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ASSESSING LINKAGES AMONG LANDSCAPE CHARACTERISTICS,
STREAM HABITAT, AND MACROINVERTEBRATE COMMUNITIES
IN THE IDAHO BATHOLITH ECOREGION

by

Andrew C. Hill

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Watershed Sciences

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2010

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ABSTRACT

Assessing Linkages Among Landscape Characteristics, Stream Habitat, and
Macroinvertebrate Communities in the Idaho Batholith Ecoregion

by

Andrew C. Hill, Master of Science

Utah State University, 2010

Major Professor: Brett B. Roper
Department: Watershed Sciences

Understanding the composition of lotic communities and the landscape processes and habitat characteristics that shape them is one of the main challenges confronting stream ecologists. In order to better understand the linkages among landscape processes, stream habitat, and biological communities and to understand how accurately our measurements represent important factors influencing biological communities, it is important to test explicit hypotheses regarding these linkages. Increasing our understanding of aquatic communities in a hierarchical context and recognizing how well our measurements represent factors structuring aquatic communities will help managers better evaluate the influence of land management practices on aquatic ecosystems, direct conservation strategies, and lead to better assessments of ecological condition.

In Chapter 2, we used spatial data, field-based habitat measurements, and macroinvertebrate community data to 1) examine the influence of landscape processes on two factors of stream habitat; maximum stream temperatures and fine sediment, and to

2) examine how well these landscape and habitat characteristics represent factors influencing gradients in macroinvertebrate community structure. The results of this study showed that spatially derived measurements may be effectively used to test hypotheses regarding landscape influences on stream habitat and that spatial data, used in conjunction with field measurements can provide important information regarding factors influencing gradients in biological communities. In addition, spatially derived measurements may provide the same or additional information regarding influences on community structure as field-based measurements, which suggests that further research should be done to assess how well our field measurements represent factors that are important in shaping stream communities.

The objective of Chapter 3 was to compare how well single field measurements and a combination of indicator variables hypothesized to be components of a single ecological processes or concept, known as a latent variable, represent thermal stress and fine sediment influences on macroinvertebrate communities. Results from this study showed that both single and latent variables explained relatively the same amount of variation in macroinvertebrate community structure. This suggests that while latent variables may have a potential to better refine how we represent ecological factors, a better basis for defining *a priori* hypotheses is needed before these variables can provide any additional information compared to single habitat measurements.

(109 pages)

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Andrew C. Hill

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CHAPTER 1

INTRODUCTION

The composition of aquatic communities is influenced by a complex interaction of physical and biological processes taking place at multiple spatial and temporal scales. Aquatic systems have long been recognized as products of the surrounding landscape (Hynes 1975) and this recognition has served as a basis for scientific investigation into the relationships among landscape processes, in-stream habitat, and stream biota. In order for aquatic organisms to persist in a local community, they must possess functional traits that allow them to adapt to environmental conditions at multiple spatial scales (Tonn 1990; Poff 1997). Therefore, the composition of local aquatic communities is comprised of taxa that have adapted to environmental conditions at scales ranging from the watershed and stream channel, to microhabitat scales.

Many stream organisms have specific environmental tolerance ranges (Malmqvist and Rundle 2002) which implies that changes in environmental conditions may lead to changes in community structure as well as shifts in community dynamics and trophic interactions (Bilby et al. 1996; Willson et al. 1998). On federal lands within the Interior Columbia River Basin (CRB), land management practices have been identified as contributing factors leading to alterations in stream habitat conditions and a decline in the distribution and abundance of native species (Kershner et al. 2004). In order to conserve aquatic ecosystems, it is important to understand the linkages among landscape processes, stream habitat, and aquatic communities and to better understand how well our field-based habitat measurements characterize important influencing stream biota.

The objectives of this research were to 1) use mapped information in conjunction with field-based habitat measurements to assess the efficacy of spatial attributes to characterize landscape factors influencing stream habitat and identify environmental gradients in macroinvertebrate community structure, 2) compare the relative efficacy of spatial attributes and field-based habitat measurements to indicate environmental influences on community structure, and to 3) test whether the combination of multiple habitat measurements hypothesized to be components of a single ecological process may more effectively characterize in-stream habitat influences on stream communities compared to single measurements. To accomplish these objectives, we focused our study on two factors of stream habitat; maximum stream temperature and fine sediment, and used macroinvertebrate community data as a biological response. High stream temperatures and increased sedimentation are two of the major aspects of stream habitat that have been identified as threats to aquatic ecosystems within the CRB (USFS and USBLM 2000) and macroinvertebrates are often used as biological indicators due to their sensitivity to changes in stream habitat (Cairns and Pratt 1992) and the relative efficiency of sample collection (Resh 2008). Macroinvertebrates are also often used in place of sampling fish species due to the potential stress biological sampling can have on sensitive fish species (Nielsen 1998).

Results from this research will provide additional insight into the efficacy of spatial attributes to represent landscape influences on stream habitat and aquatic communities in order to assess factors shaping gradients in community composition and provide a better understanding of how well our field measurements indicate the relative environmental factors important in shaping aquatic communities. These insights may

potentially provide managers with better predictive capabilities, applications that may allow the use of spatially derived landscape characteristics to factor out variation in the landscape to better assess the influence of management on aquatic ecosystems, and a means to more effectively characterize environmental processes influencing stream biota for use in monitoring programs.

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CHAPTER 2

EXPLORING GRADIENTS IN MACROINVERTEBRATE COMMUNITY
STRUCTURE USING SPATIAL DATA AND FIELD-BASED HABITAT
MEASUREMENTS**Introduction**

Conditions of aquatic habitats and the biological communities that inhabit them are shaped by a complex interaction of physical, chemical, and biological factors operating at multiple spatial and temporal scales (Poff 1997). For aquatic species to persist in a local community, they must possess a suite of functional traits that allow them to adapt to environmental conditions ranging from watershed and stream channel, to microhabitat scales (Tonn 1990; Poff 1997). The composition of local aquatic communities is therefore comprised of taxa that have adapted to environmental conditions at multiple spatial scales, where compositional shifts may result from temporal changes in local stream habitat characteristics caused by natural and anthropogenic disturbance (Gresswell 1999; Robinson et al. 2000). In order to understand how natural and anthropogenic disturbance may lead to changes in stream habitat and compositional shifts in aquatic communities, it is important to understand the environmental processes within a landscape that shape stream habitat, and the physical characteristics of stream habitat that influence aquatic communities (Imhof et al. 1996; Wang et al. 2006). A better understanding of landscape processes and the factors influencing aquatic biota is fundamental in assessing the implications that management activities may have on aquatic ecosystems and directing land management strategies that maintain and restore the integrity of aquatic systems (Minshall 1988; Palmer et al. 1997).

Within the Interior Columbia River Basin (CRB), land management practices such as livestock grazing, road construction, and timber harvest have been identified as contributing factors leading to the loss of available quality habitat and the decline of many native species (Kershner et al. 2004a). Loss in the availability of quality habitat threatens the stability and persistence of native fish populations and the structure and function of aquatic ecosystems (Rieman et al. 2000). Currently there are large scale monitoring efforts taking place on federal lands within the CRB aimed at determining whether land management and conservation strategies are effective in maintaining or restoring the structure and function of aquatic ecosystems (Whitacre et al. 2007). These efforts include field-based surveys that measure a variety of physical stream attributes to assess the status and trends of stream habitat. Determining the effectiveness of land management strategies on the status and trends of stream habitat depends on the ability to understand landscape processes influencing stream habitat conditions and to understand how well our habitat measurements represent factors important to aquatic biota.

In recent years, the use of mapped information has provided researchers with a tool for analyzing spatial data to examine relationships with the stream environment (Allan and Johnson 1997). Deriving spatial attributes from mapped data provides an efficient approach to assessing landscape influences on stream habitat across large geographic areas (Wang et al. 2006). Recent work in stream ecology has shown that a substantial amount of variation in local-scale habitat can be empirically derived from landscape features and suggests that spatially based methods may be used as an alternative to field-based habitat assessments (Wehrly et al. 2006; Zorn and Wiley 2006; Brenden et al. 2007; Burcher et al. 2007; Wehrly et al. 2009). While assessment of local

habitat characteristics based on landscape associations may be beneficial, the contribution of these methods to our understanding of environmental processes is dependent upon the ability of spatial attributes to accurately represent landscape processes influencing stream habitat.

The objectives of this study were to use mapped information in conjunction with field-based habitat measurements to assess the efficacy of spatial attributes to characterize landscape factors influencing physical stream habitat characteristics in order to identify environmental gradients in macroinvertebrate community structure and to assess how well field-based measurements indicate the influence of habitat on community structure. We focused our study on sustained periods of high stream temperatures and fine sediment accumulation because these habitat factors have been identified as major threats to aquatic ecosystems on federal lands within the CRB (USFS and USBLM 2000) and are common characteristics used in monitoring the status and trends of stream habitat. Macroinvertebrate community data was used as a biological response due to the sensitivity of macroinvertebrates to changes in stream habitat from anthropogenic influences (Cairns and Pratt 1992), the relative efficiency of sample collection (Resh 2008), and the potential stress biological sampling can have on sensitive fish species (Nielsen 1998). The use of spatial attributes in conjunction with field-based measurements provides a method to test explicit hypotheses regarding landscape influences on stream habitat in order to potentially understand environmental gradients shaping aquatic communities and assess how well our field-based habitat measurements characterize factors influencing aquatic biota. A better understanding of the influence of landscape processes on stream habitat and the habitat that is important to the biota may

potentially lead to more effective assessments of biological condition based on stream habitat relationships.

Study Area

The Idaho Batholith Ecoregion (Bailey 1995) encompasses approximately 40,000 km² of land within central Idaho and western Montana (Figure 2.1) and is defined by mountainous terrain with both deeply dissected and glacially scoured valleys primarily underlain by granitic lithologies (McGrath et al. 2002). Climate is maritime-influenced with a north to south gradient of decreasing precipitation, varying with elevation, which range from approximately 300 to 3000 m. Most precipitation in the study area falls as snow in late fall, winter and early spring, and runoff is primarily from spring snowmelt (McGrath et al. 2002). Dominant vegetation at high elevations within the study area consists of Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), Grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) at mid-elevations, and ponderosa pine (*Pinus ponderosa*) and sagebrush (*Artemisia tridentata*) at lower elevations (McGrath et al. 2002).

The study area forms the headwaters of the Bitterroot, Clearwater, and Salmon Rivers in addition to major tributaries of the Snake River. Streams draining the study area provide spawning and rearing habitat for anadromous Endangered Species Act (ESA) listed fish species such as Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) in addition to critical habitat for resident ESA listed populations of bulltrout (*Salvelinus confluentus*).

Distinct gradients of both natural and anthropogenic disturbance regimes are found in the study area. Fire is the dominant natural disturbance in the study area and

anthropogenic disturbance is predominantly associated with timber harvest and roads, with grazing and mining also occurring. Because of the varying degrees of disturbance and the presence of ESA listed species, understanding the influence of landscape process on stream habitat and the efficacy of in-stream habitat measurements to indicate factors influencing biotic communities is important in determining the impacts of disturbance on aquatic ecosystems and prioritizing restoration activities within the study area.

Methods

Study Design and Reach Selection

Our study is part of a larger program aimed at monitoring the status and trends of in-stream habitat on federal lands within the Interior Columbia River Basin (Kershner et al. 2004b). Sample watersheds were determined probabilistically using a spatially balanced sample design described in Kershner et al. (2004b). This approach first organized the Interior Columbia River Basin (CRB) into groups of 20 contiguous 6th field hydrologic code watersheds and within each of these groups, watersheds were randomly selected to determine the potential for sampling. Watersheds were then categorized as either reference or managed based on current and historical management activities. Watersheds were considered reference if they contained minimal management activities with no permitted livestock grazing in the last 30 years, less than 0.5 km/km² road density at the watershed scale and no roads within the proximate (1 km) riparian buffer, less than 10 percent timber harvest within the watershed, and no evidence of mining within riparian areas (Kershner et al. 2004b). Watersheds were considered managed if they contained higher degrees of land management activities. Within each watershed, we

located sample reaches by identifying the lowermost stream section on federally managed land with a gradient less than 3 percent and federal ownership greater than 50 percent in the upstream catchment. Reaches at the lowermost portion of the watershed were selected because they are thought to integrate the cumulative effects of upstream disturbance (Kershner et al. 2004b), and low gradient channels are likely to be more sensitive to change under variable sediment and flow regimes (Montgomery and MacDonald 2002). Further details on the study design can be found in Kershner et al. (2004b) and Al-Chokhachy et al. (2010). We attempted to control for variation in biotic assemblages that can arise from inherent differences in physiographic characteristics (Feminella 2000) by selecting a subset of reaches from this larger program dataset located within our study area that had complete physical habitat and biological stream data.

We evaluated 190 reaches on U.S. Forest Service and BLM lands located in predominantly federally managed catchments. Stream sizes at sampled reaches ranged from 1.29 to 20.78 m in bankfull width and varied in elevation from 460 to 2350 m. Reach gradients ranged from 0.03 to 2.99 percent. Contributing catchment area upstream of sample reaches varied from 1.08 km² to 145.52 km². Land management activities within upstream catchments represent the varying degrees of management found in the study area with 65 catchments considered reference and 125 considered managed.

Field Methods

We conducted field sampling from late June to early September during baseflow conditions between 2004 and 2007. Reach lengths were defined as 20 times the average bankfull width, with a minimum length of 160 m. We assessed reach lengths of 20 times

the bankfull width to increase the likelihood that multiple riffle-pool sequences were sampled in each reach (Knighton 1998). At each reach, we collected in-stream temperature, substrate, and macroinvertebrate data.

Temperature. - We recorded hourly stream temperatures from July 15th to August 31st at a point location within each reach using thermal data loggers. From these hourly temperature measurements, we summarized the seven-day moving average of maximum daily temperatures and used the maximum temperature within the warmest seven day period (hereafter referred to as weekly maximum temperature) as an indicator of sustained periods of high stream temperatures. This summary metric is used to assess compliance with Environmental Protection Agency water quality standards for salmonids in the Pacific Northwest (U. S. Environmental Protection Agency 2003) and has also been used in the investigation of species-habitat relationships (Ebersole et al. 2006).

Fine Sediment. - We collected sediment size measurements to characterize the amount of fine sediment at each reach. To accomplish this, we first established the sample reach by measuring bankfull width at four random locations and used the average of these four measurements to categorize reaches into 2 meter width categories (minimum width category = 8m, maximum = 25m). We then established transects (minimum of 20) at evenly spaced intervals of the corresponding width category along the stream.

At each transect, we collected substrate at 5 equally spaced intervals perpendicular to the channel and measured the intermediate axis of each particle (Wolman 1954). From these samples, we used particles collected within the active stream channel (no bank material) to estimate the proportion of bed material less than 4

mm (hereafter referred to as substrate < 4). The proportion of sand and finer particles within a reach is a common summary metric used in habitat monitoring programs (Roper et al. 2002) to indicate the amount of fine sediment accumulation in a reach.

Macroinvertebrates. - We collected macroinvertebrate samples at each reach prior to sampling in-stream habitat. Macroinvertebrates samples were collected at two random locations in each of the first four fast-water (riffle) habitats using a 0.09 m² Surber sampler (500- μ m mesh) for a total of eight samples. Within each 0.09 m² sample area, substrate was disturbed to a depth of 10 cm and rubbed to facilitate the dislodgment of macroinvertebrates and collection in the sampler. Samples were then combined, transferred to jars, and preserved in 95% ethanol.

Macroinvertebrate samples were sorted (Vinson and Hawkins 1996) and identified to the lowest possible taxonomic level (usually genus or species) by the National Aquatic Monitoring Center (www.usu.edu/buglab/). Due to ambiguities in taxonomic resolution that occur where organisms cannot be identified to a consistent taxonomic level (Cuffney et al. 2007), macroinvertebrates were converted into Operational Taxonomic Units (OTUs) by Charles Hawkins at The Western Center for Monitoring and Assessment of Freshwater Ecosystems (<http://www.cnr.usu.edu/wmc/>). Operational Taxonomic Units can vary in level of taxonomic resolution, but are unique from one another and are identified based on the aggregation of ambiguous taxa into an OTU or the exclusion of ambiguous taxa from the analysis. This results in all similar taxa being classified to a consistent taxonomic level.

