coarse substrate and addition of CPOM had no effects on community structure except for numeric responses of a few common taxa. The trends observed did not align with the effects due to position. Furthermore, the residual variance not explained by treatments or environmental factors suggests that other processes were responsible for the observed community assembly.

One of the main limitations of this study is the small sampling extent across space and time. To achieve the appropriate experimental design to include the desired treatments within the scope of this project, I was limited to two main catchments. Since 2017 had abnormally low flow conditions, many tributaries along the two mainstems had little to no surface flow or were inaccessible. Contrasting upstream and downstream habitat and community structure across six tributary junctions within one geographic region provides just a glimpse into the proposed processes that would benefit from future replication in different geographic regions. It would also be informative to compare these results with those from a year with a more normal hydrograph and weather patterns.

### Implications and future directions

Despite having many of the original hypotheses rejected, the findings of this study revealed and confirmed several implications for both ecological research and practitioners. First, my thesis confirms that hydrologic connectivity remains an important feature of river networks, not only for upstream-downstream linkages, but the spatial arrangement of streams in the river network (Freeman et al. 2007). I found that tributaries, regardless of size, can be important supply points of material that alters the habitat structure and resource base of disproportionately larger mainstem channels. Despite taking up the majority of total drainage length, we know that small catchments are sensitive to - and heavily impacted by - anthropocentric stressors and disturbance. Small tributaries are less conspicuous on the landscape and are subject to direct alteration (Kuglerová et al. 2017, Richardson 2019). Landscape alteration has disproportionate effects on small catchments due to the small catchment size relative to the scale of decision making (Bishop et al. 2008). Due to the limited catchment area and discharge of small streams, even modest changes to the landscape can alter relatively large proportions of the catchment area with little water volume to dilute impacts to water and habitat guality. I found that even small tributaries displayed the capacity to have measurable changes to the resource base and habitat structure, despite entering a disproportionately large mainstem. This is important on the network scale since many of these small drainages link directly with large mainstem rivers in downstream reaches. Thus, along the length of a large channel, numerous points of punctuations in ecological characteristics may take place, each being ecologically significant, particularly due to the diversity in biota and characteristics found in small streams (Finn et al. 2011, Jones and Schmidt 2016).

My second main finding highlights the need to better establish links between temporally-variable stream processes and ecosystem responses at tributary junctions. Previous conceptual models of the dynamics at tributary junctions have primarily been concerned with the spatial arrangement and characteristics of contributing basins (Rice et al. 2001a, Benda et al. 2004, Jones and Schmidt 2016) with little reference to the temporal variability of processes (except disturbance, see Benda *et al.* 2004). I attempted to capture generalized relationships between stream size and processes to predict alterations to habitat structure and resource supply at tributary junctions. However, even within my limited sampling extent, I saw considerable temporal variability in the resource and water chemistry dynamics at tributary junctions. For example, warm-and cold-water contributions from tributaries not only varied from stream to stream, but diel fluctuations of tributary temperature ranged from 2.7 °C colder to 1.9 °C warmer than the mainstem channel.

Time period did not show consistent effects on responses, but inconsistent variability due to time across tributaries further highlights the catchment-specific processes that lead to downstream effects and asynchrony among tributaries. Asynchronous patterns are a recent interest when looking at river network processes (e.g. stream metabolism (Mejia et al. 2019), hydrologic timing (Gomi et al. 2002)) and adds another consideration when trying to determine the ecological significance of tributary junctions. For example, early timing of peak flows or flash floods from small tributaries may supply large clasts of sediment that far exceed the maximum competence of the mainstem channel at average high flows. Because these hypothetical hydrographs are out of synchrony, flows from the tributary subside and do not contribute discharge to increase the stream power downstream of the confluence in the mainstem. That sediment may be a unique habitat refuge for invertebrates to avoid disturbance from peak flows in the mainstem that would otherwise be sufficient to reorganize the sediment on the channel bed upstream. Pulsed inputs of leaf litter from high wind events that run perpendicular to tributaries may lead to high concentrations of inputs to the mainstem, especially if the mainstem does not receive the same effect of the wind on inputs of CPOM. Future work should consider the context-dependency of tributary effects. Short-term studies may not reveal underlying temporal patterns that may cause tributary junctions to have intermittent or episodic ecological significance. This would require incorporating both temporally and spatially variable processes, as opposed to mean state or snapshots into current conceptual models of river networks (Palmer et al. 1997b).

My third main finding was that I did not find strong habitat-community assembly relationships indicating other, dominant factors driving observed community assembly. Previous research has shown that larger, downstream lengths of the river network are important dispersal corridors for benthic organisms (Fagan 2002, Campbell Grant et al. 2007, Meyer et al. 2007). Habitat manipulations in these areas showed little to no response with little variance explained by treatments or environment. One possibility is that these communities are strongly driven by mass-effects or neutral processes (Holyoak et al. 2005). If this is the case, it is important to consider the network arrangement of tributaries not solely for their effects on the arrangement of habitat structure and resources, but also for sources of dispersing organisms. This could have important implications as the combination of dispersing individuals that have not undergone environmental filtering may present unique species assemblages and biotic interactions that could affect other in-stream processes such as nutrient and energy cycling. Complementing future experimental research with sampling of dispersal (e.g. drift nets) may be one avenue to parse out the effects of environmental filtering and dispersal processes.

This challenging consideration of processes operating at multiple scales brings forward the issue of scale when considering sampling extent. Lastly, I found that the treatments used in this study showed little to no effect on community structure at the local patch scale. Scale is a challenging concept in most ecological research. Since processes operate across all levels of scale, this influences the degree to which we observe ecological patterns and responses (Levin 1992). Choosing the appropriate sampling extent (spatially and temporally) can greatly influence the observed magnitude and direction of the responses under study (Turner 1989). Habitat heterogeneity, for instance, can be captured differently based on sampling extent. Sampling across a larger spatial extent captures increased diversity of habitats at the patch scale. This was a particularly relevant consideration when interpreting the results from Chapter 3, where I was measuring the response of local communities within the extent of one substrate basket (490 cm<sup>2</sup>). My results align with others showing no response to habitat manipulation in larger rivers (Parker 1989, Milesi and Melo 2013). However, lack of localized responses are not indicative of a lack of effect that tributaries have on larger mainstems in general. Future research should consider incorporating experimental approaches at higher levels of scale to complement the current literature on effects of tributaries further downstream along the

length of the mainstem. Since lengths of the mainstem further downstream in the catchment integrate all the upstream tributaries, cumulative or redundant effects from upstream tributaries may be present, making it difficult to measure the effects of any single tributary at one locale.

### References

Agostinho, A. A., and M. Zalewski. 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Parana River, Brazil. Pages 141–148 *in* The importance of aquatic-terrestrial ecotones for freshwater fish. Springer.

Aho, K., D. Derryberry, and T. Peterson. 2014. Model selection for ecologists: The worldviews of AIC and BIC. Ecology 95:631–636.

Allen, D. C., and J. S. Wesner. 2016. Synthesis: Comparing effects of resource and consumer fluxes into recipient food webs using meta-analysis. Ecology 97:594–604.

Altermatt, F. 2013. Diversity in riverine metacommunities: A network perspective. Aquatic Ecology 47:365–377.

Ayres, E., H. Steltzer, B. L. Simmons, R. T. Simpson, J. M. Steinweg, M. D. Wallenstein, N. Mellor, W. J. Parton, J. C. Moore, and D. H. Wall. 2009. Home-field advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochemistry 41:606–610.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using Ime4. Journal of Statistical Software 67:1–48.

Baumgartner, M. T., A. G. de Oliveira, A. A. Agostinho, and L. C. Gomes. 2018. Fish functional diversity responses following flood pulses in the upper Paraná River floodplain. Ecology of Freshwater Fish 27:910–919.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656–2663.

Bell, S. S., E. D. McCoy, and H. R. Mushinsky. 2012. Habitat structure: The physical arrangement of objects in space. Springer Science & Business Media.

Benda, L. 1990. The influence of debris flows on channels and valley floors in the Oregon Coast Range, USA. Earth Surface Processes and Landforms 15:457–466.

Benda, L., M. A. Hassan, M. Church, and C. L. May. 2005. Geomorphology of steepland headwaters: The transition from hillslopes to channels. Journal of the American Water Resources Association 41:835–851.

Benda, L., D. Miller, P. Bigelow, and K. Andras. 2003a. Effects of post-wildfire erosion on channel environments, Boise River, Idaho. Forest Ecology and Management 178:105–119.

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: How channel networks structure riverine habitats. BioScience 54:413–427.

Benda, L., C. Veldhuisen, and J. Black. 2003b. Debris flows as agents of morphological heterogeneity at

low-order confluences, Olympic Mountains, Washington. Geological Society of America Bulletin 115:1110– 1121.

Benfield, E. 1997. Comparison of litterfall input to streams. Journal of the North American Benthological Society 16:104–108.

Bilby, R. E., and J. T. Heffner. 2016. Factors influencing litter delivery to streams. Forest Ecology and Management 369:29–37.

Biron, P. M., A. S. Ramamurthy, and S. Han. 2004. Three-dimensional numerical modeling of mixing at river confluences. Journal of Hydraulic Engineering 130:243–253.

