Long-Term Impacts of Severe Wildfire and Salvage Logging on Macroinvertebrate Assemblages and Food Web Structure in Rocky Mountain Headwater Streams

by

Amanda M. Martens

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

Master of Science

in

Water and Land Resources

Department of Renewable Resources
University of Alberta

Abstract

Wildfire is an important natural disturbance on forested landscapes influencing both physical and biological processes. The Lost Creek wildfire in 2003 was one of the more severe on Alberta's eastern slopes and provided a unique opportunity to assess the long-term impacts of wildfire on northern Rocky Mountain watersheds. The objectives of this research were to determine if persistent wildfire effects on streamflow and water quality produced effects on macroinvertebrate assemblage structure in burned and burned & salvage-logged watersheds and to evaluate potential effects on aquatic food web structure. Benthic macroinvertebrates and Cutthroat Trout (*Oncorhynchus clarkii*) were sampled eight years after the wildfire. Multivariate analysis of macroinvertebrate assemblage structure and stable isotope analysis were used to assess the long-term impacts of the wildfire on aquatic fauna. Reference, burned and burned & salvage-logged watersheds each supported a unique macroinvertebrate assemblage, suggesting that different mechanisms (resource availability and habitat limitation) were driving the ecological response in wildfire affected watersheds. Stable isotope analysis (carbon and nitrogen) showed a shift in macroinvertebrate food web structure in burned watersheds to a greater reliance on instream primary productivity. Trout showed no difference in growth metrics or resource utilization between reference and burned watersheds. Post-wildfire salvage-logging produced additional impacts to macroinvertebrate assemblages in affected watersheds highlighting the importance of addressing cumulative impacts to aquatic ecosystems.

Preface

This thesis is original work by Amanda Martens conducted under the supervision of Dr. Uldis Silins.

A portion of Chapter 2 of this thesis has been published as A.M. Martens, U. Silins, H.C. Proctor, C.H.S. Williams, M.J. Wager, M.B. Emelko, and M. Stone, "Long-term impact of severe wildfire and post-wildfire salvage logging on macroinvertebrate assemblage structure in Alberta's Rocky Mountains," *International Journal of Wildland Fire*. doi: 10.1071/WF18177. A.M. Martens was responsible for data collection, sample preparation, data analysis, and manuscript composition. C.H.S Williams and M.J. Wagner assisted with data collection and manuscript edits. H.C. Proctor, M.B. Emelko and M. Stone were involved with concept formation and manuscript edits. U. Silins was the supervisory author and involved with concept formation and manuscript composition.

Acknowledgements

I would like to thank my Supervisor, Dr. Uldis Silins for his guidance and support throughout this project and for providing me with the independence and confidence to pursue this research. I would also like to thank Dr. Heather Proctor for her guidance, support, and thoughtful insights on this project.

Dr. Monica Emelko and Dr. Mike Stone, thank you for your support and advice throughout this project, I am always grateful for our conversations! I would like to thank Dr. Kevin Bladon for his advice and assistance on this project.

The Southern Rockies Watershed Project staff tirelessly assisted with field and laboratory work, Chris Williams, Micheal Wagner, Samantha Karpyshin, Evan Luchkow and Ashley Peter-Rennich, I could not have done this without you! I would like to thank Zhouyan Song for his assistance with multivariate statistics. Thank you to my fellow graduate students Amelia Corrigan, Caitlin Watt, Sheena Spencer, Dan Greenacre, Derek Muller, Michael Stewart, Melissa Howard and Kira Puntenney for your advice and support throughout this process.

Thank you to Alberta Agriculture and Forestry, Alberta Innovates – Water Innovation Program, Canfor, the Forest Resource Improvement Association of Alberta (FRIAA), the Natural Sciences and Engineering Research Council (NSERC) and Alberta Environment and Parks for providing funding and logistical support.

I would also like to thank all of the amazing friends and family who have supported me throughout this adventure. Sam, you have been with me since 2011 when we were blissfully unware of what a round of invertebrate sampling would become and I am truly grateful! Thank you to my family for all of your love and support. Shaun, you have been constantly supportive, positive, patient and kind, thank you!

Table of Contents

Table of Tables

Table of Figures

Chapter 1 Thesis Introduction

The forested watersheds of the North American Rocky Mountains form the headwaters of several important basins including the Columbia, the Saskatchewan and the Missouri rivers, and are a vital source of water for downstream ecosystems and communities (Hauer *et al.* 2007; Emelko *et al.* 2011). These watersheds have high water quality and provide critical habitat for many species including macroinvertebrates and salmonid fishes (Hauer *et al.* 2007; Isaak *et al.* 2016). Wildfire is one of the major agents of disturbance in forested landscapes, with the potential to cause large changes in both terrestrial and aquatic ecosystems (Gresswell 1999; Moody and Martin 2001; Bixby *et al.* 2015). Climate warming is contributing to major changes in how fire behaves on the landscape, affecting fire management, human dimensions (property, recreation and drinking water), and post-fire ecosystems (Schoennagel *et al.* 2004; Flannigan *et al.* 2005; Emelko *et al.* 2011; Martin 2016).

Since the 1980s, increases in wildfire frequency, severity, duration and season length have been observed (Westerling *et al.* 2006). Comparing wildfire activity in the United States between 1970-1986 to between 1987-2003, the average wildfire season length increased by 78 days and the average time from discovering to controlling a wildfire increased from 7.5 to 37.1 days (Westerling *et al.* 2006). Understanding the effects of wildfire on forested ecosystems will be crucial to manage this threat as climate models predict a 1.4 to 5.8 °C increase in global temperature by the end of the century (Houghton 2001). It is expected that under a warming climate, the area burned in Canada will increase by 74 to 118% by the end of the 21st century (Flannigan *et al.* 2005). 60% of the observed increases in wildfire in the United States between 1970 and 2003 occurred in the Rocky Mountains (Westerling *et al.* 2006) suggesting these ecosystems will be particularly susceptible to changes in wildfire behavior induced by climate change. Indeed, major wildfires have become a regular occurrence in North America including 2018 which was the worst fire seasons in recent history in both the province of British Columbia and the state of California. Alberta has also experienced several severe wildfires in the recent decade including the Kenow Wildfire in 2017 that burned 380 km^2 (including 193 km^2 within Waterton National Park), and the Horse River (2016) and Richardson/Slave Lake (2011) wildfires that burned 5 900, and 7 100 km^2 (respectively) in northern Alberta (Parks Canada 2018; Alberta Agriculture and Forestry 2019).