Geographic Analysis

We used publicly available geographic data sets in a geographical information system (GIS; Environmental Systems Research Institute (ESRI) ArcGIS 9.2) to derive landscape characteristics hypothesized to influence sustained periods of high temperatures and fine sediment accumulation at the reach (Table 2.1). Within the GIS environment, reach locations were first identified from field geographic positioning system (GPS) coordinates and used to delineated catchment boundaries upstream of the bottom of each reach using 10-meter digital elevation models (DEMs) acquired from the U.S. Geological Survey (USGS) National Elevation Dataset (<http://www.ned.usgs.gov>). To facilitate the delineation process, we identified stream networks from the 1:24,000 scale USGS National Hydrography Dataset (NHD; <http://nhd.usgs.gov/>) and modified DEMs by lowering stream elevation values with the AGREE algorithm (Hellweger 1997).

Spatial scales. - We identified environmental characteristics at four spatially nested scales (Frissell et al. 1986) that were hypothesized to influence maximum temperatures and fine sediment accumulation at sampled reaches. Spatial scales used in this analysis included the catchment drainage, catchment stream network, stream segment, and reach scales (Figure 2.2). We defined the catchment drainage (hereafter referred to as catchment) as the contributing area upslope of the sampled reach, the catchment stream network (hereafter referred to as stream network) as the sum of streams draining the catchment, the segment as stream sections within the stream network extending from the bottom of the sampled reach upstream 1000 m in flow length, and the reach as the stream section extending from the sampled reach bottom upstream 300 m in

flow length. All stream sections had a width of 10 m, equal to the resolution of the DEMs.

Environmental influences on stream temperature. - We derived measurements from GIS at the catchment, stream network, and segment scales that were hypothesized to influence maximum stream temperatures at our sampled reaches (Table 2.1). At the catchment scale, we hypothesized that hill slope and channel structure (topography) are important in controlling the transport rate of sub-surface and surface water through a landscape (residence time) and that increases in residence times prolong the exposure of water to factors that may potentially increase surface water temperatures such as air temperature and direct solar radiation (Caissie 2006). To represent topographic controls on water residence times, we calculated the flow path distance from each cell to the catchment outlet and the flow path gradient from each cell to the outlet using DEMs. The ratio of the median flow path distance and median flow path gradient within each catchment was then calculated to represent topographic controls on stream water residence time (McGuire et al. 2005). Higher flow path distance to gradient ratios characterize catchments with longer flow paths and lower hill slope and channel gradients indicating longer residence times and a slower rate of water transport to the catchment outlet.

At the stream network scale, we hypothesized that maximum summer air temperatures were important factors contributing to extended periods of high stream water temperatures. The temperature of streams closely follows seasonal trends of the surrounding air temperature due to the convective heat transfer from air to water (Allan and Castillo 2007). To represent the influence of summer air temperatures on stream

temperatures during our period of field measurements, we calculated the average maximum July and August air temperature (PRISM Group, Oregon State University, <http://www.prismclimate.org>) within the stream network for the year field sampling occurred.

The structure and composition of riparian vegetation plays an important role in shading and insulating streams from direct solar radiation (Gregory et al. 1991) and reductions in forested riparian cover can lead to a decrease in effective shading of the stream (Moore et al. 2005). Riparian cover in closer proximities to a location along the stream continuum may also have a greater influence on localized stream temperatures than cover further upstream (Johnson 2004). To indicate the amount of shading proximal to the reach from riparian vegetation, we calculated the mean percentage of forested canopy cover (LANDFIRE, <http://www.landfire.gov>) at the segment scale.

Environmental influences on fine sediment. - We derived measurements in GIS at the catchment, stream network, and reach scales that were hypothesized to influence fine sediment deposition at our sample reaches (Table 2.1). At the catchment scale, we hypothesized that the susceptibility of hillsides to mass failure and the transport of sediment by overland flow increases with slope and that steeper hill slopes closer to the stream increase the potential supply and delivery of fine sediment to the stream. To characterize catchments with steeper slopes near the stream network, we calculated the slope for each cell within catchments using DEMs and weighted each cell based on the distance to the ridge as a fraction of the total distance from the ridge to the stream. This weighting method results in a measure for each cell between 0 and 1 indicating the proximity of a cell to the stream channel. The cell weight was then multiplied by the

slope value for each cell in the catchment and summarized as the average weighted slope within the catchment.

To indicate the sediment transport capacity of the stream, we estimated the distribution of stream energy (stream power) within the stream network. The distribution of energy within a stream network is a measure indicating the potential for fine sediment transport and storage within the stream channel (Jain et al. 2006). Stream networks with high stream power distributions would be expected to efficiently move fine sediment through the stream network leading to an expected reduction in the amount of fine sediment found at low gradient sections such as our sampled reaches. Networks with lower stream power distributions would be less adept at moving sediment through the system, where lower gradient sections would act as sinks for finer sediment. To estimate stream power, we first used the normalized excavation version of the AGREE algorithm (Baker et al. 2006) to identify stream elevation values from DEMs. Normalized excavation uses the minimum elevation within a specified local area (250m) from the stream channel to identify stream elevations to reduce topographic errors associated with elevation values where vector (NHD) and DEM stream locations may differ. We then divided the stream network into individual stream links which are defined as sections of the stream channel extending between two tributaries or between a stream source and its first junction with another stream (Kelley et al. 1988). Within each stream link, we calculated the range of elevation values and divided these results by the flow length of each link to yield a measure of channel slope (m/m) for each link. Due to the potential error in gradient estimates stemming from the simplification of channel sinuosity in raster based length estimates, we used a smoothing process to estimate average channel

gradient within a 130 meter focal radius of the stream channel from our initial link based gradient estimates.

We estimated bankfull discharge for each stream cell within the stream network using the bankfull discharge-area relationship of Castro and Jackson (2001) for the Western Cordillera Ecoregion (Omernik 1987), which encompassed a majority of our study area. This empirically derived regional curve uses a power function to estimate discharge as a function of the contributing drainage area. The equation for estimating bankfull discharge in the Western Cordillera Ecoregion is:

$$Q_{bf} = 17.28 \cdot A^{0.86}$$

where Q_{bf} = bankfull discharge (ft³/second), A = drainage area (mi²), and 17.28 and 0.86 are empirically derived coefficients and exponents, respectively.

From our link based estimates of channel slope and our continuous estimate of bankfull discharge (converting *discharge* to m³/s) within the stream network, we estimated bankfull specific stream power (Ω_{sp}) for each stream cell using the equation:

$$\Omega_{sp} = \gamma \cdot Q_{bf} \cdot s$$

where Ω_{sp} = specific stream power (watts/m), γ = the unit weight of water (9800 N/m³), Q_{bf} = bankfull discharge (m³/second), and s = the energy slope (m/m) which is considered equivalent to bed slope. The resulting values were summarized as the median network stream power (hereafter network stream power) in order to characterize the distribution of energy within the stream network (Jain et al. 2006).

While network stream power indicates the distribution of energy or the competency of a stream to transport sediment within a stream network, the presence of fine sediment at a specified location within a stream network and the competency of the

stream to initiate substrate movement may also be influenced by localized stream power.

To estimate unit stream power at the reach scale, we used equation 1.1 to estimate bankfull discharge and estimated the bankfull channel width of our reaches using the bankfull width-area relationship of Castro and Jackson (2001). The equation estimating bankfull width in the Western Cordillera Ecoregion is:

$$W_{bf} = 9.4 \cdot A^{0.42}$$

where W_{bf} = bankfull width (ft), A = drainage area (mi^2), and 9.4 and 0.42 are empirically derived coefficients and exponents, respectively. Although field measured values of bankfull width were available for each sample reach, we used estimations based on the previous equation in order to maintain the consistency of using GIS-derived measurements and to avoid potential inconsistencies stemming from field-based measurement error (Roper et al. 2010). Reach gradient (slope) was estimated from unconditioned DEMs by dividing the range of elevations in the reach by the reach flow length. Gradient values of 0 m/m were given the value of 0.1 for calculation purposes. We then estimated the stream power per unit area (Ω_u) of the reach with the equation:

$$\Omega_u = \frac{\gamma \cdot Q_{bf} \cdot s}{w_{bf}}$$

where Ω_u = unit stream power (watts/m^2), γ = the unit weight of water (9800 N/m^3), Q_{bf} = bankfull discharge (m^3/second), s = the energy slope (m/m), and w_{bf} = stream width at bankfull (m).

Analytical Methods

Assessment of landscape influences on stream habitat. - We incorporated our GIS-derived variables into ordinary least-squares multiple linear regression (MLR) analyses to assess whether the GIS measurements met our expectations regarding influences on maximum weekly temperature and fine sediment and to test the relative efficacy of GIS-derived measurements to predict field measured habitat. Prior to our final assessment, we square root transformed substrate < 4 and log transformed the flow path distance to gradient ratio, network stream power, and reach stream power (log + 1). Model assumptions were then checked for violations of normality, linearity and heteroscedascity using visual assessments of the residuals. Multicollinearity was assessed using the variance inflation factor (VIF > 10).

Macroinvertebrates. - We used the relative abundance of OTUs (hereafter referred to as taxa) to examine variation in macroinvertebrate community composition. In order to reduce noise in further analyses stemming from the presence of taxa in minimal samples, taxa that were present at fewer than five percent of the reaches were eliminated (McCune and Grace 2002) and the resulting data were $\log_{10}(x + 1)$ transformed. From the log-transformed abundance data, we converted reaches into a distance matrix using Bray-Curtis dissimilarity (BCD; Bray and Curtis 1957) based on community composition, and used Non-Metric Multi-Dimensional Scaling (Clarke 1993) to summarize multi-dimensional patterns in macroinvertebrate assemblage structure. Bray-Curtis dissimilarity compares the degree to which reaches share the same taxa (Hawkins and Norris 2000), resulting in an interpretable measure of ecological distance of taxa abundance among sampled reaches (Faith and Minchin 1987; Legendre and

Anderson 1999). NMDS is an unconstrained ordination method based on ranked distances of samples (reaches) that attempts to represent taxa in a minimal number of dimensions while preserving the distance relationships (BCD) among samples (Legendre and Legendre 1998). The multi-dimensional solution of dissimilarity from NMDS is compared to the original BCD measurement to yield a measure of fit (termed stress). Stress values are scaled from 1 to 100, with lower stress values indicating a better fit between the two distance matrices. In addition to stress, NMDS results consist of reach axis coordinates (reach scores) calculated as the weighted averages of reaches based on their order along the ordination axes that indicate gradients in reach community composition, and taxa axis coordinates (taxa scores) that represent the weighted average centroid of the taxa along the ordination axes. We used the resulting NMDS configuration of reach scores as a response variable to assess the relative efficacy of our GIS-derived variables and in-stream habitat measurements to characterize the influence of sustained periods of high stream temperatures and fine sediment accumulation on gradients in macroinvertebrate community structure. All NMDS analyses were performed using the metaMDS function in R (Oksanen et al. 2008).

Assessing landscape and habitat influences on community structure. - In order to identify and assess the relative influence of landscape and habitat characteristics shaping gradients in macroinvertebrate community structure, we fit regression models of our GIS-derived measurements and field measured habitat variables to the resulting NMDS axis reach scores. We regressed our field measured habitat variables on each NMDS axis to assess the variation in community structure along each axis accounted for by our field measurements and identify whether gradients shaping macroinvertebrate structure in our

sample were related to high stream temperatures and fine sediment accumulation. We then used the GIS-derived independent variables from our initial MLR analysis with the habitat variables to assess the variation in community structure along each axis accounted for by our GIS-derived variables. The results from these analyses were compared using adjusted coefficients of determination (R^2_{adj}) and Akaike Information Criteria (AIC) scores to assess whether our hypotheses regarding the influence of GIS-derived landscape characteristics were consistent with field measured variables and to assess the relative efficacy of our field measurements and GIS-derived measurements to represent sustained periods of high stream temperatures and fine sediment accumulation influences on macroinvertebrate community structure. Where R^2 values indicate the amount of variation in the response explained by the predictor variables, AIC calculates a score for each model that is based on model parsimony and unexplained variance (Burnham and Anderson 2002). For a set of competing models, the model with the lowest AIC score is considered to be the better model. Competing models with a difference in AIC scores < 2 suggest comparable models, while differences > 10 suggest non-comparable models (Burnham and Anderson 2002). To visualize our results, we used the envfit function in R (Oksanen et al. 2008) to additionally identify gradients in the ordination configuration correlated with each of our field and GIS-derived variables and overlaid a biplot of these variables on the NMDS configuration (Axes 1 and 2). All regression analyses were conducted in the R programming environment (R Development Core Team 2008).

Results

Assessment of Landscape Influences on Stream Habitat

Temperature. - We were able to account for 37 percent of the variation in weekly maximum temperature from our GIS variables hypothesized to influence sustained periods of high stream temperatures (Table 2.2). The resulting regression equation for the model was:

$$WMT = -0.64 + 1.23(LGradRat^a) + 0.52(MxAirT) - 1.85(Canopy\ Cover)$$

where *WMT* = weekly maximum temperature, *MxAirT* = maximum summer air temperature, *LGradRat* = the ratio of flow path length to gradient, *Canopy Cover* = forested canopy cover, and *a* indicates the log transformed variable. Each of the three GIS predictor variables was significant in the model ($P < 0.001$).

Visual assessment of the observed field measurements plotted with the GIS predicted values suggest that our model tended to over predict lower observed temperatures and under predict higher observed temperatures. This is evidenced by a number of points with lower observed temperatures occurring above the 1:1 line and a majority of higher observed temperatures occurring below the 1:1 line (Figure 2.3). The standard residual error for the model was 2.24 (C°).

Fine sediment - Our GIS variables indicating landscape influences on fine sediment accumulation accounted for 28 percent of the variation in substrate < 4 (Table 2.2). The resulting regression equation for the fine sediment model was:

$$Substrate < 4^a = 1.65 - 0.006(Slope) - 0.204(NSPwr^b) - 0.010(RSPwr^b)$$

where *Substrate* < 4 = substrate < 4 mm, *Slope* = weighted catchment slope NSP_{wr} = network stream power, RSP_{wr} = reach unit stream power, and *a* and *b* indicate square root and log transformed variables, respectively. Network stream power was statistically significant in the model ($P < 0.001$) while weighted slope and reach unit stream power were not significant ($P > 0.10$).

Assessment of the observed field measured values of substrate < 4 plotted with the GIS predicted values indicate that the regression model had a tendency to over predict the amount of substrate < 4 at reaches with low amounts of fine sediment and under predict the amount of substrate < 4 at reaches with high amounts of fine sediment (Figure 2.3). The standard residual error for the model was 1.77 (back transformed = 3.2 %).

Macroinvertebrates

A total of 163 taxa were originally identified from all sample reaches. This number was reduced to 90 taxa when only those taxa found at more than 5 percent (10 occurrences) of reaches were considered. Results from the Non Non-Metric Multi-Dimensional Scaling (NMDS) of macroinvertebrate data indicated a three dimensional solution provided the best low-dimensional fit between the original Bray-Curtis dissimilarities and the multi-dimensional dissimilarity of NMDS (final stress = 15.79). The resulting site scores from the NMDS, plotted in two-dimensional space suggest macroinvertebrate compositional similarities among many of the sites, with most outliers occurring on the positive end of NMDS Axis 1 and the negative end of NMDS Axis 2 (Figure 2). Outliers consisted of both reference and managed sites.

Taxa centroids (taxa scores) in relation to each NMDS axis resulted in *Sialis* having the highest positive taxa score (1.59) associated with NMDS Axis 1 and *Kogotus*

(-0.60) and *Rhyacophila hyalinata* (-0.60) having the highest negative taxa scores associated with Axis 1. The second NMDS Axis showed the highest positive taxa scores associated with *Atherix* (1.26), *Agapetus* (1.20), and *Pteronarcys* (1.16). Negative taxa scores along NMDS Axis 2 were associated with *Rhyacophila verrula* (-0.64) and *Prosimulium* (-0.64). Individual taxa axis scores can be found in Table A.1.