Bishop, K., I. Buffam, M. Erlandsson, J. Fölster, H. Laudon, J. Seibert, and J. Temnerud. 2008. Aqua incognita: The unknown headwaters. Hydrological Processes 22:1239–1242.

Bladon, K. D., U. Silins, M. J. Wagner, M. Stone, M. B. Emelko, C. A. Mendoza, K. J. Devito, and S. Boon. 2008. Wildfire impacts on nitrogen concentration and production from headwater streams in southern Alberta's Rocky Mountains. Canadian Journal of Forest Research 38:2359–2371.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical ecology with R. Springer, New York.

Boyer, C., D. Chaumont, I. Chartier, and A. G. Roy. 2010. Impact of climate change on the hydrology of St. Lawrence tributaries. Journal of Hydrology 384:65–83.

Brewitt, K. S., E. M. Danner, and J. W. Moore. 2017. Hot eats and cool creeks: Juvenile Pacific salmonids use mainstem prey while in thermal refuges. Canadian Journal of Fisheries and Aquatic Sciences 74:1588–1602.

Brown, B. L., C. M. Swan, D. A. Auerbach, E. H. Campbell Grant, N. P. Hitt, K. O. Maloney, and C. Patrick. 2011. Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. Journal of the North American Benthological Society 30:310–327.

Brown, B., and C. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology 79:571–580.

Brown, G. W. 1969. Predicting temperatures of small streams. Water Resources Research 5:68–75.

Brown, L. E., D. M. Hannah, and A. M. Milner. 2005. Spatial and temporal water column and streambed temperature dynamics within an alpine catchment: Implications for benthic communities. Hydrological Processes: An International Journal 19:1585–1610.

Bruns, D., G. Minshall, C. Cushing, K. Cummins, J. Brock, and R. Vannote. 1984. Tributaries as modifiers of the river continuum concept: Analysis by polar ordination and regression models. Archiv für Hydrobiologie 99:208–220.

Brusven, M., and S. Rose. 1981. Influence of substrate composition and suspended sediment on insect predation by the torrent sculpin, *cottus rhotheus*. Canadian Journal of Fisheries and Aquatic Sciences 38:1444–1448.

Bunte, K., and S. R. Abt. 2001. Sampling surface and subsurface particle-size distributions in wadable gravel-and cobble-bed streams for analyses in sediment transport, hydraulics, and streambed monitoring.

Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: A practical information-theoretic approach. Springer Science & Business Media.

Campbell Grant, E. H., W. H. Lowe, and W. F. Fagan. 2007. Living in the branches: Population dynamics and ecological processes in dendritic networks. Ecology Letters 10:165–175.

Carroll, T. M., and J. H. Thorp. 2014. Ecotonal shifts in diversity and functional traits in zoobenthic communities of karst springs. Hydrobiologia 738:1–20.

Chu, C., N. E. Jones, and L. Allin. 2010. Linking the thermal regimes of streams in the Great Lakes Basin, Ontario, to landscape and climate variables. River Research and Applications 26:221–241.

Church, M. 2006. Bed material transport and the morphology of alluvial river channels. Annu. Rev. Earth Planet. Sci. 34:325–354.

Conners, M. E., and R. J. Naiman. 1984. Particulate allochthonous inputs: Relationships with stream size in an undisturbed watershed. Canadian Journal of Fisheries and Aquatic Sciences 41:1473–1484.

Cottenie, K., E. Michels, N. Nuytten, and L. De Meester. 2003. Zooplankton metacommunity structure: Regional vs. Local processes in highly interconnected ponds. Ecology 84:991–1000.

Crow, S., G. Closs, J. Waters, D. Booker, and G. Wallis. 2010. Niche partitioning and the effect of interspecific competition on microhabitat use by two sympatric galaxiid stream fishes. Freshwater Biology 55:967–982.

Culp, J. M., and R. W. Davies. 1982. Analysis of longitudinal zonation and the river continuum concept in the Oldman–South Saskatchewan River System. Canadian Journal of Fisheries and Aquatic Sciences 39:1258–1266.

Culp, J. M., S. J. Walde, and R. W. Davies. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. Canadian Journal of Fisheries and Aquatic Sciences 40:1568–1574.

Culp, J. M., F. J. Wrona, and R. W. Davies. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. Canadian Journal of Zoology 64:1345–1351.

Death, R. 1996. The effect of patch disturbance on stream invertebrate community structure: The influence of disturbance history. Oecologia 108:567–576.

de Brouwer, J., J. Eekhout, A. Besse-Lototskaya, A. Hoitink, C. Ter Braak, and P. Verdonschot. 2017. Flow thresholds for leaf retention in hydrodynamic wakes downstream of obstacles. Ecohydrology 10:e1883.

Demars, B. O., J. Russell Manson, J. S. Olafsson, G. M. Gislason, R. Gudmundsdottír, G. Woodward, J. Reiss, D. E. Pichler, J. J. Rasmussen, and N. Friberg. 2011. Temperature and the metabolic balance of streams. Freshwater Biology 56:1106–1121.

Doane, T. A., and W. R. Horwath. 2003. Spectrophotometric determination of nitrate with a single reagent. Analytical Letters 36:2713–2722.

Dobson, M., and A. G. Hildrew. 1992. A test of resource limitation among shredding detritivores in low order streams in southern england. Journal of Animal Ecology:69–77.

Dobson Engineering Ltd. 2003. 2002 Interior Watershed Assessment Update for the Mission Creek Watershed (Penticton Forest District).

Doerr, S., S. Woods, D. Martin, and M. Casimiro. 2009. "Natural background" soil water repellency in conifer forests of the north-western USA: Its prediction and relationship to wildfire occurrence. Journal of Hydrology 371:12–21.

Downes, B. J., and J. Lancaster. 2010. Does dispersal control population densities in advection-dominated systems? A fresh look at critical assumptions and a direct test. Journal of Animal Ecology 79:235–248.

Eaton, B., R. D. Moore, and L. G. MacKenzie. 2019, January. Bceaton/bicalc: Bicalc.

Ebersole, J., W. Liss, and C. Frissell. 2001. Relationship between stream temperature, thermal refugia and rainbow trout *oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecology of Freshwater Fish 10:1–10.

Elizabeth Graham, S., R. Storey, and B. Smith. 2017. Dispersal distances of aquatic insects: Upstream crawling by benthic ept larvae and flight of adult trichoptera along valley floors. New Zealand journal of marine and freshwater research 51:146–164.

Elliott, J. 2002. Time spent in the drift by downstream-dispersing invertebrates in a lake district stream. Freshwater Biology 47:97–106.

Elliott, J. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. Freshwater Biology 48:1652–1668.

Environment and Climate Change Canada. 2018a, January. Temperature and precipitation graph for 1981 to 2010 Canadian climate normals: Kelowna East. http://climate.weather.gc.ca/climate\_normals/results\_1981\_2010\_e.html?stnID=1006&autofwd=.

Environment and Climate Change Canada. 2018b, January. Real-time hydrometric data. https://wateroffice. ec.gc.ca/mainmenu/real\_time\_data\_index\_e.html. Esri. 2017. ArcMap (v. 10.6.1).

Fagan, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83:3243–3249.

Ferguson, R., T. Hoey, S. Wathen, and A. Werritty. 1996. Field evidence for rapid downstream fining of river gravels through selective transport. Geology 24:179–182.

Fernandes, C. C., J. Podos, and J. G. Lundberg. 2004. Amazonian ecology: Tributaries enhance the diversity of electric fishes. Science 305:1960–1962.

Finlay, J. C., J. M. Hood, M. P. Limm, M. E. Power, J. D. Schade, and J. R. Welter. 2011. Light-mediated thresholds in stream-water nutrient composition in a river network. Ecology 92:140–150.

Finn, D. S., N. Bonada, C. Múrria, and J. M. Hughes. 2011. Small but mighty: Headwaters are vital to stream network biodiversity at two levels of organization. Journal of the North American Benthological Society 30:963–980.

Flannigan, M., and C. V. Wagner. 1991. Climate change and wildfire in Canada. Canadian Journal of Forest Research 21:66–72.

Fonseca, D. M., and D. D. Hart. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. Oikos:49–58.

Forman, R. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. Bio-Science 31:733–740.

Freeman, M. C., C. M. Pringle, and C. R. Jackson. 2007. Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. Journal of the American Water Resources Association 43:5–14.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environmental management 10:199–214.

Gessner, M. O., and E. Chauvet. 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology 75:1807–1817.

Gibbins, C., D. Vericat, and R. J. Batalla. 2007. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. Freshwater Biology 52:2369–2384.

Gomi, T., R. D. Moore, and A. S. Dhakal. 2006. Headwater stream temperature response to clear-cut harvesting with different riparian treatments, coastal British Columbia, Canada. Water Resources Research 42.

Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems: Headwaters differ from downstream reaches by their close coupling to hillslope

processes, more temporal and spatial variation, and their need for different means of protection from land use. BioScience 52:905–916.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology letters 4:379–391.

Government of British Columbia. 2018. Biogeoclimatic Ecosystem Classification (BEC) Map. https:// catalogue.data.gov.bc.ca/dataset/f358a53b-ffde-4830-a325-a5a03ff672c3.