When a wildfire burns it causes physical changes to the vegetation and soil surface of forested landscapes. Aquatic ecosystems are strongly influenced by these changes as the majority of water that enters a stream must first move through the terrestrial landscape. Water moving over and through burnt landscapes can transport physical and chemical contaminants including ash, charred organic matter, sediment, nutrients and heavy metals (Hynes 1975; Kelly *et al.* 2006; Kunze and Stednick 2006; Silins *et al.* 2009). The capacity of the forest canopy to intercept and store rainfall and snowmelt is reduced due to the consumption of vegetation and the development of water repellency within the soil (DeBano 2000; Martin and Moody 2001; Moody and Martin 2001; Burles and Boon 2011). These factors can contribute to faster runoff responses and higher event peakflows during precipitation and snowmelt events as well as greater overall annual water yield (Shakesby and Doerr 2006). Runoff events caused by spring snowmelt or heavy precipitation can move large amounts of sediment and debris into streams and rivers (Kunze and Stednick 2006; Rosenberger *et al.* 2011). Increased nutrient loading and changes in precipitation-runoff dynamics can alter aquatic habitat and ecosystem energy dynamics with important implications for the aquatic biota that live in wildfire affected streams.

Water quality, velocity and streambed substrate are important habitat characteristics that influence which species are able to occupy and thrive in a given location (Bjornn *et al.* 1977). The abundance of any given taxon will be greatest in the area that provides the most suitable habitat (Brittain & Eikeland, 1988). Impacts to habitat can change the relative abundance of different taxa because habitat suitability may increase for some taxa, while the abundance of disturbance sensitive taxa may decrease (Barbour *et al.* 1999; Voshell 2002). Macroinvertebrates play an important role in the breakdown of organic matter and the cycling of nutrients and energy in aquatic ecosystems (Covich *et al.* 1999). They are also an important food source for salmonid fish (e.g., trout, grayling and whitefish) (Rinne 1996; Malison and Baxter 2010). Rocky mountain watersheds in Alberta support several valuable trout fisheries, including two threated native trout, Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*) and Bull Trout (*Salvelinus confluentus*) (Alberta Environment and Parks 2014; US Fish and Wildlife Service 2017).

Previous research has shown highly variable impacts of wildfire on aquatic ecosystems. Primary productivity often increases in burned watersheds as photosynthesis is promoted when fire removes riparian vegetation, increasing water temperature and the amount of sunlight reaching the stream surface (Mihuc and Minshall 2005; Wagner *et al.* 2014). Nutrients (particularly phosphorous) are often limiting in oligotrophic mountain watersheds (Hauer *et al.* 2007); increased phosphorus and nitrogen yields following wildfire serve to further increase instream primary productivity (Mihuc and Minshall 2005; Silins *et al.* 2014). In steep watersheds, however, high peakflows can cause scouring of the streambeds washing out attached algae and reducing primary productivity (Minshall *et al.* 2001). Periphyton (the combination of algae, cyanobacteria and microbes that encrusts substrates) represents an important source of energy for aquatic consumers (Rugenski and Minshall 2014). The River Continuum Concept

(RCC) predicts that low order headwater streams will be primarily supported by terrestrial (allochthonous) energy sources (Vannote *et al.* 1980). Terrestrial energy sources include any vegetation (leaves, wood, needles, grass etc.) that is washed into the stream, where it becomes available as an energy source for aquatic consumers such as macroinvertebrates (Rounick *et al.* 1982; Zah *et al.* 2001). Burned organic material is not a valuable source of energy because combustion leaves it with limited nutritional value (Mihuc and Minshall 1995); therefore wildfire can promote increased use of instream (autocthonous) sources of energy (Spencer *et al.* 2003; Mihuc and Minshall 2005). This, in turn, can lead to changes in the biomass, abundance and diversity of macroinvertebrates as well as the composition and feeding guild structure of macroinvertebrate communities (Mihuc and Minshall 1995; Spencer *et al.* 2003; Vieira *et al.* 2004; Cooper *et al.* 2015).

The diet, growth rates and population structure of salmonid fish can be influenced by the changes in water quality, hydrology and food availability caused by wildfire (Rieman *et al.* 1997; Koetsier *et al.* 2007; Rosenberger *et al.* 2011). Warmer stream temperatures can cause stress to native cold-water species including Cutthroat Trout (*Oncorhynchus clarkii*) and Bull Trout (Isaak *et al.* 2010; Isaak *et al.* 2016). Increased fine sediment deposition can compromise spawning habitat and reduce oxygen levels for developing eggs (Minshall *et al.* 1989; Rinne 1996; Sear *et al.* 2016). This is especially important for spring spawning fish such as Cutthroat Trout as spring snowmelt can cause high sediment loading during this critical time (Silins *et al.* 2009). Macroinvertebrates are an important food source for salmonid fish (Rinne 1996), thus changes in invertebrate assemblage structure, abundance and biomass can impact fish by altering the quantity and quality of their prey base (Koetsier *et al.* 2007; Rosenberger *et al.* 2011).

Greater growth rates and increased recruitment have been observed in fish populations within wildfire-affected watersheds (Rieman *et al.* 1997; Koetsier *et al.* 2007; Silins *et al.* 2014).

Post-fire landscape management can also influence or compound the effects of fire on aquatic ecosystems by producing effects on key hydrologic and biogeochemical parameters such as runoff and sediment export (Beschta *et al.* 1995). A common type of post-wildfire management is salvage-logging, where merchantable timber is harvested to recoup economic losses (Beshta *et al.* 1995; Lindenmayer *et al.* 2004). However, as salvage logging can add additional landscape disturbance on top of recent fire disturbance the cumulative effects of timber harvest and wildfire on aquatic ecosystems must be considered. Both ground disturbance and linear features (e.g., skid trails, haul roads and stream crossings) associated with salvage logging have the potential to further increase sediment loading and habitat degradation (Wagenbrenner *et al.* 2016). The impacts to sensitive taxa such a mayflies (order Ephemeroptera) and threatened fish species such as Westslope Cutthroat Trout and Bull Trout are an important consideration prior to implementing any post-fire management activities including restoration activities.