Assessing Landscape and Habitat Influences on Community Structure

Temperature. – The linear regression results of weekly maximum temperature on each NMDS axis indicated that gradients in community composition were only moderately represented by our field measured variable. Weekly maximum temperature had a positive relationship with NMDS Axes 1-3 and accounted for approximately 21, 24, and 6 percent of the variation in community structure along each axis, respectively (Table 2.3). The multiple linear regression results of GIS-derived variables representing landscape characteristics influencing high stream temperatures on each NMDS axis indicated that our hypothesized variables explained the most variation in community structure along NMDS Axis 2 (42 percent) followed by Axis 1 (16 percent) and Axis 3 (12 percent; Table 3). All three predictor variables were statistically significant ($P < 0.01$) in the regression with Axis 2 while only maximum summer air temperature was significant in the regression with Axis 1 ($P < 0.001$; Table 4). Both air temperature and forested canopy cover were significant in the regression with Axis 3 ($P < 0.01$). AIC scores indicating model fit were lower for the weekly maximum temperature model on NMDS Axis 1, and lower for the GIS-derived model on Axes 2 and 3 (Table 2.3).

Plotting field measured weekly maximum temperature and the GIS-derived variables over the NMDS scatterplot of Axes 1 and 2 provided a visual assessment of our regression findings. Weekly maximum temperature was most associated with maximum summer air temperature and the influence of both of these variables on gradients in macroinvertebrate community structure was split between Axes 1 and 2 and had a positive relationship with both (Figure 2.4). The flow path length to gradient ratio was most strongly associated (positive) with NMDS Axis 2 and forested canopy cover also had the strongest association (negative) with Axis 2.

Fine sediment. - Regression results of substrate < 4 on each NMDS axis indicated that our field derived measurement moderately characterized the influence of fine sediment on macroinvertebrate structure. Substrate < 4 had a positive relationship with all three axes and accounted for approximately 27 percent of the variation in NMDS Axis 1, 1 percent in Axis 2, and 10 percent in Axis 3 (Table 2.3). The multiple linear regression results of the GIS-derived variables hypothesized to represent landscape influences on fine sediment accumulation on each NMDS axis explained the most variation in NMDS Axis 1 (27 percent) followed by Axis 2 (6 percent) and Axis 3 (6 percent; Table 3). Network stream power and weighted catchment slope were both statistically significant ($P < 0.01$) in the regression with NMDS Axis 1 while only slope was significant in the regression with Axis 2 ($P < 0.001$) and network stream power in the regression with Axis 3 ($P < 0.05$; Table 4). AIC scores were lower for the substrate < 4 model on NMDS Axes 1 and 3, and lower for the GIS-derived model on Axis 2 (Table 2.3).

Visual assessment of substrate < 4 and our GIS-derived fine sediment variables plotted on the NMDS scatterplot of Axes 1 and 2 substantiated our findings from the regression analysis (Figure 2.4). Substrate < 4 was had the highest positive association with NMDS Axis 1 and network stream power had a highly negative association with Axis 1. The association of reach stream power with the NMDS axes was highest along Axis 1 (negative) while slope had a slightly higher association with Axis 1 than Axis 2.

Discussion

The objectives of this study were to assess the efficacy of GIS-derived measurements to characterize landscape factors influencing sustained periods of high stream temperatures and fine sediment accumulation in order to identify gradients in community structure and assess how well field measurements indicate important factors shaping the community structure of stream macroinvertebrates. Understanding the implication of management activities on stream habitat and aquatic biota not only depends on our ability to understand how landscape processes influence stream habitat and biotic communities, but also depends on our ability to understand and accurately characterize habitat that is important to the biota. Without knowing how accurate our habitat measurements are in representing factors influencing structural gradients in aquatic communities, it is difficult to determine how changes in stream habitat may affect the condition of stream biota.

Assessment of Landscape Influences on Stream Habitat

Temperature. - The relationship of our hypothesized GIS measurements indicating landscape influences on stream temperature met our expectations regarding

their direction of influence on field measured weekly maximum temperature. Our results were also consistent with other studies indicating GIS-derived summer air temperatures and riparian shading as significant factors influencing stream temperature (Isaak and Hubert 2001; Wehrly et al. 2006; Isaak et al. 2010). Although our model accounted for a modest amount of the variation in weekly maximum temperature compared to other studies that selected GIS-derived variables using correlative methods (Brenden et al. 2007; Wehrly et al. 2009) and process based hypotheses (Isaak et al. 2010) to predict temperatures using alternative statistical methods to ordinary least-squares regression such as generalized additive modeling, kriging interpolation, and linear mixed models, our objective in fitting the GIS-derived landscape variables to each habitat variable was to validate whether our expectations regarding the influence of each variable on the response was consistent with our initial hypotheses. Thus, our concern was not about how much variation we could explain in the response variable but rather if our GIS-derived measurements met our initial hypotheses.

Fine sediment. - Both network and reach stream power met our expectations of a negative relationship with substrate < 4 while weighted slope had the opposite influence of our initial hypothesis. We initially hypothesized that steeper slopes near the stream would contribute higher amounts of fine sediment to the stream through mass wasting and overland transport. Instead we observed a negative relationship with weighted slope and substrate < 4 in the model. This opposite sign may indicate that steeper slopes near the stream may be contributing larger size classes of sediment (i.e. boulders) to the stream from landslide events. It may also indicate that steeper hill slopes near streams restrict streams from meandering which leads to higher amounts of energy expended on

the channel bed surface to steepen channel gradients and more effectively transport sediment. This interpretation may be substantiated by the correlation of weighted slope and both network ($r = 0.217$) and reach stream power ($r = 0.401$).

While some of our predictor variables met our expectations regarding their relationship with substrate < 4 , both reach stream power and slope were not statistically significant ($P > 0.10$) in the model. This finding could be due to network stream power accounting for much of the same variation as the two other measurements, or our habitat measurement representing a poor measure of fine sediment. When accounting for the negative relationship of slope to substrate < 4 in the model, all three predictors are very similar in theory regarding their influence on fine sediment and are also moderately correlated with each other. Therefore, network stream power may be accounting for much of the overlapping variation in substrate < 4 that would otherwise be accounted for by reach stream power and slope. In fact when network stream power is used as the lone predictor variable, it accounts for just as much variation in substrate < 4 (28 percent) as the full model. This may indicate that our two other predictors are poor representations of factors influencing fine sediment accumulation at the reach due to error associated with GIS-derived measurements, or that our initial hypotheses about landscape influences on fine sediment accumulation are incorrect. Further testing of GIS-derived measurements representing sources of fine sediment should be tested in order to account for variation in fine sediment accumulation stemming from processes other than transport.

*Assessing Landscape and Habitat Influences
on Community Structure*

Assessing the influence of our GIS-derived landscape measurements and our habitat variables on gradients in macroinvertebrate community structure provided insight into the potential environmental gradients shaping macroinvertebrate communities within our study area and how well our field measurements characterize habitat influences on community structure. The variation in community structure of each NMDS axis accounted for by our field measured weekly maximum temperature identified both NMDS Axis 1 and Axis 2 as gradients moderately influenced by high stream temperatures. While the gradients in community structure of Axis 1 and 2 may be due to the influences of stream temperature, it is unlikely that both gradients are directly related to sustained periods of high temperatures. Evidence from our model of GIS measurements on each axis indicates that it is likely that NMDS Axis 2 represents a gradient of community structure based on stream temperature while Axis 1 is based on landscape organization or position along the stream continuum.

Our GIS-derived model accounted for 42 percent of the variation in NMDS axis 2 which indicates that landscape influences on high temperatures are shaping the gradient in community structure along this axis. From these findings, we may be able to deduce that stream temperature is the major driver of community composition along NMDS Axis 2 where positive reach scores along this axis represent less shaded streams in catchments with higher air temperatures and longer water residence times. In contrast, the positive association of field measured weekly temperature and GIS-derived maximum summer air temperature with NMDS Axis 1 may be due to the position of reaches along the stream continuum. Evidence supporting this may be derived from observing the variation in

community structure along Axis 1 accounted for by our field derived fine sediment indicator (substrate < 4; 27 percent). As one moves longitudinally down the stream continuum, stream temperatures generally increase due to decreases in elevation and the availability of fine sediment increases due to weathering (Vannote et al. 1980). Lower gradient streams where fine sediment may accumulate are also likely to occur lower along the continuum due to landscape evolutionary processes. Therefore changes in community structure along Axis 1 may not only be due to high stream temperatures but due to the interaction of multiple environmental characteristics that are correlated along the stream continuum. Evidence of this interpretation is supported when we regressed both field measurements (substrate < 4 and weekly maximum temperature) on Axis 1 reach scores where our habitat variables accounted for 46 percent of the variation in community composition along this axis. Incorporating measures indicating position along the stream continuum such as drainage area or distance from the sample reach to catchment headwaters may be beneficial in future models in order to account for the correlation of environmental variables based on longitudinal position along the continuum.

Concluding that the gradient in community composition along NMDS Axis 2 is directly related to stream temperature or a close correlate of temperature independent of the influence of landscape position represented by Axis 1, our findings suggest that our field measurement of weekly maximum temperature may not be capturing the true variation in stream temperatures that lead to changes in community composition. Our GIS-derived model accounted for 42 percent of the variation in community composition along Axis 2 (AIC = 24.60) while the field measurement accounted for 24 percent of the

variation in this axis (AIC = 76.22). This discrepancy suggests that our initial conclusion that stream temperature defines the dominant gradient in habitat along Axis 2 may be incorrect, the environmental driver(s) of community composition along this axis is a close correlate of stream temperature, or that weekly maximum temperature as a metric may not be accurately characterizing the influence of maximum stream temperatures on stream biota. Further research is needed to understand additional factors within the landscape and stream environment that may be potential correlates of stream temperature, that in conjunction with temperature shape gradients in community structure, and to validate how well our measurements of stream temperature accurately characterize thermal influences on stream biota.

The positive association of substrate < 4 and our GIS-derived measurements associated with fine sediment accumulation indicate that the community gradient along Axis 1 may be partially related to gradients in stream substrate but may also be due to gradients in correlated habitat along the stream continuum. Substrate < 4 had a positive association and explained 28 percent of the variation in NMDS Axis 1 (AIC = 111.85). Our GIS-derived measurements also explained 28 percent of the variation in Axis 1 (AIC = 112.96). This indicates that our field measurement may be insufficiently characterizing fine sediment influences on stream biota or that our GIS measurements are capturing additional variation in community composition along Axis 1 indirectly related to fine sediment accumulation.

We summarized substrate < 4 within both riffle and pool habitat units while macroinvertebrate were sampled only in riffle units. Therefore, part of the lack of association we see between substrate < 4 and the community gradient in NMDS Axis 1

may be due to the disassociation between summarizing the habitat variable over all stream habitat units and assessing the influence of this variable on biota only associated with one of these units. This illustrates that carefully thought out hypotheses regarding the type and location of habitat data collection should be considered before conducting field surveys. In our case, the initial collection of habitat data was aimed at monitoring the status and trends of stream habitat within the Interior Columbia River Basin and is primarily aimed at habitat metrics hypothesized to be important to ESA listed fish species within the basin. By using sediment measurements in both pools and riffles, we undertook this analysis with the understanding that some error in associating substrate from both habitat units to macroinvertebrates sampled in riffles would lead to additional unexplained variance in our models.

The use of GIS variables may provide an effective means to validate the efficacy of field measurements to capture habitat influences on stream biota yet a complete understanding of what GIS-derived measurements indicate is important. While the amount of variation explained in NMDS Axis 1 by our GIS measurements is similar to the amount explained by substrate < 4, it is unknown whether the true variation that the GIS measurements is accounting for in the community gradient is directly related to fine sediment accumulation. Weighted slope and reach stream power were both non significant factors ($P > 0.10$) in assessing landscape influences on substrate < 4 yet were statistically significant ($P < 0.01$ and 0.05 , respectively) in the model relating GIS measurements to NMDS Axis 1. This may indicate that measurement error associated with substrate < 4 may be confounding the ability of the field measurement to accurately capture the effect of fine sediment on the biota and thus the influence of slope and reach

stream power are non significant, or the two variables may not be directly related to fine sediment accumulation, but instead indicate environmental factors that are close correlates to fine sediment accumulation influencing macroinvertebrate community structure. Measurement error stemming from observer variability has been recognized in substrate measurements (Roper et al. 2002; Whitacre et al. 2007) which could lead to additional errors in analyses linking landscape influences to the field measured habitat variable. In addition, our estimate of reach stream power may not purely represent influences on fine sediment accumulation but may also be representative of near-bed hydraulic conditions (i.e. velocity) which may influence community composition along the same environmental gradient as substrate (Reid and Thoms 2008). This may also be the case with our GIS-derived measurements of high stream temperatures along NMDS Axis 2 where the additional amount of variation explained by our GIS variables (~16 percent) may be due to landscape influences on in-stream primary production.

Much of the current research assessing landscape influences on aquatic ecosystems use spatial attributes to predict reach scale habitat characteristics (Davies et al. 2000; Sridhar et al. 2004; Baker et al. 2005; Creque et al. 2005; King et al. 2005; Brenden et al. 2007; Allen 2008; Wehrly et al. 2009; Isaak et al. 2010). While this research has shown that measurements derived from spatial data provide an efficient means to assess habitat conditions across large geographic areas, the applicability of predicted habitat characteristics to assess influences on aquatic communities relies on our initial ability to define and characterize in-stream habitat factors important to the biota. In this study, we used in-stream habitat measurements in conjunction with attributes derived from spatial data in order to 1) assess the efficacy of spatially derived landscape

factors to characterize influences on stream habitat, 2) identify gradients in macroinvertebrate community structure, and 3) validate how well our habitat measurements indicate temperature and fine sediment influences on aquatic biota. While some of our spatial attributes met initial expectations regarding landscape influences on maximum stream temperatures and fine sediment, integrating the landscape and habitat characteristics allowed us to more effectively identify environmental gradients shaping macroinvertebrate communities and assess how well our habitat measurements characterize factors that are important to the biota. We found that our GIS-derived models at times explained as much, to almost twice as much variation in community structure and had substantially lower AIC scores than the habitat measurements. These results further suggest that spatial methods may offer an effective alternative to field-based methods, and also indicate that our field measurements may not be accurately characterizing in-stream habitat that is important to the biota. Further research is needed in order to understand how accurate our habitat measurements are at representing the relative factors influencing aquatic communities. A better understanding of these factors will lead to more effective assessments of biological condition based on habitat relationships and provide direction in conserving and restoring the ecological function of aquatic systems.

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Table 2.1 Description of GIS-derived variables used to indicate landscape influences on field measured variables.

Field Variable	GIS Variable (units)	Indication	Scale
Weekly Maximum Temperature	Ratio of Flow Path Distance to Gradient (m)	Topographic control on water residence time	Catchment
	Maximum Summer Air Temperature (°C)	Convective heat transfer	Stream Network
	Forested Canopy Cover (%)	Riparian shading	Segment
Substrate < 4	Slope (%)	Sediment source and transport	Catchment
	Network Specific Stream Power (watts/m)	Sediment transport	Stream Network
	Reach Unit Stream Power (watts/m ²)	Initiation of Sediment Movement	Reach

Table 2.2 Multiple linear regression model results assessing the influence of GIS-derived measurements on field measured weekly maximum temperature and substrate < 4. a and b denote log and square root transformed variables, respectively.

Response Variable (Field)	Independent Variable (GIS)	Correlation w/ Response	Coefficient	Standard Error	P-value	Model R^2_{adj}
Weekly Maximum Temperature	Intercept		-0.64	2.03	0.754	0.365
	Flow Path Distance to Gradient Ratio ^a	0.356	1.23	0.07	< 0.001	
	Maximum Summer Air Temperature	0.475	0.52	0.23	< 0.001	
	Forested Canopy Cover	-0.262	-1.85	0.69	0.008	
Substrate < 4 ^b	Intercept		16.5	1.42	<0.001	0.281
	Proximity-weighted Slope	-0.233	-0.06	0.06	0.358	
	Network Stream Power ^a	-0.534	-2.04	0.27	<0.001	
	Reach Unit Stream Power ^a	-0.212	-0.10	0.13	0.462	

Table 2.3 Regression analysis results indicating the amount of variance explained (R^2) in macroinvertebrate structure along each NMDS axis by field measured variables and GIS-derived models.