Graça, M. A., V. Ferreira, C. Canhoto, A. C. Encalada, F. Guerrero-Bolaño, K. M. Wantzen, and L. Boyero. 2015. A conceptual model of litter breakdown in low order streams. International Review of Hydrobiology 100:1–12.

Grainger and Associates Consulting Ltd. 2010. Mission Creek Hydrological Risk Assessment.

Grenouillet, G., D. Pont, and C. Hérissé. 2004. Within-basin fish assemblage structure: The relative influence of habitat versus stream spatial position on local species richness. Canadian Journal of Fisheries and Aquatic Sciences 61:93–102.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Hart, D. D., and C. M. Finelli. 1999. Physical-biological coupling in streams: The pervasive effects of flow on benthic organisms. Annual review of ecology and systematics 30:363–395.

Hauer, F. R., and C. N. Spencer. 1998. Phosphorus and nitrogen dynamics in streams associated with wildfire: A study of immediate and longterm effects. International Journal of Wildland Fire 8:183–198.

Hawkins, C. P., J. N. Hogue, L. M. Decker, and J. W. Feminella. 1997. Channel morphology, water temperature, and assemblage structure of stream insects. Journal of the North American benthological society 16:728–749.

Heard, S. B., G. A. Schultz, C. B. Ogden, and T. C. Griesel. 1999. Mechanical abrasion and organic matter processing in an iowa stream. Hydrobiologia 400:179–186.

Heino, J., M. Grönroos, J. Soininen, R. Virtanen, and T. Muotka. 2012. Context dependency and metacommunity structuring in boreal headwater streams. Oikos 121:537–544.

Heino, J., and H. Myrkä. 2008. Control of stream insect assemblages: Roles of spatial configuration and local environmental factors. Ecological Entomology 33:614–622.

Herder, F., and J. Freyhof. 2006. Resource partitioning in a tropical stream fish assemblage. Journal of Fish Biology 69:571–589.

Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. Metacommunities: Spatial dynamics and ecological communities. University of Chicago Press.

Hoover, T. M., L. B. Marczak, J. S. Richardson, and N. Yonemitsu. 2009. Transport and settlement of organic matter in small streams. Freshwater Biology 55:436–449.

Hoover, T. M., and J. S. Richardson. 2009. Does water velocity influence optimal escape behaviors in stream insects? Behavioral Ecology 21:242–249.

Hoover, T. M., J. S. Richardson, and N. Yonemitsu. 2006. Flow-substrate interactions create and mediate leaf litter resource patches in streams. Freshwater Biology 51:435–447.

Hoy, T., N. Church, A. Legun, K. Glover, G. Gibson, B. Grant, J. Wheeler, and K. Dunn. 1994. Kootenay Arcview Data. http://www.empr.gov.bc.ca/Mining/Geoscience/PublicationsCatalogue/OpenFiles/1994/Pages/ 1994-8.aspx.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press.

Hunt, R. J., M. Strand, and J. F. Walker. 2006. Measuring groundwater–surface water interaction and its effect on wetland stream benthic productivity, Trout Lake watershed, northern Wisconsin, USA. Journal of Hydrology 320:370–384.

Hutchinson, G. E. 1957. Cold spring harbor symposium on quantitative biology. Concluding remarks 22:415–427.

Hynes, H. 1975. The stream and valley. Proceedings of the International Association of Theoretical and Applied Limnology 19:1–15.

Jansson, R., H. Laudon, E. Johansson, and C. Augspurger. 2007. The importance of groundwater discharge for plant species number in riparian zones. Ecology 88:131–139.

Johnson, S. L. 2004. Factors influencing stream temperatures in small streams: Substrate effects and a shading experiment. Canadian Journal of Fisheries and Aquatic Sciences 61:913–923.

Jones, N. E. 2010. Incorporating lakes within the river discontinuum: Longitudinal changes in ecological characteristics in stream–lake networks. Canadian Journal of Fisheries and Aquatic Sciences 67:1350–1362.

Jones, N. E., and B. J. Schmidt. 2016. Tributary effects in rivers: Interactions of spatial scale, network structure, and landscape characteristics. Canadian Journal of Fisheries and Aquatic Sciences 74:503–510.

Jones, N., and B. Schmidt. 2018. Influence of tributaries on the longitudinal patterns of benthic invertebrate communities. River Research and Applications 34:165–173.

Katano, I., J. N. Negishi, T. Minagawa, H. Doi, Y. Kawaguchi, and Y. Kayaba. 2009. Longitudinal macroinvertebrate organization over contrasting discontinuities: Effects of a dam and a tributary. Journal of the North American Benthological Society 28:331–351.

Kiffney, P. M., C. M. Greene, J. Hall, and J. Davies. 2006. Tributary streams create spatial discontinuities in

habitat, biological productivity, and diversity in mainstem rivers. Canadian Journal of Fisheries and Aquatic Sciences 63:2518–2530.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. Journal of the North American Benthological Society 23:542–555.

Knighton, A. 1980. Longitudinal changes in size and sorting of stream-bed material in four English rivers. Geological Society of America Bulletin 91:55–62.

Knispel, S., and E. Castella. 2003. Disruption of a longitudinal pattern in environmental factors and benthic fauna by a glacial tributary. Freshwater Biology 48:604–618.

Kostaschuk, R. 1987. Identification of debris flow hazard on alluvial fans in the Canadian Rocky Mountains. Debris flows/avalanches: process, recognition, and mitigation 7:115.

Kovalenko, K. E., S. M. Thomaz, and D. M. Warfe. 2012. Habitat complexity: Approaches and future directions. Hydrobiologia 685:1–17.

Kuglerová, L., E. M. Hasselquist, J. S. Richardson, R. A. Sponseller, D. P. Kreutzweiser, and H. Laudon. 2017. Management perspectives on aqua incognita: Connectivity and cumulative effects of small natural and artificial streams in boreal forests. Hydrological Processes 31:4238–4244.

Kuglerová, L., R. Jansson, A. Ågren, H. Laudon, and B. Malm-Renöfält. 2014. Groundwater discharge creates hotspots of riparian plant species richness in a boreal forest stream network. Ecology 95:715–725.

Lancaster, J., and A. G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. Journal of the North American Benthological Society 12:385–393.

Leach, J., and R. Moore. 2011. Stream temperature dynamics in two hydrogeomorphically distinct reaches. Hydrological Processes 25:679–690.

Leach, J., D. Olson, P. Anderson, and B. Eskelson. 2017. Spatial and seasonal variability of forested headwater stream temperatures in western oregon, usa. Aquatic sciences 79:291–307.

Leibold, M. A., and J. M. Chase. 2017. Metacommunity ecology. Book, Princeton University Press.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, and others. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leroy, C. J., and J. C. Marks. 2006. Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates. Freshwater Biology 51:605–617.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award lecture. Ecology 73:1943–1967.

Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. Ecology Letters 6:673–679.

Loreau, M., N. Mouquet, and R. D. Holt. 2005. From metacommunities to metaecosystems. Metacommunities: spatial dynamics and ecological communities. The University of Chicago Press, Chicago:418–438.

Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: A review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 49:617–628.

Mac Nally, R., E. Wallis, and P. S. Lake. 2011. Geometry of biodiversity patterning: Assemblages of benthic macroinvertebrates at tributary confluences. Aquatic Ecology 45:43–54.

Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change 102:187–223.

Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: Trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology 88:140–148.

Massol, F., D. Gravel, N. Mouquet, M. W. Cadotte, T. Fukami, and M. A. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. Ecology Letters 14:313–323.

Mathes, M. T., S. G. Hinch, S. J. Cooke, G. T. Crossin, D. A. Patterson, A. G. Lotto, and A. P. Farrell. 2009. Effect of water temperature, timing, physiological condition, and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 67:70–84.

Mayer, T. D. 2012. Controls of summer stream temperature in the pacific northwest. Journal of Hydrology 475:323–335.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, and E. Mayorga. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–312.

McSwain, M. D. 1987. Summer stream temperatures and channel characteristics of a southwestern oregon coastal stream.

Mejia, F. H., A. K. Fremier, J. R. Benjamin, J. R. Bellmore, A. Z. Grimm, G. A. Watson, and M. Newsom. 2019. Stream metabolism increases with drainage area and peaks asynchronously across a stream network. Aquatic Sciences 81:9.

Melton, M. A. 1958. Correlation structure of morphometric properties of drainage systems and their controlling agents. The Journal of Geology 66:442–460.

Melton, M. A. 1965. The geomorphic and paleoclimatic significance of alluvial deposits in southern Arizona. The Journal of Geology 73:1–38.

Merritt, R., K. Cummins, and M. Berg. 2008. An introduction to the aquatic insects of North America, 4th edn. Kendall. Hunt Publishing Company, Dubuque.

Merritt, W. S., Y. Alila, M. Barton, B. Taylor, S. Cohen, and D. Neilsen. 2006. Hydrologic response to scenarios of climate change in sub watersheds of the Okanagan basin, British Columbia. Journal of Hydrology 326:79–108.

Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman, and N. E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. Journal of the American Water Resources Association 43:86–103.

