

THESIS

AQUATIC INSECT β -DIVERSITY AMONG SMALL MOUNTAIN HEADWATER
STREAMS AND THE ROLE OF MULTIPLE MECHANISMS MAINTAINING
COMMUNITY STRUCTURE

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ABSTRACT

AQUATIC INSECT β -DIVERSITY AMONG SMALL MOUNTAIN HEADWATER STREAMS AND THE ROLE OF MULTIPLE MECHANISMS MAINTAINING COMMUNITY STRUCTURE

Despite lower local richness (α -diversity), individual headwater tributaries often retain highly distinct aquatic insect communities (β -diversity) within the overall river network. This trend is presumed especially true among high-elevation streams; where high β -diversity is driven by the effects of steep topography and harsh climatic conditions limiting dispersal between isolated mountaintop “islands.” However, inference has been predominantly drawn from observed trends along single-thread channels (higher-elevation headwaters through lower-elevation mainstems); and the increased size and hydrologic connectivity accompanying lower-elevation mainstems provide potential alternative explanations for this pattern. Controlling for habitat size, I sampled aquatic insect communities in 24 headwater streams from three adjacent river drainages spanning 2000-3500 m in elevation. I measured β -diversity among streams within each drainage (community turnover- β across elevation) and β -diversity across drainages (community dissimilarity- β within elevation “zones”). Turnover- β across elevation was consistently high and displayed no trend. Additionally, dissimilarity- β across drainages was not significantly different between high-elevation and low-elevation zones. These results provide the first evidence that β -diversity among low-elevation headwater communities is equivalent to communities at high-elevations.

Evidence suggests that high β -diversity among small headwater streams is attributed to low habitat connectivity and/or to high habitat heterogeneity, resulting from their isolated position within the dendritic network and strong responses to the surrounding environment. In order to disentangle the role of multiple mechanisms maintaining β -diversity, I utilized the unique landscape of mountain ranges, exhibiting steep gradients of spatial distance, local environmental conditions, and disturbance regimes. I characterized all 24 sites using explanatory variables categorized into spatial predictors (describing geographic location), environmental predictors (describing local habitat), and flow regime predictors (describing potential disturbances overtime). Using a series of redundancy analyses (RDA) I tested the ability of each categorized predictor group to significantly explain variation in community structure among those sites within a drainage and among those sites within an elevation zone. Further, original communities were partitioned into unique assemblages distinguished by the presence/absence of key ecological traits. Using interpretation of potential underlying mechanistic processes, I tested a priori hypotheses regarding the change in relationship between trait-partitioned assemblages. Results determined that although environmental predictors best explained community turnover- β within drainages, they were unable to explain community dissimilarity- β within any elevation zone, where habitat heterogeneity is presumably lower and inter-site network distance is higher. Additionally, dissimilarity- β among high-elevation communities was only explained by spatial predictors, supporting previous hypotheses that these communities are isolated by distance, while community dissimilarity- β among low-elevation sites was only explained by flow regime predictors. Overall, these findings suggest that despite consistent patterns in β -diversity, the relative role of mechanisms maintaining this diversity is context dependent, presenting important implications regarding the successful conservation of these dynamic systems.

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CHAPTER 1: PATTERNS OF AQUATIC INSECT β -DIVERSITY AMONG SMALL
HEADWATER STREAMS IS INDEPENDENT ACROSS ELEVATION GRADIENTS AND
BETWEEN ELEVATION ZONES

Summary

Mountain ranges provide a unique landscape for identifying and explaining multiple patterns of diversity, as environmental conditions change rapidly over a relatively small spatial scale. Specific to stream ecosystems, a negative relationship is commonly reported between local α -diversity and elevation while more recently reported relationships between regional β -diversity and elevation is often positive. These patterns are often both attributed to the harsh climatic conditions characteristic of high elevations and presumed reduction in insect dispersal ability. Consequently, high-elevation stream communities are thought to be comprised of many endemic taxa with narrow distributions. This inference has been predominantly drawn from trends along longitudinal gradients that compare higher-elevation tributaries to their lower-elevation mainstems. However, the increased size and hydrologic connectivity accompanying lower-elevation mainstems complicates direct comparisons, leading to alternative explanations for these patterns. In this work, I sampled aquatic insects in 24 similar-sized, low-order tributaries from three adjacent river drainages spanning ~2000-3500 m in elevation. From these 24 streams, over 14,000 individuals were identified to the generic level. In addition to α -diversity, I calculated β -diversity among streams within each drainage (i.e. community turnover across elevation) and β -diversity among streams across all drainages (i.e. community dissimilarity within elevation “zones”). Although the negative α -diversity trend was supported, community turnover across elevation was consistently high and displayed no trend and community

dissimilarity across high-elevation sites was not significantly different than low-elevation community dissimilarity. These results from similar-sized streams provide the first evidence that β -diversity among small, isolated headwater streams may be equivalent across broad elevation gradients.

Introduction

A fundamental objective of community ecology is identifying the patterns and processes underlying spatial variation in biodiversity (Gaston *et al.* 1995, Rosenzweig 1995). Historically, the majority of research has focused on documenting trends in the local richness within a given community (i.e. α -diversity) and/or the regional richness summed across all communities within a given landscape (i.e. γ -diversity). These efforts resulted in widely recognized large-scale patterns such as the negative correlation between diversity along increasing latitudinal and elevation gradients (Gaston 2000, Willig *et al.* 2003, Hillbrand 2004, Rahbek 2005). Until recently, significantly less consideration has been given to the relationship between regional and local diversity, measuring the variation in local diversity among communities within a region (i.e. β -diversity) (Whittaker 1960, 1972). The identification of β -diversity patterns had the potential to inform a broader understanding of the processes that regulate community assembly and maintain both regional- and local-scale diversity (Wilson and Shmida 1984, Mouquet and Loreau 2003, Soininen *et al.* 2007). Therefore, determining patterns of β -diversity presents applicable information that may be imperative to the conservation management of vulnerable ecological communities (Whittaker *et al.* 2005, Anderson *et al.* 2011); however, for many ecosystems and taxonomic groups, general trends remain uncertain (McKnight *et al.* 2007).

Stream and river ecosystems are among those in need of considerable attention with regards to how species diversity changes within and between communities. Freshwater communities are comprised of some of the most imperiled taxonomic groups in the world because they are characterized by a uniquely isolated habitat structure, taxa with reduced dispersal ability across the landscape, and specific adaptations to thermally and hydrologically dynamic environments, (Ricciardi and Rasmussen 1999, Dudgeon *et al.* 2006, Poff *et al.* 2012). Furthermore, global- and regional-scale patterns of diversity are often inconsistent within freshwater ecosystems, as many freshwater biota exhibit disproportionately higher diversity in temperate systems as compared to the distributions of marine and terrestrial taxonomic groups (Patrick 1964, Arthington 1990, Flowers 1991, Crow 1993, Master *et al.* 1998, Willig *et al.* 2003, Vinson and Hawkins 2003, Heino 2009, Pearson & Boyero 2009). Their ubiquitous distribution across the globe makes stream insects particularly useful organisms for studying patterns of biodiversity. Additionally, aquatic insects are an interesting taxonomic group to study as they exhibit a diversity of ecological roles (i.e. detritivores, herbivores, predators, etc.); and, although they spend most of their lifecycle under water, the short-lived adult stages of many species are terrestrial (Merritt *et al.* 2008).

Inspired by the foundational River Continuum Concept, diversity research in stream ecology has primarily focused on changes along longitudinal gradients, from smaller upstream headwaters to larger downstream mainstem channels (Vannote *et al.* 1980, Cushing *et al.* 1983, Minshall *et al.* 1985 *a*, Statzner and Higler 1985, Grubaugh *et al.* 1996). The River Continuum Concept hypothesizes that changes in habitat size, accompanied by differences in habitat conditions (e.g. resource input, light, temperature, etc.), are coupled with predictable changes in the richness and composition of stream insect communities (Vannote *et al.* 1980). Therefore, β -

diversity is expected to increase with increasing differences in stream size; however the rate of this change in this relationship should depend upon the rate of change in associated environmental gradients.

Several studies have applied the River Continuum Concept to montane stream systems, documenting changes in α - and β -diversity from smaller high-elevation streams to larger low-elevation streams, where environmental conditions change rapidly over a relatively small spatial scale. Similar to patterns documented in terrestrial systems, these studies have frequently reported a negative correlation between α -diversity and elevation (Allan 1975, Ward 1986, Perry and Schaeffer 1987, Omerod *et al.* 1994, Suren 1994, Jacobsen *et al.* 1997, Monaghan *et al.* 2000, Jacobsen 2003, Jacobsen 2004, Finn and Poff 2005, Finn *et al.* 2013). Theoretically, transitions in environmental conditions along an elevation gradient should be accompanied by changes in community composition, as differences in climate regimes and local habitat characteristics filter species traits (Hynes 1970, Allan and Castillo 2007, Merritt *et al.* 2008), increasing niche differentiation and β -diversity between communities within the same river network (Allan 1975, Ward 1986, Jacobsen *et al.* 1997, Jacobsen 2003, Jacobsen 2004, Finn and Poff 2005, Wang *et al.* 2012, Finn *et al.* 2013). Few studies have actually quantified the β -diversity of stream insect communities across an elevation gradient.

However, several authors have reported little change in community composition within a network, until higher elevations when sudden changes in community structure have been observed (Allan 1975, Jacobsen 2004, Finn *et al.* 2013). This pattern indicates higher β -diversity at higher elevations and is often explained by the combination of abrupt changes in environmental conditions accompanied by the loss of many widely distributed taxa that are only replaced by a limited number of taxa restricted to high-elevations (Allan 1975, Ward 1986, Perry

and Schaeffer 1987, Ward 1994, Jacobsen 2004) Additionally, higher elevations have been characterized by a significantly greater β -diversity among communities across different drainage networks than compared to mid and/or lower elevation communities (Jacobsen *et al.* 1997, Jacobsen 2003, Jacobsen 2004, Finn and Poff 2005, Finn *et al.* 2013). This pattern is often explained by the increased isolation of mountain peak “islands” separated by harsher terrestrial climates effectively creating barriers to dispersal (Ward 1994, Finn and Poff 2005). These two different concepts of β -diversity: directional β -diversity across elevation within a river drainage (i.e. community turnover) and non-directional β -diversity across river drainages within an elevation zone (i.e. community dissimilarity) (Anderson *et al.* 2011) are equally valuable measures for understanding the degree of biotic heterogeneity and maintenance of diversity in stream ecosystems across a regional-scale.

Findings of both higher community turnover and higher community dissimilarity at higher elevation systems indicates that high-elevation taxa are narrowly distributed; therefore, high elevation taxa may be dispersal limited or have narrow physiological tolerances and are expected to be considerably more vulnerable to regional scale environmental changes (Monaghan *et al.* 2005, Finn *et al.* 2013). Although high elevation communities may actually support a greater proportion of endemic taxa, results from previous elevation studies that have sampled longitudinally, observing changes in community composition from higher-elevation tributaries through lower-elevation mainstem channels, may overemphasize the influence of elevation on both α - and β -diversity patterns (Dodds and Hisaw 1925, Allan 1975, Minshall *et al.* 1985 *b*, Ward 1986, Perry and Scheffer 1987, Grubaugh *et al.* 1996, Finn and Poff 2005, Finn *et al.* 2013). The highly correlated relationship between stream size and taxonomic diversity has been well documented, and small headwater streams, regardless of elevation, typically exhibit

lower richness than larger mainstem channels (Vannote *et al.* 1980, Minshall *et al.* 1985 *b*, Ward 1986, Lake *et al.* 1994, Malmqvist and Maki 1994, Grubaugh *et al.* 1996, Vinson and Hawkins 1998, Clark *et al.* 2008, Heino 2009). Additionally, recent findings suggest that despite lower α -diversity, small isolated streams, exhibiting considerable habitat heterogeneity, maintain disproportionately high β -diversity within a network (Clarke *et al.* 2008, Finn *et al.* 2011). Thus, results from longitudinally sampled elevation studies, may actually reflect changes in larger habitat size and greater habitat connectivity at low elevations (Jacobsen 2004). The few elevation studies of aquatic insect diversity that have controlled for stream size along the elevation gradient, most of which were limited to tropical regions, have not quantified both turnover and dissimilarity of the whole community (Jacobsen *et al.* 1997, Jacobsen 2003, Jacobsen 2004, Gill *et al.* 2014); complicating comparison to patterns of diversity within temperate mountain streams.

To my knowledge, this is the first study to quantify β -diversity of entire aquatic insect communities along an elevation gradient and among elevation zones, while controlling for stream size. In an effort to gain a better understanding of the biotic diversity in temperate stream ecosystems, and the mechanisms that maintain this disproportionate heterogeneity within small isolated headwater systems, I sampled aquatic insect communities in 24 streams (1st-3rd order) ranging from ~2000-3500 m in elevation within a total of three drainages along Colorado's Front Range. I use taxonomic community composition, in order to examine patterns of richness, turnover, and dissimilarity and answer the following questions 1) Does local α -diversity of headwater streams decrease with elevation? 2) Is community turnover among small heterogeneous streams greater at higher elevations or consistent across the gradient? 3) Is

community dissimilarity among spatially isolated headwater streams greater at higher elevations or similar across all elevations?

Methods

Study Area

The study streams were located within the Southern Rocky Mountain region of Colorado and spanned three adjacent watersheds that drain the eastern slope of the state's Front Range: the Cache la Poudre (CP), the Big Thompson (BT), and the Saint Vrain (SV) (Figure 1.1). Within a single drainage, eight low order tributaries (Strahler order 1st – 3rd) were selected so that sites were distributed approximately every 200 m along the gradient, ranging from nearly 2,000 m to 3,500 m. This sampling design was repeated within each of the three drainages, resulting in a total of 24 study sites throughout the region, which are hereafter referred to by their two-letter drainage code followed by a numerical value representing their position along the elevation gradient (#1-8, increasing in elevation) (Figure 1.1, Table 1.1). In addition to being subdivided into three drainages, all 24 sites were also subdivided into one of three elevation zones determined by the eight sites with the lowest elevation (~2000-2400 m), the eight mid-elevation sites (~2450-2950 m), and the eight sites with the highest elevation (~3050-3500 m) (Table 1.1). Although maintaining an equal number of sites within each elevation zone served to eliminate statistical bias in subsequent analysis (Peres-Neto *et al.* 2006), the range of each of the delineated elevation zones roughly corresponded to previously described vegetation zones and snow cover zones within Colorado's Front Range (Peet 1981, Richer *et al.* 2013). Lower elevation sites correspond with vegetation zones dominated by *Pinus ponderosa* (~1700 to 2300-2500 m) that are characterized by intermediate snow cover (< 2550 m). Mid-elevations sites correspond with

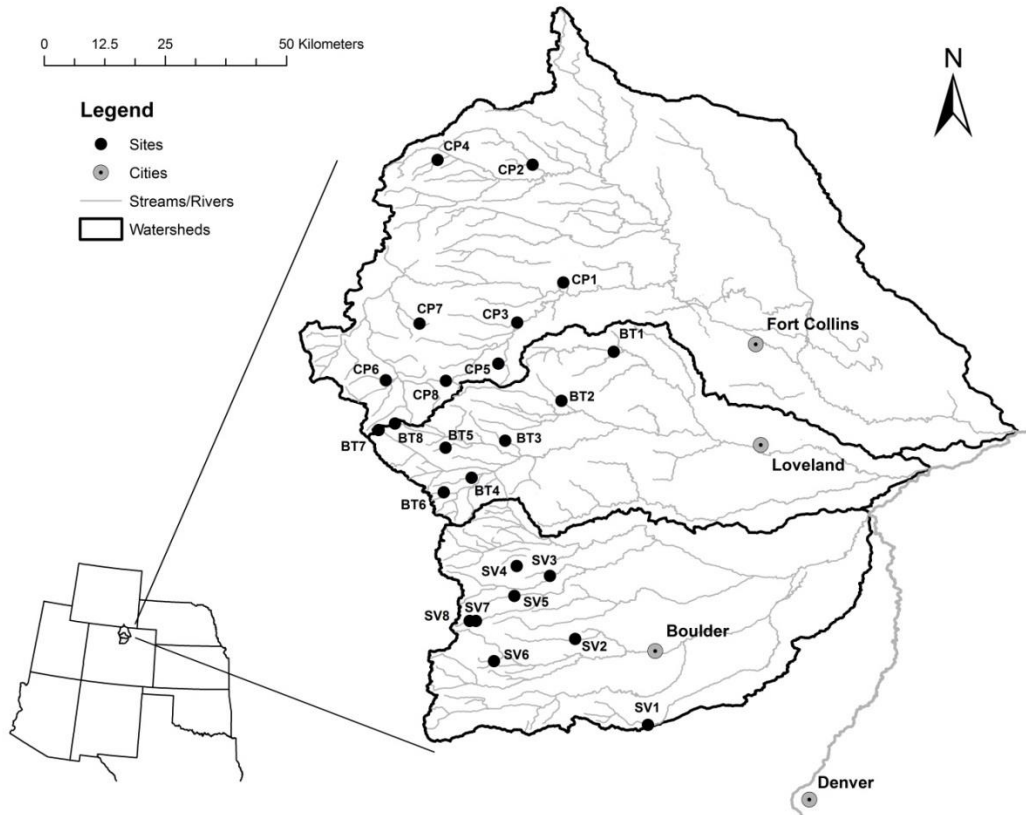


Figure 1.1. Map of the study area, depicting all 24 sampling sites. The bottom left inset locates Colorado within the United States and the three river drainages within the Colorado Rocky Mountains. Sites CP1-CP8 are located within the Cache la Poudre River drainage, sites BT1-BT8 within the Big Thompson River drainage, and sites SV1-SV8 within the Saint Vrain Creek drainage. Refer to Table 1.1 for site names and coordinates.

vegetation zones that are dominated by *Pinus contorta* (~2300-2500 to ~2700-2900) that are characterized by zones of transitional snow cover (2550-3050 m). Lastly, high-elevation sites correspond to vegetation zones dominated by *Picea abies* (~2700-2900 to ~3500) that are characterized by persistent snow cover (>3050 m) (Peet 198, Richer *et al.* 2013). Thus, the range of each of these elevation zones were expected to maintain ecological relevance.

In an effort to reduce the effects of confounding habitat diversity on patterns of community composition, site selection along the gradient controlled for comparable habitat size. Average stream width and stream width to depth ratio were not significantly correlated with

Table 1.1 Drainage, GPS coordinates, elevation (m), elevation zone, and generic richness from each site location. Alphanumeric ID's for each site indicates drainage and position along the elevation gradient. Refer to Figure 1.1 for map of site locations. * denotes sites that have no published name.

Drainage	Site Name & ID	Latitude (°N)	Longitude (°W)	Elevation (m)	Elevation Zone	Generic Richness
Cache la Poudre	Elkhorn Creek - CP1	40.7000	105.4415	1992	Low	34
	Trail Creek - CP2	40.9185	105.4984	2181	Low	30
	Little Beaver - CP3	40.6253	105.5271	2411	Low	22
	Beaver Creek - CP4	40.9277	105.6744	2590	Mid	24
	unnamed* - CP5	40.5492	105.5617	2775	Mid	15
	Corral Creek - CP6	40.5181	105.7708	3060	High	18
	E.F. Sheep Creek - CP7	40.6235	105.7080	3166	High	17
	unnamed* - CP8	40.5173	105.6589	3397	High	20
Big Thompson	Buckhorn Creek - BT1	40.5711	105.3477	2001	Low	35
	Miller Fork - BT2	40.4799	105.4448	2252	Low	21
	Black Canyon - BT3	40.4056	105.5491	2443	Mid	23
	Mill Creek - BT4	40.3368	105.6113	2573	Mid	22
	Hidden Valley - BT5	40.3926	105.6597	2900	Mid	20
	unnamed* - BT6	40.3098	105.6631	3051	High	17
	Big Thompson - BT7	40.4256	105.7840	3364	High	18
	Fall River - BT8	40.4380	105.7535	3478	High	5
Saint Vrain	Coal Creek - SV1	39.8776	105.2844	2015	Low	16
	Four Mile Creek - SV2	40.0374	105.4194	2189	Low	26
	Cave Creek - SV3	40.1547	105.4663	2388	Low	25
	Rock Creek - SV4	40.1727	105.5279	2643	Mid	21
	Beaver Creek - SV5	40.1173	105.5324	2830	Mid	25
	Caribou Creek - SV6	39.9961	105.5699	2964	Mid	18
	unnamed* - SV7	40.0707	105.6033	3249	High	14
	unnamed* - SV8	40.0709	105.6149	3348	High	15

elevation ($R^2 = 0.0627$ and $R^2 = 0.0017$, respectively). Additionally, no sites were located downstream of any major lake outlet and the most optimal sites in areas with minimal anthropogenic impact were chosen for each elevation zone. The headwaters of all three drainage basins are located within the protected areas of Rocky Mountain National Park and/or Indian Peaks Wilderness, while the lower elevation tributaries are located within either federally or municipally protected lands. All sites were sampled one time in the summer of 2011 between the dates of June 26th and August 12th. Although year round sampling has been shown to yield greater species richness of multiple aquatic insect taxa across a range of elevations (Ward, 1986), single-sample ‘snapshot’ studies are commonly used to capture the response of community composition along environmental gradients (Richards *et al.* 1997, US EPA 2006).