Environmental Factor	Predictor	Axis 1 R^2_{adj}	Axis 1 AIC	Axis 2 R^2_{adj}	Axis 2 AIC	Axis 3 R^2_{adj}	Axis 3 AIC
Sustained High Temperatures	Field Measurement	0.214	124.68	0.236	76.22	0.059	73.46
	GIS-derived Model	0.158	139.96	0.424	24.60	0.121	62.16
Fine Sediment Accumulation	Field Measurement	0.267	111.85	0.014	124.35	0.097	65.71
	GIS-derived Model	0.270	112.96	0.064	116.33	0.057	75.98

Table 2.4 Multiple linear regression results indicating regression coefficients of GIS-derived variables for each NMDS axis. Bolded numbers represent statistically significant variables in the model ($P < 0.05$)

Sustained High Temperatures		LGradRat	MxAirT	Canopy Cover
	Axis 1	-0.020	0.061	0.131
	Axis 2	0.193	0.058	-0.230
	Axis 3	0.123	-0.003	-0.194
Fine Sediment Accumulation		Slope	NSPwr	RSPwr
	Axis 1	-0.034	-0.262	-0.047
	Axis 2	0.034	-0.065	0.041
	Axis 3	0.019	0.090	0.014

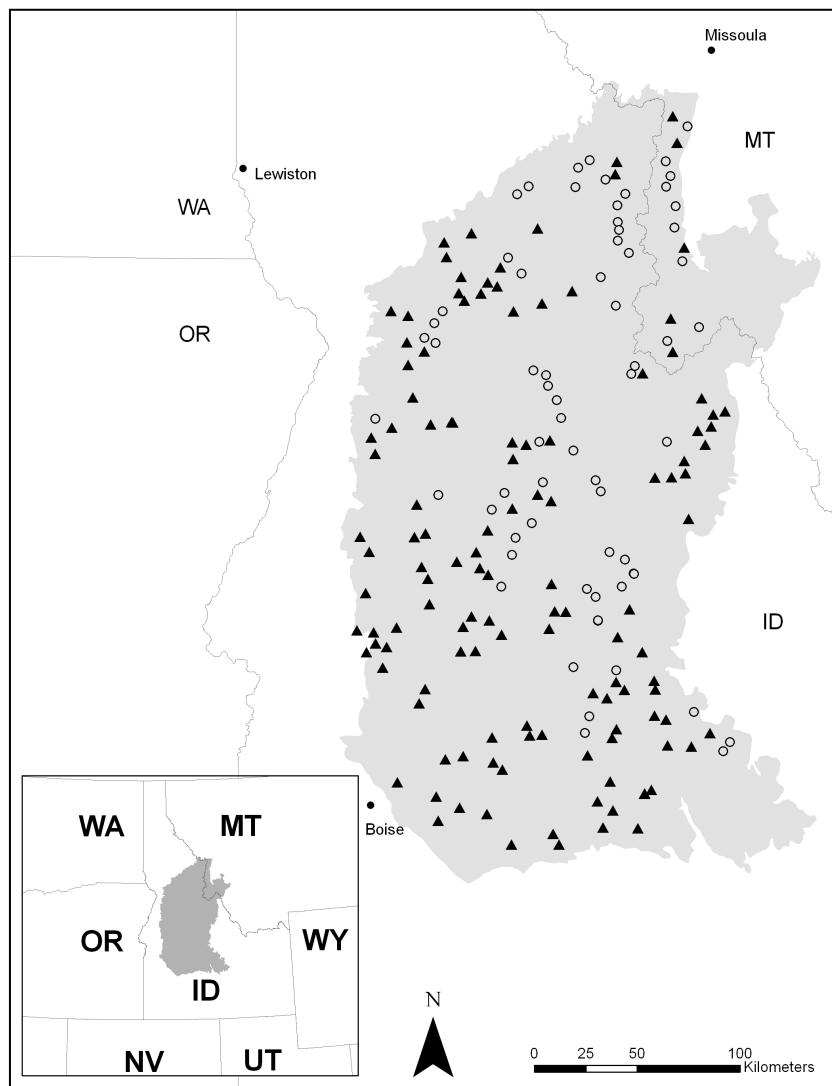


Figure 2.1 Map of study area illustrating the location of reaches in reference (circles) and managed (triangles) catchments. The Idaho Batholith Ecoregion is shown in grey.

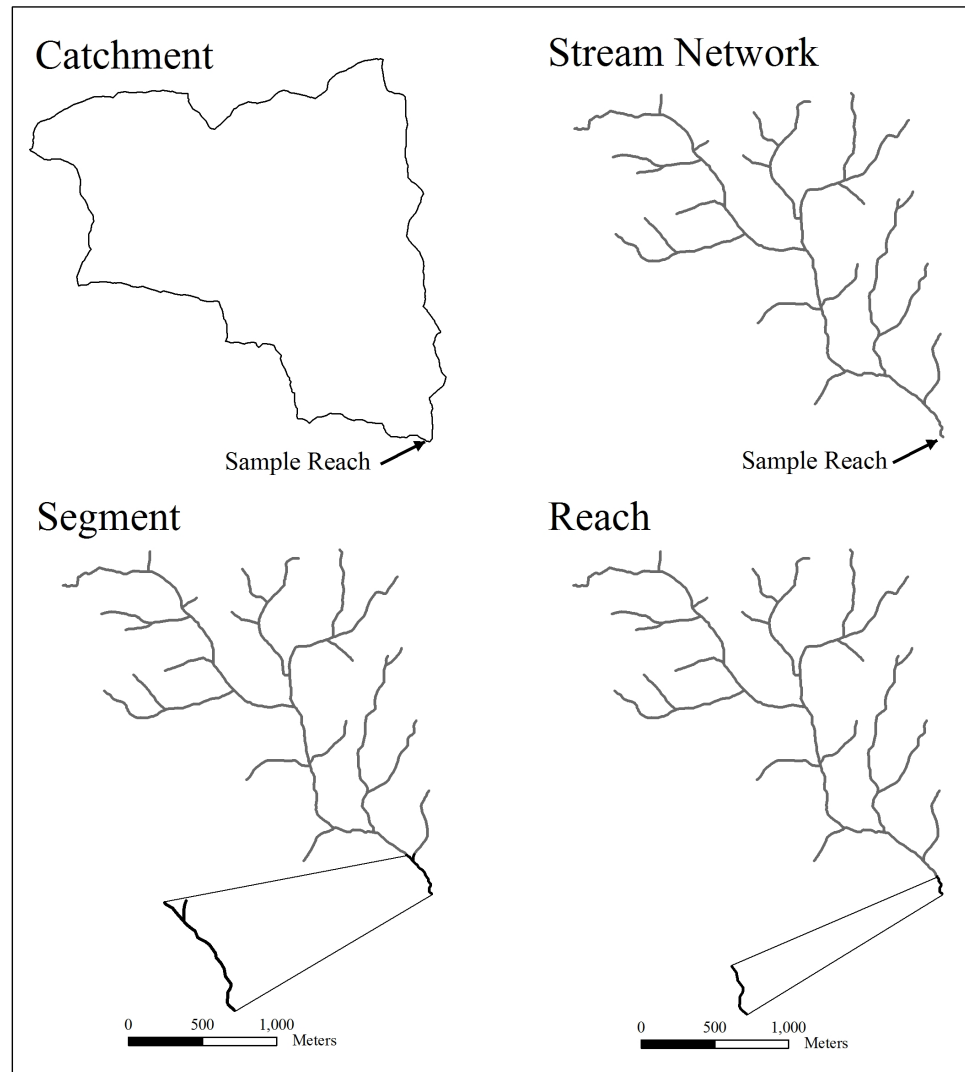


Figure 2.2 Example of spatial scales used to derive landscape characteristics hypothesized to influence weekly maximum temperature and fine sediment at field-sampled reaches. The catchment was defined as the contributing area upslope of the sampled reach and the stream network as the sum of streams draining the catchment. We defined the segments as stream sections within the stream network extending from the bottom of the sampled reach upstream 1000 m in flow length and the reach as the stream section extending from the bottom of the sampled reach upstream 300 m in flow length. All stream sections had a width of 10 m.

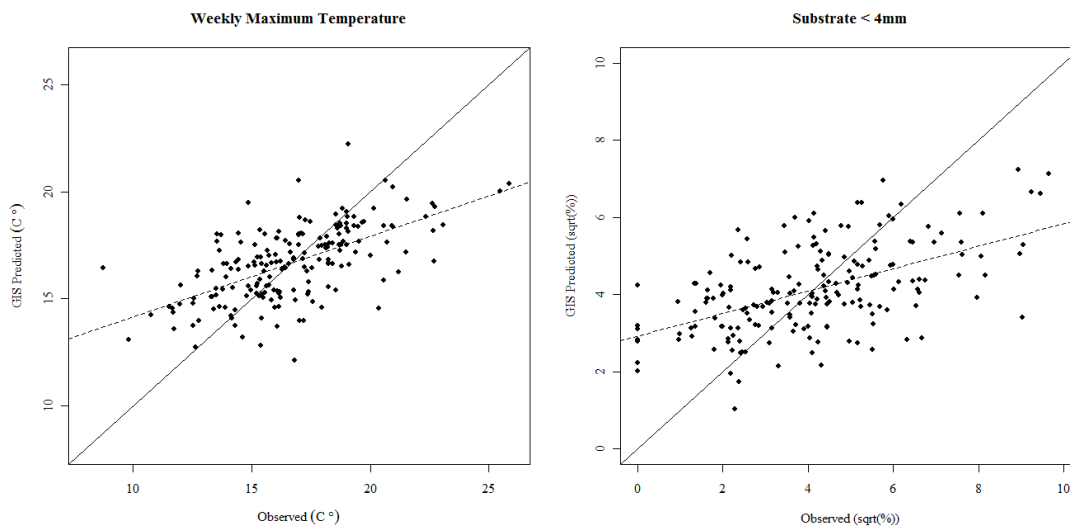


Figure 2.3 Scatterplot of field measured versus GIS predicted values for weekly maximum temperature and substrate < 4. Solid line represents a 1:1 relationship and the dashed lines represent results from the regression models. Note that the axes of the plot for substrate < 4 are scaled to the square root of the percentage of fine sediment.

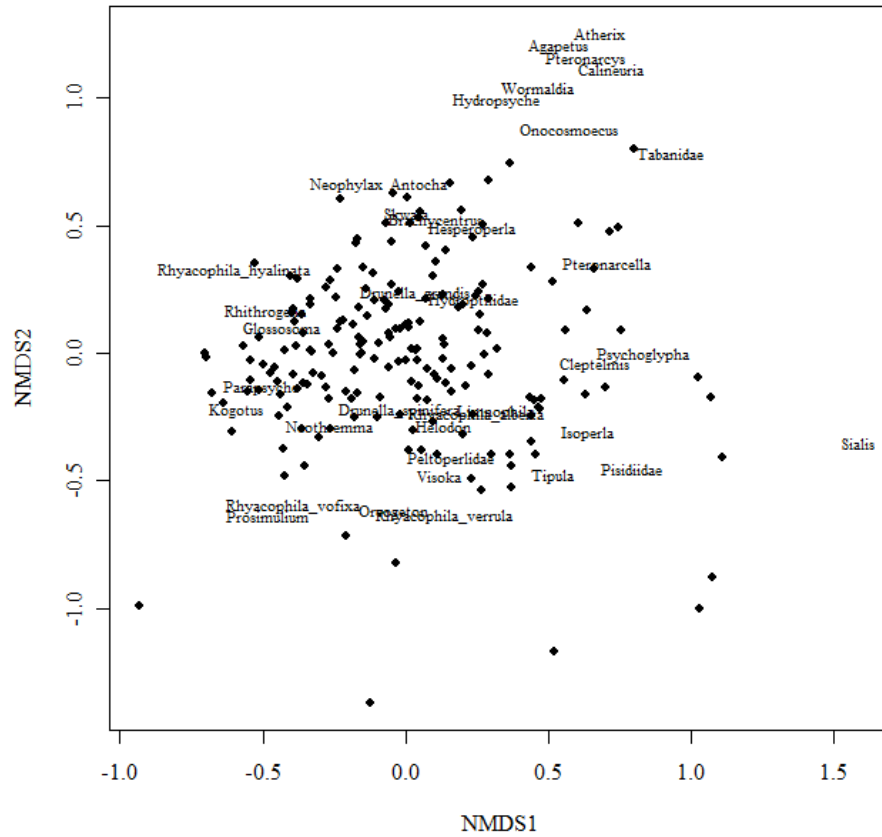


Figure 2.4 Scatterplot of Non-Metric Multi-Dimensional Scaling ordination Axes 1 and 2 of macroinvertebrate samples. Points indicate reach scores along each axis and the weighted average of taxa centroids for the taxa with the 10 highest scores along each axis are denoted by Operational Taxonomic Unit (OTU) name.

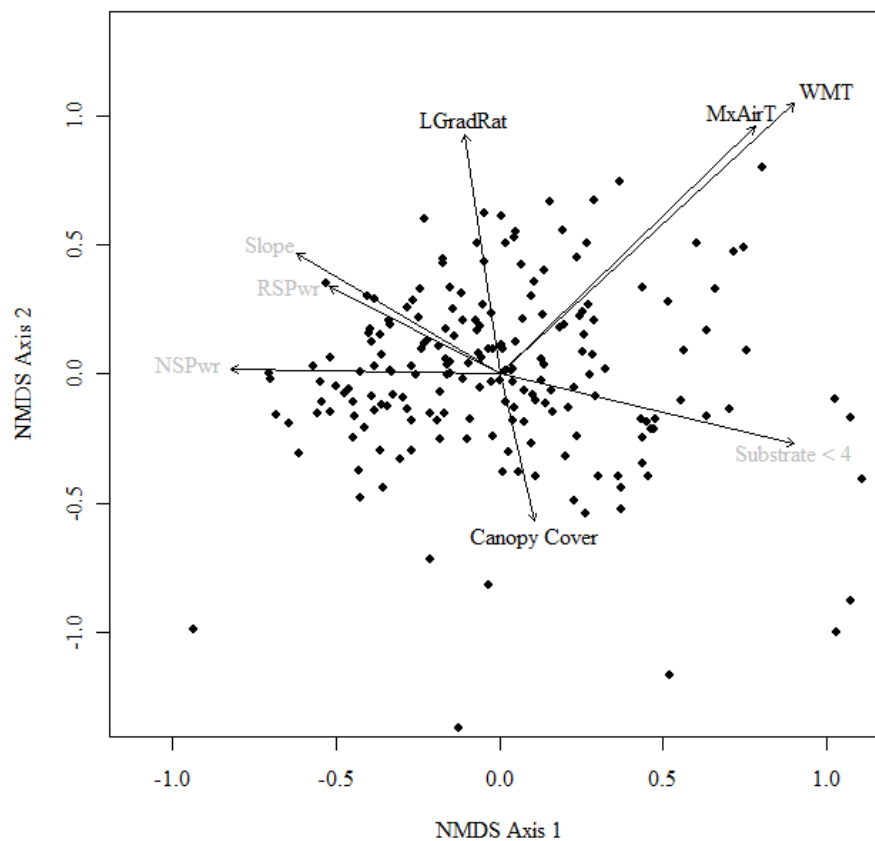


Figure 2.5 Scatterplot of Non-Metric Multi-Dimensional Scaling ordination Axes 1 and 2 of macroinvertebrate samples. Points indicate reach scores along each NMDS axis. Arrows indicate the strength and direction of correlations between field and GIS-derived measurements and each axis. Names of stream habitat and landscape variables associated with each arrow are shown in black for measurements indicating sustained high stream temperatures and in gray for measurements indicating fine sediment accumulation where WMT = weekly maximum temperature, LGradRat = the flow path length to gradient ratio, MxAirT = maximum summer air temperature, Canopy Cover = forested canopy cover, Substrate < 4 = substrate < 4, Slope = weighted catchment slope, NSPwr = network stream power, and RSPwr = reach unit stream power.