Milesi, S. V., and A. S. Melo. 2013. Conditional effects of aquatic insects of small tributaries on mainstream assemblages: Position within drainage network matters. Canadian Journal of Fisheries and Aquatic Sciences 71:1–9.

Milliman, J. D., and J. P. Syvitski. 1992. Geomorphic/tectonic control of sediment discharge to the ocean: The importance of small mountainous rivers. The journal of Geology 100:525–544.

Milner, V. S., S. M. Yarnell, and R. A. Peek. 2019. The ecological importance of unregulated tributaries to macroinvertebrate diversity and community composition in a regulated river. Hydrobiologia 829:291–305.

Molnar, L. 1996. Trapping Creek restoration project.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association.

Montgomery, D. R., and J. M. Buffington. 1997. Channel-reach morphology in mountain drainage basins. Geological Society of America Bulletin 109:596–611.

Moore, R. D., and S. Wondzell. 2005. Physical hydrology and the effects of forest harvesting in the Pacific Northwest: A review. Journal of the American Water Resources Association 41:763–784.

Moore, R., M. Nelitz, and E. Parkinson. 2013. Empirical modelling of maximum weekly average stream temperature in british columbia, canada, to support assessment of fish habitat suitability. Canadian Water Resources Journal 38:135–147.

Moore, R., D. Spittlehouse, and A. Story. 2005a. Riparian microclimate and stream temperature response to forest harvesting: A review. Journal of the American Water Resources Association 41:813–834.

Moore, R., P. Sutherland, T. Gomi, and A. Dhakal. 2005b. Thermal regime of a headwater stream within a clear-cut, coastal british columbia, canada. Hydrological Processes: An International Journal 19:2591–2608.

Muneepeerakul, R., E. Bertuzzo, H. J. Lynch, W. F. Fagan, A. Rinaldo, and I. Rodriguez-Iturbe. 2008. Neutral metacommunity models predict fish diversity patterns in Mississippi–Missouri basin. Nature 453:220.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:31–36.

Naiman, R. J., H. Décamps, J. Pastor, and C. A. Johnston. 1988. The potential importance of boundaries of fluvial ecosystems. Journal of the North American Benthological Society 7:289–306.

Naiman, R. J., J. M. Melillo, M. A. Lock, T. E. Ford, and S. R. Reice. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68:1139–1156.

Naman, S. M., J. S. Rosenfeld, and J. S. Richardson. 2016. Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. Canadian Journal of Fisheries and Aquatic Sciences 73:1292–1305.

Negishi, J. N., and J. S. Richardson. 2003. Responses of organic matter and macroinvertebrates to placements of boulder clusters in a small stream of southwestern British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 60:247–258.

Negishi, J. N., and J. S. Richardson. 2006. An experimental test of the effects of food resources and hydraulic refuge on patch colonization by stream macroinvertebrates during spates. Journal of Animal Ecology 75:118–129.

Nelson, K. C., and M. A. Palmer. 2007. Stream temperature surges under urbanization and climate change: Data, models, and responses. Journal of the American Water Resources Association 43:440–452.

Nilsson, C., L. E. Polvi, J. Gardeström, E. M. Hasselquist, L. Lind, and J. M. Sarneel. 2015. Riparian and in-stream restoration of boreal streams and rivers: Success or failure? Ecohydrology 8:753–764.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2018. Vegan: Community ecology package.

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997a. Ecological theory and community restoration ecology. Restoration Ecology 5:291–300.

Palmer, M. A., C. C. Hakenkamp, and K. Nelson-Baker. 1997b. Ecological heterogeneity in streams: Why variance matters. Journal of the North American Benthological Society 16:189–202.

Palmer, M. A., K. L. Hondula, and B. J. Koch. 2014. Ecological restoration of streams and rivers: Shifting strategies and shifting goals. Annual Review of Ecology, Evolution, and Systematics 45:247–269.

Palmer, M. A., and N. L. Poff. 1997. Heterogeneity in streams: The influence of environmental heterogeneity on patterns and processes in streams. Journal of the North American Benthological Society 16:169–173.

Paola, C., G. Parker, R. Seal, S. K. Sinha, J. B. Southard, and P. R. Wilcock. 1992. Downstream fining by selective deposition in a laboratory flume. Science 258:1757–1760.

Parker, M. S. 1989. Effect of substrate composition on detritus accumulation and macroinvertebrate distribution in a southern Nevada desert stream. The Southwestern Naturalist:181–187.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual review of Ecology and Systematics 32:333–365.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2018. nlme: Linear and nonlinear mixed effects models.

Poff, N. L., and J. Ward. 1990. Physical habitat template of lotic systems: Recovery in the context of historical pattern of spatiotemporal heterogeneity. Environmental management 14:629.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual review of ecology and systematics 28:289–316.

Pond, G. J., K. M. Fritz, and B. R. Johnson. 2016. Macroinvertebrate and organic matter export from headwater tributaries of a central Appalachian stream. Hydrobiologia 779:75–91.

Poole, G. C. 2002. Fluvial landscape ecology: Addressing uniqueness within the river discontinuum. Freshwater Biology 47:641–660.

Powell, D. M. 1998. Patterns and processes of sediment sorting in gravel-bed rivers. Progress in Physical Geography 22:1–32.

Power, G., R. Brown, and J. Imhof. 1999. Groundwater and fish—insights from northern North America. Hydrological Processes 13:401–422.

Power, M. E., and W. E. Dietrich. 2002. Food webs in river networks. Ecological Research 17:451–471.

Presa Abos, C., F. Lepori, B. McKie, and B. Malmqvist. 2006. Aggregation among resource patches can promote coexistence in stream-living shredders. Freshwater Biology 51:545–553.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652–661.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rhoads, B. L. 1987. Changes in stream channel characteristics at tributary junctions. Physical Geography 8:346–361.

Rice, S. 1998. Which tributaries disrupt downstream fining along gravel-bed rivers? Geomorphology 22:39– 56.

Rice, S., and M. Church. 1998. Grain size along two gravel-bed rivers: Statistical variation, spatial pattern and sedimentary links. Earth Surface Processes and Landforms 23:345–363.

Rice, S. P. 2016. Tributary connectivity, confluence aggradation and network biodiversity. Geomorphology.

Rice, S. P., M. T. Greenwood, and C. Joyce. 2001a. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. Canadian Journal of Fisheries and Aquatic Sciences 58:824–840.

Rice, S. P., M. T. Greenwood, and C. B. Joyce. 2001b. Macroinvertebrate community changes at coarse sediment recruitment points along two gravel bed rivers. Water Resources Research 37:2793–2803.

Rice, S. P., P. Kiffney, C. Greene, and G. R. Pess. 2008. The ecological importance of tributaries and confluences. Pages 209–242 *in* River confluences, tributaries and the fluvial network. John Wiley & Sons, England.

Richardson, J. S. 2019. Biological diversity in headwater streams. Water 11.

Richardson, J. S., and R. J. Mackay. 1991. Lake outlets and the distribution of filter feeders: An assessment of hypotheses. Oikos:370–380.

Richardson, J. S., R. J. Naiman, F. J. Swanson, and D. E. Hibbs. 2005. Riparian communities associated with pacific northwest headwater streams: assemblages, processes, and uniqueness. Journal of the American Water Resources Association 41:935–947.

Roni, P., K. Hanson, and T. Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. North American Journal of Fisheries Management 28:856–890.

Sabo, J. L., K. Bestgen, W. Graf, T. Sinha, and E. E. Wohl. 2012. Dams in the Cadillac Desert: Downstream effects in a geomorphic context. Annals of the New York Academy of Sciences 1249:227–246.

Sabo, J. L., M. Caron, R. Doucett, K. L. Dibble, A. Ruhi, J. C. Marks, B. A. Hungate, and T. A. Kennedy. 2018. Pulsed flows, tributary inputs and food-web structure in a highly regulated river. Journal of Applied Ecology 55:1884–1895.

Sabo, J. L., and E. M. Hagen. 2012. A network theory for resource exchange between rivers and their watersheds. Water Resources Research 48.

Sabo, J., and M. Power. 2002. River–watershed exchange: Effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83:1860–1869.

Sánchez-Piñero, F., and G. A. Polis. 2000. Bottom-up dynamics of allochthonous input: Direct and indirect effects of seabirds on islands. Ecology 81:3117–3132.

Schiarizza, P., and N. Church. 1996. Digital Geology Data, Thompson - Okanagan (East Part). http://www. empr.gov.bc.ca/mining/geoscience/publicationscatalogue/openfiles/1996/pages/1996-20.aspx.

Schnetger, B., and C. Lehners. 2014. Determination of nitrate plus nitrite in small volume marine water samples using vanadium (iii) chloride as a reduction agent. Marine Chemistry 160:91–98.

Shakesby, R., and S. Doerr. 2006. Wildfire as a hydrological and geomorphological agent. Earth-Science

#### Reviews 74:269–307.

Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography:1–20.

Skaug, H., D. Fournier, B. Bolker, A. Magnusson, and A. Nielsen. 2016. Generalized linear mixed models using 'AD Model Builder'.