Aquatic insects

In each study site, benthic macroinvertebrate samples were collected along a 200 m reach using a D-frame kicknet (mesh size 500 μm). As opposed to a fixed quadrat sampler, this semi-quantitative sampling technique was chosen because it enables the sampling of multiple microhabitats and is more comprehensive of total richness (Resh and Rosenberg 1984). Sampling effort per site was standardized using a 5 minute timed collection in which time spent per microhabitat was adjusted according to the proportion of each microhabitat type per site (e.g. riffles, runs, pools, boulders, and woody debris). The semi-quantitative method allowed for the estimation of relative density of all taxa per site which, with the exception of chironomids, identified to the family level, were used for the subsequent β -diversity analyses. Samples were preserved in 95% ethanol and later identified (usually to the generic level) and enumerated

(Hauer and Lamberti 2007); over 14,000 individuals were identified from all 24 streams (Appendix I).

Statistical analyses

Study site α -diversity for taxonomic groups were summed for each site and plotted against site elevation to calculate regression statistics. All β -diversity calculations and subsequent statistical tests were performed using PC-ORD (McCune and Mefford 2011). Community turnover along the elevation gradients were determined using pairwise calculations of β -diversity between all adjacent pairs of sites within a single drainage and plotted against average elevation. Using relative abundance in multivariate taxonomic space, I quantified values of β -diversity between adjacent pairs of sites using the quantitative Sørensen Index (i.e. Bray-Curtis multivariate index). The quantitative Sørensen Index was selected because pairwise multivariate measurements of β -diversity are recommended for measuring changes in turnover along a gradient (Anderson *et al.* 2011). Additionally, compared to similar multivariate indices, the quantitative Sørensen index exhibits less sensitivity to the abundance of the most dominant species and is commonly used to quantify changes in ecological communities along gradients (Morlon *et al.* 2008, Anderson *et al.* 2011). Values for each pair of sites, ranging from zero (i.e. no β -diversity) to one (i.e. no similarity), were regressed against the average elevation between the two sites; regression statistics were calculated individually with each drainage, as well as, all values plotted together. I note that pairwise turnover calculations are inherently non-independent and therefore, significance of the regression was generated using Mantel tests with 1000 random permutations (Manly 1991, Anderson *et al.* 2011).

For dissimilarity analyses all 24 sites were divided into one of three elevation zones based on site elevation instead of drainage. The lowest eight sites ranged from approximately ~2000 – 2450 m, the middle eight sites ranged from ~2450 – 2950 m, and the highest eight sites ranged from a~ 3050-3500 m. Using Sørensen's distance measure I applied a multi-response permutation procedure (MRPP) in PC-ORD to test for significant differences in taxonomic community composition between the three low-, mid-, and high-elevation zones (McCune and Mefford 2011). Community dissimilarity among drainages was determined using pairwise calculations of β -diversity between all possible pairs of sites within each of the elevation zones. In order to facilitate comparison with values of community turnover, I used the quantitative Sørensen Index to calculate the ecological distance between all pairs of sites plotted in multivariate space. Although all multivariate measurements of β -diversity using abundance data are sensitive to differences in species richness and relative abundance, there were no a priori expectations of significant differences in α -diversity among sites within elevation zones (Koleff et al. 2003). Furthermore, thorough and equal sampling among was ensured to reduce this potential bias. Therefore, the quantitative Sørensen Index, also commonly used to dissimilarity between a group of sites, is also appropriate for quantifying β -diversity within elevation zones (Brown and Swan 2010, Anderson *et al.* 2011, Finn et al. 2013). An MRPP was applied on the resulting distance matrices to test differences in community dissimilarity between low-, mid-, and high- elevation sites.

Results

Aquatic insects and α -diversity

Overall a total number of 68 distinct stream insect taxa from all 24 study locations were identified (Appendix I). Local richness at individual sites (α -diversity) displayed a significantly negative relationship with increasing elevation ($p < 0.001$, $R^2 = 0.55$) with the number of individual taxa ranging from 35 taxa at site BT_1 (in the lowest elevation zone) to 5 taxa at site BT_8 (in the highest elevation zone) (Figure 1.2). Of the 68 total taxa identified, 54 of these

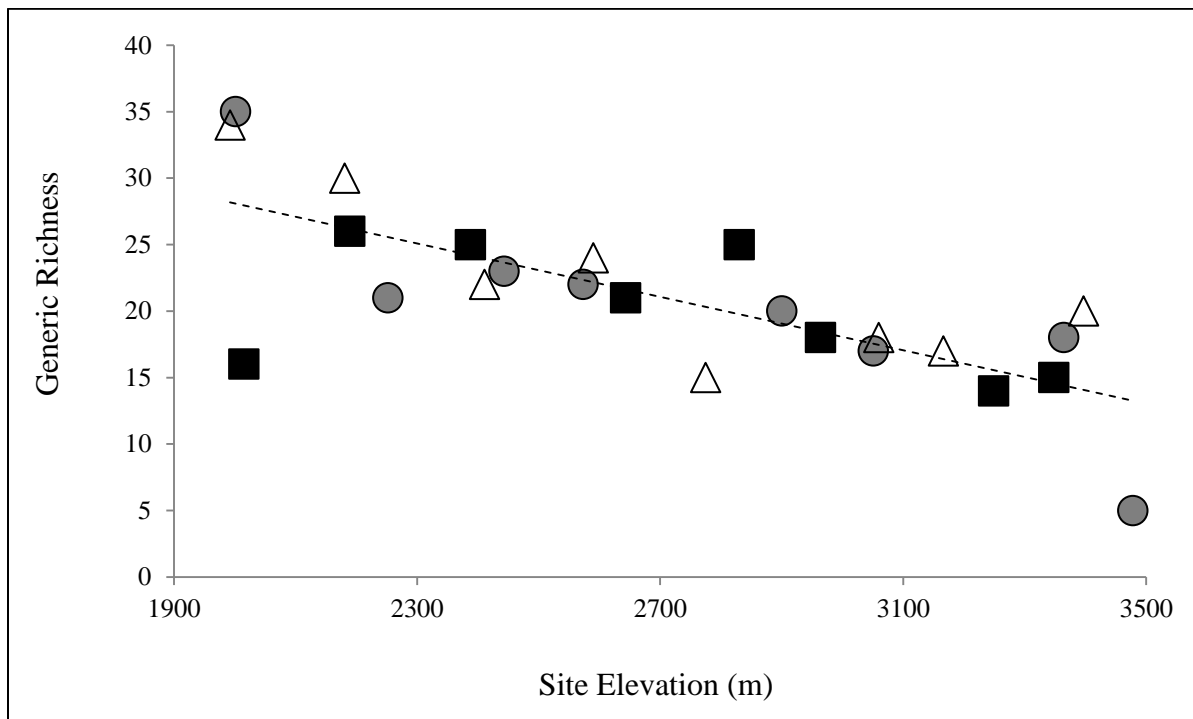


Figure 1.2. Regression plot of the generic richness at each site across the elevation gradient (m), with a dashed line indicating the significance of the relationship ($R^2 = 0.55$, $p < 0.001$) (Sites within the Cache la Poudre River drainage are depicted as \triangle ; within the Big Thompson River drainage as \bullet ; and within the Saint Vrain Creek drainage as \blacksquare).

were present at low-elevation sites (Zone 1), 43 at mid-elevation sites (Zone 2), and 39 at high-elevation sites (Zone 3); indicating the presence of unique taxa within each elevation zone (Figure 1.3). Results from the MRPP confirmed that the community structure among the three groups was significantly different ($A = 0.10$, $p < 0.0001$, all pairwise comparisons: $p < 0.005$).

Community turnover

Community turnover of taxonomic composition along was not significantly correlated with elevation when data from all three drainage were analyzed together ($p = 0.18$, $R^2 = 0.014$), nor when drainages were considered independently (BT: $p = 0.21$, $R^2 = 0.087$; CP: $p = 0.84$, $R^2 =$

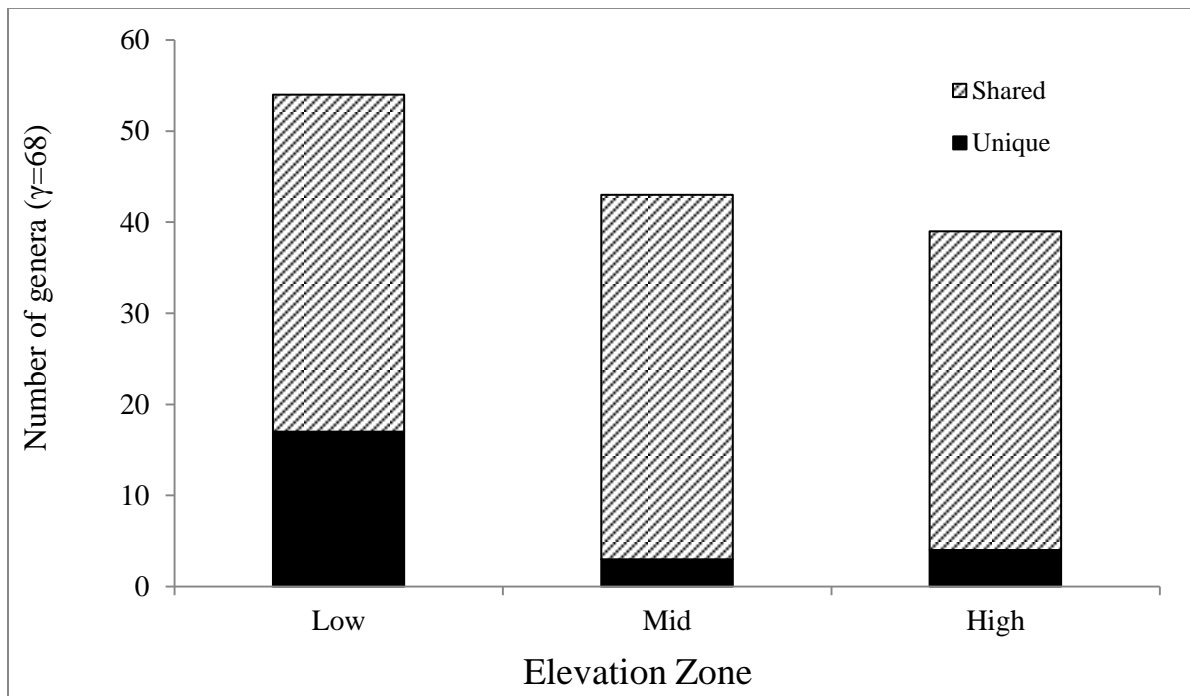


Figure 1.3. Histogram depicting the number of genera collected within each elevation zone (i.e. low, mid, or high) out of the total 68 taxa identified. Within each elevation zone the total number of taxa are partitioned into the number of taxa that were unique to each individual zone (solid fraction) and the number of taxa shared with other zones (diagonal lined fraction).

0.002; SV: $p = 0.06$, $R^2 = 0.183$) (Figure 1.4a-d). However, community turnover was consistently high across the elevation gradient, with an average rate of 0.54 ($\sigma = 0.17$) and highest values peaking at high elevation sites in both the Big Thompson and Cache la Poudre drainages (Figure 4b&c), and at low-elevation sites in all three drainages (Figure 1.4a-d).

Community dissimilarity

Community dissimilarity was significantly higher among high-elevation communities when compared to mid-elevation communities ($\mu = 0.63$ and 0.46 , respectively; $\sigma = 0.23$ and 0.10 , respectively) (MRPP, $p < 0.001$) and also higher among low-elevation communities when compared to mid-elevation communities ($\mu = 0.61$ and 0.46 , respectively; $\sigma = 0.15$ and 0.10 , respectively) ($p < 0.001$). However, the community dissimilarity among high-elevation and low-elevation communities was not significantly different from one another ($p = 0.11$) (Figure 1.5).

Discussion

Aquatic insects and α -diversity

Local α -diversity of benthic macroinvertebrate taxa decreased along the elevation gradient, with greatest taxonomic richness at lowest elevation sites (Figure 1.2). The negative trend found in these results is consistent with the majority of findings from elevation studies of stream insects, including four longitudinal studies conducted in Colorado (Allan 1975, Ward 1986, Perry and Schaeffer 1987, Finn and Poff 2005). It is often hypothesized that this inverse correlation may be explained by higher rates of mutation and speciation in warmer lower elevation systems, younger systems at higher elevations due to differences in geologic history, decrease in regional area at higher elevations, and/or harsh thermal conditions at higher

elevations selecting for limited taxa tolerant of these conditions (Rohde 1992, Ward 1994, Rohde 1999, Jacobsen *et al.* 1997, Jacobsen 2003, Finn and Poff 2005). While generic richness at high-elevation sites was similar to values reported in previous longitudinal studies conducted in Colorado, richness values at low-elevation sites were lower than those previously reported at comparable elevations (Ward 1986, Perry and Schaeffer 1987). The relationship between stream

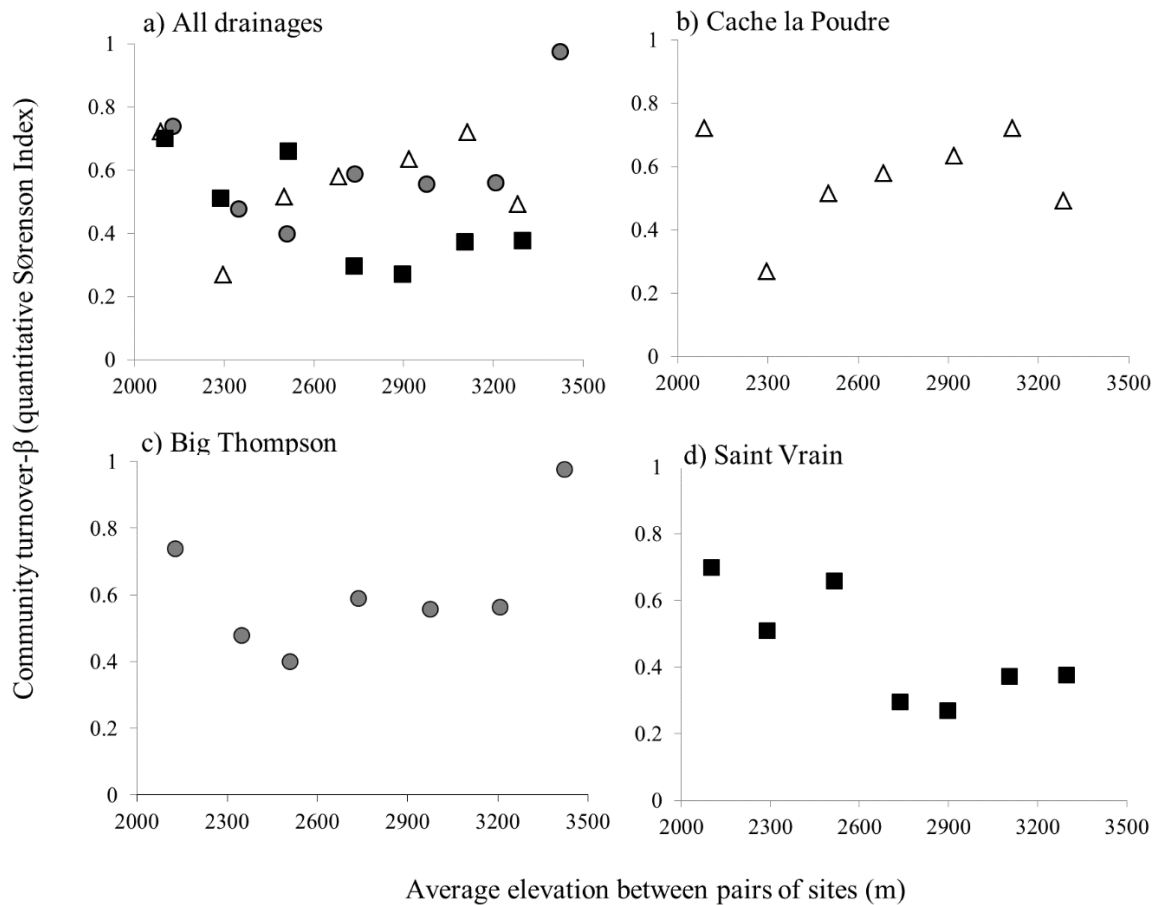


Figure 1.4. Regression plots depicting pairwise community turnover values (quantitative Sørensen Index) across the average elevation between all pairs of adjacent sites within a drainage. Values are plotted for all sites within a.) combined drainages; and for sites within, b.) the Cache la Poudre River drainage = \triangle ; c.) the Big Thompson River drainage = \bullet ; and, d.) the Saint Vrain Creek drainage = \blacksquare .

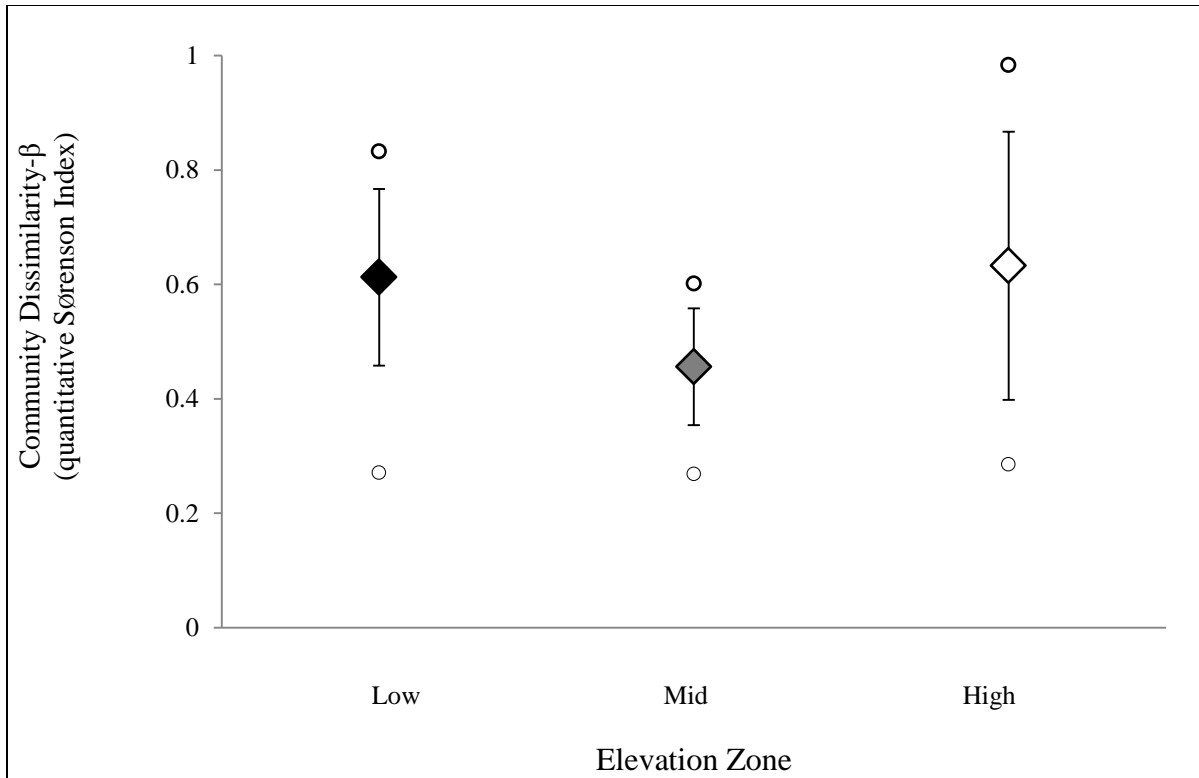


Figure 1.5. Mean pairwise community dissimilarity (quantitative Sørensen Index) within each elevation zone (i.e. low, mid, or high). Error bars depict \pm one standard between all pairwise values within each elevation zone. Maximum and minimum pairwise community dissimilarity values from each zone are displayed (\circ).

order and taxonomic richness implies that this inconsistency in α -diversity at lower elevations can be attributed to differences in habitats size (Vannote *et al.* 1980, Grubaugh *et al.* 1996, Vinson and Hawkins 1998); and thus, the influence of elevation on local α -diversity may be overestimated by previous studies along single-thread, mainstem, channels.