CHAPTER 3

COMPARING TWO APPROCHES TO ASSESS THE INFLUENCE OF STREAM
HABITAT METRICS ON MACROINVERTEBRATE COMMUNITIES**Introduction**

The physical stream environment forms a habitat template that influences the composition of aquatic communities by limiting the persistence of species to those that have adopted strategies to exist within a specific range of environmental conditions (Poff and Ward 1990; Fisher et al. 2007). Many stream organisms have specific thermal and hydrological tolerance ranges, which implies that changes in physical habitat can have major consequences for stream biota (Malmqvist and Rundle 2002). Potential consequences of changes may lead to physical stressors on individual taxa and shifts in community structure, dynamics, and trophic interactions (Bilby et al. 1996; Willson et al. 1998). In order to protect stream ecosystems, it is important to understand the influence of both natural and anthropogenic factors on stream habitat as well as the influence of physical processes on aquatic communities (Imhof et al. 1996; Fausch et al. 2002; Wang et al. 2006). Understanding environmental processes and the factors influencing aquatic communities is fundamental in directing strategies that maintain and restore aquatic systems (Minshall 1988; Palmer et al. 1997).

Changes in stream habitat leading to persistent conditions that border on the upper and lower limits of natural variation have primarily been a result of human modification to the physical environment (Bohn and Kershner 2002). In the Interior Columbia River Basin (CRB), land management practices such as livestock grazing, road construction, and timber harvest have been identified as contributing factors to changes in stream

habitat leading to degraded conditions (Kershner et al. 2004a). This degradation has led to the reduction and fragmentation of quality habitat to smaller patches in headwater streams primarily managed by federal agencies (Thurow et al. 1997).

On U.S. Forest Service and Bureau of Land Management managed lands within the CRB, two of the major environmental factors identified as threats to aquatic ecosystems are high summer water temperatures and increased sedimentation (USFS and USBLM 2000). Grazing, road construction, and timber harvest near streams may indirectly influence stream temperatures by reducing the amount of riparian shading, thereby increasing direct solar radiation to the stream. These activities within a watershed can also increase runoff rates, which reduce stream baseflow levels (Hicks et al. 1991) and decreases the buffering capacity of streams to direct solar radiation (Poole and Berman 2000). Poorly managed forest land use practices may also lead to increased amounts of fine sediment delivered to the stream through stream bank and upland soil erosion (Platts 1981; Hicks et al. 1991; Gucinski et al. 2001).

Increased water temperatures and sedimentation are considered major threats to aquatic ecosystems because both temperature and sediment play a dominant role in shaping biological communities (Allan and Castillo 2007) and are two of the fundamental physical characteristics of stream habitat templates (Poff and Ward 1990). Water temperatures above a species tolerance range leads to thermal stress which results in decreased growth, increased metabolic function rates, and influences in migration and emergence timing (Vannote and Sweeney 1980). Continued or repeated exposure of coldwater adapted species to thermal stressors may eventually lead to species emigration or death (Allan and Castillo 2007). Therefore, the distribution and persistence of species

is partially dependent upon their biological adaptations to thermal stressors that limit the occurrence of temperature intolerant species to those individuals with high thermal tolerances or preferences (Vannote and Sweeney 1980).

Increased levels of fine sediment can fill interstitial spaces and reduce the availability of habitat (Waters 1995) that organisms use to feed and seek refuge from predators and sub-optimal environmental conditions (Stickler et al. 2008). Fine sediment deposition can also clog the feeding apparatus of filter feeders (Rabeni et al. 2005) and coat larger substrate, inhibiting periphyton and macrophyte growth (Wood and Armitage 1997). Additionally, fine sediment accumulation can have a direct effect on the egg-to-fry survival of salmonids (Bjornn and Reiser 1991) and reduce food subsidies of juvenile salmonids (Suttle et al. 2004). A reduction in the quality and quantity of habitat due to fine sediment accumulation may therefore lead to a shift in biotic communities consisting of species that have adopted strategies to persist in natural conditions of low fine sediment levels to taxa that are more tolerant of higher levels of fine sediment (Lanat et al. 1981; Harrison et al. 2007).

Currently, large scale monitoring efforts are taking place on federal lands within the CRB to determine whether land management and conservation strategies are effective in maintaining or restoring the structure and function of aquatic ecosystems (Whitacre et al. 2007). These efforts include field surveys that measure a variety of physical stream attributes to assess the status and trends of stream habitat which is then used as a surrogate of biological condition.

Physical habitat measurements hypothesized to be important to stream biota are often times used in place of monitoring biological conditions due to the relative

efficiency of data collection and the temporal variability of biological communities (Dauwalter et al. 2009). Although logistically practical, the general acceptance of this strategy is based on the assumed linkages between habitat and biota (Rabeni et al. 2002). Although we have a basic understanding of the physical habitat requirements necessary to sustain the structure and function of aquatic ecosystems, the effectiveness of field measured habitat variables to accurately characterize the direct environmental processes influencing stream biota is still uncertain. In order to better understand whether our assumptions regarding the linkages between habitat measurements and biota are valid and whether these measurements accurately characterize processes influencing the biota, it is necessary to examine the relationship between stream biota and field measured attributes, and test alternative methods of characterizing process based influences on the biota.

One of the limitations to directly measuring and testing process based influences on aquatic biota is that our measurements are limited by time and resources (Lane and Brown 2006). Because of these limitations, we often use proximal measures hypothesized to be an indicator or representation of the direct process we want to examine (Loehlin 2004). Most measurements we make are proximal measures of ecological processes and concepts we seek to represent. While proximal indicators provide an efficient means to represent ecological processes, measurement error associated with indicators may lead to uncertainty about the true underlying influence of ecological processes on biota.

Many measurements used as explanatory variables in ecological analyses are also often times highly correlated among each other (Graham 2003). Collinearity can confound the statistical validity and ecological interpretation of analyses by magnifying

or obscuring relationships between explanatory and response variables (Graham 2003; King et al. 2005; Baker and Wiley 2009). To avoid collinearity and simplify analyses, we often choose single indicator variables to represent environmental factors, which may lead to results that are dependent upon the methodology used to measure the indicator (Grace 2006).

An alternative to using single indicator variables is to combine indicator variables hypothesized to be components of a single ecological processes or concept. The similarity of indicator variables, assessed by the shared covariance among variables may be used to represent underlying environmental processes that each proximal variable is hypothesized to indicate (Grace 2006). These underlying processes or theoretical constructs are known as latent variables. The use of latent variables in ecological research has the potential to extend and refine ecological concepts in order to explicitly test hypotheses about environmental – species relationships.

The objectives of this study were to examine the influence of thermal stress and fine sediment on aquatic biota and to compare the relative efficacy of single and latent variables to characterize thermal stress and fine sediment influences on biological communities. We use macroinvertebrate community data as a biological response due to the sensitivity of macroinvertebrates to changes in stream habitat from anthropogenic influences (Cairns and Pratt 1992), the relative efficiency of sample collection (Resh 2008), and the potential stress biological sampling can have on sensitive fish species (Nielsen 1998). Results from this study will further our knowledge as to the degree of influence thermal stress and fine sediment have in shaping macroinvertebrate

communities and help determine the potential of latent variables to characterize environmental factors influencing stream biota.

Study Area

The Idaho Batholith Ecoregion (Bailey 1995) encompasses approximately 40,000 km² of land within central Idaho and western Montana (Figure 3.1). The topography of the study area is defined by mountainous terrain with both deeply dissected and glacially scoured valleys primarily underlain by granitic lithologies (McGrath et al. 2002). Climate is maritime-influenced with a north to south gradient of decreasing precipitation, varying with elevation, which range from approximately 300 to 3000 m. Most precipitation falls as snow in late fall, winter and early spring, and runoff is primarily from spring snowmelt (McGrath et al. 2002). Dominant vegetation within the study area consists of Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at higher elevations, Grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) at mid-elevations, and ponderosa pine (*Pinus ponderosa*) and sagebrush (*Artemisia tridentata*) at lower elevations (McGrath et al. 2002).

The study area forms the headwaters of the Bitterroot, Clearwater, and Salmon Rivers in addition to major tributaries of the Snake River. Streams draining the study area provide spawning and rearing habitat for anadromous Endangered Species Act (ESA) listed fish species such as Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) in addition to critical habitat for resident ESA listed populations of bulltrout (*Salvelinus confluentus*).

Distinct gradients of both natural and anthropogenic disturbance regimes are found in the study area. Fire is the dominant natural disturbance in the study area and

anthropogenic disturbance is predominantly associated with timber harvest and roads, with grazing and mining also occurring. Because of the varying degrees of disturbance and the presence of ESA listed species, monitoring the status of in-stream habitat and assessing the influence of in-stream habitat on biotic communities is important in determining the impacts of disturbance on aquatic ecosystems and prioritizing restoration activities within the study area.

Methods

Study Design and Reach Selection

This study is part of a larger program aimed at monitoring the status and trends of in-stream habitat on federal lands within the Interior Columbia River Basin (CRB; (Kershner et al. 2004b). In brief, watersheds were determined probabilistically using a spatially balanced sample design described in (Kershner et al. 2004b). This approach first organized the CRB into groups of 20 contiguous 6th field hydrologic code watersheds. Within these groups, watersheds were randomly selected to determine the potential for sampling. Each watershed was then categorized as either reference or managed based on current and historical management activities. Reference watersheds contained minimal management activities with no permitted livestock grazing in the last 30 years, less than 0.5 km/km² road density at the watershed scale and no roads within the proximate (1 km) riparian buffer, less than 10 percent timber harvest within the watershed, and no evidence of mining within riparian areas (Kershner et al. 2004b). Watersheds subject to higher degrees of land management activities were considered managed. Within each watershed, sample reaches were located by identifying the

lowermost stream section on federally managed land having a gradient less than 3 percent and greater than 50 percent federal ownership in the upstream catchment. We selected reaches at the lowermost portion of the watershed because they are thought to integrate the cumulative effects of upstream disturbance (Kershner et al. 2004b), and low gradient channels are likely to be more sensitive to change under variable sediment and flow regimes (Montgomery and MacDonald 2002). Additional details on study design and reach selection can be found in (Kershner et al. 2004b) and (Al-Chokhachy et al. 2010). From this larger program dataset, we attempted to control for variation in biotic assemblages that can arise from inherent differences in physiographic characteristics (Feminella 2000) by selecting a subset of reaches located within our study area that had complete physical habitat and biological stream data.

We evaluated 190 reaches located on U.S. Forest Service and Bureau of Land Management lands within our study area. Stream sizes ranged from 1.29 to 20.78 m in bankfull width and varied considerably in elevation (range = 460 to 2350 m). Reach gradient ranged from 0.03 to 2.99 percent. Catchments upstream of sample reaches represent the varying degrees of management in the study area with 65 catchments considered reference and 125 considered managed.

Field Methods

We conducted field sampling between 2004 and 2007 from late June to early September during baseflow conditions. Survey reach lengths were defined as 20 times the average bankfull width, with a minimum length of 160 m. A reach length of 20 times the bankfull width increases the likelihood that multiple riffle-pool sequences are

sampled in each reach (Knighton 1998). At each reach, we collected in-stream macroinvertebrates, temperature, and substrate data.

Macroinvertebrates. - Prior to in-stream habitat sampling, macroinvertebrate samples were collected at each reach. We collected two random samples in each of the first four fast-water (riffle) habitats using a 0.09 m² Surber sampler (500- μ m mesh) for a total of eight samples. Within the 0.09 m² sample area, substrate was disturbed to a depth of 10 cm and rubbed to facilitate the dislodgment of macroinvertebrates and collection in the sampler. Samples were then combined to provide a single sample for each reach, transferred to jars, and preserved in 95% ethanol.

Macroinvertebrates were sorted using criteria outlined by (Vinson and Hawkins 1996) and identified to the lowest possible taxonomic level (usually genus or species) by the National Aquatic Monitoring Center. Due to ambiguities in taxonomic resolution that occur during identification where organisms cannot be identified to a consistent taxonomic level (Cuffney et al. 2007), macroinvertebrates were converted into Operational Taxonomic Units (OTUs) by Charles Hawkins at The Western Center for Monitoring and Assessment of Freshwater Ecosystems. OTUs can vary in their level of taxonomic resolution, but are unique from one another and are identified based on the aggregation of ambiguous taxa into an OTU or the exclusion of ambiguous taxa from the analysis. This results in a dataset where all similar taxa are classified to a consistent taxonomic level.

Temperature. - We collected stream temperature at a point location within each reach. Temperature was recorded hourly from July 16th to August 26th using thermal data loggers. From the hourly temperature data, we derived the average daily maximum

temperature of the warmest consecutive seven day period (hereafter referred to as weekly maximum temperature), the number of days exceeding 16 degrees Celsius (hereafter referred to as days >16), and the percent of hourly observations greater than the 90th percentile of temperature values for all sampled reaches (hereafter referred to as the percent of observations > the 90th percentile). Each temperature metric was hypothesized to represent prolonged exposure of aquatic biota to thermal stressors.

Fine sediment. - To characterize stream substrate, we collected sediment size and pool tail fine sediment measurements at each reach. For our sediment size measurements, we first established the overall reach by measuring bankfull width at four random locations and used the average of these four measurements to categorize reaches into 2 meter width categories with a minimum width category of 8 m and a maximum of 25 m. We then established transects (minimum of 20) along the stream at evenly spaced intervals of the corresponding width category.

At each transect, we collected substrate at 5 equally spaced intervals and the intermediate axis of each particle was measured (Wolman 1954). Only particles collected within the active stream channel (no bank material) were included for the analysis. From our samples, we estimated the median particle size (d_{50}) and the proportion of bed material less than 4 mm (hereafter referred to as substrate <4).

We estimated the amount of substrate covered by surface fines at pool tail locations within the reach. Pool habitat units were defined as areas where the stream bed is both laterally and longitudinally concave in profile and bounded by an upstream break in slope (i.e. pool head) and a downstream break in slope (i.e. pool tail). Criteria for defining a pool also include the designations that the maximum depth was ≥ 1.5 times

deeper than the water depth at the pool tail, the length of the habitat unit was \geq the wetted channel width, and the habitat unit was \geq 50 percent of the wetted width at its widest part. Pool tails were identified as the lowermost 10 percent of each habitat unit (Heitke et al. 2007).

At each pool tail within the sample reach, we conducted grid measurements to estimate the amount of substrate covered by surface fines. Grid measurements were carried out by placing a 0.35 by 0.35 meter grid with 50 intersections at three equidistant locations across the wetted width of the lowermost portion of the pool. For each grid, we counted the number of intersections that corresponded with particles < 2 mm and < 6 mm. The average percent fines of each size category was then estimated for each pool from the three grids and the total percent fines < 2 mm (hereafter referred to as fines < 2) and < 6 mm (hereafter referred to as fines < 6) was averaged for the reach. We also calculated the ratio of $\log_{10}(x + 1)$ substrate < 4 and $\log_{10}(x + 1)$ d_{50} (hereafter referred to as the ratio of substrate < 4 and d_{50}) to indicate the potential entrainment of smaller streambed particles in interstitial spaces leading to the embedding of larger substrate (Lisle, 1989).

Analytical Methods

Macroinvertebrates. - We used the relative abundance of OTUs (hereafter referred to as taxa) to examine variation in macroinvertebrate community composition. In order to reduce noise in further analyses stemming from the presence of taxa in minimal samples, taxa that were present at fewer than five percent of the reaches were eliminated (McCune and Grace 2002) and the resulting data were $\log_{10}(x + 1)$ transformed. From the log-transformed abundance data, we converted reaches into a

distance matrix using Bray-Curtis dissimilarity (BCD; Bray and Curtis 1957) based on community composition, and used Non-Metric Multi-Dimensional Scaling (NMDS; (Clarke 1993) to summarize multi-dimensional patterns in macroinvertebrate assemblage structure. Bray-Curtis dissimilarity compares the degree to which reaches share the same taxa (Hawkins and Norris 2000), resulting in an interpretable measure of ecological distance of taxa abundance among sampled reaches (Faith and Minchin 1987; Legendre and Anderson 1999). NMDS is an unconstrained ordination method based on ranked distances of samples (reaches) that attempts to represent taxa in a minimal number of dimensions while preserving the distance relationships (BCD) among samples (Legendre and Legendre 1998). The multi-dimensional solution of dissimilarity from NMDS is compared to the original BCD measurement to yield a measure of fit (termed stress). Stress values are scaled from 1 to 100, with lower stress values indicating a better fit between the two distance matrices. In addition to stress, NMDS results consist of reach axis coordinates (reach scores) calculated as the weighted averages of reaches based on their order along the ordination axes, and taxa axis coordinates (taxa scores) representing the weighted average centroid of the taxa along the ordination axes. We used the resulting NMDS configuration of reach scores as a response variable to assess the relative efficacy of single variables and latent variables to characterize the influence of thermal stress and fine sediment on macroinvertebrate community structure. All NMDS analyses were performed using the metaMDS function in R (Oksanen et al. 2008; R Development Core Team 2008).