Smith, H. G., G. J. Sheridan, P. N. Lane, P. Nyman, and S. Haydon. 2011. Wildfire effects on water quality in forest catchments: A review with implications for water supply. Journal of Hydrology 396:170–192.

Smith, K., and M. Lavis. 1975. Environmental influences on the temperature of a small upland stream. Oikos:228–236.

Southwood, T. R. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46:337–365.

Staelens, J., L. Nachtergale, S. Luyssaert, and N. Lust. 2003. A model of wind-influenced leaf litterfall in a mixed hardwood forest. Canadian Journal of Forest Research 33:201–209.

Stone, D. M. 1977. Leaf dispersal in a pole-size maple stand. Canadian Journal of Forest Research 7:189– 192.

Swan, C. M., and B. L. Brown. 2017. Metacommunity theory meets restoration: Isolation may mediate how ecological communities respond to stream restoration. Ecological Applications 27:2209–2219.

Tanentzap, A. J., B. W. Kielstra, G. M. Wilkinson, M. Berggren, N. Craig, P. A. del Giorgio, J. Grey, J. M. Gunn, S. E. Jones, J. Karlsson, C. T. Solomon, and M. L. Pace. 2017. Terrestrial support of lake food webs: Synthesis reveals controls over cross-ecosystem resource use. Science Advances 3:e1601765.

Tanentzap, A. J., E. J. Szkokan-Emilson, B. W. Kielstra, M. T. Arts, N. D. Yan, and J. M. Gunn. 2014. Forests fuel fish growth in freshwater deltas. Nature Communications 5:4077.

Tavernini, D., and T. Hoover. 2016.. Unpublished data.

Thompson, R., and C. Townsend. 2006. A truce with neutral theory: Local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. Journal of Animal Ecology 75:476–484.

Thorp, J. H., and M. D. Delong. 1994. The riverine productivity model: An heuristic view of carbon sources and organic processing in large river ecosystems. Oikos:305–308.

Thorp, J. H., M. C. Thoms, and M. D. Delong. 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. River Research and Applications 22:123–147.

Tomanova, S., P. A. Tedesco, M. Campero, P. A. Van Damme, N. Moya, and T. Oberdorff. 2007. Longitudinal and altitudinal changes of macroinvertebrate functional feeding groups in neotropical streams: A test of the

river continuum concept. Fundamental and Applied Limnology/Archiv für Hydrobiologie 170:233–241.

Tonkin, J. D., F. Altermatt, D. S. Finn, J. Heino, J. D. Olden, S. U. Pauls, and D. A. Lytle. 2018. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. Freshwater Biology 63:141–163.

Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society:36–50.

Turner, M. G. 1989. Landscape ecology: The effect of pattern on process. Annual review of ecology and systematics 20:171–197.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Vellend, M., and A. Agrawal. 2010. Conceptual synthesis in community ecology. The Quarterly Review of Biology 85:183–206.

Vogel, S. 2009. Glimpses of creatures in their physical worlds. Book, Princeton University Press.

Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. Nature 424:1035.

Wallace, J. B., T. Cuffney, J. Webster, G. Lugthart, K. Chung, and B. Goldowitz. 1991. Export of fine organic particles from headwater streams: Effects of season, extreme discharges, and invertebrate manipulation. Limnology and Oceanography 36:670–682.

Wallace, J. B., S. Eggert, J. L. Meyer, and J. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

Wallis, E., R. Mac Nally, and S. Lake. 2009. Do tributaries affect loads and fluxes of particulate organic matter, inorganic sediment and wood? Patterns in an upland river basin in south-eastern Australia. Hydrobiologia 636:307–317.

Walther, D. A., and M. R. Whiles. 2011. Secondary production in a southern illinois headwater stream: Relationships between organic matter standing stocks and macroinvertebrate productivity. Journal of the North American Benthological Society 30:357–373.

Ward, J. V., and J. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Dynamics of lotic ecosystems 10:29–42.

Webb, B. W., D. M. Hannah, R. D. Moore, L. E. Brown, and F. Nobilis. 2008. Recent advances in stream and river temperature research. Hydrological Processes: An International Journal 22:902–918.

Webb, B., and Y. Zhang. 1997. Spatial and seasonal variability in the components of the river heat budget. Hydrological Processes 11:79–101.

Webb, B., and Y. Zhang. 1999. Water temperatures and heat budgets in dorset chalk water courses. Hydrological Processes 13:309–321.

Wehrly, K. E., M. J. Wiley, and P. W. Seelbach. 2003. Classifying regional variation in thermal regime based on stream fish community patterns. Transactions of the American Fisheries Society 132:18–38.

Welsh Jr, H. H., G. R. Hodgson, B. C. Harvey, and M. F. Roche. 2001. Distribution of juvenile coho salmon in relation to water temperatures in tributaries of the Mattole River, California. North American Journal of Fisheries Management 21:464–470.

Westrek Geotechnical Services. 2000. Upper Mission Creek Terrain Stability Study for Riverside Forest Products Ltd., Kelowna Division.

Wetmore, S. H., R. J. Mackay, and R. W. Newbury. 1990. Characterization of the hydraulic habitat of brachycentrus occidentalis, a filter-feeding caddisfly. Journal of the North American Benthological Society 9:157–169.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81–120.

Williams, D., and H. Hynes. 1976. The recolonization mechanisms of stream benthos. Oikos 27:265–272.

Wilson, M. J., and M. E. McTammany. 2014. Tributary and mainstem benthic macroinvertebrate communities linked by direct dispersal and indirect habitat alteration. Hydrobiologia 738:75–85.

Wilson, M. J., and M. E. McTammany. 2016. Spatial scale and dispersal influence metacommunity dynamics of benthic invertebrates in a large river. Freshwater Science 35:738–747.

Winemiller, K. O., A. S. Flecker, and D. J. Hoeinghaus. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. Journal of the North American Benthological Society 29:84–99.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: Contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. Canadian Journal of Fisheries and Aquatic Sciences 54:1259–1269.

Wipfli, M. S., and D. P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern alaska: Implications for downstream salmonid production. Freshwater Biology 47:957–969.

Wolman, M. G. 1954. A method of sampling coarse river-bed material. EOS, Transactions American Geophysical Union 35:951–956.

Wooster, D., and A. Sih. 1995. A review of the drift and activity responses of stream prey to predator presence. Oikos:3–8.

# Appendix

Appendix A: Supporting information for Chapter 2.

Table A1: Plot location upstream and downstream of tributary, distance along the river (rkm) from upstreammost site, and geographic coordinates for each site.

Stream	Tributary	Upstream	Downstream	River km	Latitude	Longitude
Mission Creek	Belgo Creek	120	180	0	49°52'1.41"N	119° 9'14.84"W
	Dave's Creek	270	35	10.3	49°51'13.51"N	119°17'5.89"W
	KLO Creek	70	30	18.3	49°50'38.61"N	119°21'45.93"W
West Kettle River	Kallis Creek	25	50	0	49°41'34.26"N	119° 6'1.75"W
	Trapping Creek	100	35	17.7	49°33'49.39"N	119° 3'18.29"W
	Wilkinson Creek	35	50	26	49°30'13.27"N	119° 6'54.99"W



Figure A1: Validation of modeled downstream mainstem nitrate concentration by comparing predicted and observed values. Black line indicates 1:1 ratio between the two values, meaning no error in modeled values.



Figure A2: Validation of modeled downstream mainstem TDP concentration by comparing predicted and observed values. Black line indicates 1:1 ratio between the two values, meaning no error in modeled values.



Figure A3: Validation of modeled downstream mainstem TP concentration by comparing predicted and observed values. Black line indicates 1:1 ratio between the two values, meaning no error in modeled values.



Figure A4: Observed nitrate concentration across the three sampling periods (panels 1-3) in the mainstem (red) and tributary (blue) with the corresponding basin area of the upstream catchment.



Figure A5: Observed total dissolved phosphorus concentration across the three sampling periods (panels 1-3) in the mainstem (red) and tributary (blue) with the corresponding basin area of the upstream catchment.



Figure A6: Observed total phosphorus concentration across the three sampling periods (panels 1-3) in the mainstem (red) and tributary (blue) with the corresponding basin area of the upstream catchment.



Figure A7: Mainstem (black) and tributary (grey) hourly temperature at each of the six tributaries.



Figure A8: Mainstem (black) and tributary (grey) hourly temperature at each of the six tributaries across first ten days of sampling. The shorter timespan compared to Figure A7 is to more clearly display the tributary-mainstem comparison. Note that during this time period, there were no data available for for the mainstem in KLO Creek.

# Appendix B: Supporting information for Chapter 3.

(Appendix begins on next page due to the size of Table B1)

Table B1: Summary statistics of taxa included (black) and omitted (grey) from analysis. Mean represents mean number of individuals in samples (± 1 SD). Total abundance is total across all samples. Percent of samples present is the percentage of total samples that the taxa was identified and present in. "MS" represents morphospecies that were not positively identified.