Community turnover

Although rates of community turnover were consistently high, turnover within drainages showed no trend along the elevation gradient (Figure 1.4a-d). To my knowledge, the current study is the first to present these findings; which were unexpected as results from many previous

studies indicate relatively low rates of turnover along the gradient, with higher peaks in community turnover at high elevations (Allan 1975, Ward 1986, Perry and Shaeffer 1987, Jacobsen *et al.* 1997, Jacobsen 2004, Finn *et al.* 2013). Several potential explanations may account for the discrepancy among the current results and other findings from temperate systems. First, given their small size, headwater streams are strongly influenced by the conditions of the surrounding terrestrial ecosystem; and therefore, small streams tend to exhibit stronger responses to subtle differences in local conditions and often display high inter-site habitat heterogeneity among streams (Lowe and Likens 2005, Meyer *et al.* 2007). If local habitat conditions filter species according to their physiological and ecological traits, then high habitat heterogeneity at the regional-scale is expected result in distinct communities, increasing β -diversity (Leibold *et al.* 2004). The previously documented pattern of greater community turnover associated with high elevations has often been described as the loss of broadly distributed taxa reaching the upper range of their altitudinal limits and simultaneously, the moderate gain of cold-adapted taxa restricted to higher elevations. These transitions' in community structure are often attributed to the gradual or abrupt shifts into harsh thermal regimes associated with high-elevation regions (Ward 1986, Perry and Shaeffer 1987, Ward 1994).

Although it is predicted that temperate systems as a whole display highly variable annual thermal regimes (Janzen 1967), the thermal regimes among small headwater streams may exhibit greater distinctions potentially accounting for the inconsistency in community turnover between these results and previous longitudinal studies. Despite broadly fluctuating ambient temperatures, the higher water volume accumulated in larger channels enhances the buffering capacity and significantly dampens the response to changes in temperature (Vannote *et al.* 1980). Additionally, downstream temperatures are further buffered from the input of cold upstream

source water (Mosley 1983), and thermal conditions within a highly connected mainstem channel may remain fairly stable, changing only moderately, along the majority of the elevation gradient. However, further up in elevation, as stream size decreases considerably; reduced buffering capacity may result in abrupt changes in thermal conditions. Therefore, the turnover of taxa typically reported at high-elevations may be driven by this abrupt transition into thermally harsh environments. In contrast, low-elevation headwater streams, closely linked to their surrounding environment, also lack strong buffering capacity (Ward 1985, Lowe and Likens 2005). Throughout an annual cycle poorly buffered streams in seasonal temperate systems are likely to experience a wide range of temperatures; broadly overlapping with other streams positioned along the elevation gradient (Ward 195). However, despite these overlapping thermal ranges, headwater streams partitioned along the elevation gradient are expected to exhibit considerable differences in maximum annual temperature, timing of maximum and minimum extremes, and cumulative degree days (Ward 1985). These thermal variables may be more ecologically meaningful measurements of thermal regime, setting the distributional limits of many taxa, and driving consistently high rates of turnover along the gradient (Ward 1985, Ward and Stanford 1982). Differences in thermal regime extremes may account for the turnover peaks observed at lower elevations in all drainages (Figure 1.4a-d), as higher maximum temperatures may allow for the persistence of taxa primarily distributed among plains streams while limiting taxa primarily distributed within the montane streams.

In addition to the potentially higher inter-site habitat heterogeneity (e.g. temperature, productivity, slope, substrate size, etc.) among small streams, higher degrees of spatial isolation and lower habitat connectivity among headwater streams, may also account for inconsistencies in turnover patterns. The dendritic network characteristic of stream systems inherently results in the

hierarchical connectivity of habitats and differential rates of dispersal (Grant *et al.* 2007, Clarke *et al.* 2008). Although some immature aquatic insects do exhibit net upstream dispersal (Berger and Ward 1989); in-stream dispersal is strongly oriented in the direction of flow; therefore, mainstem channels experience significantly higher rates of in-stream dispersal from upstream communities across the network (MacKay 1992, Brown and Swan 2010). Theoretically, high-dispersal rates outweigh the effects of local environmental filters, enabling populations to persist in habitats where they may otherwise be eliminated and effectively reducing β -diversity among communities (Mouquet and Loreau 2003). Evidence from recent studies have suggested that turnover of most aquatic taxonomic groups is strongly correlated with network distance, as opposed to straight-line or Euclidean distance; therefore, communities that are hydrologically connected to one another exhibit lower β -diversity. Accordingly, mainstem channels experiencing higher rates of instream dispersal have been documented to maintain significantly lower β -diversity than headwater streams within the same network (Brown and Swan 2010, Rouquette *et al.* (2013). Aquatic insects adults are also capable of overland dispersal, although evidence suggests that female flight is often restricted the network corridor where distances between small streams are effectively larger; and although headwater specialists are more likely to disperse in straight-line distances, dispersal is often limited to the closest adjacent streams (Clarke *et al.* 2008, Rouquette *et al.* 2013). These dispersal-driven processes offer further insight into understanding the inconsistencies among turnover patterns. Previously reported values of lower turnover at along the elevation gradient may be attributed to high habitat connectivity and rather than elevation, as turnover among dispersal limited headwater streams was high.

In general, the consistently high rates of directional turnover along the elevation gradient found in these analyses implies that, compared to mainstem systems, many taxa inhabiting

headwater stream communities exhibit narrow distributions, regardless of position along the elevation gradient. While high β -diversity within the network is probably a result of both changing habitat conditions and low dispersal rates, the rate of aquatic insect dispersal is often adequate to maintain colonization within a network (Palmer *et al.* 1996, Poff 1997, Heino and Mykrä 2008). Therefore, changes in local microhabitat conditions are probably predominately responsible for distribution along the elevation gradient.

Community dissimilarity

Greater community dissimilarity across drainages within both high- and low-elevation zones was an unexpected result; and to my knowledge, has never before been reported (Figure 1.5). Most studies, regardless of sampling gradient or latitude, have consistently documented higher dissimilarity among high-elevation communities when compared to mid and/or lower elevation communities (Jacobsen *et al.* 1997, Jacobsen 2003, Jacobsen 2004, Finn & Poff 2005, Finn *et al.* 2013). Although streams in adjacent watersheds may be in close proximity, dispersal limitation is expected to play a larger role in structuring communities across drainages, since flight is often restricted the network corridor (Clarke *et al.* 2008, Rouquette *et al.* 2013).

Several temperate studies have attributed community dissimilarity among high-elevations to limited dispersal, which is expected to be even greater given the physical isolation of mountain peak “islands” separated by steep topography and harsh terrestrial environments (Ward 1994, Finn and Poff 2005, Finn *et al.* 2013). Relocation of immature aquatic insects inhabiting any headwater stream may require migration through potentially unfavorable higher order systems (Creed 2006, Meyer *et al.* 2007); and thus, winged adults are primarily responsible for dispersal to new habitats (Bunn and Hughes 1997). However, high wind, steep mountain terrain,

and harsh climatic conditions in alpine systems have been documented to hinder insect flight and dispersal (Deshmukh 1986, Finn and Poff 2008). Recent studies have found that the population structure of several aquatic insect populations are related to spatial distance among high-elevation headwater streams, providing evidence in support of the hypothesis that dispersal limitation and geographic distance may regulate community assembly and maintain β -diversity in high-elevation systems (Hughes *et al.* 1999, Wishart and Hughes 2003, Finn *et al.* 2006, Finn *et al.* 2007, Finn and Adler 2006). Interestingly though, several of these studies found that similarity in population structure was strongly predicted by Euclidean, out-of-network distance, indicating that dispersal over steep topography, across drainage basins, is more prevalent than network dispersal across lower elevation valleys (Finn *et al.* 2006, Finn *et al.* 2007). Given the consistent findings of high community dissimilarity among high-elevation headwater streams, and the evidence in support of isolation by distance mechanisms of both adult overland dispersal and instream network dispersal, the role of dispersal limitation offers a plausible mechanistic explanation for maintaining high β -diversity at high elevations.

For reasons formerly discussed, inconsistencies in community dissimilarity across drainages within low-elevation zones, is most likely due differences in habitat size and connectivity between mainstem and headwater systems. However, compared to high community turnover, and high community dissimilarity at high-elevations, the role of dispersal limitation vs. habitat heterogeneity driving high community dissimilarity among low-elevation streams is less certain. Dispersal limitation may contribute to high dissimilarity because overland dispersal is predominantly limited to streams in close proximity, within the network (Clarke *et al.* 2008). Additionally, while the spatial landscape among low-elevation sites does not impose any apparent barriers to dispersal, overall spatial distance between sites spanning the three drainages

is significantly greater than the average distance between high-elevation sites, where steeper slopes result in less spatial distance between sites ranging ~200 m apart in elevation ($p < 0.01$). However, the average spatial distance between mid-elevation sites was not statistically different from low-elevations ($p = 0.14$), despite that among drainage β -diversity was significantly lower. Additionally, other elevation-independent studies among low-elevation headwater streams have failed to find a strong relationship between community dissimilarity and spatial distance spanning multiple watersheds, instead reporting that environmental variables are stronger predictors of community structure and β -diversity (Mykrä *et al.* 2007, Grönroos *et al.* 2013). However, the role of local habitat heterogeneity in maintaining high community dissimilarity among low-elevation streams is also fairly uncertain. In contrast to predictable changes in environmental conditions along the elevation gradient, there was no a priori expectation regarding the degree of heterogeneity among low-elevation communities. Additionally, there were no expectations regarding differences in habitat heterogeneity among different elevations zones, nor am I aware any fundamental differences that may account for higher habitat heterogeneity among low-elevation sites. Further, analysis of multiple reach scale variables collected June-August 2011 (N.L. Poff, unpublished data) shows no indication of higher habitat heterogeneity at among low-elevation sites compared to mid-elevation sites where β -diversity was significantly lower.

Alternatively, high β -diversity within a system that is unable to be explained by either environmental variation or spatial isolation may reflect the effects of recent disturbances (Finn and Poff 2011). Leger *et al.* (2008) found that spatial variability of high magnitude disturbances increased β -diversity in algal communities by creating the simultaneous existence of multiple habitats exhibiting different successional phases. Although, accounting for this variation in

community structure without knowledge of the recent disturbance history would be unlikely, the potential mechanism of disturbance variability in maintaining high β -diversity appears plausible. In contrast to the annual snowmelt disturbances characteristic of high-elevations, disturbances among low-elevation streams in the region are predominantly driven by large but spatially isolated convective storms occurring anytime from late spring to early fall. Compared to high-elevation snowmelt disturbances, these large rain events are variable both in space (among headwater watersheds) and time (from year to year) (Jarrett & Costa 1983, Wohl 2005, Pitlick 1994). It is probable that this stochastic variability promotes biotic heterogeneity among low elevation sites by promoting opportunities for both dispersal-driven dynamics as well as local habitat filtering.

Conclusion

Although this study specifically focuses on patterns of diversity resulting from the unique structure of stream networks, findings of patterns along the elevation gradient may also apply to other types of isolated and/or fragmented ecosystems. In general, these results suggest that community turnover across elevation was consistently high and displayed no trend and that community dissimilarity across high-elevation communities was not significantly different than low-elevation community dissimilarity. Therefore, these results from similar-sized streams indicate that β -diversity among low-elevation communities is equivalent to high-elevation communities, providing the first evidence that streams across broad elevation gradients are inhabited by many unique taxa (Figure 1.2). In addition to environmental heterogeneity along the elevation gradient, dispersal limitation and disturbance variability between isolated communities

may potentially contribute to maintaining considerable biotic heterogeneity among isolated communities along mountain ranges.

Specifically to stream networks, findings from the current study support the previous understanding that despite low α -diversity, headwater streams exhibit high β -diversity, effectively contributing disproportionately to the regional diversity of stream networks (Clarke *et al.* 2008, Finn *et al.* 2011). Narrow distributions of taxa may be driven by a combination of reduced dispersal ability and/or specific niche requirements and therefore headwater stream communities, regardless of elevation, are potentially similarly vulnerable to climate change and anthropogenic disturbance. This possibility presents important implications for understanding the impacts habitat fragmentation and habitat homogenization on the diversity of headwater systems. However, the relative influence of these regional and local mechanisms likely varies across the region; and elucidating these patterns still requires considerable attention. Further examination of the relationship between both community composition and key dispersal traits in response to environmental, spatial, and disturbance variability across elevations may illuminate a greater understanding regarding the conservation of biodiversity among these complex systems.

CHAPTER 1 LITERATURE CITED

- Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* **56**:1040-1053.
- Allan, J. D. and M. M. Castillo. 2007. *Stream ecology: structure and function of running waters*. Springer-Verlag, Dordrecht.
- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of β -diversity: a roadmap for the practice ecologist. *Ecology Letters* **14**:19-28.
- Arthington, A. H. 1990. Latitudinal gradients in insect species richness of Australian lotic systems: a selective review. *Tropical Freshwater Biology* **2**:179-196.
- Bergey, E. A. and J. V. Ward. 1989. Upstream-downstream movements of aquatic invertebrates in a Rocky Mountain stream. *Hydrobiologia* **185**: 71-82.
- Brown, B.L. and C.M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology* **79**:571-580.
- Bunn, S. E. and J. M. Hughes. 1997. Dispersal and recruitment in streams: evidence from genetic studies. *Journal of the North American Benthological Society* **16**:338-346.
- Clarke, A., R. Mac Nally, N. Bond, and P. S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology* **53**:1707-1721.
- Creed, R. P. 2006. Predator transitions in stream communities: a model and evidence from field studies. *Journal of the North American Benthological Society* **25**:533-544.
- Crow, G. E. 1993. Species diversity in aquatic angiosperms: latitudinal patterns. *Aquatic Botany* **44**:229-386.
- Cushing, C. E., C. E. McIntire, K. W. Cummins, G. W. Minshall, R. C. Petersen, J. R. Sedell, and R. L. Vannote. 1983. Relationships among chemical, physical, and biological indices along river continua based on multivariate analyses. *Archiv für Hydrobiologie* **98**:317-326.
- Deshmukh, I. 1986. *Ecology and tropical biology*. Blackwell Scientific Publications, Palo Alto, California.

- Dodds, G. S. and F. L. Hisaw. 1925. Ecological studies on aquatic insects. IV. Altitudinal zonation of mayflies, stoneflies, and caddisflies in the Colorado Rockies. *Ecology* **6**:380-390.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naimen, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status, and conservation challenges. *Biological Reviews* **81**:163-182.
- Finn, D.S. and N. L. Poff. 2005. Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology* **50**:243-261.
- Finn, D. S. and P. H. Adler. 2006. Population genetic structure of a rare high-elevation black fly, *Metacnephia coloradensis*, occupying Colorado lake outlet streams. *Freshwater Biology* **51**:2240-2251.
- Finn, D. S., D. M. Theobald, W. C. Black, and N. L. Poff. 2006. Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology* **15**:3553-3566.
- Finn, D. S., M. S. Blouin, and D. A. Lytle. 2007. Population genetic structure reveals terrestrial affinities for a headwater stream insect. *Freshwater Biology* **52**:1881-1897.
- Finn, D. S. and N. L. Poff. 2008. Emergence and flight activity of alpine stream insects in two years with contrasting winter snowpack. *Arctic, Antarctic, and Alpine Research* **40**:638-646.
- 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 North American Benthological Society* **30**:963-980.
- Finn, D. S. and Poff, N. L. 2011. Examining spatial concordance of genetic and species diversity patterns to evaluate the role of dispersal limitation in structuring headwater metacommunities. *Journal for North American Benthological Society* **30**:273-283.
- Finn, D. S., K. Khamis, and A. M. Milner. 2013. Loss of small glaciers will diminish beta diversity in Pyrenean streams at two levels of biological organization. *Global Ecology and Biogeography* **22**:40-51.
- Flowers, R. W. 1991. Diversity of stream-living insects in northwestern Panamá. *Journal of the North American Benthological Society* **10**:322-334.
- Gill, B. A., R. A. Harrington, B. C. Kondratieff, K. R. Zamudio, N. L. Poff, and W. C. Funk. 2014. Morphological taxonomy, DNA barcoding, and species diversity in Southern Rocky Mountain headwater streams. *Freshwater Science* **33**:288-301.

- Gaston, K. J., P. H. Williams, P. Eggleston, C. J. Humphries. 1995. Large scale patterns of biodiversity: spatial variation in family richness. *Proceedings of the Royal Society of London B – Biological Sciences* **260**:149-154.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* **405**:220-227.
- Grant, E. H. C., W. H. Lowe, W. F. Fagan. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* **10**:165-175.
- Grönroos, M., J. Heino, T. Siqueira, V. L. Landerio, J. Kotanen, and L. M. Bini. 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution* **3**:4473-4487.
- Grubaugh, J. W., J. B. Wallace, and E. S. Houston. 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:896-909.
- Hauer, F. R. and G. A. Lamberti. 2007. *Methods in Stream Ecology*. Elsevier. Burlington, Massachusetts, U.S.A.
- Heino, J. and H. Mykrä. 2008. Control of stream insect assemblages: roles of spatial configuration and local environmental factors. *Ecological Entomology* **33**:614-622.
- Heino, J. 2009. Biodiversity of aquatic insects: spatial gradients and environmental correlates of assemblage-level measures at large scales. *Freshwater Reviews* **2**:1-29.
- Heino, J., M. Grönroos, J. Ilmonen, T. Karhu, M. Niva, and L. Paasivirta. 2013. Environmental heterogeneity and β diversity of stream macroinvertebrate communities at intermediate spatial scales. *The Society for Freshwater Science* **32**:142-154.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist* **163**:192-211.
- Hughes, J. M., P. B. Mather, A. L. Sheldon, and F. W. Allendorf. 1999. Genetic structure of the stonefly, *Yoraperla brevis*, populations: the extent of gene flow among adjacent montane streams. *Freshwater Biology* **41**:63-72.
- Hynes, H. B. N. 1970. *The Ecology of Running Waters*. Liverpool University Press.
- Jacobsen, D., R. Schultz, and A. Encalada. 1997. Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology* **38**:247-261.
- Jacobsen, D. 2003. Altitudinal changes in diversity of macroinvertebrates from small streams in the Ecuadorian Andes. *Archiv für Hydrobiologie* **158**:145-167.

- Jacobsen, D. 2004. Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology* **49**:1293-1305.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *The American Naturalist* **101**:233-249.
- Jarrett, R. D., and J. E. Costa. 1983. Multidisciplinary approach to the flood hydrology of foothill streams in Colorado. Pp 565-568 in A.I. Johnson and R. A. Clark (eds.), American Water Resources Association International Symposium on Hydrometeorology, Denver, CO, American Water Resources Association.
- Jarrett, R. D. 1990. Paleohydrologic techniques used to define the spatial occurrence of floods. *Geomorphology* **3**:181-195.
- Koleff, P., K. J. Gaston, J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* **72**:367-382.
- Lake, P. S., E. S. G. Schreiber, B. J. Milne, and R. G. Pearson. 1994. Species richness in streams: patterns over time, with stream size and with latitude. *Verhandlungen der Internationalen Vereinigung Limnologie* **25**:1822-1826.
- Ledger, M. E., R. M. L. Harris, P. D. Armitage, and A. M. Milner. 2008. Frequency influences patch dynamics in stream benthic algal communities. *Oecologia* **155**:809-819.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. Elsevier Science B.V. Amsterdam, The Netherlands.
- Lowe, W. H., and G. E. Likens. 2005. Moving headwater streams to the head of the class. *BioScience* **55**:196-197.
- MacKay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:617-628.
- Malmqvist, B. and M. Maki. 1994. Benthic macroinvertebrate assemblages in north Swedish streams: environmental relationships. *Ecography* **17**:9-16.
- Manly, B. F. J. 1991. *Randomization and Monte Carlo Methods in Biology*. Chapman and Hall, London, U.K.
- Master, L. L., S. R. Flack, and B. A. Stein. 1998. *Rivers of Life: Critical Watersheds for Protecting Freshwater Biodiversity*. The Nature Conservancy, Arlington, Virginia, U.S.A.
- McCune, B. and M. J. Mefford. 2011. *PC-ORD. Multivariate Analysis of Ecological Data. Version 6*. MjM Software, Gleneden Beach, Oregon, U.S.A.