Single variables. - We used weekly maximum temperature and substrate < 4 as proximal variables characterizing thermal stress and fine sediment, respectively. The

weekly maximum temperature is often used as a temperature summary metric to assess compliance with water quality standards for salmonids in the Pacific Northwest (U.S. Environmental Protection Agency 2003) and has also been used in the investigation of species-habitat relationships (Ebersole et al. 2006). Substrate < 4 is a proximal measure representing the proportion of sand and finer particles within a reach which is a common summary metric used in habitat monitoring programs (Roper et al. 2002). Weekly maximum temperature and substrate < 4 were used as single, independent variables in further analyses assessing the influence of these variables on community composition and compared with results from the latent variable models.

Latent variable models. - In contrast to single variables, latent variable models are built upon the concept that combining multiple indicator variables may more accurately characterize and represent ecological processes (Fabricius and De'Ath 2004). The combination of these indicator variables may be used to represent underlying causes as unmeasured factors or theoretical constructs known as latent variables (Grace 2006). Latent variables are hypothetical or theoretical factors that may not be directly observed but are hypothesized to be common among multiple indicators (Hershberger *et al.* 2003). Latent variable models are structural models that explicitly identify and describe the statistical relationship between the observed indicator variables and the latent variable (Bollen 1989).

We constructed latent variable models and used confirmatory factor analysis (CFA) to evaluate the covariance structure among proximal indicators hypothesized to represent two latent, environmental factors influencing macroinvertebrate community composition; thermal stress and fine sediment accumulation. While CFA is conceptually

similar to principal components analysis (PCA), CFA specifies direct links between observed variables and the latent factor and assumes that the latent variables are true representations of the underlying factor, measured without error, while the observed variables contain measurement error (Grace 2006). In contrast, PCA attempts to account for a maximum amount of variance in the data by allowing all observed variables to load on all factors (components), and makes the assumption that observed variables are measured without error (Grace 2006). Because all variables are allowed to load on all factors in PCA, PCA is generally considered an unreliable method leading to interpretable factors (Grace 2006).

Confirmatory factor analysis uses linear combinations of the observed variables to account for the covariance among descriptors, resulting in a latent variable that explains the covariance structure of the observed variables in relation to the hypothesized latent factor (Legendre and Legendre 1998). The covariance among observed variables is assessed using maximum likelihood estimation resulting in standardized path coefficients or factor loadings, that are scaled from 0 to 1 and describe the relative contribution of each indicator variable to the latent factor, and a measure that represents the variation of each indicator accounted for by the factor.

We used three variables in each of two latent variable models to represent the latent factors thermal stress and fine sediment accumulation (Figure 3.2). Variables used in each model represent hypothesized proximal indicators of the two latent factors. For the thermal stress latent variable model, we used the weekly maximum temperature, days > 16, and the percent of observations > the 90th percentile as proximal indicators of thermal stress. Days > 16 indicates the upper limit of the optimal range for juvenile

salmon and trout rearing (USEPA 2003) and probability of bull trout occurrence (Dunham et al. 2003). The percent of observations > the 90th percentile provides a regional context to reaches with repeated periods of high temperatures. All measures are hypothesized to characterize sustained periods of high stream temperatures that may limit the distribution and community composition of aquatic biota.

For the fine sediment accumulation latent variable model, we used substrate < 4, fines < 6, and the ratio of substrate < 4 and d₅₀ as proximal indicators of fine sediment deposition at the reach. Fines < 6 represents the amount of fine sediment accumulation at pool tails and is commonly used as a summary metric in habitat monitoring programs (Roper et al. 2002; Al-Chokhachy et al. 2010). The ratio of substrate <4 and d₅₀ indicates the potential filling of substrate interstitial spaces, leading to a reduction in habitat availability (Richards and Bacon 1994; Waters 1995). Each proximal measure of fine sediment were hypothesized to represent fine sediment accumulation that may lead to shifts in biological communities (Lanat et al. 1981; Harrison et al. 2007).

From the results of the CFA, we derived factor scores from each latent variable model using the regression method of Thomson (1951). Thomson's regression method calculates the z-score of the sum of the products of indicator values and factor loadings. The CFA was conducted using the stats package within the R programming environment (R Development Core Team 2008). We used the latent variable derived factor scores (hereafter referred to as latent variables) along with the single variables for thermal stress and fine sediment as independent variables to compare the relative efficacy of each variable to account for the variation in macroinvertebrate community composition.

Comparison of Single and Latent Variables

To assess the relative efficacy of single variables and latent variables to characterize the influence of thermal stress and fine sediment on macroinvertebrate community composition, we compared the overall variation in community structure explained by the single and latent variables. The overall variation in community composition was assessed by fitting variables to the NMDS results using the `envfit` function in R (Oksanen et al. 2008). The `envfit` function finds the gradient in the ordination configuration with the highest correlation to each environmental variable. This results in a measure that expresses the total amount of variation in community composition explained by the environmental variable (R^2). To visualize the strength and direction of influence of thermal stress and fine sediment on community structure and to examine whether compositional differences in reference and managed catchments were related to the environmental factors, we overlaid a biplot of the single and latent variables on a scatterplot of NMDS Axes 1 and 2 reach and taxa scores.

Due to the uncertainty of statistical estimates within a single dataset to accurately assess the influence of environmental factors on community composition within a population, we used a bootstrap procedure to assess the accuracy and potential bias of R^2 estimates within our dataset. Bootstrapping is a nonparametric resampling procedure used to estimate the sampling variance of a statistic where adequate replication of data is difficult (Efron 1982). We used 1000 randomly drawn samples with replacement to estimate R^2 values resulting from the analysis of single and latent variables on the NMDS results. The resulting distributions of values were used to compare the reliability of single and latent variables to assess the influence of thermal

stress and fine sediment on macroinvertebrate community composition. The reliability of estimates was assessed by comparing the median, mean, bias (difference between the mean of bootstrap estimates and the original estimate), 95 percent confidence intervals, and 1st and 3rd quantiles of bootstrapped values between the single and latent variables.

Results

Macroinvertebrates

In total, 163 OTUs (taxa) were originally identified from all sample reaches. This number was reduced to 90 taxa when only those taxa found at more than 5 percent (10 occurrences) of sampled reaches were considered. Results from the Non Non-Metric Multi-Dimensional Scaling (NMDS) of macroinvertebrate data indicated a three dimensional solution provided the best low-dimensional fit between the original Bray-Curtis dissimilarities and the multi-dimensional dissimilarity of NMDS (final stress = 15.79). The resulting reach scores from the NMDS, plotted in two-dimensional space suggest macroinvertebrate compositional similarities among many of the reaches, including both reference and managed reaches (Figure 3.3). Outliers consisted of reaches in both reference and managed catchments. A fairly distinct separation between reaches in reference catchments and a portion of reaches in managed catchments occurred along NMDS Axis 1 (≈ 0.5) and to a lesser degree along NMDS Axis 2 (≈ 0.5).

Taxa centroids (taxa scores) in relation to each NMDS axis resulted in *Sialis* having the highest positive taxa score (1.59) associated with NMDS Axis 1 and *Kogotus* (-0.60) and *Rhyacophila hyalinata* (-0.60) having the highest negative taxa scores associated with Axis 1. The second NMDS Axis showed the highest positive taxa scores

associated with *Atherix* (1.26), *Agapetus* (1.20), and *Pteronarcys* (1.16). Negative taxa scores along NMDS Axis 2 were associated with *Rhyacophila verrula* (-0.64) and *Prosimulium* (-0.64). Individual taxa axis scores can be found in Table A.1.

Latent Variable Models

Results from the latent variable models showed relatively strong relationships among indicator variables comprising each hypothesized factor and latent variable derived factor scores (Table 3.1). For the thermal stress model, 86.5 percent of the covariance among the thermal stress indicators weekly maximum temperature, days > 16, and the percent of observations > the 90th percentile was attributed to the latent variable (Figure 3.4). Latent variable factor loadings (γ) on each indicator variable were consistent among variables with weekly maximum temperature having the highest factor loading ($\gamma = 0.934$) followed by days > 16 ($\gamma = 0.930$) and the percent of observations > the 90th percentile ($\gamma = 0.927$). The amount of variation in each indicator variable accounted for by the latent variable was consistent with the factor loadings where weekly maximum temperature had the highest amount of variation explained by the latent factor (87.2%) followed by days > 16 (86.4%) and the percent of observations > the 90th percentile (86.0%).

Eighty three percent of the covariance among substrate < 4, fines < 6, and the ratio of substrate < 4 and d_{50} was accounted for by the latent variable representing fine sediment accumulation (Figure 3.4). The fine sediment accumulation latent variable loaded highest on substrate < 4 ($\gamma = 0.973$), followed by the ratio of substrate < 4 and d_{50} ($\gamma = 0.895$) and fines < 6 ($\gamma = 0.843$). The latent variable accounted for 94.6 percent of

the variation in substrate < 4 and 81.1 and 71.0 percent of the variation in the ratio of substrate < 4 and d_{50} and fines < 6, respectively.

Thermal Stress and Fine Sediment Influences on Community Structure

Pearson product-moment correlations of the thermal stress and fine sediment single and latent variables on individual NMDS axes indicate that both environmental factors are influential in shaping gradients in macroinvertebrate community structure (Table 3.2; Figure 3.1). Both of the thermal stress variables were positively correlated with NMDS Axis 1 and 2, and negatively correlated with NMDS Axis 3. The two fine sediment variables were positively correlated with NMDS Axis 1 and 3, and negatively correlated with NMDS Axis 2.

Comparison of Single and Latent Variables

Comparison of the amount of variation explained (R^2) between the single and latent variables in overall community structure showed that each variable was relatively equal in characterizing thermal stress and fine sediment influences on macroinvertebrates (Table 3.3). The thermal stress single and latent variables explained nearly equal amounts of variation (52.3 and 51.8 %, respectively) in overall community composition using our initial dataset and were significant at $P < 0.001$. Results from the bootstrapping of thermal stress single and latent variables on overall community structure were consistent with our initial findings. The single variable consistently exhibited higher R^2 estimates for the median, mean, and 95 percent confidence intervals of bootstrapped values. All bootstrapped values were significant at $P < 0.0001$. Both of the initial single and latent variable R^2 estimations were negatively biased, indicating that the

initial values tended to overestimate R^2 values. Figures illustrating differences in the distribution of bootstrap R^2 estimates for thermal stress and fine sediment single and latent variables with overall macroinvertebrate community structure can be found in Figure A.1.

The fine sediment single variable initially explained slightly less (0.3 %) variation in overall community structure compared to the fine sediment latent variable which initially explained 42.8 percent (Table 3.3). Bootstrap results were consistent with the comparison of initial R^2 estimates for the fine sediment variables with the latent variable exhibited higher median, mean, and confidence interval bootstrap estimations of R^2 . All bootstrapped values were significant at $P < 0.0001$. Both of the initial single and latent variable R^2 estimations were negatively biased when compared to the distribution of bootstrapped R^2 values. This suggests that both fine sediment variables tended to overestimate R^2 in the initial dataset, while the single variable overestimated R^2 values slightly more than the latent variable.

Discussion

Thermal Stress and Fine Sediment Influences on Community Structure

The objectives of this study were to examine the influence of thermal stress and fine sediment on aquatic community composition and compare the relative efficacy of single and latent variables to assess the influence of thermal stress and fine sediment on macroinvertebrate community structure. Results examining the variation in community structure explained by the thermal stress and fine sediment variables indicate that both

thermal stress and fine sediment are important factors influencing the structure of macroinvertebrate communities.

We were able to account for 52 percent of the variation in community structure with our thermal stress variables and 43 percent of the variation in community structure with our fine sediment variables. The correlations of thermal stress and fine sediment variables on each NMDS axis suggest that both factors were influential in structuring community gradients along NMDS Axis 1 while thermal stress was more influential in on community gradients defining Axis 2. The shared moderately high correlations of the two factors on Axis 1 may indicate an expected gradient in stream habitat templates leading to a corresponding gradient in community structure related to the location of reaches along the stream continuum (Vannote et al. 1980). The interpretation of habitat gradients corresponding with community structure is supported by our *post hoc* analysis using Geographic Information Systems where Axis 1 had a positive correlation ($r = 0.407$) with mean summer air temperature and a negative correlation with field measured stream gradient ($r = -0.336$). This indicates that community structure is influenced by a continuum of stream habitat along Axis 1 that ranges from steeper, higher elevation streams (negative values) to lower elevation streams with lower stream gradients (positive values) where fine sediment may accumulate.

The structure of community composition along Axis 2 may also be related to this same gradient of reach position along the stream continuum which is evidenced by the negative correlation of reach elevation with Axis 2 reach scores ($r = -0.437$). This suggests that the total variation in community structure cannot be solely attributed to a

single factor but instead may be influenced by the interaction of multiple physical factors whose relationship is based on landscape position along the stream continuum.

Differences in community structure between reference and managed catchments indicate that both thermal stressors and fine sediment play a factor in differentiating these communities. A majority of reaches in both reference and managed catchments overlapped in the scatterplot of NMDS Axes 1 and 2 (Figure 3.3). This suggests that community composition in many managed catchments is similar to those in reference catchments. Deviations from this overlap do occur though along Axis 1 and 2 where reaches with higher positive values which are correlated with higher levels of thermal stress and fine sediment are dominated by managed catchments. While differences in community structure between reaches in reference and managed catchments may be attributed to different levels of thermal stress and fine sediment, it is unclear what these differences stem from. A majority of forest land management practices occur in terrain at lower elevations where natural resources are more easily accessible. Therefore it is difficult to assess whether differences in community structure resulting from thermal stressors and fine sediment accumulation are directly related to anthropogenic influences, landscape position, or a combination of these two factors. Our findings illustrate the importance of accounting for the natural variation in watershed characteristics when comparing stream habitat (Kershner et al. 2004a; Al-Chokhachy et al. 2010) and biotic communities (Cao et al. 2007) between reference and managed watersheds.

Latent Variable Models

Results from the latent variable models indicate that a substantial amount of covariation among indicator variables characterizing thermal stress and fine sediment was

captured by each model. In the thermal stress latent variable model, standardized regression coefficients were relatively high and weighted evenly among indicator variables. This indicates that our *a priori* hypothesis about indicator variable similarities is valid, but also suggests that the thermal stress indicator variables are redundant, resulting in a latent variable that is nearly equivalent to each indicator. Evidence supporting the latter is confirmed by observing the correlations between the latent variable derived factor scores and thermal stress indicator variables, where the lowest Pearson product-moment correlation between the factor scores and indicators was 0.951 (Table 3.1).

In the fine sediment model, differences in standardized regression coefficients and the amount of variation explained for each indicator variable by the latent variable most likely reflects differences in sampling locations and methods. Substrate < 4 was measured at evenly spaced transects in both pool and riffle/run habitats, fines < 6 were measured at pool tail locations, and the ratio of substrate < 4 and d_{50} is a ratio of measurements in pool and riffle/run habitats. Therefore, the discontinuity among indicator variable regression weights may be partially due to the different habitat types in which the measurements were taken and the covariance among variables may be more representative of fine sediment within all reach habitat types. Differences in the variance explained by the latent variable may also be due to differences in sampling methods. Substrate < 4 was estimated from (Wolman 1954) pebble counts which may bias observations toward larger particles (Marcus et al. 1995) and has been associated with higher observer variability when summarizing the percent of fine sediment from these measurements (Roper et al. 2002; Whitacre et al. 2007). Methods used to measure fines

< 6 have been associated with low signal to noise ratios stemming from observer variability (Roper et al. 2002). The recognition of observer variability in substrate measurements illustrates how combining multiple measurements hypothesized to be a component of the latent factor (fine sediment) and assessing the covariation among indicators may more precisely reflect the underlying structure of the environmental factor by reducing the effects of measurement error. This also suggests that latent variable models may be a preferred method used to account for sources of variability associated with substrate measurements where failure to account for this variability may result in a decreased ability to meet habitat monitoring objectives (Olsen et al. 2005).