Taxon	Mean ( ± 1SD)		Total Abundance	% Samples Present	Total Relative Abundance (%)
Chironomidae_orthocladiinae_spp	21.1	± 30.97	1876	95.51	6.88%
Lepidostomatidae_lepidostoma	113.2	± 245.78	10076	95.51	36.94%
Baetidae_baetis	10.4	± 13.49	926	91.01	3.39%
Chironomidae_tanytarsini	12.1	± 25.31	1078	91.01	3.95%
Elmidae_narpus	3.7	± 3.98	328	84.27	1.20%
Chironomidae_brillia	45.8	± 89.22	4074	82.02	14.94%
Chironomidae_tanypodinae	3.9	± 4.47	349	80.90	1.28%
Ameletidae_ameletus	5.7	± 7.35	508	79.78	1.86%
Pternarcyidae_pteronarcys	5.7	± 5.91	508	77.53	1.86%
Chloroperlidae_haploperla	2.2	± 2.62	199	75.28	0.73%
Brachycentridae_brachycentrus	6.8	± 15.88	605	75.28	2.22%
Chironomidae_corynoneura	7.3	± 16.04	651	71.91	2.39%
Ephemerellidae_serratella	7.8	± 11.62	691	70.79	2.53%
Hydropsychidae_hydropsyche	16.7	± 25.06	1482	69.66	5.43%
Heptageniidae_rithrogena	6.9	± 10.52	615	59.55	2.25%
Perlodidae_skwala	2.1	± 3.57	190	57.30	0.70%
Ephemerellidae_drunella_spp	3.2	± 5.83	285	52.81	1.04%
Hydropsychidae_arctopsyche	3.8	± 7.63	337	50.56	1.24%
Nemouridae_zapada	4.1	± 9.53	366	50.56	1.34%
Perlidae_claassenia	0.9	± 1.11	77	48.31	0.28%
Pternarcyidae_pteronarcella	1.2	± 1.81	108	47.19	0.40%
Chloroperlidae_suwallia	1.9	± 2.91	171	43.82	0.63%
Leptophlebidae_paraleptophlebidae	1.1	± 1.97	101	41.57	0.37%
Tipulidae_MS1	2.9	± 8.37	261	41.57	0.96%
Heptageniidae_cinygma	1.5	± 3.44	135	34.83	0.49%
Simuliidae_simulium	1.4	± 3.46	123	33.71	0.45%
Brachycentridae_micrasema	0.9	± 2.93	79	31.46	0.29%
Ephemerellidae_drunella_doddsi	1.5	± 4.02	132	28.09	0.48%
Rhyachophilidae_rhyachophila	0.3	± 0.71	30	24.72	0.11%
Perlodidae_MS2	0.4	± 0.79	34	24.72	0.12%
Perlidae_perlesta	0.3	± 0.69	24	20.22	0.09%
Ephemerellidae_ephemerella	1.1	± 3.66	101	19.10	0.37%
Perlodidae_setvena	0.3	± 0.79	28	17.98	0.10%
Heptageniidae_cinygmula	0.4	± 0.97	33	17.98	0.12%
Baetidae_heterocloeon	1.5	± 4.58	132	17.98	0.48%
Limnephilidae_dicosmoecus	0.2	± 0.50	18	15.73	0.07%
Heptageniidae_epeorus	0.4	± 1.25	32	15.73	0.12%
Tipulidae_hexatoma	0.2	± 0.80	22	13.48	0.08%
Chloroperlidae_plumiperla	0.3	± 1.08	28	13.48	0.10%
Apataniidae_pedomoecus	0.3	± 0.82	23	12.36	0.08%
Glossosomatidae_agapetus	1.1	± 4.21	94	12.36	0.34%
Ephemerellidae_timpanoga	0.1	± 0.32	10	11.24	0.04%
Chironomidae_MS2	0.2	± 0.47	14	11.24	0.05%
Elmidae_heterlimnius	0.9	± 2.94	76	10.11	0.28%
Table B1 (cont.). Summary statistics of taxa included (black) and omitted (grey) from analysis. Mean represents mean number of individuals in samples (± 1 SD). Total abundance is total across all samples. Percent of samples present is the percentage of total samples that the taxa was identified and present in. "MS" represents morphospecies that were not positively identified.

Таха	Mea	in ( ± 1SD)	Total Abundance	% Samples Present	Total Relative Abundance
Dytiscidae_MS1	0.1	± 0.59	12	8.99	0.04%
Chironomidae_tanytarsus	0.3	± 1.43	25	8.99	0.09%
Coleoptera_MS6_adult	0.1	± 0.32	8	7.87	0.03%
Tipulidae_MS2	0.1	± 0.52	11	7.87	0.04%
Chironomidae_chironominae_spp	0.2	± 1.02	17	7.87	0.06%
Brachycentridae_MS3	0.8	± 5.75	73	7.87	0.27%
Brachycentridae_MS2	0.2	± 0.89	20	6.74	0.07%
Perlodidae_isoperla	0.1	± 0.23	5	5.62	0.02%
Tipulidae_dicranota	0.1	± 0.28	5	4.49	0.02%
Baetidae_spp	0.1	± 0.33	6	4.49	0.02%
Chloroperlidae_suwallia_MS1	0.1	± 0.64	11	4.49	0.04%
Elmidae_lara	0.0	± 0.26	4	3.37	0.01%
Limnephilidae_MS2	0.0	± 0.26	4	3.37	0.01%
Hydroptilidae_MS1	0.1	± 0.35	5	3.37	0.02%
Coleoptera_MS7_adult	0.0	± 0.15	2	2.25	0.01%
Perlodidae_MS1	0.0	± 0.15	2	2.25	0.01%
Tipulidae_MS3	0.0	± 0.15	2	2.25	0.01%
Ephemerellidae_anthopotamus	0.0	± 0.24	3	2.25	0.01%
Tipulidae_dicranota_MS2	0.0	± 0.24	3	2.25	0.01%
Chloroperlidae_rickera	0.0	± 0.33	4	2.25	0.01%
Chironomidae_MS1	0.0	± 0.11	1	1.12	0.00%
Coleoptera_MS2_adult	0.0	± 0.11	1	1.12	0.00%
Diptera_MS2	0.0	± 0.11	1	1.12	0.00%
Dixidae_dixa	0.0	± 0.11	1	1.12	0.00%
Hemiptera_MS1	0.0	± 0.11	1	1.12	0.00%
Hydropsychidae_smicridea	0.0	± 0.11	1	1.12	0.00%
Leptophlebidae_MS2	0.0	± 0.11	1	1.12	0.00%
Nemouridae_malenka	0.0	± 0.11	1	1.12	0.00%
Perlidae_calineuria	0.0	± 0.11	1	1.12	0.00%
Perlidae_eccoptera	0.0	± 0.11	1	1.12	0.00%
Perlodidae_megarcys	0.0	± 0.11	1	1.12	0.00%
Tipulidae_MS4	0.0	± 0.11	1	1.12	0.00%
Trichoptera_MS1	0.0	± 0.11	1	1.12	0.00%
Trichoptera_MS2	0.0	± 0.11	1	1.12	0.00%
Uenoidae_neophylax	0.0	± 0.11	1	1.12	0.00%
Chironomidae_podonominae	0.0	± 0.21	2	1.12	0.01%
Coleoptera_MS5_adult	0.0	± 0.21	2	1.12	0.01%
Heptageniidae_MS1	0.0	± 0.21	2	1.12	0.01%
Tubellaria	0.0	± 0.42	4	1.12	0.01%
		Total	27277		100.00%
		Included in Analysis	27030		99.09%

Table B2: Top 15 (out of 32) model ranking results predicting rarefied taxonomic richness based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank			Model Equation	on			k	L-L	AICc	$\Delta AICc$	$w_i$
1	<b>y</b> = β0					+ Velocity	10	-175.48	373.78	0.00	0.17
2	$y = \beta 0$						9	-176.85	373.98	0.20	0.15
3	y = $\beta$ 0	 + CPOM x Pos				+ Velocity	11	-174.82	375.07	1.29	0.09
4	y = $\beta$ 0		+ Substrate x Pos			+ Velocity	11	-174.95	375.34	1.56	0.08
5	y = $\beta$ 0	 + CPOM x Pos					10	-176.29	375.39	1.61	0.07
6	y = $\beta$ 0		+ Substrate x Pos				10	-176.32	375.45	1.68	0.07
7	y = $\beta$ 0	 + CPOM x Pos	+ Substrate x Pos			+ Velocity	12	-174.29	376.68	2.90	0.04
8	y = $\beta$ 0			+ CPOMAccum		+ Velocity	11	-175.71	376.85	3.07	0.04
9	y = $\beta$ 0	 + CPOM x Pos	+ Substrate x Pos				11	-175.75	376.92	3.14	0.03
10	y = $\beta$ 0			+ CPOMAccum			10	-177.11	377.05	3.27	0.03
11	$y = \beta 0$				+ Depth	+ Velocity	11	-175.93	377.29	3.51	0.03
12	y = $\beta$ 0				+ Depth		10	-177.25	377.31	3.53	0.03
13	$y = \beta 0$	 + CPOM x Pos		+ CPOMAccum		+ Velocity	12	-175.07	378.24	4.46	0.02
14	y = $\beta$ 0		+ Substrate x Pos	+ CPOMAccum		+ Velocity	12	-175.18	378.47	4.69	0.02
15	y = $\beta$ 0	 + CPOM x Pos		+ CPOMAccum			11	-176.56	378.54	4.77	0.02