- McKnight, M. W., P. S. White, R. I. McDonald, J. F. Lamoreux, W. Schrest, R.S. Ridgely, S. N. Stuart. 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in the extreme. *PLoS Biology* **5**:2424-2432.
- Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque, Iowa, U.S.A.
- Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Egger, 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.
- Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote. 1985 *a*. Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:1045-1055.
- Minshall, G. W., R. C. Petersen, and C. F. Nimz. 1985 *b*. Species richness in streams of different sizes from the same drainage basin. *The American Naturalist* **125**:16-38.
- Monaghan, K. A., M. R. Peck, P. A. Brewin, M. Masiero, E. Zarate, P. Turcotte, and S. J. Ormerod. 2000. Macro-invertebrate distribution in Ecuadorian hill streams: the effect of altitude and land use. *Archiv für Hydrobiologie* **149**:421-440.
- Monaghan, M. T., C. T. Robinson, P. Spaak, J. Ward. 2005. Macroinvertebrate diversity in fragmented Alpine streams: implications for freshwater conservation. *Aquatic Sciences* **67**:454-464.
- Morlon, H., G. Chuyong, R. Condit, S. Hubbell, S. Kenfack, D. Thomas, R. Valencia, J. L. Green. 2008. A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters* **11**:904-917.
- Mosley, M. P. 1983. Variability of water temperature in the braided Ashley and Rakaia Rivers, N. Z. *Australian Journal of Marine and Freshwater Research* **17**:331-342.
- Mouquet, N. and M. Loreau. 2003. Community patterns in source-sink metacommunities. *The American Naturalist* **162**:544-557.
- Mykrä, H., J. Heino, and T. Muotka. 2007. Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography* **16**:149-159.
- Omerod, S. J., S. D. Rundle, S. M. Wilkinson, G. P. Daly, K. M. Dale, and I. Juttner. 1994. Altitudinal trends in the diatoms, bryophytes, macroinvertebrates, and fish of a Nepalese river system. *Freshwater Biology* **32**:309-322.

- Palmer, M. A., J. D. Allan, C. A. Butman. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology & Evolution* **11**:322-326.
- Patrick, R. 1966. The Catherwood Foundation Peruvian Amazon Expedition: limnological and systematic studies. *Monographs of The Academy of Natural Sciences of Philadelphia* **14**:1-495.
- Pearson, R. G. and L. Boyero. 2009. Gradients in regional diversity of freshwater taxa. *Journal of the North American Benthological Society* **28**:504-514.
- Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. *Vegetatio* **45**:3-75
- Perry, J. A. and D. J. Schaeffer. 1987. The longitudinal distribution of riverine benthos: A river dis-continuum? *Hydrobiologia* **148**:257-268.
- Phillipsen, I. C. and D. A. Lytle. 2013. Aquatic insects in a sea of desert: population genetic structure is shaped by limit dispersal in a naturally fragmented landscape. *Ecography* **36**:731-743.
- Pitlick, J. 1994. Relation between peak flows, precipitation, and physiography for five mountainous regions in the western USA. *Journal of Hydrology* **158**:219-240.
- Poff, N. L. and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **46**:1805-1818.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of North American Benthological Society* **16**:391-409.
- Poff, N. L., J. D. Olden, and D. S. Strayer. 2012. Climate change and freshwater extinction risk *in* L. Hannah, editors. *Saving a Million Species: Extinction Risk from Climate Change*. Island Press, Washington, DC.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**:224-239.
- Resh, V. H. and D. M. Rosenberg. 1984. *The Ecology of Aquatic Insects*. Praeger Publishers, New York, New York, U.S.A.
- Ricciardi, A. and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* **13**:1200-1222.
- Richards, C., R. J. Haro, L. B. Johnson, and G. E. Host. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* **37**:219-230.

- Richer, E. E., S. K. Kampf, S. R. Fassnacht, and C. C. Moore. 2013. Spatiotemporal index or analyzing controls on snow climatology: application in the Colorado Front Range. *Physical Geography* **34**:85-107.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**:514-527.
- Rohde, K. 1999. Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of gradients? *Ecography* **22**:593-613.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, New York.
- Rouquette, J. R., M. Dallimer, P. R. Armsworth, K. J. Gaston, L. Maltby, and P. H. Warren. 2013. Species turnover and geographic distance in an urban river network. *Diversity and Distributions* **19**:1429-1439.
- Soininen, J., R. McDonald, and H. Hillebrand. 2007. The distance decay of similarity in ecological communities. *Ecography* **30**:648-655.
- Statzner, B. and B. Higler. 1985. Questions and comments on the River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:1038-1044.
- Suren, A. M. 1994. Macroinvertebrate communities of streams in western Nepal: effects of altitude and land use. *Freshwater Biology* **32**:323-336.
- Tate, C. M. and J. S. Heiny. 1995. The ordination of benthic invertebrate communities in the South Platte River basin in relation to environmental factors. *Freshwater Biology* **33**:439-454.
- U.S. Environmental Protection Agency. 2006. *Wadeable Streams Assessment: A Collaborative Survey of the Nation's Streams*. EPA 841-B-06-002. U.S. Environmental Protection Agency, Office of Research and Development and Office of Water, Washington, D.C., USA.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:130-137.
- Vinson, M. R. and C. P. Hawkins. 1998. Biology of stream insects: Variation at local, basin, and regional scales. *Annual Review of Entomology* **43**:271-293.
- Vinson, M. R. and C. P. Hawkins. 2003. Broad-scale geographical patterns in local stream insect genera richness. *Ecography* **26**:751-767.

- Wang, J., J. Soininen, Y. Zhang, B. Wang, X. Yang, J. Shen. 2012. Patterns of elevation beta diversity in micro- and macroorganisms. *Global Ecology and Biogeography* **21**:743-750.
- Ward, J. V. and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* **27**:97-117.
- Ward, J. V. 1985. Thermal characteristics of running waters. *Hydrobiologia* **121**:31-46.
- Ward, J. V. 1986. Altitudinal zonation in a Rocky Mountain stream. *Archiv für Hydrobiologie* **74**:133-199.
- Ward, J. V. 1994. Ecology of alpine streams. *Freshwater Biology* **32**:277-294.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monography* **30**:279-338.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* **21**:213-251.
- Willig, M. R., D. M. Kaufman, R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* **34**:273-309.
- Wilson, M. V. and A. Shmida. 1984. Measuring beta diversity with presence-absence. *Journal of Ecology* **72**:1055-1064.
- Wishart, M. J. and J. M. Hughes. 2003. Genetic population structure of the net-winged midge, *Elporia barnardi* (Diptera: Blephariceridae) in streams of the south-western Cape, South Africa: implications for dispersal. *Freshwater Biology* **48**:28-38.
- Wohl, E. 2005. Virtual rivers: Understanding historical human impacts on rivers in the context of restoration. *Ecology and Society* **10**, online at:
<http://www.ecologyandsociety.org/vol10/iss2/art2/>

CHAPTER 2: MECHANISMS MAINTAINING AQUATIC INSECT β -DIVERSITY IN ISOLATED MOUNTAIN STREAMS VARIES BETWEEN ELEVATION GRADIENTS AND ELEVATION ZONES

Summary

Despite low local richness (α -diversity), aquatic insects inhabiting the isolated branches of stream networks (i.e. headwater tributaries) retain highly distinct communities (β -diversity); and therefore, as a whole, these small streams are an important component of overall diversity within the system. In general, theory suggests that high β -diversity is maintained via regional-scale dispersal driven dynamics (e.g. dispersal limitation), local-scale environmental dynamics (e.g. niche differentiation), or a combination of the two processes. However, due to the inherent spatial and environmental complexity of river networks, previous efforts to decipher the relative role of these mechanisms have failed to produce consistent results.

In the current study, I utilize the unique landscape of mountain ranges, characterized by a range of climatic conditions and topographic features within a confined region, in order to detect relationships between the multiple drivers of aquatic insect biodiversity in headwater streams. In this work, aquatic insects were sampled in 24 similar-sized, low-order tributaries from three adjacent river drainages spanning ~2000-3500 m in elevation. From these 24 streams, over 14,000 individuals were identified to the generic level. Using multiple spatial, environmental, and flow regime variables to explain variation in community structure (β -diversity) I quantify the significance of these relationships among sites grouped along the elevation gradient of each drainage (i.e. community turnover) and among sites grouped across drainages within low-, mid-, or high-elevations zones (i.e. community dissimilarity). Drawing conclusions from these series

of relationships, it was found that environmental predictors best explained community turnover within drainages, while, environmental predictors were poorly associated with community dissimilarity among drainages. However, despite greater inter-site distance among elevation zones, it was found that spatial predictors only accounted for community dissimilarity among high-elevation sites. I partitioned original community data into unique assemblages determined by the presence of key dispersal and ecological traits; and test a priori hypothesis regarding underlying mechanistic processes to strengthen the validity of these relationships. Despite previous inconsistencies in reported findings, and the spatial and environmental complexities inherent among headwater systems, these results suggest the potential for predicting the role of regional and local-scale factors maintaining diversity among unique headwater systems.

Introduction

Historically, the field of community ecology has emphasized local-scale mechanisms (i.e. biotic interactions and habitat conditions) for their role in niche-differentiation and the regulation of biological organization within a single community (MacArthur 1958, Whittaker 1972, Tilman 1982). Although the influence of regional-scale mechanisms across the landscape (i.e. dispersal limitation) on local community structure has not been overlooked entirely (MacArthur and Wilson 1967), only recently has the development of metacommunity theory (i.e. multiple communities, linked via dispersal) shifted focus towards the direction of incorporating both spatial and environmental processes into our understanding of regional community assembly dynamics and subsequent patterns of biodiversity (Ricklefs 1987, Wilson 1992, Poff 1997, Leibold *et al.* 2004). Theoretically, novel information resulting from this integration will be critical to the successful conservation of many diverse ecological systems (Nekola and White

1999, Whittaker *et al.* 2005, Wiersma and Urban 2005, Wang *et al.* 2012); and as a result, identifying patterns and relationships of biotic heterogeneity (i.e. β -diversity) across the landscape continues to garner substantial attention (Tuomisto and Ruokolainen 2004, McKnight *et al.* 2007, Anderson *et al.* 2011, Heino *et al.* 2013).

Current hypotheses accounting for the role of regional vs. local processes are primarily distinguished by their assumptions regarding the degree of dispersal ability vs. limitation (Leibold *et al.* 2004). Therefore, depending on which mechanisms dominate, β -diversity is most often expected to respond positively to environmental heterogeneity and/or spatial distance (Figure 2.1a-b). Under conditions of no dispersal limitation, mechanisms of local niche differentiation (i.e. species-sorting dynamics) are expected to locally govern community assembly, and diversity will be positively correlated environmental distance (Whittaker 1972, Leibold *et al.* 2004) (Figure 2.1a). Alternatively, communities encountering high dispersal limitation (i.e. neutral dynamics) will be negatively correlated across spatial distance, exhibiting a simple distance-decay relationship (Hubbell 2001) (Figure 2.1b). However, in systems dominated by higher scale processes, underlying local effects may persist due to differences in species traits; in the case of high dispersal limitation, subsequent local conditions are expected to filter those taxa with highest rates of dispersal (Bonada *et al.* 2005, Bonada *et al.* 2007) (Figure 2.1e). Alternatively, very high rates of dispersal (i.e. mass-effects) can enable the persistence of taxa that might otherwise be eliminated by suboptimal environmental conditions (including biotic interactions), thus community similarity is expected to remain low, regardless of the gradient (Mouquet and Loreau 2003, Leibold *et al.* 2004) (Figure 2.1c). Under the dynamics of high dispersal, local-effects may also persist, filtering those taxa with lowest rates of dispersal (Figure 2.1f). In addition to the rate of dispersal, the relative role of regional vs. local scale

mechanisms may be further convoluted under high temporal stochasticity and spatial variability of the disturbance regime (i.e. patch-dynamics hypothesis), in which intermediate levels of disturbance frequency, magnitude, and predictability within the system facilitate the coexistence of both competitively dominant taxa and taxa exhibiting strong resilient to disturbance (Hutchinson 1951, Townsend 1989) (Figure 2.1d). If community structure reflects the effects of recent disturbance, underlying local-effects may persist, filtering non- resilient taxa among the least disturbed systems (Figure 2.1h). Given the complexity of mechanisms operating simultaneously, disentangling the relative role of regional vs. local processes can prove to be a challenge. Therefore, despite increased consideration in recent years, the relative role of processes responsible for governing community structure and maintaining β -diversity remain largely uncertain among many spatial gradients, ecosystems and taxonomic groups (McKnight *et al.* 2007).

Stream and river ecosystems, by virtue of their dendritic network structure, exhibit a range of habitat types increasing in both size and connectivity across the landscape (Grant *et al.* 2007). Hierarchical organization of the spatial and ecological processes fundamental to stream and river dynamics, offers a unique system for identifying patterns of β -diversity with a strong potential to disentangling the relative influence of regional vs. local mechanisms regulating community structure (Vannote *et al.* 1980, Brown *et al.* 2011). Furthermore, because stream insects are ubiquitous across the globe this taxonomic group is particularly useful for studying patterns of biodiversity among stream systems. Additionally, aquatic insects are an interesting taxonomic group to study as they not only exhibit a range of ecological roles (e.g. detritivores, herbivores, predators, etc.) and tolerance to disturbances (e.g. resilient, sensitive, etc.), but also considerable variation in dispersal ability (Lytle and Poff 2004, Macneale *et al.* 2005, Poff *et al.*

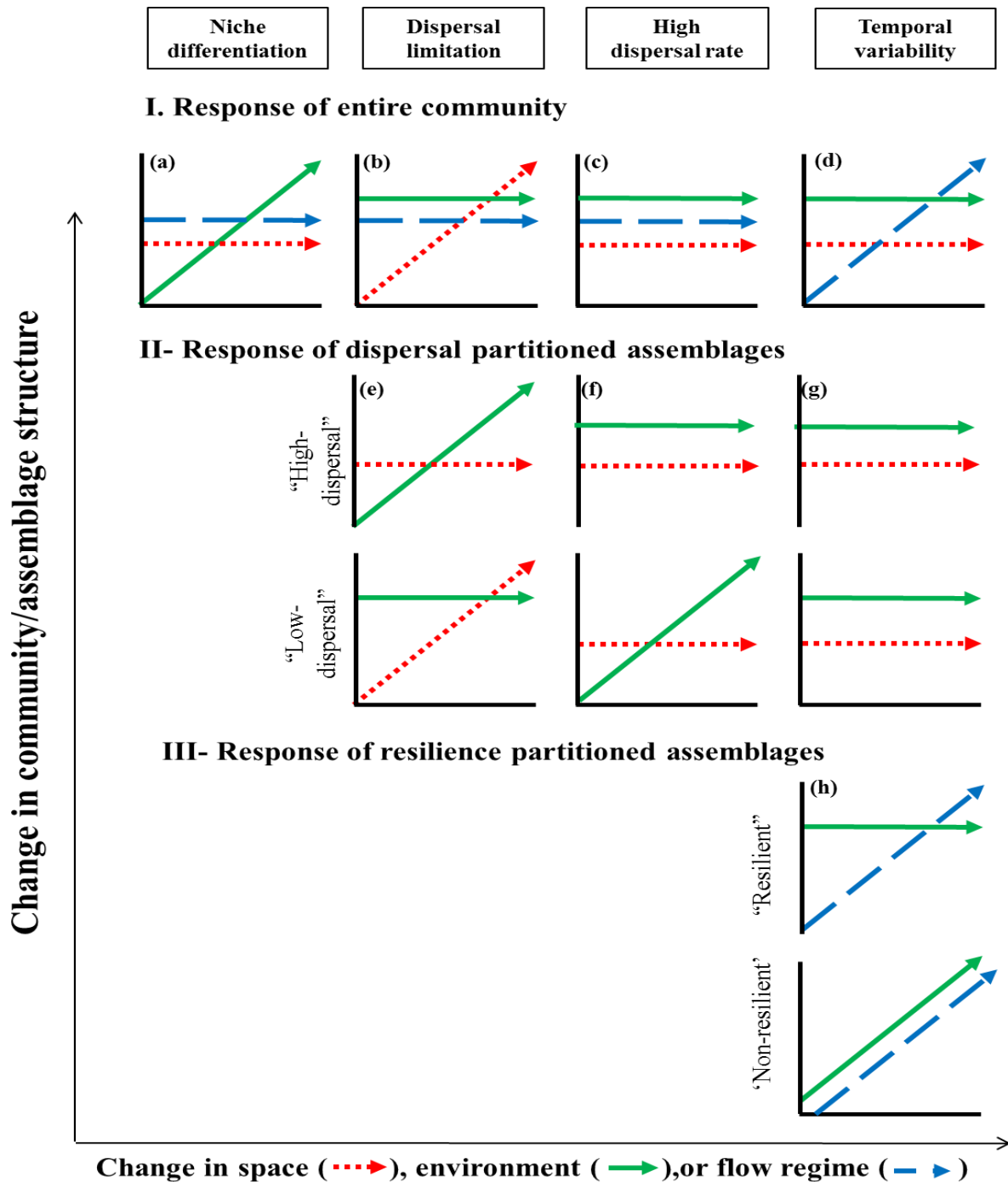


Figure 2.1. Conceptual framework illustrating the hypothesized trends between the change in community structure (i.e. β -diversity) related to the change in spatial, environmental, and/or flow regime (a surrogate for disturbance in stream ecosystems). Panel I depicts whole community relationships depending upon mechanisms of niche filtering, dispersal limitation, high dispersal rate, and, temporal variability. Panel II and III depict a priori hypotheses regarding the change in relationship between trait partitioned assemblage structure.

2006, Merritt *et al.* 2008). Although they spend most of their lifecycle under water, the adult stages of many species are terrestrial and capable of overland dispersal and in some cases may maintain colonization among streams with little to no hydrologic connectivity (Bunn and Hughes 1997, Macneale *et al.* 2005, Masters *et al.* 2007, Clarke *et al.* 2008, Merritt *et al.* 2008). However, the short-life span of most adults results in relatively low rates of dispersal limited to adjacent streams (Griffith *et al.* 1998, Peterson *et al.* 2001); and in some species instream dispersal of immature insects may be primarily responsible for maintaining colonization (Schultheis *et al.* 2002).

Recent evidence has suggested that aquatic insect communities inhabiting small isolated headwater streams typically maintain disproportionately high rates of β -diversity when compared to communities inhabiting larger mainstem channels Meyer *et al.* 2007, Clarke *et al.* 2008, Finn *et al.* 2011). This distinction is often attributed to the low habitat connectivity among small streams within the network and further driven by the flow oriented instream dispersal of immature aquatic insects, resulting in significantly lower rates of colonization in headwater streams (Brown and Swan 2010). Additionally, small streams are often tightly linked to the surrounding terrestrial ecosystem, heavily influenced by small-scale variations in the environment, and thus, the high β -diversity characterizing many headwater systems is also commonly attributed to high inter-site habitat heterogeneity (Lowe and Likens 2005, Meyers *et al.* 2007). However, many studies have credited the regulation of aquatic insect community structure in headwater streams to regional processes, local processes, temporal dynamics, a combination of processes, or have failed to find strong effects all together (Thompson and Townsend 2006, Mykrä *et al.* 2007, Heino *et al.* 2012, Heino 2013, Grönroos *et al.* 2013). This discrepancy among results may be attributed to dissimilarities in habitat heterogeneity,

disturbance variability, and/or spatial isolation among headwater streams in different systems. Furthermore, the substantial variation in both dispersal ability and resilience to disturbance among species at both immature and adult stages further adds to this complexity because mechanisms acting differentially upon species may be undetected at the community level. This contextual complexity renders evidence accounting for high β -diversity within headwater streams inconsistent, and generalizable explanations and applicable conservation strategies remain uncertain (Lowe and Likens 2005, Dudgeon *et al.* 2006, Durance and Omerod 2007). However, few studies have explicitly focused their observations across multiple spatial and environmental gradients. Additionally, few studies have addressed the dependency of regional and local filters on differences in species traits, both reasons that potentially account for these inconsistencies.