Comparison of Single and Latent Variables

Results from the comparison of thermal stress and fine sediment single and latent variables on overall macroinvertebrate community structure suggest that our thermal stress latent variable was not as effective in characterizing the influence of thermal stress on community structure as the single variable while the fine sediment latent variable was more effective at characterizing the influence of fine sediment on community structure compared to the single variable. The thermal stress single variable initially explained a higher percentage in overall community composition compared to the latent variable and these results were further supported by the results of the bootstrap analysis. This suggests that important information in the variance of the single variable that relates to macroinvertebrate composition may have been lost when the single variable was combined with similar proximal measures in the latent variable model. Although the difference in the initial amount of variation explained by the two models was small (0.5%), the bootstrap results indicate that the single variable was consistently more

effective at representing the influence of thermal stress on community structure. This is confirmed in the lower bootstrap bias estimate of the single variable, which differed from the latent variable by 1.9 percent and indicates that the single variable may also be more effective at representing the influence of thermal stress on macroinvertebrates outside of our original dataset of sample reaches.

The high correlation of the thermal stress single variable with the latent variable ($r = 0.958$; Table 3.1) also indicates that the two variables are nearly identical. Therefore, we should not have expected that one variable should account for a substantially more amount of variation than the other. Including alternative proximal measures of thermal stress in the latent variable model that were not as highly correlated may have aided us in developing a more effective latent variable. For example, stream temperature summary metrics may not be the only indicators of thermal stress on aquatic biota. High stream temperatures can also lead to a decrease in dissolved oxygen (DO) levels and an increase in organism metabolic rates (Allan and Castillo 2007) that may lead to a shift in community composition toward species more tolerant of high DO levels. Developing a latent variable model that incorporates DO or other close correlates of sustained high stream temperatures along with temperature summary metrics and assessing the covariance among these variables may lead to a latent variable that is more effective in characterizing the influence of thermal stressors on macroinvertebrate community structure.

The fine sediment latent variable initially explained 0.3 percent more of the variation in overall macroinvertebrate community structure than the fine sediment single variable. Results of the bootstrap analysis support these initial findings where each of the

bootstrapped summary statistics (Table 1.3) were higher for the latent variable than the single variable and the difference between the resulting bootstrap distribution means was 1.1 %. The bias of the latent variable was also smaller (0.8%) than that of the single variable which indicates that the latent variable may be a more reliable estimate of fine sediment influences on macroinvertebrates in sample populations outside our initial dataset. Although the differences in the amount of variation explained by the two variables were small, these results suggest that the latent variable was more effective in characterizing the influence of fine sediment on community structure than the single variable.

Similar to the high correlation between the thermal stress single and latent variable, our fine sediment variables were highly correlated ($r = 0.997$). Therefore, the difference in the amount of variation explained between the two variables may be attributed to the other proximal variables in the model and their covariation with substrate < 4 . Fines < 6 and the ratio of substrate < 4 and d_{50} had moderately high correlations with substrate < 4 ($r = 0.843$ and $r = 0.871$, respectively). This suggests that the two variables are somewhat distinct indicators of our hypothesized latent factor and the relationship among the variables, assessed through their covariance may be more representative of the underlying influence of fine sediment on macroinvertebrate community structure than the single variable. The small amount of additional variation explained by the latent variable may not be enough to warrant using the latent variable in place of the single variable in further analyses, but it does provide evidence for the potential of latent variables to more accurately characterize factors influencing stream biota.

While our fine sediment latent variable did explain slightly more variation in community structure than our single variable, a more effective model may have been constructed by using alternative proximal measures of fine sediment that are more spatially relevant to where biotic samples are taken. Alternative measures of fine sediment such as those that more accurately indicate embedded substrate (McHugh and Budy 2005) and are not as highly correlated with or derived from other measurements in the model may have resulted in a more effective latent variable. A more effective model may also have been attained if all proximal indicator variable measurements were conducted in riffles where macroinvertebrate samples were taken. These considerations should be employed when developing theoretical and statistical models aimed at representing factors influencing a target biological community.

In this analysis, we were limited to physical stream attributes used to monitor the status and trends of in-stream habitat. While many of these attributes are used to assess the effect of land management on stream habitat, the reliability of many of these measurements to characterize factors influencing aquatic biota is still uncertain. Considerable effort has been taken to assess the reliability of observer variation in measuring physical stream attributes (Roper et al. 2002; Olsen et al. 2005; Whitacre et al. 2007). Results from these studies have helped us to understand which measurements are more reliable in characterizing in-stream habitat. Given our increased understanding of the reliability of in-stream habitat measurements, the next step may be to examine the reliability of these measurements to assess influences on stream biota. While our ability to characterize in-stream habitat may be sufficient, our ability to measure attributes

representing environmental factors directly affecting the biota is limited by our understanding of these factors and the resources to measure them.

Including additional measurements in our habitat assessments that are proximal indicators of the environmental factors effecting stream communities will allow us to test the efficacy of multiple habitat measurements to characterize their influence on stream biota. By combining multiple proximal indicators with ecologically similar attributes into latent variable models, we may be able to more accurately characterize and assess the ecological processes influencing the biota. The use of latent variables to represent underlying processes or factors provides a potentially effective alternative to single habitat measurements. Although their use has been limited in the aquatic sciences, latent variables have been successful in representing unmeasured theoretical factors in other ecological analyses (Grace and Pugsek 1997; Malaeb et al. 2000; Baker and Wiley 2009). Further refining of conceptual models based on underlying processes may be especially beneficial to researchers investigating habitat-landscape and species-habitat relationships in lotic environments and further our understanding of the factors influencing aquatic communities.

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Table 3.1 Pearson product-moment correlations between field measured variables and latent variable model derived factor scores representing indicators of thermal stress and fine sediment accumulation.

Environmental Factor	Indicator Variable				
Thermal Stress	Weekly Maximum Temperature	1			
	Days > 16	0.868	1		
	Observations > 90th Percentile	0.866	0.862	1	
	Latent Variable	0.958	0.953	0.951	1
Fine Sediment	Substrate < 4	1			
	Fines < 6	0.843	1		
	RatioSubstrate < 4 and d ₅₀	0.871	0.757	1	
	Latent Variable	0.997	0.867	0.896	1

Table 3.2 Pearson product moment correlations of thermal stress and fine sediment single and latent variables with individual NMDS axis site score. The thermal stress variables were significantly correlated with each axis at $P < 0.0001$ and the fine sediment variables were at $P < 0.001$.

Environmental Factor	Variable			
Thermal Stress		NMDS Axis 1	NMDS Axis 2	NMDS Axis 3
	Single	0.471	0.488	-0.250
	Latent	0.422	0.505	-0.292
Fine Sediment		NMDS Axis 1	NMDS Axis 2	NMDS Axis 3
	Single	0.550	-0.203	0.284
	Latent	0.554	-0.215	0.273

Table 3.3 Initial R-squared (R^2) estimates and statistical summaries of bootstrapped R^2 values for thermal stress and fine sediment single and latent variables with overall community structure. Lower CI and Upper CI represent the lower and upper 95% confidence intervals of bootstrap values.

Environmental Factor	Variable	Initial R^2	Median	Mean	Bias	Lower CI	Upper CI
Thermal Stress							
	Single	0.523	0.465	0.463	-0.060	0.374	0.548
	Latent	0.518	0.438	0.439	-0.079	0.354	0.521
Fine Sediment							
	Single	0.425	0.350	0.349	-0.075	0.239	0.456
	Latent	0.428	0.359	0.360	-0.068	0.249	0.474

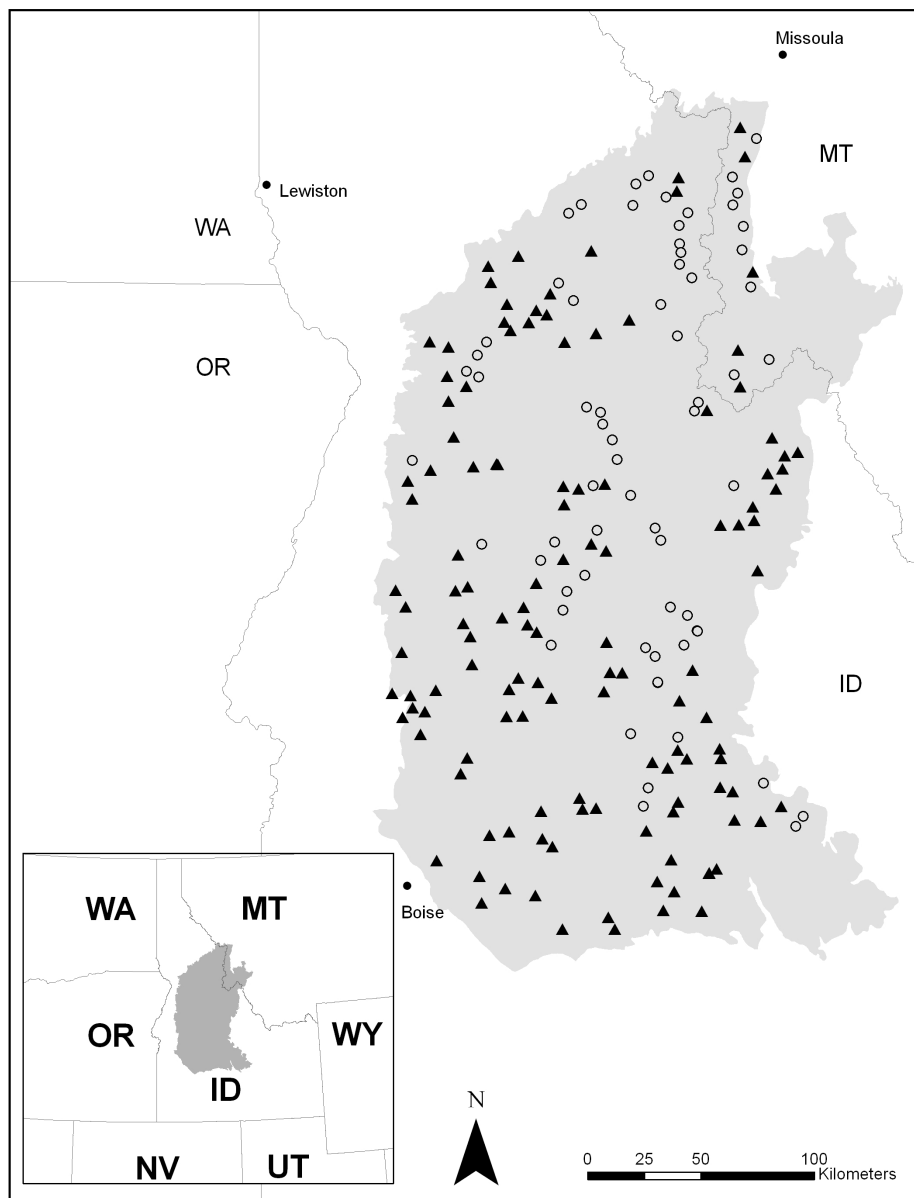


Figure 3.1 Map of study area illustrating the location of reference (circles) and managed (triangles) reaches. The Idaho Batholith Ecoregion is shown in grey.

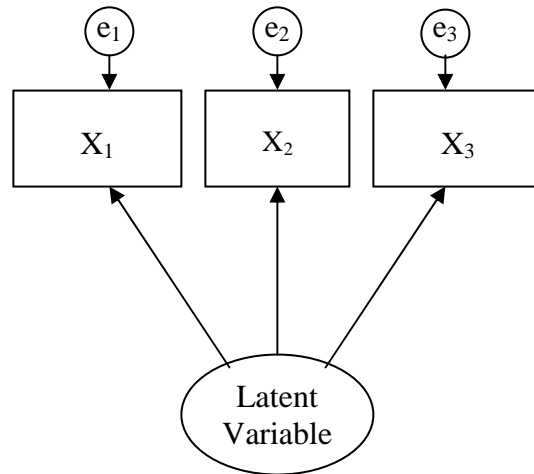


Figure 3.2 Schematic path diagram of a latent variable model. Circles (e_i) represent error associated with each indicator variable (X_i), which are represented by rectangles. Arrows from circles to indicator variables represent the influence of error associated with each measured variable. The oval represents the latent variable. Arrows pointing from the latent variable to each indicator variable symbolize that each indicator is an element of the latent factor.

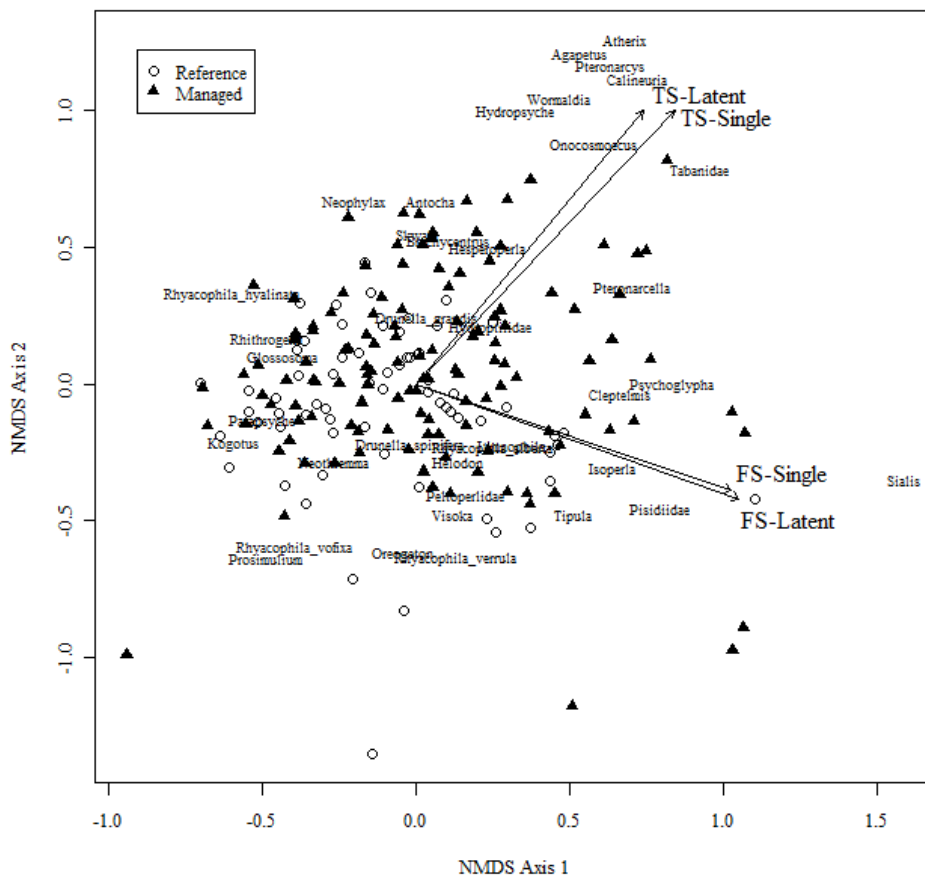


Figure 3.3 Scatterplot of Non-Metric Multi-Dimensional Scaling ordination Axes 1 and 2 of macroinvertebrate samples. Open circles and triangles indicate site scores for reference and managed sites, respectively. Species are denoted by name and represent the 10 highest species scores associated with NMDS Axes 1-3. Arrows indicate the strength and direction of correlations between single and latent variables and each NMDS axis. Identification of arrows are as follows; TS-Single = the thermal stress single variable, TS-Latent = the thermal stress latent variable, FS-Single = the fine sediment single variable, and FS-Latent = the fine sediment latent variable.