Table B3: Top 15 (out of 32) model ranking results predicting Shannon index based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank	Model Equation						k	L-L	AICc	$\Delta {\rm AICc}$	wi
1	<b>y</b> = β0						9	-37.29	94.86	0.00	0.50
2	$y = \beta 0$					+ Velocity	10	-36.63	96.08	1.22	0.27
3	$y = \beta 0$	 + CPOM x Pos					10	-38.31	99.45	4.59	0.05
4	$y = \beta 0$		+ Substrate x Pos				10	-38.32	99.45	4.59	0.05
5	$y = \beta 0$	 + CPOM x Pos				+ Velocity	11	-37.46	100.35	5.49	0.03
6	$y = \beta 0$		+ Substrate x Pos			+ Velocity	11	-37.71	100.85	5.99	0.03
7	$y = \beta 0$				+ Depth		10	-39.37	101.56	6.70	0.02
8	$y = \beta 0$			+ CPOMAccum			10	-39.49	101.80	6.94	0.02
9	$y = \beta 0$				+ Depth		11	-38.62	102.67	7.82	0.01
10	$y = \beta 0$			+ CPOMAccum		+ Velocity	11	-38.84	103.10	8.24	0.01
11	$y = \beta 0$	 + CPOM x Pos	+ Substrate x Pos				11	-39.34	104.11	9.25	0.00
12	$y = \beta 0$	 + CPOM x Pos	+ Substrate x Pos			+ Velocity	12	-38.54	105.19	10.33	0.00
13	$y = \beta 0$		+ Substrate x Pos		+ Depth		11	-40.36	106.15	11.29	0.00
14	$y = \beta 0$	 + CPOM x Pos			+ Depth		11	-40.39	106.21	11.35	0.00
15	$y = \beta 0$	 + CPOM x Pos		+ CPOMAccum			11	-40.51	106.46	11.60	0.00

Table B4: Top 15 (out of 32) model ranking results predicting total abundance based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank	Model Equation						k	L-L	AICc	$\Delta {\rm AICc}$	wi
1	y = β0		+ Substrate x Pos				10	-517.98	1058.79	0.00	0.12
2	$y = \beta 0$						9	-519.39	1059.05	0.26	0.10
3	$y = \beta 0$					+ Velocity	10	-518.29	1059.40	0.61	0.09
4	$y = \beta 0$		+ Substrate x Pos			+ Velocity	11	-517.06	1059.55	0.77	0.08
5	$y = \beta 0$		+ Substrate x Pos	+ CPOMAccum			11	-517.33	1060.09	1.31	0.06
6	$y = \beta 0$			+ CPOMAccum			10	-518.79	1060.40	1.61	0.05
7	$y = \beta 0$		+ Substrate x Pos		+ Depth		11	-517.64	1060.71	1.93	0.04
8	$y = \beta 0$			+ CPOMAccum		+ Velocity	11	-517.79	1061.01	2.22	0.04
9	$y = \beta 0$		+ Substrate x Pos	+ CPOMAccum		+ Velocity	12	-516.50	1061.11	2.32	0.04
10	$y = \beta 0$				+ Depth		10	-519.18	1061.19	2.40	0.04
11	$y = \beta 0$	 + CPOM x Pos	+ Substrate x Pos				11	-517.92	1061.28	2.49	0.03
12	$y = \beta 0$		+ Substrate x Pos		+ Depth	+ Velocity	12	-516.65	1061.41	2.62	0.03
13	$y = \beta 0$				+ Depth	+ Velocity	11	-518.02	1061.47	2.68	0.03
14	$y = \beta 0$	 + CPOM x Pos					10	-519.33	1061.49	2.70	0.03
15	$y = \beta 0$	 + CPOM x Pos				+ Velocity	11	-518.28	1061.99	3.20	0.02

Table B5: Top 15 (out of 32) model ranking results predicting Pielou's evenness based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank	Model Equation					k	L-L	AICc	$\Delta {\rm AICc}$	wi
1	y = β0					9	64.44	-108.60	0.00	0.87
2	$y = \beta 0$				+ Velocity	10	63.17	-103.52	5.08	0.07
3	$y = \beta 0$	 + CPOM x Pos				10	62.27	-101.72	6.88	0.03
4	$y = \beta 0$		+ Substrate x Pos			10	62.12	-101.43	7.17	0.02
5	$y = \beta 0$			+ CPOMAccum		10	61.08	-99.34	9.26	0.01
6	$y = \beta 0$	 + CPOM x Pos			+ Velocity	11	61.21	-96.99	11.62	0.00
7	$y = \beta 0$		+ Substrate x Pos		+ Velocity	11	60.84	-96.25	12.35	0.00
8	$y = \beta 0$	 + CPOM x Pos	+ Substrate x Pos			11	59.96	-94.49	14.12	0.00
9	$y = \beta 0$			+ CPOMAccum	+ Velocity	11	59.84	-94.26	14.35	0.00
10	$y = \beta 0$	 + CPOM x Pos		+ CPOMAccum		11	58.90	-92.38	16.22	0.00
11	$y = \beta 0$		+ Substrate x Pos	+ CPOMAccum		11	58.77	-92.11	16.50	0.00
12	$y = \beta 0$	 + CPOM x Pos	+ Substrate x Pos		+ Velocity	12	58.88	-89.65	18.96	0.00
13	$y = \beta 0$	 + CPOM x Pos		+ CPOMAccum	+ Velocity	12	57.86	-87.62	20.99	0.00
14	$y = \beta 0$		+ Substrate x Pos	+ CPOMAccum	+ Velocity	12	57.51	-86.92	21.69	0.00
15	$y = \beta 0$	 + CPOM x Pos	+ Substrate x Pos	+ CPOMAccum		12	56.59	-85.08	23.52	0.00

Table B6: Top 15 (out of 32) model ranking results predicting abundance of *Lepidostoma* sp. based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank			Model Equati	on			k	L-L	AICc	$\Delta {\rm AICc}$	$w_i$
1	$y = \beta_0$				+ Depth		10	-390.06	802.94	0.00	0.27
2	$y = \beta_0$			+ CPOMAccum	+ Depth		11	-389.45	804.33	1.39	0.14
3	$y = \beta_0$				+ Depth	+ Velocity	11	-389.77	804.97	2.02	0.10
4	$y = \beta_0$	 + CPOM x Pos	NA		+ Depth		11	-389.99	805.41	2.47	0.08
5	$y = \beta_0$		+ Substrate x Pos		+ Depth		11	-390.03	805.48	2.53	0.08
6	y = $\beta_0$			+ CPOMAccum	+ Depth	+ Velocity	12	-389.21	806.52	3.57	0.05
7	$y = \beta_0$	 + CPOM x Pos		+ CPOMAccum	+ Depth		12	-389.36	806.82	3.87	0.04
8	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum	+ Depth		12	-389.42	806.94	4.00	0.04
9	$y = \beta_0$	 + CPOM x Pos			+ Depth	+ Velocity	12	-389.72	807.54	4.59	0.03
10	y = $\beta_0$		+ Substrate x Pos		+ Depth	+ Velocity	12	-389.73	807.56	4.62	0.03
11	y = $\beta_0$						9	-393.66	807.60	4.66	0.03
12	$y = \beta_0$	 + CPOM x Pos	+ Substrate x Pos		+ Depth		12	-389.95	808.01	5.06	0.02
13	y = $\beta_0$	 + CPOM x Pos		+ CPOMAccum	+ Depth	+ Velocity	13	-389.13	809.12	6.18	0.01
14	$y = \beta_0$		+ Substrate x Pos	+ CPOMAccum	+ Depth	+ Velocity	13	-389.17	809.18	6.24	0.01
15	y = $\beta_0$			+ CPOMAccum			10	-393.31	809.43	6.49	0.01

Table B7: Top 15 (out of 32) model ranking results predicting abundance of *Pteronarcys* sp. based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank			Model Equati	on			k	L-L	AICc	$\Delta {\rm AICc}$	$w_i$
1	$y = \beta_0$			+ CPOMAccum		+ Velocity	11	-191.64	408.70	0.00	0.13
2	y = $\beta_0$					+ Velocity	10	-192.95	408.71	0.01	0.13
3	y = $\beta_0$			+ CPOMAccum	+ Depth	+ Velocity	12	-190.76	409.63	0.93	0.08
4	y = $\beta_0$				+ Depth	+ Velocity	11	-192.17	409.76	1.06	0.08
5	y = $\beta_0$	 + CPOM x Pos				+ Velocity	11	-192.36	410.15	1.45	0.06
6	y = $\beta_0$	 + CPOM x Pos		+ CPOMAccum		+ Velocity	12	-191.18	410.46	1.75	0.05
7	$y = \beta_0$						9	-195.20	410.67	1.97	0.05
8	y = $\beta_0$		+ Substrate x Pos			+ Velocity	11	-192.95	411.32	2.62	0.04
9	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum		+ Velocity	12	-191.63	411.37	2.67	0.03
10	y = $\beta_0$			+ CPOMAccum			10	-194.30	411.42	2.72	0.03
11	y = $\beta_0$	 + CPOM x Pos			+ Depth	+ Velocity	12	-191.71	411.52	2.81	0.03
12	y = $\beta_0$	 + CPOM x Pos		+ CPOMAccum	+ Depth	+ Velocity	13	-190.42	411.69	2.99	0.03
13	y = $\beta_0$				+ Depth		10	-194.46	411.73	3.03	0.03
14	$y = \beta_0$	 + CPOM x Pos					10	-194.64	412.10	3.40	0.02
15	$\mathbf{y} = \beta_0$		+ Substrate x Pos	+ CPOMAccum	+ Depth	+ Velocity	13	-190.70	412.25	3.55	0.02