The persistence of wildfire effects on aquatic communities is dependent upon a number of factors governing stream recovery, including the severity of the wildfire, the geology of the region, vegetation recovery, the occurrence of drought or flooding, and any application of forest management treatments (Lindenmayer *et al.* 2004; Shakesby and Doerr 2006; Malison and Baxter 2010; Rugenski and Minshall 2014). While extensive wildfire research has been conducted, important knowledge gaps remain including understanding the impacts of wildfire over longer time frames (>5 years) and cumulative impacts of post-wildfire management such as salvage logging (Beshta *et al.* 1995; Gresswell 1999; Bisson *et al.* 2003; Bixby *et al.* 2015). Minshall *et al*. (1989) defined the temporal effects of fire on aquatic ecosystems as immediate (active burning to the first runoff event), delayed (first event to 4 years post-fire) and long-term (greater than 4 years post-fire). The majority of previous wildfire studies have focused on immediate and delayed effects (Rinne 1996; Minshall *et al.* 1997; Malison and Baxter 2010, Bixby *et al.* 2015), however longer-term effects of wildfire on aquatic ecology are less well understood.

Accordingly, the goals of my research were to evaluate some of the longer-term impacts (> 5 years) of wildfire and salvage-logging on both macroinvertebrates and fish in the Front Range watersheds of Alberta's Rocky Mountains. The Lost Creek wildfire burned over 210 km^2 in south-west Alberta in 2003 and was one of the more severe fires in that region in recent decades. All of the forest canopy and forest floor organic material was effectively removed. The Southern Rockies Watershed Project (SRWP) was established to document the effects of the wildfire and post-wildfire salvage-logging on hydrology, biogeochemistry and aquatic ecology. Continuous monitoring (11 years) of streamflow, precipitation, water quality, sediment and primary productivity have demonstrated that the effects of the wildfire have been persistent (Silins *et al.* 2014; Wagner *et al.* 2014; Emelko *et al.* 2016; Silins *et al.* 2016). Given the persistence of effects on the physical factors that regulate aquatic ecology, benthic macroinvertebrates and fish were sampled in the fall of 2011 to determine if there were also persistent effects on aquatic biota and food web structure. The specific objectives of this research were to:

1) investigate if persistent wildfire effects on streamflow and water quality produced any lasting effects on the macroinvertebrate assemblage structure in burned and burned & salvage-logged watersheds (reported in Chapter 2);

2) evaluate potential wildfire effects on aquatic food web structure and the relative importance of instream and terrestrial energy resources to benthic macroinvertebrates and a salmonid fish, Cutthroat Trout (reported in Chapter 3).

Literature Cited

Alberta Agriculture and Forestry, 2019. Historical wildfire database - Alberta Wildfire Records.

Alberta Environment and Parks (2014) 'Alberta species at risk.' Available at http:// aep .alberta.ca/fish-wildlife/species-at-risk/documents/SpeciesAssessedConservation-2014a.pdf [Accessed 4-14-17].

Barbour MT, Snyder BD, Stribling JB, 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, D.C.

Beschta RL, Frissell CA, Gresswell RE, Hauer FR, Karr JR, Minshall GW, Perry DA, Rhodes JJ (1995) Wildfire and salvage logging: recommendations for ecologically sound post-fire salvage logging adn other post-fire treatments on Federal lands in the west., Oregon State University, Corvallis OR.

Bisson PA, Rieman BE, Luce C, Hessburg PF, Lee DC, Kershner JL, Reeves GH, Gresswell RE (2003) Fire and aquatic ecosystems of the western USA: current knowledge and key questions. *Forest Ecology and Management* **178**, 213-229.

Bixby R, Cooper S, Gresswell R, Brown L, Dahm C, Dwire K (2015) Fire effects on aquatic ecosystems: an assessment of the current state of the science. *Freshwater Science* **34**, 1340-1350.

Bjornn T, Brusven M, Molnau M, Milligan J, Klamt R, Cacho E, Schaye C (1977) Transport of granitic sediment in streams and its effects on insects and fish. *Idaho Forest Wildfire and Range Experiment Station Bulletin* **17**, 11-20.

Brittain J, Eikeland T (1988) Invertebrate drift - a review. *Hydrobiologia* **166**, 77-93.

Burles K, Boon S (2011) Snowmelt energy balance in a burned forest plot, Crowsnest Pass, Alberta, Canada. *Hydrological Processes* **25**, 3012-3029.

Cooper S, Page H, Wiseman S, Klose K, Bennett D, Even T, Sadro S, Nelson C, Dudley T (2015) Physicochemical and biological responses of streams to wildfire severity in riparian zones. *Freshwater Biology* **60**, 2600-2619.

Covich A, Palmer M, Crowl T (1999) The role of benthic invertebrate species in freshwater ecosystems - Zoobenthic species influence energy flows and nutrient cycling. *Bioscience* **49**, 119-127.

DeBano L (2000) The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology* **231**, 195-206.

Emelko MB, Silins U, Bladon K, Stone M (2011) Implications of land disturbance on drinking water treatability in a changing climate: Demonstrating the need for "source water supply and protection" strategies. *Water Research* **45**, 461-472.

Emelko MB, Stone M, Silins U, Allin D, Collins AL, Williams CHS, Martens AM, Bladon KD (2016) Sediment-phosphorus dynamics can shift aquatic ecology and cause downstream legacy effects after wildfire in large river systems. *Global Change Biology* **22**, 1168-1184.

Flannigan M, Logan K, Amiro B, Skinner W, Stocks B (2005) Future area burned in Canada. *Climatic Change* **72**, 1-16.

Gresswell R (1999) Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* **128**, 193-221.

Hauer FR, Stanford JA, Lorang MS (2007) Pattern and process in Northern Rocky Mountain headwaters: ecological linkages in the headwaters of the Crown of the Continent. *Journal of the American Water Resources Association* **43**, 104-117.

Houghton J (2001) The science of global warming. *Interdisciplinary Science Reviews* **26**, 247-257.

Hynes HBN (1975) The stream and its valley. *Proceedings of the International Association of Theoretical and Applied Limnology* **19**, 1-15.

Isaak DJ, Young M, Luce C, Hostetler S, Wenger S, Peterson E, Hoef J, Groce M, Horan D, Nagel D (2016) Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 4374-4379.