To my knowledge, this is the first study to examine these relationships in headwater streams across a range of spatial, environmental, and disturbance gradients, while also examining differences among communities varying in key ecological traits. Mountain ranges provide a unique landscape for studying patterns of biodiversity and community structure as abiotic conditions and disturbance regimes differentially vary along distinct spatial gradients (i.e. altitudinal vs. latitudinal). Furthermore, the spatial structure of parallel watersheds along a mountain profile offers an optimal design for examining patterns of hydrologically connected communities along steep environmental gradients (i.e. community turnover within a drainage), as well as, patterns of non-hydrologically connected communities within similar environmental regions (i.e. community dissimilarity across drainages in different elevation zones). This landscape structure is well suited to test hypotheses regarding the role of regional vs. local filtering dynamics that maintain β -diversity among small isolated streams.

In this study, I sampled stream insect communities in 24 small (wadeable) streams ranging from ~2000-3500 m in elevation within a total of three drainages along Colorado's Front Range. In an effort to gain insight into possible mechanisms contributing to community differences across multiple spatial, environmental, and disturbance gradients, I grouped sites by those within a single drainage (along the elevation gradient), as well as, sites among drainages (within low-, mid-, and high- elevation zones). I use a combination of whole community composition, as well as communities partitioned into "high-" and "low-dispersal" assemblages, and into "resilient" and "non- resilient" assemblages to test for relationships with changes in spatial, environmental, and flow regime (a surrogate for disturbance in streams). Specifically, I ask the following questions: 1) Is the influence of local environmental predictors stronger within drainages, where habitat heterogeneity is presumably high along the elevation gradient (e.g. thermal regime, substrate size, riparian cover, etc.) but inter-site spatial distance is low? 2) Is the influence of regional, spatial predictors stronger across drainages, within elevation zones, where habitat heterogeneity is presumably lower but spatial distance is greater? 3) How might the influence of regional vs. local mechanisms vary between elevation zones characterized by different climatic regimes and topographic landscape features? 4) Does the partitioning of communities into "high-" and/or "low-dispersal" assemblages increase the relationship with environmental predictors (Figure 2.1e-f)? 5) Does the partitioning of communities into "non-resilient" assemblages increase the relationship with environmental predictors (Figure 2.1h)?

Methods

Study area

The study streams were located within the Southern Rocky Mountain region of Colorado and spanned three adjacent watersheds that drain the eastern slope of the state's Front Range: the Cache la Poudre (CP), the Big Thompson (BT), and the Saint Vrain (SV) (Figure 2.2). Higher

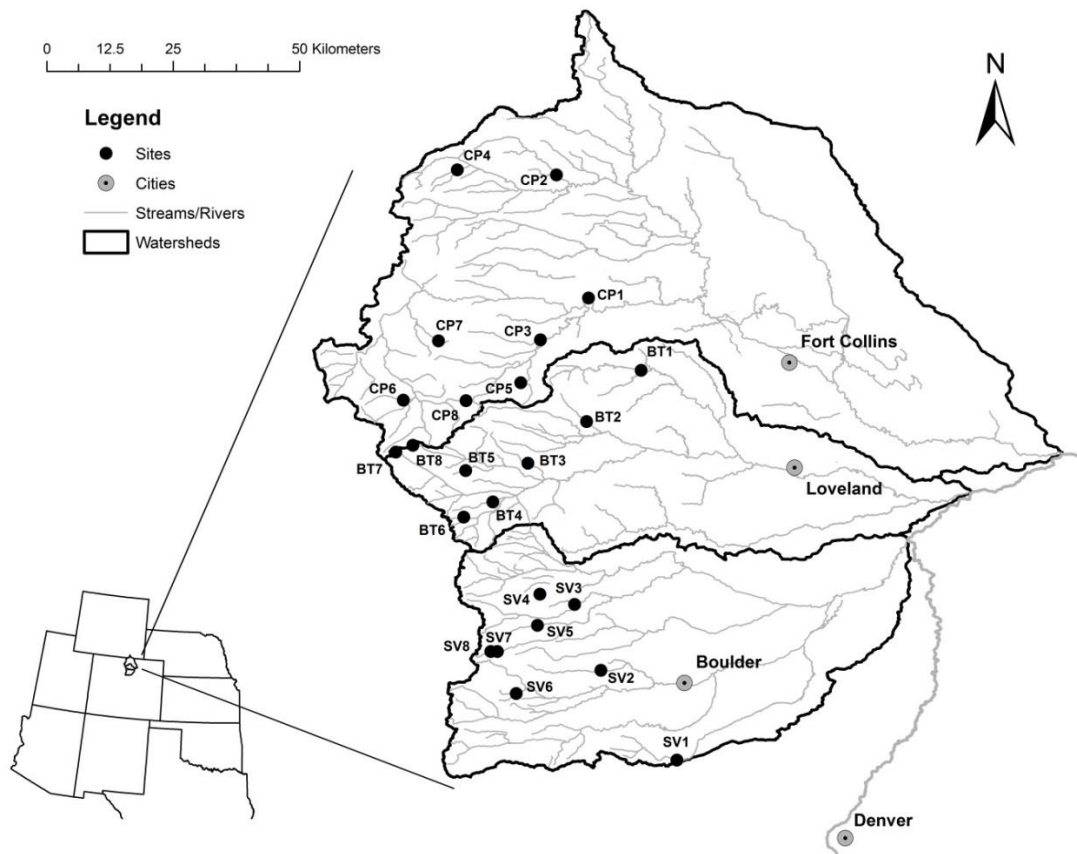


Figure 2.1. Map of the study area, depicting all 24 sampling sites. The bottom left inset locates Colorado within the United States and the three river drainages within the Colorado Rocky Mountains. Sites CP1-CP8 are located within the Cache la Poudre River drainage, sites BT1-BT8 within the Big Thompson River drainage, and sites SV1-SV8 within the Saint Vrain Creek drainage. Refer to Table 2.1 for site names and coordinates.

elevation streams in the region are generally characterized by a snowmelt-driven hydrograph, peaking in late spring or early summer (Jarrett 1990, Pitlick 1994, Wohl 2005, Richer *et al.* 2013), while disturbances in lower elevation streams are generated from large isolated convective storms that are more variable in time and space than the snow-melt disturbances in alpine systems (Jarrett and Costa 1983, Wohl 2005). Within a single drainage, eight low order tributaries (Strahler order 1st – 3rd) were selected so that sites were distributed approximately every 200 m along the gradient, ranging from nearly 2,000 m to almost 3,500 m. This sampling design was repeated within each of the three drainages, resulting in a total of 24 study sites throughout the region, which are hereafter referred to by their two-letter drainage code followed by a numerical value representing their position along the elevation gradient (#1-8, increasing in elevation) (Figure 2.2, Table 2.1). In addition to being subdivided into three drainages, all 24 sites were also subdivided into one of three elevation zones determined by the eight sites with the lowest elevation (~2000-2400 m), the eight mid-elevation sites (~2450-2950 m), and the eight sites with the highest elevation (~3050-3500 m) (Table 2.1). Although maintaining an equal number of sites within each elevation zone served to eliminate statistical bias in subsequent analysis (Peres-Neto *et al.* 2006), the range of each of the delineated elevation zones roughly corresponded to previously described vegetation zones and snow cover zones within Colorado's Front Range (Peet 1981, Richer *et al.* 2013). Lower elevation sites correspond with vegetation zones dominated by *Pinus ponderosa* (~1700 to 2300-2500 m) that are characterized by intermediate snow cover (< 2550 m). Mid-elevations sites correspond with vegetation zones that are dominated by *Pinus contorta* (~2300-2500 to ~2700-2900) that are characterized by zones of transitional snow cover (2550-3050 m). Lastly, high-elevation sites correspond to vegetation zones dominated by *Picea abies* (~2700-2900 to ~3500) that are characterized by persistent snow

Table 2.1. Drainage, elevation (m), and elevation zone each site location. Alphanumeric ID's for each site indicates drainage and position along the elevation gradient. Refer to Figure 2.1 for map of site locations. * denotes sites without a published name.

Drainage	Site Name	Site ID	Elevation(m)	Elevation Zone
Big Thompson	Buckhorn Creek	BT1	2001	Low
	Miller Fork	BT2	2252	Low
	Black Canyon	BT3	2443	Mid
	Mill Creek	BT4	2573	Mid
	Hidden Valley	BT5	2900	Mid
	unnamed*	BT6	3051	High
	Big Thompson	BT7	3364	High
	Fall River	BT8	3478	High
Cache la Poudre	Elkhorn Creek	CP1	1992	Low
	Trail Creek	CP2	2181	Low
	Little Beaver	CP3	2411	Low
	Beaver Creek	CP4	2590	Mid
	unnamed*	CP5	2775	Mid
	Corral Creek	CP6	3060	High
	E.F. Sheep Creek	CP7	3166	High
	unnamed*	CP8	3397	High
Saint Vrain	Coal Creek	SV1	2015	Low
	Four Mile Creek	SV2	2189	Low
	Cave Creek	SV3	2388	Low
	Rock Creek	SV4	2643	Mid
	Beaver Creek	SV5	2830	Mid
	Caribou Creek	SV6	2964	Mid
	unnamed*	SV7	3249	High
	unnamed*	SV8	3348	High

cover (>3050 m) (Peet 198, Richer *et al.* 2013). Thus, the range of each of these elevation zones were expected to maintain ecological relevance.

In an effort to reduce the effects of confounding habitat diversity on patterns of community composition, site selection along the gradient controlled for comparable habitat size. Average stream width and stream width to depth ratio were not significantly correlated with elevation ($R^2 = 0.0627$ and $R^2 = 0.0017$, respectively). Additionally, no sites were located downstream of any major lake outlet and the most optimal sites in areas with minimal anthropogenic impact were chosen for each elevation zone. The headwaters of all three drainage basins are located within the protected areas of Rocky Mountain National Park and/or Indian Peaks Wilderness, while the lower elevation tributaries are located within either federally or municipally protected lands. Contributing watershed area was correlated with elevation ($R^2 = 0.59$). All sites were sampled one time in the summer of 2011 between the dates of June 26th and August 12th. Although year round sampling has been shown to yield greater species richness of multiple macroinvertebrate groups across a range of elevations (Ward, 1986), single-sample ‘snapshot’ studies are commonly used to capture the response of community composition along environmental gradients (Richards *et al.*, 1997, US EPA 2006).

Aquatic Insects

In each study site, macroinvertebrate samples were collected along a 200 m reach using a D-frame kicknet (mesh size 500 μm). As opposed to a fixed quadrat sampler, this semi-quantitative sampling technique was chosen, as it enables the sampling of multiple microhabitats and is more efficient at sampling total richness of a stream reach (Resh and Rosenberg 1984). Sampling effort per site was standardized using a 5 minute timed collection in which the

proportion of 5 minutes spent per microhabitat was adjusted according to the visually estimated fraction of each microhabitat type per site (e.g. riffles, runs, pools, boulders, and woody debris). The semi-quantitative method allowed for the estimation of relative density of all taxa per site which, with the exception of chironomids, identified to the family level, were used for the subsequent multivariate analyses. Samples were preserved in 95% ethanol and later identified (usually to the generic level) and enumerated (Hauer and Lamberti 2007); over 14,000 individuals were identified from all 24 streams (Appendix I).

All identified taxa (except one to a few individuals of *Hybomitra* sp., *Dixa* sp., *Tropisternus* sp., which lack of trait information in the literature) were then classified using a total of 9 functional traits categorizing the dispersal ability and degree of resilience to disturbance exhibited by either the juvenile and/or terrestrial adult stages of each taxa (see Table 1 in Poff *et al.* 2006). Each trait consisted of two or three trait states, indicating either the binary presence/absence state of the trait (e.g. ability or inability to survive desiccation) or the categorical state within the trait range (e.g. strong, weak, or no swimming ability). After all taxa were classified by each of the nine traits, the cumulative taxonomic composition from each of the 24 individual communities was partitioned into one of two assemblages using five functional traits characterizing the level of dispersal ability. The 24 “high-dispersal” assemblages were composed of all taxa from each community that possessed at least one of the follow trait states: strong adult flying strength, high female dispersal, strong swimming ability, high crawling rate, and/or abundant or common occurrence in drift. The 24 “low-dispersal” assemblages were composed of all remaining taxa from each original community that lacked all of the “high-dispersal” traits and instead exhibited: weak adult flying strength, low female dispersal, weak- or no swimming ability, low- or very low crawling rate, and common or rare occurrence in drift.

Additionally, cumulative taxonomic composition from each of the individual 24 communities was separately partitioned into one of two assemblages using five functional traits characterizing resistance to disturbance. The 24 “resilient” assemblages were composed of all taxa from each community that possessed at least one of the following trait states: multivoltinism, nonseasonal development, poorly synchronized emergence of adults, ability to survive desiccation, ability to exit the stream, and/or high crawling rate. The 24 “non- resilient” assemblages from each community were composed of all remaining taxa from each original community that lacked all of the “resilient” traits and instead exhibited: uni- or semivoltinism, slow- or fast seasonal development, well synchronized emergence of adults, inability to survive desiccation, and low or very low crawling rate.

Predictor Variables

For each site, I quantified several explanatory variables that were grouped into one of three categories in order to characterize changes along the spatial, environmental, and disturbance gradients (Appendix II). *Spatial predictors* are variables that identify the geographic location of each (i.e. latitude, longitude, elevation), *environmental predictors* are primarily static variables that characterize the structural habitat conditions of each site, and *flow regime predictors* are temporal variables that estimate ecologically relevant variables of disturbance dynamics. Measurements of environmental predictors collected in the field included: slope of the reach (%), wetted width (cm), width/depth (cm), and percentage of riparian cover averaged across several increments along the 200 m reach, conductivity ($\mu\text{S}/\text{cm}$), dissolved oxygen (mg/L), and pH measured with a multiparameter sonde (YSI Inc., Yellow Springs, OH), and median substrate size (d50) (mm), size of large particle fraction of bed (d84) (mm), percentage

of fine-grained particles (< 2.0 mm), percentage of boulder sized substrate, percentage of embedded substrate, and the coefficient of variation of substrate size each calculated from a random sample of 100 particles (d50-cv). Additionally, fine particulate benthic matter and epilithon samples were collected and filtered in the field for subsequent processes in the laboratory in order to obtain an average ash free dry mass of benthic organic matter (BOM) (g/m^2) and an average concentration of chlorophyll-*a* (mg/m^2) for each site. However, the quality of epilithon samples was compromised from a two of the sites, and these data were not used in the subsequent analyses (Appendix II).

Temperature recording devices (iButtons) were deployed and measured water temperature four times a day for approximately one year. I used the daily mean from these ~290 days to calculate total mean, total max, total degree days, percentage of winter days (subtracted from the proportion of days where temperature was ≥ 1.0 °C for at least three consecutive days), winter mean, winter coefficient of variation (CV), summer mean, and summer CV (calculated from the previously classified winter days and those days remaining; respectively); however, devices at five sites failed completely. Initial analyses indicated that thermal regime variables from the remaining 19 sites which explained a significant amount of variation in community structure were all highly correlated ($R^2 \geq 0.80$) to the total annual mean. Therefore, in order to include mean annual temperature in subsequent analyses (categorized as an environmental predictor), the annual mean for the five sites missing data was determined using a linear regression from the 19 sites where data was obtained ($R^2 = 0.834$, $p < 0.001$).

Mean annual discharge (Q) (categorized as an environmental predictor) and all flow regime predictors for each site were acquired using the web-based Geographic Information System (GIS) application, StreamStats, developed by the U.S. Geological Survey (2012)

(Appendix II). StreamStats is a tool that estimates stream flow statistics for ungauged sites by calculating basin characteristics and extrapolating statistics from reference gauged sites. For each site I obtained the watershed slope and basin area, mean annual discharge, monthly mean discharge variables, and peak discharge values for the 2-year flood and the 100-year flood (Q2 & Q100). Mean annual discharge (Q) was used to characterize the local environmental conditions, while remaining variables were used to calculate flow regime predictors. I calculated the ratio between both the corresponding two-year peak flow and the 100-year peak flow statistics with the mean annual discharge ($Q2/Q_m$ and $Q100/Q_m$; respectively) in order to quantify the relative magnitude of both frequent and rare disturbances. Additionally, I calculated the coefficient of variation between the 12 monthly mean discharge variables in order to quantify the relative annual flow variability at each site. Further, in order to estimate bed mobility as a surrogate for potential disturbance magnitude (e.g., Townsend et al. 1997 *a*), I used the following formula “Bed Mobility Index” = $W.S.Slope * (A^{0.4} / d84^{0.8})$, originally developed by Hack (1957) and modified by Bagnold (1980) in order to scale watershed slope and area (a surrogate for “stream power”) to local sediment size and calculate the ratio of erosional forces to resistant forces (B. Bledsoe, Dept. CEE, CSU, pers. Comm.). Differences between bed mobility index values among sites reflect differences in the *potential* disturbance magnitude among streams for a precipitation event of standard magnitude.

Statistical Analyses

I used a multi-response permutation procedure (MRPP) in PC-ORD to test for significant differences in taxonomic community composition between the three low-, mid-, and high-elevation zones (McCune and Mefford 2011). Analysis was completed using Sørensen’s distance

measure and taxonomic relative abundance data. I then used a non-metric multidimensional scaling analysis (NMS) also in PC-ORD, selecting the solution with the lowest stress after 200 iterations, in order to visualize the distribution in community structure among all 24 streams within the region (McCune and Grace, 2002). Incorporating the influence of predictor variables on community structure, a canonical redundancy analyses (RDA) was applied to the taxonomic composition data from all sites. RDA was selected for the analysis because total density among sites varied considerably and RDA avoids the heavily weighted contribution of densely populated communities to the regression that is inherent in other constrained ordination (Legendre and Gallagher 2001). However, because species often respond unimodally across broad gradients, the Euclidean-based distance utilized in RDA is typically considered inappropriate for community data with many joint absences (Legendre and Gallagher 2001). Overcoming this pitfall, a Hellinger-transformation was applied to the taxonomic abundance data, effectively creating a distance based RDA using Hellinger distances, as it has been demonstrated as an appropriate transformation for the use of species abundance data and linear ordinations while providing a better compromise between linearity and resolution than other transformations (Legendre and Gallagher 2001). Initially the RDA was applied for all 24 sites using all predictor variables from the spatial, environmental and disturbance categories. The RDA was then applied again using only the predictors that correlated most strongly with the first ($R^2 \geq 0.35$) and/or the second axis ($R^2 \geq 0.12$). In order to test for the significance of the community variation explained by the predictor variables, the recommended Monte Carlo randomization test (999 permutations) was used to infer a p-value associated with these relationships (Manly 1991, Legendre *et al.* 2011). The RDA applied to all 24 sites, as well as, all

subsequent RDAs applied to subdivided groups of sites were also carried out in PC-ORD (McCune and Medfford 2011).

In order to test the relationships between spatial, environmental and flow regime predictors and community turnover within drainages, as well as, community dissimilarity among drainages, a series of three individual RDAs for each of the six subdivided groups (within drainage: BT, CP, SV and among drainage: Low, Mid, High) was performed. Initially, in order to eliminate statistical bias resulting from different numbers of predictor variables, I used a forward selection procedure to select the three environmental predictors and three flow regime predictors that cumulatively explained the most variation in community structure, to facilitate comparison with the three spatial variables. All forward selection procedures were determined using the program DISTLM_forward (Anderson 2004). RDAs for each subdivided group of communities were then performed using the three selected predictors from each of the spatial, environmental and flow regime categories. In order to test for the significance of the community variation explained by the predictor variables, the recommended Monte Carlo randomization test (999 permutations) was used to infer a p-value associated with these relationships (Manly 1991, Legendre *et al.* 2011).