Table B8: Top 15 (out of 32) model ranking results predicting abundance of *Brachycentrus* sp. based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank			Model Equati	on			k	L-L	AICc	$\Delta {\rm AICc}$	$w_i$
1	$y = \beta_0$			+ CPOMAccum			10	-206.82	436.46	0.00	0.15
2	y = $\beta_0$						9	-208.29	436.86	0.40	0.12
3	$y = \beta_0$		+ Substrate x Pos	+ CPOMAccum			11	-206.05	437.53	1.07	0.09
4	y = $\beta_0$			+ CPOMAccum	+ Depth		11	-206.17	437.76	1.31	0.08
5	$y = \beta_0$			+ CPOMAccum		+ Velocity	11	-206.35	438.13	1.67	0.06
6	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum	+ Depth		12	-205.11	438.32	1.86	0.06
7	$y = \beta_0$		+ Substrate x Pos				10	-207.83	438.49	2.03	0.05
8	y = $\beta_0$					+ Velocity	10	-207.95	438.71	2.25	0.05
9	$y = \beta_0$	 + CPOM x Pos		+ CPOMAccum			11	-206.80	439.02	2.56	0.04
10	y = $\beta_0$			+ CPOMAccum	+ Depth	+ Velocity	12	-205.54	439.18	2.72	0.04
11	y = $\beta_0$	 + CPOM x Pos					10	-208.25	439.31	2.86	0.03
12	$y = \beta_0$		+ Substrate x Pos	+ CPOMAccum		+ Velocity	12	-205.65	439.41	2.95	0.03
13	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum	+ Depth	+ Velocity	13	-204.56	439.97	3.51	0.03
14	y = $\beta_0$	 + CPOM x Pos	+ Substrate x Pos	+ CPOMAccum			12	-206.03	440.17	3.71	0.02
15	$y = \beta_0$	 + CPOM x Pos		+ CPOMAccum	+ Depth		12	-206.15	440.40	3.94	0.02

Table B9: Top 15 (out of 32) model ranking results predicting abundance of Hydropsychidae spp. based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank			Model Equati	on			k	L-L	AICc	$\Delta {\rm AICc}$	$w_i$
1	$y = \beta_0$		+ Substrate x Pos		+ Depth	+ Velocity	12	-182.12	392.34	0.00	0.36
2	$y = \beta_0$				+ Depth	+ Velocity	11	-183.86	393.15	0.82	0.24
3	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum	+ Depth	+ Velocity	13	-182.02	394.90	2.56	0.10
4	$y = \beta_0$	 + CPOM x Pos	+ Substrate x Pos		+ Depth	+ Velocity	13	-182.04	394.92	2.59	0.10
5	y = $\beta_0$			+ CPOMAccum	+ Depth	+ Velocity	12	-183.77	395.65	3.31	0.07
6	y = $\beta_0$	 + CPOM x Pos			+ Depth	+ Velocity	12	-183.83	395.77	3.43	0.07
7	y = $\beta_0$	 + CPOM x Pos	+ Substrate x Pos	+ CPOMAccum	+ Depth	+ Velocity	14	-181.96	397.60	5.26	0.03
8	y = $\beta_0$	 + CPOM x Pos	NA	+ CPOMAccum	+ Depth	+ Velocity	13	-183.75	398.36	6.02	0.02
9	y = $\beta_0$		+ Substrate x Pos			+ Velocity	11	-187.86	401.15	8.81	0.00
10	y = $\beta_0$					+ Velocity	10	-189.51	401.83	9.50	0.00
11	$y = \beta_0$		+ Substrate x Pos	+ CPOMAccum		+ Velocity	12	-187.63	403.37	11.03	0.00
12	y = $\beta_0$	 + CPOM x Pos	+ Substrate x Pos			+ Velocity	12	-187.71	403.52	11.18	0.00
13	y = $\beta_0$		+ Substrate x Pos		+ Depth		11	-189.22	403.86	11.52	0.00
14	y = $\beta_0$	 + CPOM x Pos				+ Velocity	11	-189.22	403.88	11.54	0.00
15	y = $\beta_0$			+ CPOMAccum		+ Velocity	11	-189.33	404.09	11.76	0.00

Table B10: Top 15 (out of 32) model ranking results predicting abundance of Heptageniidae spp. based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank			Model Equati	on			k	L-L	AICc	$\Delta {\rm AICc}$	$w_i$
1	$y = \beta_0$						9	-255.26	530.79	0.00	0.23
2	$y = \beta_0$					+ Velocity	10	-254.90	532.61	1.82	0.09
3	$y = \beta_0$				+ Depth		10	-254.94	532.70	1.91	0.09
4	$y = \beta_0$			+ CPOMAccum			10	-255.11	533.05	2.26	0.08
5	y = $\beta_0$	 + CPOM x Pos					10	-255.14	533.10	2.31	0.07
6	$y = \beta_0$		+ Substrate x Pos				10	-255.26	533.33	2.54	0.07
7	y = $\beta_0$				+ Depth	+ Velocity	11	-254.56	534.55	3.76	0.04
8	$y = \beta_0$	 + CPOM x Pos				+ Velocity	11	-254.74	534.90	4.11	0.03
9	y = $\beta_0$	 + CPOM x Pos			+ Depth		11	-254.76	534.94	4.15	0.03
10	$y = \beta_0$			+ CPOMAccum		+ Velocity	11	-254.80	535.03	4.24	0.03
11	$y = \beta_0$			+ CPOMAccum	+ Depth		11	-254.81	535.04	4.25	0.03
12	y = $\beta_0$		+ Substrate x Pos			+ Velocity	11	-254.89	535.21	4.42	0.03
13	$y = \beta_0$		+ Substrate x Pos		+ Depth		11	-254.94	535.30	4.51	0.02
14	y = $\beta_0$	 + CPOM x Pos		+ CPOMAccum			11	-254.99	535.40	4.61	0.02
15	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum			11	-255.11	535.65	4.86	0.02

Table B11: Top 15 (out of 32) model ranking results predicting abundance of *Baetis* sp. based on measured AICc values. k indicates number of terms included in model, L-L is the log-likelihood of model i,  $\Delta$ AICc is the difference between AICc of model i and the top ranked model,  $w_i$  is the model weighting of model i relative to all other fitted models to form a cumulative weighting score of 1. Ellipses represent fixed factors that were consistent across all models (position + substrate + CPOM + mainstem + period)

Rank			Model Equati	on			k	L-L	AICc	$\Delta {\rm AICc}$	$w_i$
1	$y = \beta_0$			+ CPOMAccum	+ Depth	+ Velocity	12	-254.51	537.12	0.00	0.19
2	y = $\beta_0$			+ CPOMAccum		+ Velocity	11	-256.35	538.14	1.01	0.11
3	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum	+ Depth	+ Velocity	13	-253.69	538.24	1.11	0.11
4	y = $\beta_0$	 + CPOM x Pos		+ CPOMAccum	+ Depth	+ Velocity	13	-253.95	538.76	1.63	0.08
5	y = $\beta_0$	 + CPOM x Pos		+ CPOMAccum		+ Velocity	12	-255.68	539.47	2.35	0.06
6	y = $\beta_0$				+ Depth	+ Velocity	11	-257.14	539.71	2.59	0.05
7	y = $\beta_0$	 + CPOM x Pos	+ Substrate x Pos	+ CPOMAccum	+ Depth	+ Velocity	14	-253.17	540.02	2.90	0.04
8	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum		+ Velocity	12	-255.96	540.03	2.91	0.04
9	y = $\beta_0$	 + CPOM x Pos			+ Depth	+ Velocity	12	-256.26	540.63	3.51	0.03
10	y = $\beta_0$			+ CPOMAccum	+ Depth		11	-257.71	540.84	3.72	0.03
11	y = $\beta_0$		+ Substrate x Pos	NA	+ Depth	+ Velocity	12	-256.41	540.92	3.79	0.03
12	y = $\beta_0$			+ CPOMAccum			10	-259.06	540.95	3.83	0.03
13	y = $\beta_0$					+ Velocity	10	-259.27	541.36	4.24	0.02
14	y = $\beta_0$	 + CPOM x Pos	+ Substrate x Pos	+ CPOMAccum		+ Velocity	13	-255.33	541.51	4.39	0.02
15	y = $\beta_0$		+ Substrate x Pos	+ CPOMAccum	+ Depth		12	-256.77	541.65	4.52	0.02



Figure B1: Probability of significant difference (p < 0.05) in rarefied taxonomic richness due to position across 100 simulations using generated data based on variance derived from observed data.