Isaak DJ, Luce CH, Rieman BE, Nagel DE, Peterson EE, Horan DL Parkes S, Chandler GL (2010) Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* **20**, 1350-1371.

Kelly E, Schindler D, St Louis V, Donald D, Vlaclicka K (2006) Forest fire increases mercury accumulation by fishes via food web restructuring and increased mercury inputs. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 19380-19385.

Koetsier P, Tuckett Q, White J (2007) Present effects of past wildfires on the diets of stream fish. *Western North American Naturalist* **67**, 429-438.

Kunze M, Stednick J (2006) Streamflow and suspended sediment yield following the 2000 Bobcat Fire, Colorado. *Hydrological Processes* **20**, 1661-1681.

Lindenmayer D, Foster D, Franklin J, Hunter M, Noss R, Schmiegelow F, Perry D (2004) Ecology - Salvage harvesting policies after natural disturbance. *Science* **303**, 1303-1303.

Malison RL, Baxter CV (2010) Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. *Journal of the North American Benthological Society* **29**, 1324-1338.

Martin D (2016) At the nexus of fire, water and society. *Philosophical Transactions of the Royal Society B-Biological Sciences* **371**,

Martin D, Moody J (2001) Comparison of soil infiltration rates in burned and unburned mountainous watersheds. *Hydrological Processes* **15**, 2893-2903.

Mihuc T, Minshall G (1995) Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. *Ecology* **76**, 2361-2372.

Mihuc TB, Minshall GW (2005) The trophic basis of reference and post-fire stream food webs 10 years after wildfire in Yellowstone National Park. *Aquatic Sciences* **67**, 541-548.

Minshall GW, Andrews DA, Brock JT, Robinson CT, Lawrence DE (1989) Changes in wild trout habitat following forest fire. In 'Wild Trout IV Symposium. Yellowstone National Park, Wyoming, USA', September 18-19, 1989.

Minshall GW, Brock JT, Andrews DA, Robinson CT (2001) Water quality, substratum and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek fire. *International Journal of Wildland Fire* **10**, 185-199.

Minshall GW, Andrews DA, Brock JT, Robinson CT, Lawrence DE (1989) changes in wild trout habitat following forest fire. In 'Wild Trout IV Symposium. Yellowstone National Park, Wyoming, USA', September 18-19, 1989.

Minshall GW, Robinson CT, Lawrence DE (1997) Postfire responses of lotic ecosystems in Yellowstone National Park, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2509-2525.

Moody J, Martin D (2001) Initial hydrologic and geomorphic response following a wildfire in the Colorado Front Range. *Earth Surface Processes and Landforms* **26**, 1049-1070.

Parks Canada (2018) 'Kenow Wildfire.' Available at https://www.pc.gc.ca/en/pn-np/ab/waterton/securite-safety/feu-fire-kenow [Accessed March 10, 2019].

Rieman B, Lee D, Chandler G, Meyers D, J Greenlee (Ed.) (1997) 'Does wildfire threaten extinction for salmonids? Responses of redband trout and bull trout following recent large fires on the Boise National Forest, Fire Effects on Rare and Endangered Species and Habitats Conference.' Coeur d'Alene, Idaho. (International Association of Wildland Fire)

Rinne JN (1996) Management briefs: short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *North American Journal of Fisheries Management* **16**, 653-658.

Rosenberger AE, Dunham JB, Buffington JM, Wipfli MS (2011) Persistent effects of wildfire and debris flows on the invertebrate prey base of rainbow trout in Idaho streams. *Northwest Science* **85**, 55-63.

Rounick JS, Winterbourn MJ, Lyon GL (1982) Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New-Zealand streams - A Stable Carbon Isotope Study. *Oikos* **39**, 191-198.

Rugenski AT, Minshall GW (2014) Climate-moderated responses to wildfire by macroinvertebrates and basal food resources in montane wilderness streams. *Ecosphere* **5**, 25.

Schoennagel T, Veblen T, Romme W (2004) The interaction of fire, fuels, and climate across rocky mountain forests. *Bioscience* **54**, 661-676.

Sear D, Jones J, Collins A, Hulin A, Burke N, Bateman S, Pattison I, Naden P (2016) Does fine sediment source as well as quantity affect salmonid embryo mortality and development? *Science of the Total Environment* **541**, 957-968.

Shakesby R, Doerr S (2006) Wildfire as a hydrological and geomorphological agent. *Earth-Science Reviews* **74**, 269-307.

Silins U, Anderson A, Bladon KD, Emelko MB, Stone M, Spencer SA, Williams CHS, Wagner MJ, Martens AM, Hawthorn K (2016) Southern Rockies Watershed Project. *Forestry Chronicle* **92**, 39-42.

Silins U, Bladon K, Kelly E, Esch E, Spence J, Stone M, Emelko M, Boon S, Wagner M, Williams C, Tichkowsky I (2014) Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. *Ecohydrology* **7**, 1508-1523.

Silins U, Stone M, Emelko MB, Bladon KD (2009) Sediment production following severe wildfire and post-fire salvage logging in the Rocky Mountain headwaters of the Oldman River Basin, Alberta. *Catena* **79**, 189-197.

Spencer C, Gabel K, Hauer F (2003) Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management* **178**, 141-153.

US Fish and Wildlife Service (2017) 'Environmental conservation online system.' Available at https://ecos.fws.gov/ecp0/pub/SpeciesReport.do?groups=E&listingType=L&mapstatus=1 [Accessed 4-14-17].

Vannote R, Minshall G, Cummins K, Sedell J, Cushing C (1980) River continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130-137.

Vieira N, Clements W, Guevara L, Jacobs B (2004) Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology* **49**, 1243-1259.

Voshell JR (2002) 'A Guide to Common Freshwater Invertebrates of North America.' (The McDonald and Woodward Publishing Company: Blacksburg, Virginia)

Wagenbrenner J, Robichaud P, Brown R (2016) Rill erosion in burned and salvage logged western montane forests: Effects of logging equipment type, traffic level, and slash treatment. *Journal of Hydrology* **541**, 889-901.