If community variation within any subdivision of communities was not significantly explained by environmental predictors, two further tests were run. First, for communities that were partitioned into “high-dispersal” vs. “low-dispersal” assemblages, RDAs were run using both the spatial and environmental predictors. I used the results from the “high-dispersal” assemblages to examine the potential for dispersal limitation as a mechanism explaining community structure and to test whether local environmental predictors are able to significantly explain variation among “high dispersal” assemblages (Figure 2.1e). Additionally, I used results

from the “low-dispersal” assemblages to examine the potential that mass-effects dynamics predominantly regulate community structure, and to test whether local environmental predictors are able to significantly explain variation among “low dispersal” assemblages (Figure 2.1f).

Second, using “resilient” and “non- resilient” partitioned assemblages, RDAs were run using both flow regime and environmental predictors. I used the results from “non- resilient” assemblages to examine the potential for temporal patch-dynamics as a mechanism explaining community structure, and to test whether local environmental predictors are able to significantly explain variation among “non- resilient” taxa that are presumed to exhibit greater competitive ability (Figure 2.1h). In order to test for the significance of the variation among partitioned assemblages explained by the predictor variables, I used the recommended Monte Carlo randomization test (999 permutations) to infer a p-value associated with these relationships (Manly 1991, Legendre *et al.* 2011). I use these derived p-values to compare the ability of spatial and environmental variables to explain variation in these partitioned “high-” and “low-dispersal” assemblages versus the whole taxonomic communities. Also these derived p-values were used to compare the ability of flow regime and environmental variables to explain variation in these partitioned “resilient” and “non- resilient” assemblages versus the whole taxonomic communities.

Results

Diversity relationships among all sites

Across all 24 sites, a total of 68 aquatic insect taxa from a total of five orders, consisting of 13 Ephemeroptera, 14 Plecoptera, 19 Trichoptera, 16 Diptera, and 6 Coleoptera were identified (Appendix I). Of these 68, a total of 54 were present among low-elevation

communities, 43 among mid-elevation communities, and 39 among high-elevation communities, and the community structure among the three groups was determined to be significantly different (MRPP $A = 0.10$, $p < 0.0001$). After 200 iterations, NMS analysis determined a three-dimensional final solution to be most stable (stress 10.33, instability 0.0000), the three axes cumulatively accounting for a significant majority of the community variation across the region (cumulative $R^2 = 0.89$). Communities were predominantly distributed according to elevation zone, with no apparent clustering of sites within drainages (Figure 2.3).

Cumulatively, taxonomic variation among communities was significantly explained by the predictor variables ($p = 0.019$). RDA axes 1-3 explained a total of 32.5% of the variation, with 16.0% explained in the first axis (Figure 2.4). Both mean annual temperature and mean annual discharge, were strongly associated with the first axis, in which communities were predominantly distributed according to their position along the elevation gradient. Reach scale variables, BOM and % embeddedness, were associated with both of the axes equally, explaining variation both along the elevation gradient and across drainages. Additionally, the 100-year disturbance variable (Q_{100}/Q_m), orthogonal to the elevation gradient, helped to explain some variation across drainages (Figure 2.4).

Diversity relationships within and among drainages

Analyses independently testing the relationships between spatial, environmental, and flow regime predictors within subdivided groups were used to test the hypotheses that: 1.) local environmental predictors maintain a stronger role structuring communities along elevation gradients, 2.) regional spatial predictors maintain a stronger role structuring communities across drainages where habitat heterogeneity is presumably lower but spatial distance is greater, and to

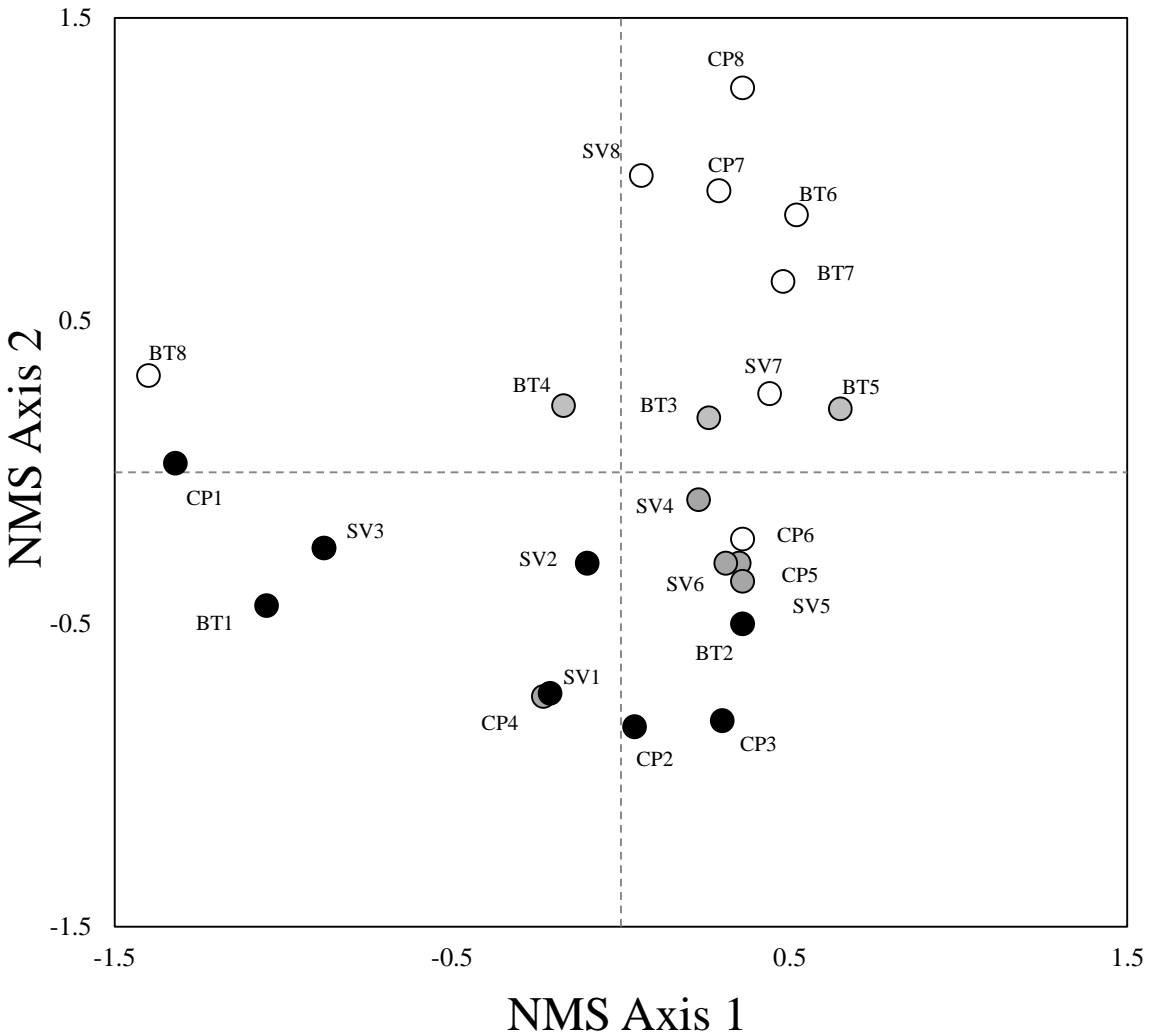


Figure 2.3. Scatterplot of the first and second axes from the non-metric multidimensional scaling ordination with all 24 headwater streams (depicted by site ID) according to taxonomic community structure. Black circles = low-elevation sites; grey circles = mid-elevation sites; white circles = high-elevation sites. The first two axes accounted for 70% of the variation, while the third axis (not displayed) accounted for an additional 19%. Refer to Figure 2 for site locations. Refer to Table 2.1 for site ID notation.

determine if, 3.) the role of regional vs. local filters varies among elevation zones? Community turnover within all three drainages was significantly explained by environmental predictors (BT: $p = 0.01$; CP: $p = 0.04$; SV: $p = 0.02$) (Table 2.2). Predictors included in the analysis with environmental predictors consisted of: BT-mean annual Q, conductivity & slope, ($R^2 = 0.31$);

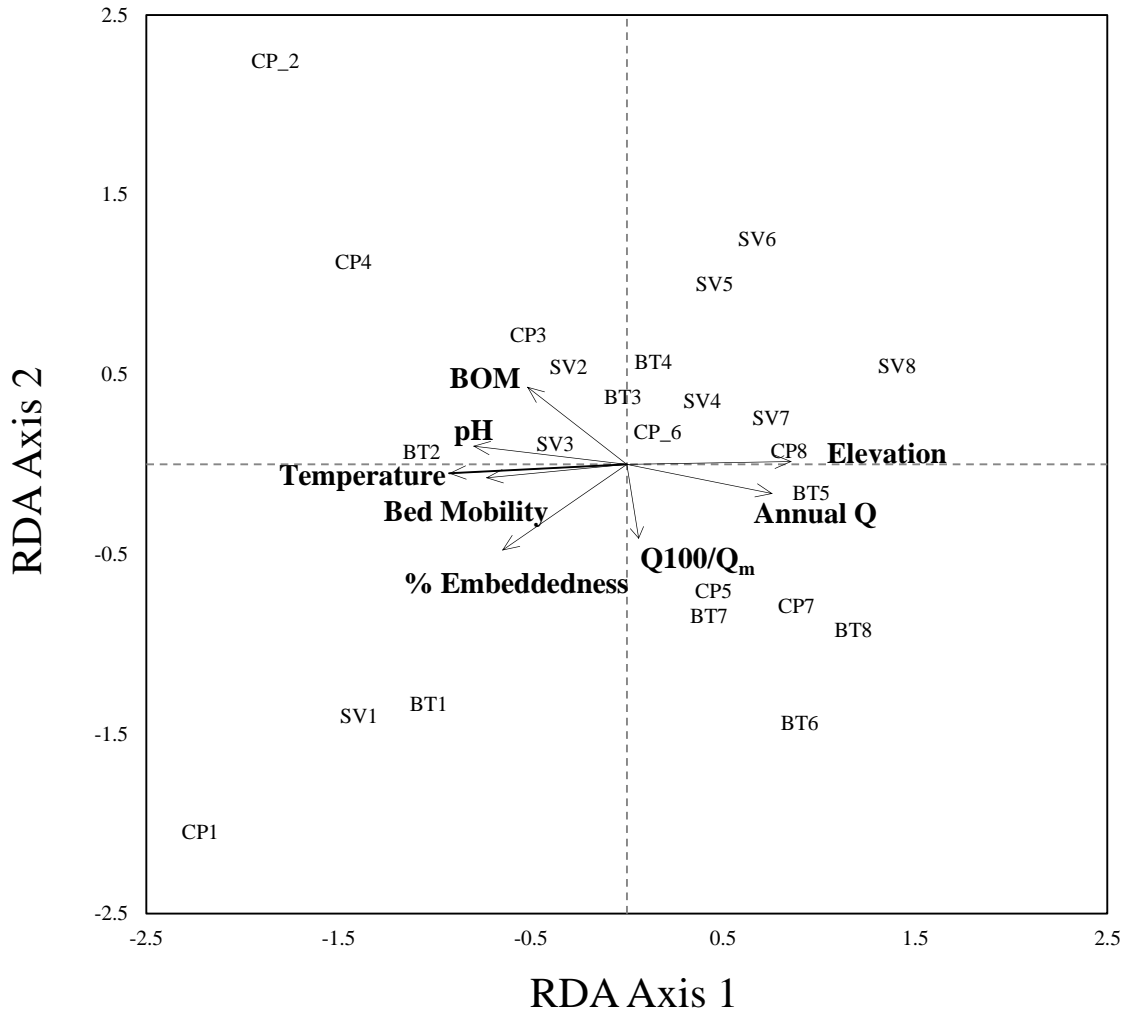


Figure 2.4. Biplot of the first and second RDA axes for taxonomic community variation among 24 headwater streams (depicted by site ID) explained by spatial, environmental, and flow regime predictors (arrows). The first two axes accounted for 25.3% of the variation explained, while the third axes (not displayed) accounted for an additional 7.2%. Refer to Table 2.1 for site ID notation.

CP - mean annual temperature, % embeddedness, & d50-cv, ($R^2 = 0.29$); and SV- mean annual Q, conductivity, % boulder, ($R^2 = 0.26$). However, the cumulative variation explained by the three spatial predictors and top three flow regime predictors were unable to significantly explain community turnover within any drainage and significance was variable (Table 2.2).

Table 2.2. Results from the RDAs of entire taxonomic community structure for each subset of sites within drainages (i.e. BT, CP, SV) and each subset of sites across drainages (i.e. Low, Mid, High). Refer to Table 2.1 for categorization of sites. Reported p-values from the Monte-Carlo test indicate the ability of predictor variables (i.e. spatial, environmental, flow regime) to significantly explain taxonomic community structure within each subset of sites. Bolded values indicate significance $p < 0.05$.

Subset of sites	Spatial Predictors	Environmental Predictors	Flow Regime Predictors
BT	0.14	0.01	0.06
CP	0.06	0.04	0.13
SV	0.12	0.02	0.30
Low	0.60	0.51	0.02
Mid	0.43	0.12	0.08
High	0.01	0.51	0.82

When sites were grouped across drainages, community dissimilarity within low-, mid-, and high-elevation zones was not significantly explained by the top three environmental predictors (Low: $p = 0.51$; Mid: $p = 0.12$; High: $p = 0.51$) (Table 2.2). Interestingly, the dissimilarity in community structure explained by the top three flow regime predictors was only significant for low-elevation sites (Low: $p = 0.02$) (Table 2.2). Also, variation in community structure explained by the top three spatial predictors was only significant only for the high-elevation sites ($p = 0.01$) (Table 2.2). Thus, community dissimilarity among low-elevation sites was only significantly explained by flow regime predictors, community dissimilarity among

high-elevation sites was only significantly explained by spatial predictors, and community dissimilarity among mid elevations sites was not significantly explained by environmental, spatial, or flow regime predictors (Table 2.2).

Diversity relationships among trait-partitioned assemblages

Spatial and environmental RDA analyses using dispersal-partitioned assemblages were performed in order to test the hypothesis that spatially structured communities are predominantly dispersal limited; and therefore, the taxa maintaining higher dispersal rates are filtered by local environmental processes (Figure 2.1e). Alternatively, the following analyses were also used to test the hypothesis that communities unable to be explained by spatial, environmental, or environmental predictors may exhibit high dispersal ability, swamping the role of weak local environmental filters that are only effective in filtering the few individuals with reduced dispersal ability (Figure 2.1f).

For high-elevation communities, spatial predictors continued to explain much variation in the “low-dispersal” assemblages ($p = 0.06$ compared to $p = 0.01$), whereas environmental predictors remained non-significant ($p = 0.60$ compared to $p = 0.51$). In contrast, for “high-dispersal” assemblages, spatial predictors become non-significant ($p = 0.34$ compared to $p = 0.01$), while the relationship between environmental predictors explaining variation among “high-dispersal” assemblages increased ($p = 0.03$ compared to $p = 0.51$) (Table 2.3).

Environmental predictors included in the analysis of high elevation “high-dispersal” assemblages consisted of: mean annual temperature, pH, and % embeddedness ($R^2 = 0.26$). For both mid- and low-elevation sites, partitioning into “high-dispersal” assemblages did not alter the ability of spatial or environmental predictors to explain variation in community structure (Table 2.3).

Table 2.3. A priori hypotheses and results from the RDAs of dispersal-partitioned assemblage structure for each subset of sites across drainages (i.e. Low, Mid, High). Hypotheses for individual assemblages were based on Figure 2.1 and the RDA results from entire community structure (i.e. total) reported in Table 2.2, in which no hypotheses were made (i.e. n/a). Hypotheses are depicted by a \uparrow for an expected increase in the relationship, a \downarrow for an expected decrease in the relationship, and a – when relationships were not hypothesized to change. Reported p-values from the Monte-Carlo test indicate the ability of predictor variables (i.e. spatial, environmental, and flow regime) to significantly explain taxonomic assemblage structure within each subset of sites. Bolded values indicate significance $p < 0.05$. * denotes results where expected increases or decreases were found.

Zone	Assemblage	Spatial Predictors		Environmental Predictors	
		Hypothesis	Results	Hypothesis	Results
Low	Total	n/a	0.60	n/a	0.51
	High-Dispersal	-	0.57	-	0.45
	Low-Dispersal	-	0.33	-	0.07
Mid	Total	n/a	0.43	n/a	0.12
	High-Dispersal	-	0.60	-	0.17
	Low-Dispersal	-	0.43	-	0.02
High	Total	n/a	0.01	n/a	0.51
	High-Dispersal	\downarrow	0.34*	\uparrow	0.03*
	Low-Dispersal	-	0.06	-	0.60

Additionally, “low-dispersal” assemblages remained unexplained by spatial predictors for both low- and mid-elevation sites (Table 2.3). However, for both low- and mid-elevation zones, the relationship between the environmental predictors and “low-dispersal” assemblages increased significantly (Mid: $p = 0.02$ compared to $p = 0.12$) or near-significantly (Low: $p = 0.07$

compared to $p = 0.51$) (Table 2.3). Environmental predictors included in the analysis of mid- and low-elevation “low-dispersal” assemblages consisted of: Mid- mean annual temperature, B.O.M., and pH ($R^2 = 0.33$).

Flow regime and environmental RDA analyses using “resilient” and “non- resilient” partitioned assemblages, were performed in order to test the hypotheses that community structure significantly explained by flow regime predictors are predominantly regulated by temporal stochasticity and disturbance variability; and therefore, local environmental filters are presumably only effective in filtering “non- resilient” individuals that are less resilient to disturbance and therefore likely to inhabit more stable streams (Figure 2.1h). For low-elevation communities, flow regime predictors significantly explained variation among cumulative, “resilient” and “non- resilient” assemblages ($p = 0.02$, $p = 0.01$, $p = 0.03$; respectively) whereas environmental predictors consistently was unable to explain variation in community structure among cumulative, “resilient” and “non- resilient” assemblages ($p = 0.51$, $p = 0.31$, $p = 0.55$; respectively) (Table 2.4). After partitioning, mid-elevation “resilient” assemblages remained unexplained by both environmental and flow regime predictors ($p = 0.12$, $p = 0.11$; respectively). However, while “non- resilient” mid-elevation assemblages also remained unexplained by environmental predictors, the relationship between community variance and flow regime variables became significant ($p = 0.17$, $p = 0.02$; respectively) (Table 2.4). At high-elevation sites, flow regime and environmental predictors remained unable to significantly explain the variation for both “resilient” and “non- resilient” assemblages (Table 2.4).

Table 2.4. A priori hypotheses and results from the RDAs of resilience-partitioned assemblage structure for each subset of sites across drainages (i.e. Low, Mid, High). Hypotheses for individual assemblages were based on Figure 2.1 and the RDA results from entire community structure (i.e. total) reported in Table 2.2, in which no hypotheses were made (i.e. n/a). Hypotheses are depicted by a ↑ for an expected increase in the relationship, a ↓ for an expected decrease in the relationship, and a – when relationships were not hypothesized to change. Reported p-values from the Monte-Carlo test indicate the ability of predictor variables (i.e. spatial, environmental, and flow regime) to significantly explain taxonomic assemblage structure within each subset of sites. Bolded values indicate significance $p < 0.05$. * denotes results where expected increases or decreases were found.

Zone	Assemblage	Environmental Predictors		Flow Regime Predictors	
		Hypothesis	Results	Hypothesis	Results
Low	Total	n/a	0.51	n/a	0.02
	Resilient	-	0.31	-	0.01
	Non- resilient	↑	0.55	-	0.03
Mid	Total	n/a	0.12	n/a	0.08
	Resilient	-	0.12	-	0.11
	Non- resilient	-	0.17	-	0.02
High	Total	n/a	0.51	n/a	0.82
	Resilient	-	0.35	-	0.32
	Non- resilient	-	0.26	-	0.66

Discussion

In this study, I aimed to explain patterns of community variation among small, isolated headwater streams across a 1500 m elevation gradient, where changes in annual water temperature, mean flow, flow disturbance, riparian vegetation, stream slope and other factors are

pronounced. With this unique study design I hoped to distinguish among several possible mechanisms that have been invoked to explain patterns of variation in aquatic insect communities across the landscape.