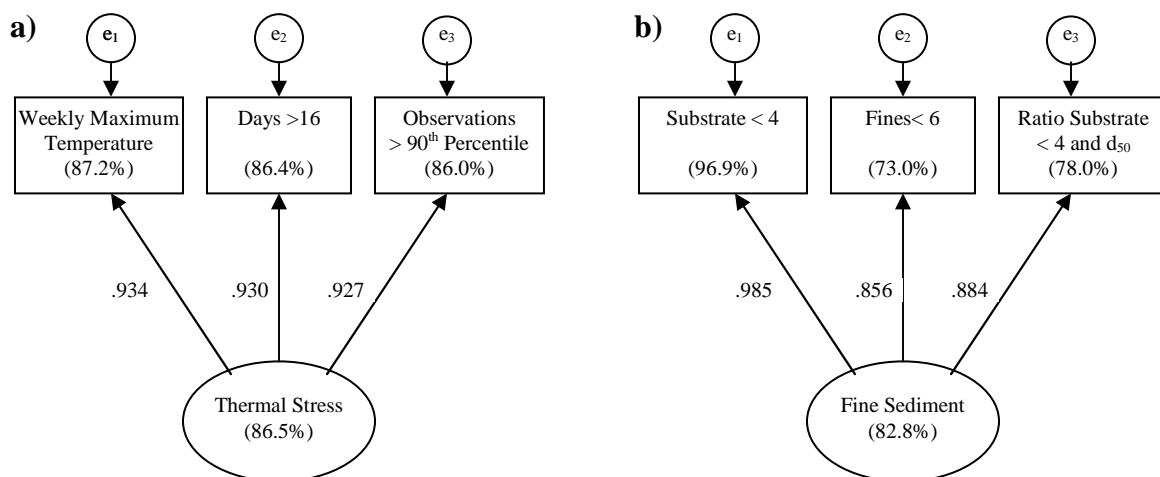


Figure 3.4 Latent variable model results for a) thermal stress and b) fine sediment. Values within indicator variable rectangles represent the amount of variation explained by the latent factor. Standardized path coefficients, or factor loadings of the latent factor on indicator variables are located next to each arrow. Values within ovals indicate the total variation among indicator variables explained by the latent variable.

CHAPTER 4

CONCLUSION

Understanding the linkages among landscape processes, in-stream habitat, and aquatic biota is one of the major objectives and challenges of stream ecology. While much knowledge has been gained in recent years regarding these linkages, a further, more complete understanding of these linkages is needed. This understanding is an essential step in assessing the influence of land management activities on aquatic ecosystems in order to direct conservation strategies aimed at protecting aquatic resources.

In Chapter 2, we used spatial data, field-based habitat measurements, and macroinvertebrate community data to examine the influence of landscape processes on maximum stream temperatures and fine sediment, and to examine how well landscape and habitat characteristics represent factors influencing gradients in macroinvertebrate community structure. Regression results of the spatially derived landscape variables on weekly maximum temperature indicated that water residence time, maximum summer air temperatures, and riparian shading were all significant factors influencing maximum stream temperatures. Results of the landscape variables on fine sediment indicated that network specific stream power was a significant influence on fine sediment accumulation at the reach while proximity-weighted slope and reach unit stream power were not significant. These results indicate that our initial hypotheses regarding the influence of proximity-weighted slope and reach stream power may have been incorrect, but most likely reflects either our inability to accurately characterize these factors using spatial data or the fact that network stream power accounted for much of the same variation as

the other two variables in the model as indicated by the moderate correlations among the three.

Interpretation of the linear regression results of the field and GIS-derived measurements on non-metric multidimensional scaling (NMDS) results of the macroinvertebrate community data suggested that macroinvertebrate community structure along NMDS Axis 1 most likely reflects a gradient in longitudinal position along the stream continuum. This gradient, based on the location of sampled reaches along the continuum may be influenced by a combination of factors relating to both landscape processes and in-stream habitat characteristics where reaches further from steeper headwater streams at lower elevations tended to have increased levels of fine sediment accumulation and higher temperatures. Changes in macroinvertebrate community structure associated with NMDS Axis 2 most likely reflect a gradient in maximum stream temperatures or a close environmental correlate of temperature and may also indicate a shift in community structure from heterotrophic to autotrophic dominated communities. While both of these patterns in macroinvertebrate community composition have previously been recognized (Vannote et al. 1980), our ability to accurately characterize the landscape processes influencing these patterns may allow us to factor out variation in the landscape in order to better understand the implication of land management practices on in-stream habitat and aquatic biota.

What may be most interesting is that our GIS-derived model consisting of measurements hypothesized to influence maximum stream temperatures explained almost twice as much variation in macroinvertebrate community structure along NMDS Axis 2 compared to the field measurement of weekly maximum temperature and had a

substantially lower AIC score. Also, the GIS-derived model representing landscape influences on fine sediment explained roughly the same amount of variation in community structure along NMDS Axis 1 and had a similar AIC score compared to the field measurement of fine sediment. These results indicate that characteristics within the landscape may play a more dominant role than in-stream habitat in structuring aquatic communities, that the GIS-derived measurements may be accounting for additional variation in community structure indirectly related to the field measurements, or that our field measurements may not be accurately characterizing in-stream habitat important to the biota. The results also provide evidence that spatial methods may offer an alternative method to assess patterns in stream communities and suggest that more research is needed in order to understand how accurate our habitat measurements are at representing the relative factors structuring aquatic communities.

In Chapter 3, we compared the relative efficacy of single field measurements and latent variables to characterize the influence of thermal stress and fine sediment accumulation on macroinvertebrate community composition. Results showed that the latent variable indicating thermal stress was less reliable than the single variable at characterizing the influence of high temperature on macroinvertebrate community structure and that the latent variable indicating fine sediment accounted for only a limited amount of additional variation compared to the single variable regarding the influence of fine sediment accumulation on community structure. These results suggest that while latent variables may provide a potentially effective alternative to single habitat measurements, their ability to more accurately represent underlying processes or ecological factors important to aquatic biota compared to single measurements is

uncertain. Further work is needed to refine hypotheses in order to develop more effective latent variables and more research is needed to determine how well our habitat measurements characterize factors influencing aquatic biota.

One common question throughout this research was how well do our in-stream habitat measurements represent factors influencing aquatic biota? While our results do not provide a definitive answer to this question, they do suggest that further research should be directed at comparing alternative in-stream habitat measurements to determine how well these measurements characterize factors important to the biota. This may be accomplished by testing additional single habitat measurements or alternative means of representing ecological processes such as latent variables. Our results also suggest that additional research is needed to refine methods used to characterize landscape processes from spatial data. Further testing and improvements of methods used to characterize landscape processes will allow us to better assess landscape influences on stream habitat and aquatic biota, better understand the implications of land management practices on aquatic ecosystems, and eventually may reduce our reliance on field based methods. Improving how well our field and spatial measurements represent factors influencing aquatic ecosystems will lead the way to better environmental assessments and help guide strategies aimed at conserving aquatic resources.

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APPENDICES

Table A.1 Operational Taxonomic Unit (OTU) names, non-metric multidimensional scaling (NMDS) Axis 1-3 scores, and frequencies of occurrence of all macroinvertebrate OTUs with at least 10 occurrences (5%) in the dataset. OTUs are listed in order of rank (positive to negative) along NMDS Axis 1.

Operational Taxonomic Unit (OTU) Name	NMDS Axis 1	NMDS Axis 2	NMDS Axis 3	Frequency (%)	Frequency (<i>n</i>)
Sialis	1.589	-0.344	0.014	5.79	11
Tabanidae	0.926	0.788	0.034	6.84	13
Psychoglypha	0.835	0.000	0.484	7.89	15
Pisidiidae	0.796	-0.440	0.449	16.84	32
Calineuria	0.714	1.119	-0.753	5.79	11
Pteronarca	0.698	0.369	0.335	8.42	16
Atherix	0.672	1.256	-1.285	6.32	12
Cleptelmis	0.668	-0.039	0.194	48.95	93
Isoperla	0.648	-0.315	0.404	16.84	32
Pteronarcys	0.623	1.156	-1.103	6.32	12
Malenka	0.591	0.657	0.101	8.42	16
Onocosmoecus	0.559	0.909	-0.208	6.32	12
Agapetus	0.531	1.207	-0.036	7.37	14
Lepidostoma	0.528	0.305	-0.036	29.47	56
Tipula	0.518	-0.476	0.336	22.11	42
Paraleptophlebia	0.492	0.271	-0.034	24.74	47
Wormaldia	0.461	1.052	0.153	7.89	15
Hesperoconopa	0.426	0.540	0.227	5.79	11
Apatania	0.422	0.263	0.089	21.05	40
Oreodytes	0.416	0.528	0.063	9.47	18
Tanypodinae	0.395	-0.122	0.151	67.89	129
Dipheter	0.344	0.156	0.049	26.84	51
Limnophila	0.322	-0.227	0.737	16.32	31
Hydropsyche	0.316	0.991	-0.334	15.26	29
Micrasema	0.313	0.067	0.180	68.95	131
Optioservus	0.293	0.583	-0.273	61.58	117
Other_Oligochaeta	0.284	0.136	-0.110	21.05	40
Zaitzevia	0.255	0.654	-0.292	42.63	81
Rhyacophila_alberta_group	0.254	-0.232	0.493	10.00	19
Hydroptilidae	0.240	0.207	-0.385	11.05	21

Table A.1 continued Operational Taxonomic Unit (OTU) names, non-metric multidimensional scaling (NMDS) Axis 1-3 scores, and frequencies of occurrence of all macroinvertebrate OTUs with at least 10 occurrences (5%) in the dataset. OTUs are listed in order of rank (positive to negative) along NMDS Axis 1.

Operational Taxonomic Unit (OTU) Name	NMDS Axis 1	NMDS Axis 2	NMDS Axis 3	Frequency (%)	Frequency (<i>n</i>)
Hesperoperla	0.232	0.487	-0.478	29.47	56
Pericoma_Telmatoscopus	0.226	0.382	0.253	15.79	30
Amiocentrus	0.211	0.322	0.219	10.00	19
Acari	0.202	0.121	0.390	30.00	57
Ceratopogoninae	0.200	0.038	0.213	57.37	109
Narpus	0.170	0.536	-0.230	22.63	43
Peltoperlidae	0.169	-0.413	0.751	41.05	78
Helodon	0.149	-0.278	0.830	5.79	11
Rhyacophila_verrula_group	0.140	-0.623	0.858	9.47	18
Visoka	0.131	-0.481	0.796	15.26	29
Chironominae	0.129	0.003	0.111	82.11	156
Rhabdomastix	0.122	-0.166	0.364	14.21	27
Clinocera	0.104	0.170	0.370	6.84	13
Brachycentrus	0.102	0.529	-0.358	35.79	68
Dicranota	0.063	0.062	0.212	25.26	48
Simulium	0.057	0.064	0.011	74.74	142
Antocha	0.045	0.667	-0.152	28.42	54
Heterlimnius	0.031	-0.058	0.187	87.37	166
Orthoclaadiinae	0.024	0.031	0.019	96.84	184
Hexatoma	0.020	-0.036	0.162	73.16	139
Drunella_grandis	0.010	0.270	-0.379	5.26	10
Skwala	0.004	0.541	-0.453	8.42	16
Drunella_spinifera	-0.015	-0.223	0.479	38.42	73
Chelifera_Metachela_Neoplasta	-0.015	0.055	0.180	20.00	38
Arctopsyche	-0.018	0.555	-0.329	38.42	73
Oreogeton	-0.032	-0.631	0.644	10.53	20
Lara	-0.033	0.609	-0.099	17.89	34
Serratella	-0.056	0.147	0.113	56.32	107
Glutops	-0.056	0.223	0.211	33.16	63
Other_Chloroperlidae	-0.077	-0.078	0.032	95.79	182
Caudatella	-0.087	0.277	0.098	39.47	75

Table A.1 continued Operational Taxonomic Unit (OTU) names, non-metric multidimensional scaling (NMDS) Axis 1-3 scores, and frequencies of occurrence of all macroinvertebrate OTUs with at least 10 occurrences (5%) in the dataset. OTUs are listed in order of rank (positive to negative) along NMDS Axis 1.

Operational Taxonomic Unit (OTU) Name	NMDS Axis 1	NMDS Axis 2	NMDS Axis 3	Frequency (%)	Frequency (<i>n</i>)
Ameletus	-0.089	-0.228	0.271	56.84	108
Doroneuria	-0.098	0.068	0.170	52.63	100
Rhyacophila brunnea vemna group	-0.125	-0.052	0.154	80.00	152
Dolophilodes	-0.184	0.545	-0.046	20.00	38
Baetis	-0.203	0.063	-0.076	92.63	176
Neophylax	-0.211	0.679	-0.027	15.79	30
Ephemerella	-0.215	0.041	0.367	13.68	26
Neothremma	-0.257	-0.289	0.511	17.37	33
Zapada	-0.262	-0.171	0.246	61.58	117
Dicosmoecus	-0.272	0.048	-0.009	14.74	28
Rhyacophila_sibirica_group	-0.275	-0.019	0.365	24.21	46
Leuctridae	-0.294	-0.119	0.227	21.05	40
Acentrella	-0.299	0.128	-0.311	15.79	30
Megarcys	-0.313	-0.013	0.192	54.74	104
Rhyacophila_vofixa_group	-0.389	-0.607	0.036	17.89	34
Rhyacophila_betteni_group	-0.415	-0.126	0.136	45.79	87
Rhyacophila_angelita_group	-0.441	0.121	-0.517	19.47	37
Cinygmula	-0.458	-0.143	0.020	64.21	122
Drunella_doddsii	-0.458	0.087	-0.125	63.68	121
Drunella_coloradensis_flavilinea	-0.473	-0.043	0.099	55.79	106
Prosimulium	-0.484	-0.635	0.094	14.21	27
Rhithrogena	-0.488	0.156	-0.249	52.63	100
Capniidae	-0.492	0.150	0.120	10.00	19
Parapsyche	-0.500	-0.142	0.188	38.42	73
Glossosoma	-0.520	0.123	-0.039	39.47	75
Epeorus	-0.522	0.102	-0.259	64.74	123
Rhyacophila_hyalinata_group	-0.601	0.332	-0.050	20.00	38
Kogotus	-0.602	-0.197	0.137	18.42	35
Oligophlebodes	-0.929	0.361	0.081	6.84	13

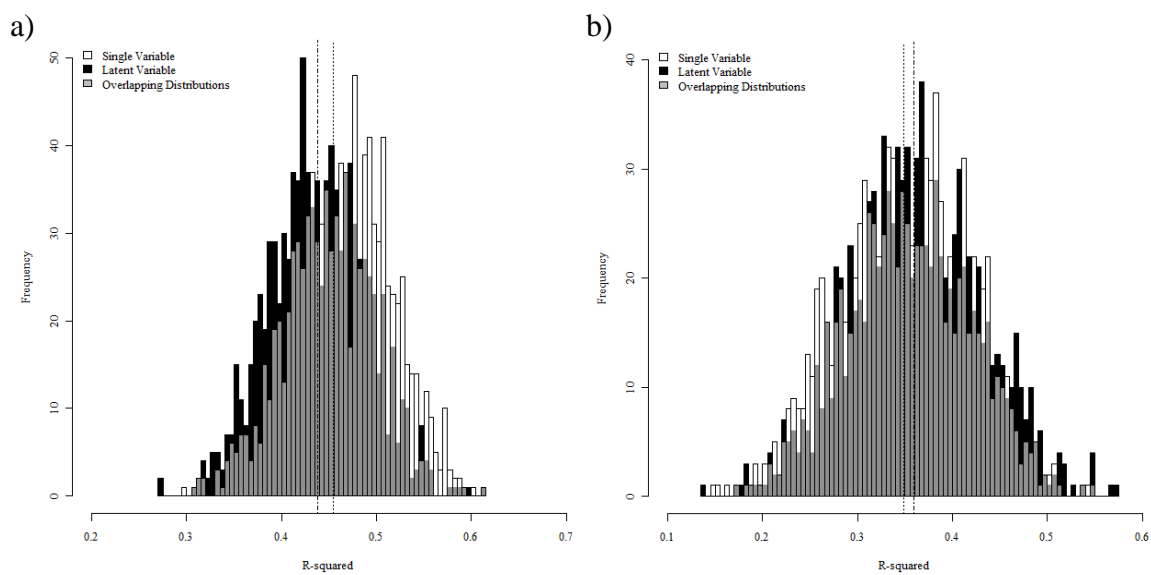


Figure A.1 Bootstrap ($n = 1000$) distribution results of R-squared (R^2) values for a) thermal stress and b) fine sediment accumulation single (white) and latent (black) variables on overall macroinvertebrate community structure. Vertical dotted and dashed/dotted lines represent the median bootstrap R^2 values for the single and latent variable, respectively. Areas in grey represent overlapping distributions.