Wagner MJ, Bladon KD, Silins U, Williams CHS, Martens AM, Boon S, MacDonald RJ, Stone M, Emelko MB, Anderson A (2014) Catchment-scale stream temperature response to land disturbance by wildfire governed by surface-subsurface energy exchange and atmospheric controls. *Journal of Hydrology* **517**, 328-338.

Westerling A, Hidalgo H, Cayan D, Swetnam T (2006) Warming and earlier spring increase western US forest wildfire activity. *Science* **313**, 940-943.

Zah R, Burgherr, P Bernasconi S, Uehlinger U (2001) Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology* **46**, 871-882.

Chapter 2 Long-Term Impact of Severe Wildfire on Macroinvertebrate Assemblage Structure in Alberta's Rocky Mountains[1]

2.1 Introduction

Wildfire is an important natural disturbance that can strongly influence both physical and biological processes (Gresswell 1999; Moody and Martin 2001; Hauer *et al.* 2007). Since the 1980s, increases in wildfire frequency, severity, duration and season length in the western United States have been correlated with warming atmospheric temperatures (Schoennagel *et al.* 2004; Westerling *et al.* 2006). Between 1970 and 2003, 60% of the observed increases in wildfire activity occurred in the Rocky Mountains (Westerling *et al.* 2006). These ecosystems will be particularly susceptible to climate-change induced shifts in wildfire behavior and it is expected that by the end of the 21st century the annual area burned in Canada will increase by 74 to 118% compared to the latter half of the 20th century (1959-1997) (Flannigan *et al*. 2005). Such increases in area burned will have strong effects on both terrestrial and freshwater ecosystems (Romme *et al.* 2011).

Forested mountain watersheds provide critical habitat for many species, including macroinvertebrates and salmonid fish (Hauer *et al*. 2007; Isaak *et al*. 2016). These streams typically have higher water quality than lowland streams (Hauer *et al*. 2007), and are highly sensitive to the changes in vegetation and soils caused by wildfire (Hynes 1975; Hauer *et al.* 2016). Wildfire alters rainfall-runoff dynamics which can change sediment and nutrient regimes,

[1] A portion of this chapter has been published as A.M. Martens, U. Silins, H.C. Proctor, C.H.S. Williams, M.J. Wager, M.B. Emelko, and M. Stone, "Long-term impact of severe wildfire and post-wildfire salvage logging on macroinvertebrate assemblage structure in Alberta's Rocky Mountains," *International Journal of Wildland Fire.* doi 10.1071/WF18177

channel morphology and water temperature (Gresswell 1999). Elevated sediment loading, export of nutrients (nitrogen, phosphorous and dissolved organic carbon), export of heavy metals (e.g., mercury and methyl mercury) and stream temperature are commonly reported after wildfire in mountain watersheds (Hauer and Spencer 1998; Kelly *et al.* 2006; Shakesby and Doerr 2006; Writer *et al.* 2012; Wagner *et al.* 2014). Increased nutrients stimulate microbial activity and autochthonous primary productivity (Spencer et al. 2003; Mihuc and Minshall 2005) while the influx of fine sediment can impact the availability and quality of instream habitat and food resources (Bjornn *et al.* 1977; Jones *et al.* 2012). Macroinvertebrate assemblages invariably respond to water-quality changes associated with wildfire (Barbour *et al.* 1999; Minshall 2003). Assemblage composition often shifts to favor disturbance-adapted taxa, while more sensitive taxa can decline in abundance or be excluded entirely (Mihuc *et al.* 1996; Minshall *et al.* 2001a; Minshall *et al.* 2001b; Malison and Baxter 2010b). Changes in biomass and density are less predictable but are often related to factors such as primary productivity, water chemistry and the occurrence of drought or flooding in the months or years following wildfire (Verkaik *et al.* 2015). Rinne (1996) documented large declines (70-90%) in invertebrate density following high flow events with heavy sediment loads after a wildfire in Arizona. In contrast, Malison & Baxter (2010b) reported greater invertebrate productivity in severely burned reaches following the Diamond Peak wildfire in Idaho and associated this with increases in food resources. The extent of wildfire effects on macroinvertebrate assemblages depends on fire severity, local watershed characteristics including hydro-climatic setting, vegetation type, topography, soils and geology as well as the influences of climate change including warming and changes in precipitation patterns (Moody and Martin 2001; Shakesby and Doerr 2006; Rugenski and Minshall 2014).

Macroinvertebrates are an important component of Rocky Mountain stream ecosystems. They contribute to nutrient cycling and provide a critical food source for fish and riparian insectivores (Mihuc *et al.* 1996; Rinne 1996; Minshall 2003; Malison and Baxter 2010a). Despite their importance in the trophic structure of stream ecosystems, little is known about the long-term effects of wildfire on macroinvertebrate assemblages. Previous post-fire invertebrate studies report on shorter-term (1-5 year) impacts (Rinne 1996; Minshall *et al.* 1997; Spencer *et al.* 2003; Malison and Baxter 2010a; Malison and Baxter 2010b). However, fire can produce longer-term changes in the physical stream environment and water-quality conditions regulating stream ecology (Silins *et al.* 2014; Emelko *et al.* 2016). While several studies in the United States have reported wildfire impacts on macroinvertebrate assemblages lasting as long as 5-10 years (Minshall *et al.* 1989; Roby 1989; Mihuc *et al.* 1996; Vieira *et al.* 2004; Malison and Baxter 2010b), both the longevity of fire effects on macroinvertebrates and factors regulating longer-term patterns of ecosystem recovery are presently not well understood across more northern mountain environments (Bixby *et al*. 2015).

The Lost Creek wildfire was one of the more severe fires in recent decades on the eastern slopes of Alberta's Rocky Mountains and provided an opportunity to assess the long-term impacts of wildfire on northern Rocky Mountain watersheds. The Southern Rockies Watershed Project (SRWP) was established to document the effects of the wildfire and post-wildfire salvage-logging on hydrology, biochemistry and aquatic ecology (Silins *et al.* 2016). Eleven years of continuous monitoring have demonstrated that wildfire effects on water quality and biogeochemistry are persistent in the study watersheds, with many parameters including sediment production, nutrient (phosphorous and dissolved organic carbon) export and primary productivity showing no signs of recovery over a decade post-wildfire (Silins *et al.* 2009;

Emelko *et al*. 2011; Silins *et al.* 2014; Wagner *et al.* 2014; Emelko *et al.* 2016; Silins *et al.* 2016). Given these persistent impacts on hydrology and water quality, disturbance-associated effects on macroinvertebrate abundance and assemblage structure between reference and wildfire-affected watersheds were also expected. Greater abundance was expected in the more productive wildfire affected watersheds, and greater diversity was expected in the unburned systems. The objectives of this study were to:

1) quantify differences in macroinvertebrate abundance and assemblage structure in three disturbance categories, reference (unburned), burned and burned & salvage-logged;
2) determine the environmental parameters (water quality, streamflow and periphyton productivity) that best explain variation in macroinvertebrate assemblage structure;
3) analyze the variation in ecological traits of more abundant taxa along a disturbance gradient (reference, burned and burned & salvage-logged) to establish mechanisms governing response of macroinvertebrate assemblages after wildfire.