Relationships of community turnover

It was found that turnover of community structure within all three drainages was significantly explained by environmental predictors (Table 2.2), supporting the commonly proposed hypothesis that local-scale filtering of the regional species pool dominates the regulation of aquatic insect community structure, and maintains β -diversity among headwater streams (Heino and Mykrä 2008, Brown and Swan 2010, Patrick and Swan 2011, Heino *et al.* 2013, Swan and Brown 2014). Specifically, both mean annual temperature and mean annual flow, strongly co-varied ($R^2 = -0.77$), were highly correlated along the elevation gradient and explained a considerable amount of variation in community turnover (Figure 2.3). This is not surprising, as the distributional ranges of many aquatic insect species within a given region are often attributed to physiological limits in response to temperature (Sweeney and Vannote 1978, Ward and Stanford 1982). The thermal regimes of high-elevation systems in the Colorado Rocky Mountains are generally characterized by long winter seasons and lower annual variation in temperature (Richer *et al.* 2013). Previous studies conducted from high-elevation headwaters through low-elevation mainstems have attributed both the reduced richness and increased turnover at high-elevations to the presence of few remaining euryzonal taxa persisting at the limit of their range in these thermally harsh conditions (Ward 1986, Ward 1994). Although it was found that richness did decrease with elevation, variation in community structure was consistent between sites along the gradient (Figures 2.3, 2.4). These results suggest that the replacement of

taxa along the gradient is potentially driven by greater differentiation of thermal regimes between poorly buffered headwater streams than mainstem channels.

Although I selected small streams that were relatively spatially (and hydrologically) isolated, the relationship between spatial predictors and community turnover was weaker and less consistent (Table 2.2). I note that there was a strong correlation between environmental conditions and geographic distance due to the steep elevation gradient in this study. This fact potentially masks the ability to accurately partition the influences of regional-scale spatial dynamics vs. local-scale environmental dynamics on the turnover of community structure. However, these results are consistent with the basic premise that the dispersal rate of many stream insects is high enough to maintain colonization throughout a network (Palmer *et al.* 1996, Poff 1997, Heino and Mykrä 2008).

Interestingly, flow regime predictors were also unable to significantly explain turnover in taxonomic community structure within any of the three drainages (Table 2.2). One potential explanation is that although flow regime predictors are confounded with elevation (and thus temperature), shifting from more stable, snowmelt-driven disturbances at high elevations to more variable, rainfall-driven disturbances at lower elevation streams (Pitlick 1994, Wohl 2005, Richer *et al.* 2013), the filtering mechanisms of disturbance regimes operate across a coarser spatial- and temporal-scale than local reach-scale habitat conditions (Poff 1997, Brown *et al.* 2011). Therefore these results are perhaps not surprising, as they are consistent with the theoretical and empirical support that the role of hydrologic regimes in regulating community structure is typically associated with species trait characterization of communities (Poff and Ward 1989, Townsend 1989, Poff and Allan 1995, Townsend *et al.* 1997 *b*, Lytle and Poff 2004).

Relationships of community dissimilarity

Although environmental habitat conditions significantly explained community turnover within all three drainages, environmental predictors were unable to explain community variance among streams located in low-, mid-, or high-elevation zones (Table 2.2). Heino *et al.* (2013) have argued that species-sorting dynamics are more likely to govern community assembly processes along stronger environmental gradients (such as the elevation gradient of temperature.) with greater differences in habitat conditions among sites functioning as coarse local-scale filters. Therefore, environmental conditions may play less of a role among regions that retain a greater degree of habitat similarity (such as the gradients across drainages) with lower variation in conditions among sites functioning as fine local-scale filters (Heino *et al.* 2013). Despite weak relationships with environmental predictors, it was found that relationships between community structure and both spatial and flow regime predictors varied substantially between low-, mid-, and high-elevation zone communities (Table 2.2), suggesting an important role for context dependency of both regional- and local-scale filters.

Results from redundancy analyses across drainages determined that community dissimilarity among high-elevation sites was significantly explained by spatial predictors, but unable to be explained by environmental or flow regime predictors (Table 2.2). Because high-elevation communities exhibited relatively high community dissimilarity, the significant correlation with spatial predictors suggests that community structure among high elevation streams is strongly influenced by dispersal limitation. Several authors have argued that spatial dynamics play a larger role in structuring communities at higher elevations due to greater isolation of mountain peak “islands” separated by steep topography harsh terrestrial environments (Ward 1994, Finn and Poff 2005). Recent studies of high-elevation stream taxa

have revealed a significant pattern of population structure and isolation by distance, providing evidence in support of the dispersal limited neutral processes (Hughes *et al.* 1999, Wishart and Hughes 2003, Finn *et al.* 2006, Finn *et al.* 2007, Phillipson and Lytle 2013). However, to my knowledge, the current study is the first to examine and find a significant relationship between spatial distance and whole community composition of aquatic insects among high-elevation streams.

Under the assumption that dispersal limitation is responsible for the regulation of community structure at high-elevations, it was expected that the positive relationship between community dissimilarity and spatial distance would weaken when community structure among exclusively “high-dispersal” assemblages is considered (Figure 2.1e). In effect, the results from the partitioning of communities into “high-dispersal” assemblages did detect a weakened relationship with spatial predictors, which was not observed among “low-dispersal” assemblages, strengthening support for the isolation by distance hypothesis (Table 2.3). Furthermore, theoretical and empirical evidence suggests that taxa not restricted by dispersal limitation within a region are better able to track habitat conditions at the local scale (Poff 1997, Leibold *et al.* 2004, Bonada *et al.* 2005, Bonada *et al.* 2007, Grönroos *et al.* 2013, Heino 2013). Partitioning of communities into “high-dispersal” assemblages did detect a stronger positive relationship between community dissimilarity and environmental predictors (Table 2.3), supporting the idea that, although the relative strength of regional- vs. local-scale mechanisms may vary, they often function simultaneously. Additionally, these findings confirm the understanding that the role of local environmental filters is stronger when the role of regional dispersal limiting filters is weaker.

In contrast to the results from high-elevation sites, across drainage community dissimilarity among low-elevation sites was unable to be explained by either spatial or environmental predictors (Table 2.2). Partitioning low-elevation communities into both “low-” and “high-dispersal” assemblages did not alter the relationship between community dissimilarity and spatial predictors; however, the relationship between “low-dispersal” assemblages and environmental predictors was strengthened (although remained non-significant) (Table 2.3a). These results suggest that overall, low-elevation community structure is not regulated by dispersal limitation and in fact, high dispersal rates of many taxa may swamp effects of local environmental filters (Thompson and Townsend 2006, Brown *et al.* 2011). Interestingly, the putative higher dispersal ability among low-elevation streams does not result in the expected lowered β -diversity among communities (Mouquet and Loreau 2003, Brown and Swan 2010) (Figure 2.3), suggesting that other mechanisms may dominate.

A significant relationship between community dissimilarity and flow regime predictors along these sites was found, and it is reasonable to propose that disturbance variability is a mechanism regulating the variation in community structure (Table 2.2). Disturbances among low-elevation streams in the region are predominantly driven by large but spatially isolated convective storms occurring anytime from late spring to early fall. Furthermore, these large rain events are variable both in space (among headwater watersheds) and time (from year to year) (Jarrett and Costa 1983, Wohl 2005, Pitlick 1994). This hydro-climatology stands in stark contrast to high-elevation streams, which are dominated by predictable, annual snowmelt with moderate inter-annual variation in magnitude (Pitlick 1994). In low-elevation streams, the potential magnitude of these unusual flow disturbances can be approximated using watershed area and slope, and reach-scale streambed particle size; and variation among sites in this “bed

mobility index” is significant ($\mu = 26.5 \times 10^4$, $\sigma = 10.3 \times 10^4$) (Figure 2.4). Therefore, it is possible that this variation in community structure at low-elevations may be explained by variability in disturbance among sites, as organisms with strong colonization and dispersal ability are more persistent in frequently disturbed environments (Fritz and Dodds 2004, Vieira *et al.* 2004).

Given the temporal and spatial degree of disturbance variability it might be expected that the community structure of partitioned “non- resilient” assemblages would exhibit a stronger relationship with environmental predictors, as habitat heterogeneity among less disturbed streams should increase the influence of biotic interactions and niche differentiation (Townsend 1989). Interestingly, the partitioning of communities into “resilient” and “non- resilient” assemblages did not strengthen the relationship with environmental predictors, nor did it weaken the relationship with flow regime predictors (Table 2.4). One potential explanation accounting for this observation is that, despite variation in potential magnitude, the timing of disturbances among all sites is unpredictable (both seasonally and inter-annually); and all communities are stochastically reset across the landscape. Local habitat conditions, biotic interactions, and spatial distance may well contribute to community structure, but lacking information on the recent flow disturbance history of each low-elevation site, potential assembly mechanisms cannot be disentangled with a one-time snapshot sampling of these communities.

Unlike, both high- and low-elevation sites, variation in community structure at mid-elevations was not only lower, but also unable to be significantly explained by spatial, environmental, and flow regime predictors (Table 2.2). Although less consistent, partitioning of community structure into both “high-” and “low-dispersal” assemblages, as well as, “resilient” and “non- resilient” assemblages, provided some insight in to the range of possible regional- and local-scale mechanisms regulating community dissimilarity among mid-elevation streams. As

previously explained, the observed increase in the relationship between “low-dispersal” assemblages and environmental predictors suggests that overall higher rates of dispersal within the communities may swamp local environmental filters via source-sink dynamics (Thompson and Townsend 2006, Brown *et al.* 2011) (Table 2.3). Although the role of regional mass-effects is often supported in larger channels and rarely attributed to the regulation of community structure in isolated headwater streams (Brown and Swan 2010), the contribution of higher dispersal ability, relative to high-elevation systems, is plausible considering the lower dissimilarity observed among mid-elevation communities (Figure 2.2). Additionally, the strengthened relationship between “non- resilient” assemblages and flow regime predictors indicates that at least some degree of variability in the disturbance regime, though lower compared to low-elevations, contributes to the regulation of community structure and maintains the observed community dissimilarity (Table 2.4).

Conclusion

In summary, these analyses indicate that the characteristically high β -diversity among many headwater streams is maintained by a combination of spatial dispersal-driven dynamics and local environmental-filtering dynamics, as well as, disturbance variability across time and space. It was found that environmental predictors best explained community turnover within drainages, where environmental conditions changed rapidly along the elevation gradient, but inter-site spatial distance is low. However, environmental conditions were weak predictors of community structure among drainages, where environmental conditions are more similar and distance among sites is greater. Notably, a strong relationship with spatial predictors, indicating dispersal limitation, only accounted for community dissimilarity among high-elevation sites and

not among mid- and low-elevation sites. This discrepancy implies that in the absence of physical dispersal barriers (e.g. steep mountain topography), aquatic insects are not dispersal limited and dispersal rates are sufficient to maintain colonization across a regional landscape. Conversely, high dissimilarity among low-elevation sites, where disturbance events are spatially and temporally unpredictable, was almost entirely explained by flow regime predictors.

In general, these results suggest that spatial, environmental, and disturbance factors are potentially all important for maintaining high β -diversity among headwater streams.

Furthermore, results indicate that the relative influence of these regional- and local-scale processes relies not only upon the strength of spatial and environmental gradients but also upon differences in the disturbance regimes and physical landscape features among regions. Therefore, it is expected that these comprehensive relationships would commonly apply to other montane stream systems characterized by similar spatial features, environmental conditions, and disturbance regimes. However, general ideas concerning the relative influence of these mechanisms from individual drainages and elevation zones should translate to other headwater systems with high spatial isolation, habitat heterogeneity, and/or disturbance variability. For example, the importance of dispersal limitation should apply to headwater systems exhibiting physical barriers to dispersal (e.g. canyon streams). Alternatively, the importance of temporal and spatial stochasticity should apply to headwater streams exhibiting high variability among disturbance regimes (e.g. intermittent desert streams). Additionally, differences in biogeographic history (e.g. age and geologic events) may be expected to operate under different dynamics, as higher regional diversity may eventually strengthen the role of biotic interactions (Ricklefs 1987). Due to the context dependency regarding the relative role of regional vs. local processes, it can be concluded that applying these spatial, environmental, or disturbance processes to the

regulation community structure and maintenance of β -diversity within an individual system should emphasize the biological details that are unique to a particular system.

Nevertheless, considering the range of features unique to a specific region, the ability to predict the role of regional- vs. local-scale processes maintains significant potential and critical implications. Already facing a disproportionate risk of extinction, freshwater biota as a whole, are anticipated to experience considerable vulnerability resulting from the impacts of climate change (Ricciardi and Rasmussen 1999, Poff *et al.* 2012). However, the magnitude of response from individual systems are projected to vary ranging from regional geographic location and network orientation (Meisner *et al.* 1988, Matthews and Zimmerman 1990, Poff 1992, Fagan *et al.* 2002, Poff *et al.* 2002, Isaak and Rieman, 2013) down to the ecological, physiological, and dispersal behaviors characterizing local populations (Poff *et al.* 2010, Poff *et al.* 2012). Therefore, utilizing the concepts of the regional and local processes in order to identify the dynamics regulating community structure within a particular system, presents critical implications regarding the successful conservation of these uniquely diverse systems.

CHAPTER 2 LITERATURE CITED

- Anderson, M. J. 2004. DISTLM_forward. Department of Statistics, University of Auckland, New Zealand.
- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V. Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of β -diversity: a roadmap for the practice ecologist. *Ecology Letters* **14**:19-28.
- Bonada, N., C. Zamora-Muñoz, M. Rieradevall, and N. Prat. 2005. Ecological and historical filters constraining spatial caddisfly distribution in mediterranean rivers. *Freshwater Biology* **50**:781-797.
- Bonada, N., S. Dolédec, and B. Statzner. 2007. Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology* **13**:1658-1671.
- Brown, B.L. and C.M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology* **79**:571-580.
- Brown, B. L., C. M. Swan, D. A. Auerbach, E. H. C. 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 North American Benthological Society* **30**:310-327.
- Bunn, S. E. and J. M. Hughes. 1997. Dispersal and recruitment in streams: evidence from genetic studies. *Journal of the North American Benthological Society* **16**:338-346.
- Clarke, A., R. Mac Nally, N. Bond, and P. S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology* **53**:1707-1721.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naimen, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status, and conservation challenges. *Biological Reviews* **81**:163-182.
- Durance, I. and S. J. Ormerod. 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology* **13**:942-957.
- Fagan, W. F., P. J. Unmack, C. Burgess, and W. L. Minckley. 2002. Rarity, fragmentation, and extinction risk in desert fish. *Ecology* **83**:3250-3256.

- Finn, D.S. and N. L. Poff. 2005. Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology* **50**:243-261.
- Finn, D. S., D. M. Theobald, W. C. Black, and N. L. Poff. 2006. Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology* **15**:3553-3566.
- Finn, D. S., M. S. Blouin, and D. A. Lytle. 2007. Population genetic structure reveals terrestrial affinities for a headwater stream insect. *Freshwater Biology* **52**:1881-1897.
- 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 North American Benthological Society* **30**:963-980.
- Fritz, K. M. and W. K. Dodds. 2004. Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. *Hydrobiologia* **527**:99-112.
- Grant, E. H. C., W. H. Lowe, W. F. Fagan. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* **10**:165-175.
- Griffith, M. B., E. M. Barrows, and S. A. Perry. 1998. Lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera) following emergence from headwater streams in forested Appalachian catchments. *Annals of the Entomological Society of America* **91**:195-201.
- Grönroos, M., J. Heino, T. Siqueira, V. L. Landerio, J. Kotanen, and L. M. Bini. 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution* **3**:4473-4487.
- Hauer, F. R. and G. A. Lamberti. 2007. *Methods in Stream Ecology*. Elsevier. Burlington, Massachusetts, U.S.A.
- Heino, J. and H. Mykrä. 2008. Control of stream insect assemblages: roles of spatial configuration and local environmental factors. *Ecological Entomology* **33**:614-622.
- 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. 2013. Environmental heterogeneity, dispersal mode, and co-occurrence in stream macroinvertebrates. *Ecology and Evolution* **3**:344-355.
- Heino, J., M. Grönroos, J. Ilmonen, T. Karhu, M. Niva, and L. Paasivirta. 2013. Environmental heterogeneity and β diversity of stream macroinvertebrate communities at intermediate spatial scales. *The Society for Freshwater Science* **32**:142-154.

- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton New Jersey, U.S.A.
- Hughes, J. M., P. B. Mather, A. L. Sheldon, and F. W. Allendorf. 1999. Genetic structure of the stonefly, *Yoraperla brevis*, populations: the extent of gene flow among adjacent montane streams. *Freshwater Biology* **41**:63-72.
- Hutchinson, G. E. 1951. Copepodology for the Onithologist. *Ecology* **32**:571-577.
- Isaak, D. J., and B. E. Rieman. 2013. Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. *Global Change Biology* **19**:742-751.
- Jarrett, R. D., and J. E. Costa. 1983. Multidisciplinary approach to the flood hydrology of foothill streams in Colorado. Pp 565-568 in A.I. Johnson and R. A. Clark (eds.), *American Water Resources Association International Symposium on Hydrometeorology*, Denver, Colorado, USA.
- Jarrett, R. D. 1990. Paleohydrologic techniques used to define the spatial occurrence of floods. *Geomorphology* **3**:181-195.
- Legendre, P. and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* **129**:271-280.
- Legendre, P., J. Oksanen, C. J. F. ter Braak. 2011. Testing the significance of canonical axes in redundancy analysis. *Methods in Ecology and Evolution* **2**:269-277.
- Leibold, M. A., M. Holyoak, M. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**:601-613.
- Lowe, W. H., and G. E. Likens. 2005. Moving headwater streams to the head of the class. *BioScience* **55**:196-197.
- Lytle, D. A. and N. L. Poff. Adaptation to natural flow regimes. 2004. *Trends in Ecology & Evolution* **19**:94-100.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**:599-619.
- MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey., U.S.A.

- Macneale, K. H., B. L. Peckarsky, and G. E. Likens. 2005. Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. *Freshwater Biology* **50**:1117-1130.
- Manly, B. F. J. 1991. *Randomization and Monte Carlo Methods in Biology*. Chapman and Hall, London, U.K.
- Masters, Z., I. Peteresen, A. G. Hildrew, and S. J. Omerod. 2007. Insect dispersal does not limit the biological recovery of streams from acidification. *Aquatic Conservation: Marine and Freshwater Ecosystems* **17**:375-383.
- McCune, B. and J. B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon, U.S.A.
- McCune, B. and M. J. Mefford. 2011. *PC-ORD. Multivariate Analysis of Ecological Data. Version 6*. MjM Software, Gleneden Beach, Oregon, U.S.A.
- Matthews, W. J. and E. G. Zimmerman. 1990. Potential effects of global warming on native fishes of the southern Great Plains and the Southwest. *Fisheries* **15**:26-32.
- McKnight, M. W., P. S. White, R. I. McDonald, J. F. Lamoreux, W. Schrest, R.S. Ridgely, S. N. Stuart. 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in the extreme. *PLoS Biology* **5**:2424-2432.
- Meisner, J. D., J. S. Rosenfeld, and H. A. Regier. 1988. The role of groundwater in the impact of climate warming on stream salmonines. *Fisheries* **13**:2-8.
- Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque, Iowa, U.S.A.
- Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Egger, 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.
- Mouquet, N. and M. Loreau. 2003. Community patterns in source-sink metacommunities. *The American Naturalist* **162**:544-557.
- Mykrä, H., J. Heino, and T. Muotka. 2007. Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography* **16**:149-159.
- Nekola, J. C. and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26**:867-878.