2.2 Methods

2.2.1 Site Description

The Lost Creek wildfire burned 211.6 km^2 in the forested region of the Crowsnest and Castle River watersheds in southern Alberta, Canada from July to September 2003. Seven research watersheds were established including three burned watersheds (South York, Lynx and Drum Creek) and two reference (unburned) watersheds (Star and North York Creek) (Table 2.1, Figure 2.1). Two watersheds (Lyons East and Lyons West Creek) were salvage-logged and instrumented in 2005. Clear-cut salvage harvest occurred over the winters of 2004 and 2005; 2.6

km^2 and 2.4 km^2 (19.9% and 33.6% of the watershed area) were harvested in Lyons East and Lyons West respectively (Table 2.1, Figure 2.1). Although the wildfire burned between 53.2% and 100% of the study watersheds (Table 2.1), effectively all of the forest cover and forest floor organic material were consumed. Unburned regions of the watersheds consisted of treeless rocky alpine zones with little available fuel.

The hydrologic regime of these watersheds is snowmelt dominated. The highest flows occur in late May to early June during the peak of spring snowmelt. Mean annual precipitation in the reference, burned and burned & salvage-logged watersheds was 1087 mm (898-1398 mm), 1146 mm (950-1431 mm), and 775 mm (582-971 mm), respectively (2004-2014). Mean annual, area-weighted discharge in the reference, burned and burned & salvage-logged watersheds over the same period was 744 mm (483-1080 mm), 871 mm (571-1091 mm), and 592 mm (373-887 mm) respectively. Forest cover prior to the fire was predominantly lodgepole pine (*Pinus contorta* var. *latifolia*) at lower elevations, Englemann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) at mid elevations, and alpine meadow vegetation and bare rock at higher elevations characteristic of upper alpine ecozones. While no pre-disturbance hydrologic, water quality, or aquatic ecological data existed in the study area (as is typical for most wildfire studies) modest replication (2-3) of undisturbed (reference) and disturbed (burned and burned & salvage-logged) watersheds with similar physical and environmental characteristics have been previously used to support broader inferences on wildfire and salvage-logging impacts (Spencer *et al.* 2003; Reid *et al.* 2010). This assumes that disturbed watersheds would behave similarly to reference watersheds had the disturbance not occurred.

2.2.2 Environmental Parameters

All parameters used in this analysis were calculated from data collected eight years after the wildfire, during the ice-free period from April to October 2011 (Table 2.2). Water samples were collected every two weeks and analyzed according to Standard Methods (Rice 2012; US Environmental Protection Agency (EPA) 2012) for ammonium (NH_4^+), nitrate + nitrite (NO_3^- + NO_2^-), soluble reactive phosphorous (SRP), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), alkalinity (as $CaCO_3$), total suspended solids (TSS) and total dissolved solids (TDS). Total inorganic nitrogen (TIN) was determined by calculating the sum of ammonium, nitrate and nitrite.

Stream discharge ($m^3\ s^{-1}$) was measured every two weeks using a Sontek acoustic Doppler velocity meter (Flow Tracker ADV, Sontek/YSI, San Diego, CA, USA). Stage was recorded every 10 minutes using HOBO water level loggers suspended in PVC stilling wells (U20-001-04; Onset Computer Corporation, Bourne, MA, USA) or with a dry gas bubbler and pressure transducer (Waterlog Model H-350 Lite and H-355, Design Analysis Associates Inc., Logan, UT, USA) connected to a measurement and control data logger (CR1000, Campbell Scientific, Logan, UT, USA). Discharge and manual stage measurements were used to develop rating curves for each stream and calculate continuous discharge. Stream temperature was recorded either every 60 minutes using HOBO temperature data loggers or every 10 minutes using HOBO temperature and water level loggers (H08-001-02 or U20-001-04; Onset Computer Corporation, Bourne, MA, USA).

Periphyton samples were collected using three replicate unglazed ceramic tiles (155 cm^2) anchored to the streambed in the study reaches of all seven watersheds in late April/early May after ice-out. Tiles were scrubbed clean in running stream water prior to deployment and periphyton was allowed to colonize naturally. Samples were collected monthly (June to October) by scraping and rinsing periphyton from the tile surface into acid-washed (10% HCl) HDPE Nalgene sample bottles. Samples were frozen prior to determination of ash-free dry mass (AFDM; Aloi, 1990).

Riparian canopy cover was measured as a proxy indicator of variation in reach-scale allochthonous (terrestrial primary productivity) loading among study watersheds. Riparian canopy cover was quantified by taking hemispherical photographs using a Nikon Coolpix 4500 camera with a Nikon FC-E8 0.21x Fisheye Converter (Nikon Inc., Melville, NY, USA). Nine photos were taken along each 100 m invertebrate sampling transect on the left and right stream banks and in the center of the stream at 0 m, 50 m and 100 m. Percent canopy openness was determined using Gap Light Analyzer (version 2.0) imaging software (Frazer *et al.,* 1999).

2.2.3 Macroinvertebrate Sampling

Macroinvertebrate sampling was conducted at the end of the growing season in October 2011. A Surber sampler (500 µm mesh; 0.096 m^2) was used to collect invertebrates from eight randomly chosen riffle sections along a 100 m transect upstream of each hydrometric gauging station. The sampler was placed on the streambed facing upstream. Large rocks within the sampling area were rubbed clean and removed, then the bed material was vigorously disturbed for 2 minutes. Sampler contents were placed in a white plastic basin and large debris (e.g., whole leaves, twigs and rocks) were rinsed and removed. Macroinvertebrates, associated plant material and detritus were transferred to HDPE Nalgene sample bottles and preserved in 95% ethanol. The 500 µm mesh of the Surber sampler permitted the collection of larger bodied water mites and later insect instars. Macroinvertebrates were sorted, enumerated and identified to the lowest practical taxonomic unit (usually family) using a dissecting microscope and the following keys (Clifford 1991; Thorp and Covich 2009). Identification of freshwater macroinvertebrates to the level of family has been shown to be sufficient for multivariate analyses comparing assemblage structure between disturbed and undisturbed systems (Bowman and Bailey 1997; Bailey *et al.* 2001).

Roundworms (Nematoda) and the water mite family Feltriidae were excluded from the analysis as the large mesh size (500 µm) prevented consistent collection of a representative sample. Specimens that could not be identified to class were also excluded. Individuals from the stonefly families Capniidae and Leuctriidae were too young to be distinguished from each other and were grouped for this analysis as Capniidae+Leuctridae. Excluded specimens represented 2.61% of the total specimens collected.

Parameters describing community composition (taxonomic richness, diversity and evenness) were calculated using formulae from Morris *et al.* (2014). Taxonomic richness (*S*) is the total number of taxa observed in each watershed (Equation 2.1). Diversity (*D*) was calculated using Simpsons Index of Diversity where p_i is the proportion of individuals of taxon *i* (Equation 2.2). Evenness (*E*) was calculated using Simpson's Evenness (Equation 2.3).

$$S = number\ of\ unique\ taxa \tag{2.1}$$

$$D = 1 - \sum p_1^2 \tag{2.2}$$

$$E = {}^{D}/_{S} \tag{2.3}$$

2.2.4 Statistical Analysis

Statistical analyses were conducted using R (R Core Team, 2018). Community ordination and analysis were conducted using the vegan package (Oksanen *et al.*, 2019). One-way analysis of variance (ANOVA) was used to test for an effect of disturbance category on univariate environmental predictors (streamflow, temperature, water chemistry, canopy openness and primary productivity). Parameters that did not meet the assumptions of parametric tests (normal distribution and equal variance) were either log transformed or analyzed using a non-parametric Kruskal-Wallis rank sum test. Post-hoc comparisons between treatments were conducted following one-way ANOVA using Tukey's honest significant difference (Tukey's HSD) test or following Kruskal-Wallis rank sum test with Fisher's least significant difference test. Permutational multivariate analysis of group dispersions (PERMDISP2) was used to test for multivariate homogeneity of group dispersions. Tukey's HSD test was used to conduct post-hoc pairwise comparisons of dispersion between treatments. A multivariate analysis of variance (mANOVA) was conducted on the Bray-Curtis dissimilarity matrix to test for significant differences in taxonomic composition between watersheds and treatments.

Non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity matrices was used to visualize the variability of invertebrate taxa in multidimensional space and evaluate the similarity of invertebrate assemblages among watersheds within disturbance categories. NMDS ordinations were conducted using both raw counts and log(x+1) transformed data. Since invertebrate abundance was considerably higher in the burned watersheds, ordinations using counts were heavily influenced by burned watersheds. To reduce this effect, ordinations were also conducted using relative abundances instead of counts to compute the dissimilarity matrix.

Redundancy analysis (RDA) was used to determine the strongest environmental correlates of macroinvertebrate assemblage structure among disturbance categories. Environmental variables used in the RDA are summarized in Table 2. Detrended correspondence analysis (DCA) indicated RDA was the appropriate model, as axis lengths were less than 3 standard deviations (between 1.75 and 2.34) (Borcard *et al.* 2011). Variables with high multicollinearity (variance inflation factor > 10) were removed prior to the selection of the most important environmental parameters using a forward stepwise selection procedure (ordiR2step). A Hellinger transformation was applied to the species counts and environmental parameters were standardized to mean zero and unit variance prior to fitting the RDA model (Legendre and Gallagher 2001).

2.3 Results

2.3.1 Environmental Parameters

Stream discharge in 2011 was similar between reference, burned and burned & salvage-logged (Q_{daily} = 0.36 m^3 s^{-1} ± 0.02, 0.30 m^3 s^{-1} ± 0.02 and 0.35 m^3 s^{-1} ± 0.03, respectively; χ^2 = 7.8498, P = 0.0197). The annual flow regime (range of flows) varied more between treatments than did mean discharge (Figure 2.2). Reference watersheds were the least variable, with the least pronounced snowmelt and stormflow peaks and the lowest peak discharge (2.03 m^3 s^{-1}). The burned watersheds were intermediate with a peak discharge of 2.11 m^3 s^{-1}. Burned & salvage-logged watersheds were the most variable with steeper snowmelt and stormflow limbs and the highest peak discharge (5.18 m^3 s^{-1}). Mean daily stream temperature was significantly different between treatments (χ^2 = 38.492, P < 0.001). Stream temperature was highest and most variable in the burned & salvage-logged watersheds (6.51°C ± 0.24 compared to 4.64°C ± 0.11 and 3.58°C ± 0.11 in the reference and burned watersheds, respectively; Figure 2.3).

Periphyton productivity (AFDM) varied throughout the growing season in all watersheds (Figure 2.4), mean seasonal AFDM was lowest in the reference watersheds and greatest in the burned and burned & salvage-logged watersheds (0.09 mg cm^{-2} ± 0.03, 0.21 mg cm^{-2} ± 0.05 and 0.28 mg cm^{-2} ± 0.07 in the reference, burned and burned & salvage-logged watersheds, respectively). AFDM was significantly lower in the reference streams compared to the burned and burned & salvage-logged watersheds ($F_{1,61} = 7.504$, $P < 0.01$).

Water chemistry values are summarized in Table 2.2. Total inorganic nitrogen (TIN), total dissolved solids (TDS), dissolved inorganic carbon (DIC), and alkalinity were greatest in the reference and lowest in the burned & salvage-logged watersheds, showing a generally monotonic pattern across disturbance categories. In contrast, soluble reactive phosphorus (SRP), total suspended sediment (TSS) and dissolved organic carbon (DOC) were greatest in the burned & salvage-logged watersheds following a pattern of burned & salvage-logged > burned > reference.