- Palmer, M. A., J. D. Allan, C. A. Butman. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology & Evolution* **11**:322-326.
- Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. *Vegetatio* **45**:3-75.
- Peterson, B. D., J. H. Winterbottom, S. Orton, N. Friberg, A. G. Hildrew, D. C. Spiers, and W. S. C. Gurney. 1999. Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, UK. *Freshwater Biology* **42**:401-416.
- Phillipsen, I. C. and D. A. Lytle. 2013. Aquatic insects in a sea of desert: population genetic structure is shaped by limited dispersal in a naturally fragmented landscape. *Ecography* **36**:731-743.
- Patrick, C. J. and C. M. Swan. 2011. Reconstructing the assembly of a stream-insect metacommunity. *Journal of the North American Benthological Society* **30**:259-272.
- Pitlick, J. 1994. Relation between peak flows, precipitation, and physiography for five mountainous regions in the western USA. *Journal of Hydrology* **158**:219-240.
- Poff, N. L. and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **46**:1805-1818.
- Poff, N. L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbances in streams. *Journal of North American Benthological Society* **11**:86-92.
- Poff, N. L. and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology* **76**:606-627.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of North American Benthological Society* **16**:391-409.
- Poff, N. L., M. Brinson, and J. B. Day. 2002. Freshwater and coastal ecosystems and global climate change: a review of projected impacts for the United States. Pew Center on Global Climate Change, Arlington, Virginia, U.S.A.
- Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, M. P. Simmons, and B. C. Kondratieff. 2006. North American lotic insects: trait-based ecological applications in light of phylogenetic relationships. *Journal of North American Benthological Society* **25**:730-755.
- Poff, N. L., M. I. Pyne, B. P. Bledsoe, C. C. Cuhaciyan, and D. M. Carlisle. 2010. Developing linkages between species traits and multiscaled environmental variation to explore

- vulnerability of stream benthic communities to climate change. *Journal for North American Benthological Society* **29**:1441-1458.
- Poff, N. L., J. D. Olden, and D. S. Strayer. 2012. Climate change and freshwater extinction risk *in* L. Hannah, editors. *Saving a Million Species: Extinction Risk from Climate Change*. Island Press, Washington, DC, U.S.A.
- Resh, V. H. and D. M. Rosenberg. 1984. *The Ecology of Aquatic Insects*. Praeger Publishers, New York, New York, U.S.A.
- Ricciardi, A. and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* **13**:1200-1222.
- Richards, C., R. J. Haro, L. B. Johnson, and G. E. Host. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* **37**:219-230.
- Richer, E. E., S. K. Kampf, S. R. Fassnacht, and C. C. Moore. 2013. Spatiotemporal index or analyzing controls on snow climatology: application in the Colorado Front Range. *Physical Geography* **34**:85-107.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167-171.
- Schultheis, A. S., L. A. Weigt, and A. C. Hendricks. 2002. Gene flow, dispersal, and nested clade analysis among populations of the stonefly *Peltoperla tarteri* in the southern Appalachians. *Molecular Ecology* **11**:317-327.
- Swan, C. M. and B. L. Brown. 2014. Using rarity to infer how dendritic network structure shapes biodiversity in riverine communities. *Ecography* **37**:1-9.
- Sweeney, B. W., and R. L. Vannote. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science* **200**:444-446.
- 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.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey, U.S.A.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* **8**:36-50.

- Townsend, C. R., M. R. Scarsbrook, S. Dolédec. 1997 *a*. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society* **16**: 531-534.
- Townsend, C. R., S. Dolédec, and M. R. Scarsbrook. 1997 *b*. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat template theory. *Freshwater Biology* **37**:367-387.
- Tuomisto, H. and K. Ruokolaine. 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. *Ecological Society of America* **87**:2697-2708.
- U.S. Environmental Protection Agency. 2006. *Wadeable Streams Assessment: A Collaborative Survey of the Nation's Streams*. EPA 841-B-06-002. U.S. Environmental Protection Agency, Office of Research and Development and Office of Water, Washington, D.C., USA.
- U.S. Geological Survey. 2012. The StreamStats program for Colorado, online at: <http://water.usgs.gov/osw/streamstats/colorado.html>.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*. **37**:130-137.
- Vieira, N. M., W. H. Clements, L. S. Guevara, and B. F. Jacobs. 2004. Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology* **49**:1243-1259.
- Wang, J., J. Sojininen, Y. Zhang, B. Wang, X. Yang, J. Shen. 2012. Patterns of elevation beta diversity in micro- and macroorganisms. *Global Ecology and Biogeography* **21**:743-750.
- Ward, J. V. and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* **27**:97-117.
- Ward, J. V. 1994. Ecology of alpine streams. *Freshwater Biology* **32**:277-294.
- Ward, J. V. 1986. Altitudinal zonation in a Rocky Mountain stream. *Archiv für Hydrobiologie* **74**:133-199.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* **21**:213-251.
- Whittaker, R. J., M. B. Araújo, P. Jepsen, R. J. Ladle, J. E. M. Watson, and K. J. Willis. 2005. Conservation Biogeography: assessment and prospect. *Diversity and Distributions* **11**:3-23.
- Wiersma, Y. F. and D. L. Urban. 2005. Beta diversity and nature reserve system design in the Yukon, Canada. *Conservation Biology* **19**:1262-1272.

- Wilson, D. S. 1992. Complex interaction in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* **73**:1984-2000.
- Wishart, M. J. and J. M. Hughes. 2003. Genetic population structure of the net-winged midge, *Elporia barnardi* (Diptera: Blephariceridae) in streams of the south-western Cape, South Africa: implications for dispersal. *Freshwater Biology* **48**:28-38.
- Wohl, E. 2005. Virtual rivers: Understanding historical human impacts on rivers in the context of restoration. *Ecology and Society* **10**, online at:
<http://www.ecologyandsociety.org/vol10/iss2/art2/>

APPENDIX I

Abundance of taxa collected at each study site, in number of individuals per five minutes of sampling.

	BT1	BT2	BT3	BT4	BT5	BT6	BT7	BT8	CP1	CP2	CP3	CP4	CP5	CP6	CP7	CP8	SV1	SV2	SV3	SV4	SV5	SV6	SV7	SV8
Ephemeroptera																								
<i>Paraleptophlebia</i> sp.	32	-	8	-	-	-	-	-	48	2	-	4	-	-	2	-	-	8	1	4	4	-	-	-
<i>Siphonurus</i> sp.	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Ecdyonurus</i> sp.	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-	-	153	-	-	-	-	-	-	-
<i>Rhithrogena</i> sp.	12	-	20	13	1	-	22	-	1	-	-	-	120	53	-	4	-	-	-	92	-	44	-	-
<i>Epeorus</i> sp.	108	117	188	98	16	-	58	-	112	90	69	50	16	434	-	120	32	224	40	92	164	77	228	300
<i>Cinygmula</i> sp.	28	44	553	172	41	28	228	-	-	8	1	124	116	190	15	490	-	32	5	636	524	158	252	208
<i>Acentrella</i> sp.	12	-	-	-	-	-	-	-	50	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fallceon quilleri</i>	29	40	-	-	-	-	-	-	1	30	10	44	-	-	-	-	-	88	49	-	8	2	-	-
<i>Baetis</i> sp.	230	874	460	249	361	156	156	2	67	738	569	624	932	242	87	36	608	268	80	1148	1064	506	860	97
<i>Timpanoga hecuba</i>	8	-	-	-	-	-	-	-	41	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ephemerella</i> sp.	4	16	76	107	-	-	-	-	6	170	8	208	-	-	-	-	-	96	248	24	96	7	-	-
<i>Drunella</i> sp.	208	13	88	54	7	32	6	1	152	4	30	33	64	3	17	4	4	1	19	72	36	106	68	232
<i>Ameletus</i> sp.	4	27	-	-	5	189	8	-	1	4	2	28	8	2	9	4	-	20	1	-	-	7	20	76
Plecoptera																								
<i>Pteronarcella badia</i>	8	-	-	-	-	-	-	-	23	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Classenia sabulosa</i>	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hesperoperla pacifica</i>	131	5	-	4	-	256	-	-	1	1	-	7	-	16	-	-	-	9	-	-	-	-	-	-
<i>Sweltsa</i> sp.	-	-	20	8	16	8	18	-	-	-	2	-	8	12	20	-	8	-	2	36	4	2	-	8
Chloroperlidae gn.	48	36	48	24	9	-	6	-	103	44	35	16	-	46	16	105	40	64	31	56	36	18	12	24
<i>Kogotus modestus</i>	-	36	27	3	32	-	-	-	-	-	1	-	-	22	3	-	-	8	-	4	36	13	32	-
<i>Isoperla</i> sp.	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	8	-
<i>Megarcys signata</i>	-	-	1	-	5	-	67	-	-	-	-	-	4	-	-	96	-	-	-	6	-	-	96	125
<i>Pictetiella expansa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6

APPENDIX I (continued)

	BT1	BT2	BT3	BT4	BT5	BT6	BT7	BT8	CP1	CP2	CP3	CP4	CP5	CP6	CP7	CP8	SV1	SV2	SV3	SV4	SV5	SV6	SV7	SV8
Perlodidae gn.	4	-	24	12	14	-	-	-	19	-	-	-	-	-	-	24	-	-	4	-	8	-	-	24
<i>Malenka</i> sp.	16	-	-	12	-	-	-	-	9	4	-	12	-	-	-	-	-	20	-	-	8	-	-	-
<i>Zapada</i> sp.	12	88	164	360	136	113	148	-	1	6	8	20	145	27	163	302	4	20	-	156	72	23	444	281
Leuctridae gn.	-	-	-	-	7	4	8	-	-	-	-	-	8	-	7	-	-	-	-	36	-	-	-	-
Taeniopterygidae gn.	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
Trichoptera																								
<i>Ochrotrichia</i> sp.	4	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hydropsyche</i> sp.	266	-	-	-	-	-	-	-	69	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Cheumatopsyche</i> sp.	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Arctopsyche grandis</i>	-	4	-	-	-	-	-	-	-	-	3	22	-	-	-	-	-	-	-	-	1	-	-	-
<i>Agapetus</i> sp.	12	-	-	-	-	-	-	-	9	4	-	4	-	-	-	-	4	-	-	-	-	-	-	-
<i>Glossosoma</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	20	-	-	-
<i>Lepidostoma</i> sp.	184	-	12	-	-	-	-	-	18	-	3	17	-	-	-	-	-	24	4	8	-	-	-	-
<i>Rhyacophila</i> sp.	16	99	190	48	162	101	87	-	13	32	6	5	42	27	29	12	-	109	13	113	74	25	220	128
<i>Brachycentrus</i> sp.	226	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Micrasema bactro</i>	72	44	44	4	-	-	-	-	-	8	5	144	-	10	-	-	-	16	-	-	36	-	-	-
<i>Oecetis</i> sp.	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptoceridae gn.	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chyranda centralis</i>	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dicosmoecus</i> sp.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Psychoglypha</i> sp.	-	-	-	-	2	8	2	-	-	-	-	-	-	-	-	-	-	-	3	-	-	2	-	-
<i>Hesperophylax</i> sp.	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	20	3	-	1	-	-	-	-	-
Limnephilidae gn.	-	-	-	-	-	12	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-
<i>Neothremma alicia</i>	-	-	531	4	-	112	-	-	-	-	-	-	140	-	16	-	-	-	-	360	24	-	-	-

APPENDIX I (continued)

	BT1	BT2	BT3	BT4	BT5	BT6	BT7	BT8	CP1	CP2	CP3	CP4	CP5	CP6	CP7	CP8	SV1	SV2	SV3	SV4	SV5	SV6	SV7	SV8
<i>Allomyia</i> sp.	-	-	-	-	34	-	2	-	-	-	-	-	-	-	2	16	-	-	-	-	-	-	-	-
Diptera																								
<i>Pericoma</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Hybomitra</i> sp.	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Culicoides</i> sp.	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Palpomyia</i> sp.		8								0						6		6						-
<i>Dixa</i> sp.	-	-	-	-	2	-	-	-	-	-	-	-	-	-	2	4	4	-	-	4	-	-	-	-
<i>Chelifera</i> sp.	32	-	16	-	9	-	-	-	2	10	2	4	4	-	-	-	-	32	1	12	-	-	4	-
<i>Clinocera</i> sp.	-	-	4	4	11	-	4	25	3	-	-	-	-	-	5	173	4	12	-	68	12	-	8	40
<i>Simulium</i> sp.	64	8	4	100	-	-	-	-	183	32	2	380	-	24	-	12	176	4	7	-	28	-	-	-
<i>Prosimulium</i> sp.	4	40	-	164	-	-	-	115	16	2	-	-	200	-	-	-	404	76	74	284	-	-	-	-
<i>Helodon</i> sp.	-	-	76	-	145	60	192	-	-	-	-	-	-	2	157	924	-	-	-	-	12	27	304	576
<i>Antocha</i> sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Limnophila</i> sp.	-	-	-	-	-	-	-	-	-	6	-	4	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hexatoma</i> sp.	-	-	-	-	-	-	-	-	-	8	2	-	-	1	-	-	-	-	-	-	3	-	-	-
<i>Dicronota</i> sp.	4	4	-	-	-	6	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tipula</i> sp.	1	-	-	-	-	-	11	-	2	-	1	-	-	-	2	18	-	8	2	-	-	-	-	1
Tipulidae gn.	4	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	4	2	-	-	-	-	-
Coleoptera																								
<i>Agabus</i> sp.	-	-	-	-	-	-	-	-	1	4	-	-	-	-	-	-	4	-	2	-	-	-	-	-
<i>Tropisternus</i> sp.	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-
<i>Zaitzevia parvula</i>	56	-	-	-	-	-	-	-	-	-	-	52	-	-	-	-	-	-	-	-	-	-	-	-
<i>Optioservus</i> sp.	620	-	-	-	-	-	-	-	128	60	-	60	-	-	-	-	-	4	-	-	-	-	-	-
<i>Narpus concolor</i>	20	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-
<i>Heterlimnius corpulentus</i>	68	384	368	140	-	-	2	-	-	4	85	132	-	118	-	-	-	288	10	164	516	54	-	-

APPENDIX II

All explanatory variables for each category of spatial, environmental, and flow regime predictors from all 24 sites.

	BT1	BT2	BT3	BT4	BT5	BT6	BT7	BT8
Spatial Predictors								
Elevation (m)	2001	2252	2443	2573	2900	3051	3364	3478
Latitude (°N)	40.5711	40.4799	40.4056	40.3368	40.3926	40.3098	40.4256	40.4380
Longitude (°W)	105.3477	105.4448	105.5491	105.6113	105.6597	105.6631	105.7840	105.7535
Environmental Predictors								
Mean annual temp. (°C)	4.60	3.70	2.70	2.20	1.50	1.80	0.60	0.20
Mean annual Q (cms/km ²)	0.007	0.009	0.013	0.021	0.024	0.041	0.033	0.039
Width (cm)	500.7	433.3	310.0	200.0	313.7	260.0	180.0	200.0
Width/Depth	19.3	18.8	21.1	6.3	11.8	8.4	24.5	22.2
Channel slope (%)	1.75	4.38	6.00	3.00	8.50	7.00	15.50	25.00
Riparian cover (%)	61.83	82.92	79.67	72.08	55.25	54.83	4.42	0.00
BOM (g/m ²)	27.68	57.64	12.60	22.20	38.63	58.63	14.85	15.11
Conductivity (µS/cm)	43.14	22.23	18.56	9.80	10.86	6.01	15.29	25.74
Dissolved oxygen (mg/L)	7.63	9.21	8.11	8.16	9.13	7.96	7.31	8.65
pH	7.97	7.78	6.99	6.66	6.46	6.38	7.32	6.15
d50 (mm)	11.1	22.7	11.1	32.1	32.1	90.1	64.1	32.1
d50-cv (mm)	0.65	0.61	0.66	0.50	0.57	0.59	0.21	0.36
% Fine sized substrate	18.0	17.0	21.6	15.0	18.0	23.5	0.0	4.0
% Boulder sized substrate	2.0	6.0	2.9	0.0	4.0	10.8	3.0	0.0
% Embedded substrate	22.0	14.0	0.0	0.0	7.0	16.7	6.0	0.0
Flow Regime Predictors								
Q2/Q _m	7.63	9.28	10.39	11.08	13.02	18.05	15.26	18.85
Q100/Q _m	27.99	28.18	28.02	25.46	29.64	34.39	36.05	45.19
Monthly Q – cv	1.41	1.50	1.50	1.48	1.55	1.57	1.67	1.75
Bed Mobility Index	30.95	22.94	22.58	11.12	11.46	13.27	2.34	4.91

APPENDIX II (continued)

	CP1	CP2	CP3	CP4	CP5	CP6	CP7	CP8
Spatial Predictors								
Elevation (m)	1992	2181	2411	2590	2775	3060	3166	3397
Latitude (°N)	40.7000	40.9185	40.6253	40.9277	40.5492	40.5181	40.6235	40.5173
Longitude (°W)	105.4415	105.4984	105.5271	105.6744	105.5617	105.7708	105.7080	105.6589
Environmental Predictors								
Mean annual tem. (°C)	5.60	5.10	3.60	3.60	1.50	2.00	1.50	1.10
Mean annual Q (cms/km ²)	0.005	0.005	0.006	0.009	0.011	0.025	0.013	0.019
Width (cm)	496.7	379.0	423.3	195.0	280.0	372.3	210.0	760.0
Width/Depth	14.8	15.8	13.1	5.0	10.2	10.5	10.3	39.3
Channel slope (%)	2.50	2.50	6.00	2.50	8.00	2.50	11.00	3.50
Riparian cover (%)	61.00	35.83	39.67	22.42	69.67	27.83	53.00	0.00
BOM (g/m ²)	42.85	203.53	29.07	140.77	19.75	7.66	46.93	17.09
Conductivity (µS/cm)	62.27	87.41	20.33	55.37	12.77	12.85	16.57	9.39
Dissolved oxygen (mg/L)	8.21	7.95	7.51	8.13	8.87	7.88	7.57	7.72
pH	8.10	8.19	6.83	8.09	7.60	7.23	6.73	6.91
d50 (mm)	32.1	9.6	45.1	22.7	5.7	64.1	32.1	22.7
d50-cv (mm)	0.54	0.67	0.50	0.66	0.71	0.34	0.50	0.40
% Fine sized substrate	19.0	19.4	14.0	28.0	14.9	4.9	10.0	4.0
% Boulder sized substrate	2.0	1.0	0.0	2.0	2.0	0.0	0.0	0.0
% Embedded substrate	29.0	16.5	1.0	18.0	12.9	1.0	17.0	1.0
Flow Regime Predictors								
Q2/Q _m	7.28	6.80	7.46	8.27	10.21	11.21	10.06	12.13
Q100/Q _m	34.11	26.14	26.39	27.48	31.85	23.39	31.81	32.03
Monthly Q – cv	1.46	1.46	1.49	1.56	1.60	1.45	1.64	1.61
Bed Mobility Index	22.90	28.56	19.44	8.86	13.09	8.72	3.48	7.36

APPENDIX II (continued)

	SV1	SV2	SV3	SV4	SV5	SV6	SV7	SV8
Spatial Predictors								
Elevation (m)	2015	2189	2388	2643	2830	2964	3249	3348
Latitude (°N)	39.8776	40.0374	40.1547	40.1727	40.1173	39.9961	40.0707	40.0709
Longitude (°W)	105.2844	105.4194	105.4663	105.5279	105.5324	105.5699	105.6033	105.6149
Environmental Predictors								
Mean annual temp. (°C)	6.20	3.90	3.30	2.40	2.30	1.80	1.40	0.90
Mean annual Q (cms/km ²)	0.009	0.009	0.011	0.017	0.017	0.020	0.037	0.034
Width (cm)	316.7	341.7	323.3	286.7	484.3	377.7	262.0	163.3
Width/Depth	19.0	12.3	14.7	17.6	12.7	9.9	13.6	9.6
Channel slope (%)	2.50	3.50	5.25	9.00	6.00	1.00	10.00	18.00
Riparian cover (%)	46.75	82.33	81.50	79.50	64.42	1.33	58.67	18.00
BOM (g/m ²)	31.79	24.69	37.78	19.29	30.85	18.71	46.80	29.13
Conductivity (µS/cm)	200.81	24.36	24.20	10.59	15.88	12.79	10.63	7.30
Dissolved oxygen (mg/L)	7.92	8.74	8.84	8.92	7.81	8.44	7.93	8.04
pH	8.06	7.74	7.80	7.58	7.10	7.35	7.07	7.07
d50 (mm)	11.1	32.1	32.1	22.7	180	45.1	90.1	128.1
d50-cv (mm)	0.62	0.48	0.50	0.51	0.40	0.27	0.40	0.29
% Fine sized substrate	18.6	12.4	12.0	9.8	13.7	5.0	13.0	4.2
% Boulder sized substrate	0.0	1.0	8.0	2.0	0.0	0.0	0.0	0.0
% Embedded substrate	29.4	10.3	18.0	9.8	4.9	0.0	10.0	3.4
Flow Regime Predictors								
Q2/Q _m	8.89	8.90	9.47	11.62	10.01	10.77	16.21	15.87
Q100/Q _m	32.91	28.64	28.08	29.56	24.45	25.30	39.09	33.59
Monthly Q – cv	1.47	1.50	1.53	1.55	1.48	1.49	1.74	1.60
Bed Mobility Index	29.80	23.52	9.93	14.45	7.26	10.89	2.52	7.98