Variation in canopy openness reflected smaller stream reach-scale variation in both riparian canopy density prior to the fire and crown consumption among burned stream reaches. Canopy openness was lowest and relatively homogeneous in the reference watersheds (26.77 % ± 0.94) whereas the burned and burned & salvage-logged study reaches had higher and more variable percent canopy openness (42.67 % ± 3.65 and 42.31 % ± 4.05 respectively). The greater variability in the burned and burned & salvage-logged watersheds was due to portions of the riparian area associated with the specific sampling transects remaining unburned due to fire skips. This pattern was particularly evident in study reaches in the Drum and South York (burned) and Lyons West (burned & salvage-logged) watersheds.

2.3.2 Macroinvertebrate Assemblage Structure

A total of 21409 individuals from 29 taxonomic groups were identified, enumerated and included in this analysis (Table 2.3; 2.4). Insects (Ephemeroptera, Plecoptera, Trichoptera, Diptera and Coleoptera) made up the majority of the macroinvertebrate assemblages (94.0%, 94.3% and 97.7% in the reference, burned and burned & salvage-logged watersheds respectively). Flatworms (Platyhelminthes: Turbellaria), aquatic mites (Acariformes: Prostigmata: Parasitengonina: Hydrachnidiae), and ostracods (Crustacea) comprised the remainder of the assemblages.

Macroinvertebrates were most abundant in burned streams with a mean density of 5959.6 ± 577.1 individuals m^2 (Figure 2.5). Abundance was similar between reference and burned & salvage-logged streams with densities of 2529.5 ± 405.5 and 2731.1 ± 421.5 individuals m^2 respectively. Taxonomic richness (S) was similar across watersheds (S = 25.0 ± 3.0, 26 ± 0.0 and 23.5 ± 0.5 in the reference, burned and burned & salvage-logged watersheds respectively). All taxa sampled were represented at least once in each of the reference, burned and burned & salvage-logged watersheds with the exception of two aquatic mite families. The family Hygrobatidae was absent from the burned & salvage-logged watersheds and the family Torrenticolidae was absent from the reference and burned watersheds; both families were relatively rare across watersheds accounting for 0.03% and 0.02% of the total individuals sampled respectively. Diversity (D) and evenness (E) were moderately higher in reference watersheds and similar across the wildfire affected watersheds (D = 0.85 ± 0.01, 0.80 ± 0.05 and 0.79 ± 0.01 and E = 0.28 ± 0.06, 0.22 ± 0.05 and 0.21 ± 0.01 in the reference, burned and burned & salvage-logged watersheds respectively). Counts and relative abundances of all taxonomic groups are summarized by disturbance category in Tables 2.3 and 2.4.

Reference watersheds were characterized by high relative abundances of stoneflies (Plecoptera) (41.9% compared to 13.1% and 24.2% in the burned and burned & salvage-logged watersheds respectively). In particular the relative abundance of Capniidae+Leuctridae was high (4.15% compared to 0.72% and 0.47% in the burned and burned & salvage-logged watersheds).

Burned watersheds showed high relative abundances of both true flies (Diptera) and mayflies (Ephemeroptera) (22.0% and 45.1% compared to 11.8% and 31.5%, and 11.1% and 29.44% in the reference and burned & salvage-logged watersheds respectively). In particular the true fly families Chironomidae and Psychodidae and the mayfly family Baetidae were abundant in burned watersheds. The burned & salvage-logged watersheds were characterized by particularly high abundances of riffle beetles (Coleoptera: Elmidae) (28.63% compared to 0.76% and 4.01% in the reference and burned watersheds, respectively) as well as crane flies (Diptera: Tipulidae) (1.59% compared to 0.13% and 0.30% in the reference and burned watersheds, respectively). The burned & salvage-logged watersheds had particularly low numbers of flatworms; only 2 individuals were collected representing 0.05% of the macroinvertebrate assemblage compared to 1.84% and 3.56% in the reference and burned watersheds respectively.

2.3.3 Multivariate Analysis of Macroinvertebrate Assemblage Structure

Invertebrate assemblages formed distinct groups according to watershed and disturbance category in NMDS ordinations (Figure 2.6). Multivariate ANOVA of the Bray-Curtis dissimilarity matrices confirmed significant differences in assemblage structure between watersheds ($F = 7.845$, $P < 0.01$) and treatments ($F = 11.403$, $P < 0.01$). The test of homogeneity of multivariate dispersions (PERMDIPS2) indicated that beta diversity was homogeneous between disturbance category (N.perm = 999, $F = 2.821$, $P = 0.07$). This was confirmed using Tukey's HSD test ($P > 0.12$).

Several taxonomic groups were strongly associated ($P < 0.01$) with study watersheds across disturbance categories (Figure 2.7). Heptageniidae (HEPTA) and Capniidae+Leuctridae (CA_LE) were strongly associated with reference watersheds. Burned watersheds were positively associated with the families Baetidae (BAET), Psychodidae (PSYCH) and

Chironomidae (CHIRO) while Tipulidae (TIPUL) and Elmidae (ELMI) were strongly associated with burned & salvage-logged sites. Several taxa were also associated with watersheds in two disturbance categories including Peltoperlidae (PELTO), Brachycentridae (BRAC) and Turbellaria (TURB) associated with both reference and burned watersheds and Chloroperlidae (CHLOR) which was characteristic of both reference and burned & salvage-logged watersheds.

The RDA model explained 34.4% of the variance in invertebrate assemblage structure ($P < 0.01$, Figure 2.8). The first two RDA axes explained 20.3% and 7.8% of the variation respectively. The variables selected by the model in decreasing order of strength were: dissolved organic carbon (DOC), stream discharge (Q), periphyton productivity (AFDM), and total dissolved solids (TDS). Reference reaches were characterized by higher discharge and lower periphyton productivity. The burned watersheds were highly variable; Drum had particularly high TDS, South York was characterized by low discharge and DOC and Lynx was more similar to the reference sites having high discharge and low DOC. Burned & salvage-logged sites were characterized by high DOC and elevated periphyton productivity. Environmental predictors are summarized in Table 2.2.

2.4 Discussion

Persistent wildfire effects on macroinvertebrate assemblages were observed in burned and burned & salvage-logged watersheds eight years after the Lost Creek wildfire (Figure 2.6). This observation is consistent with the slow post-wildfire recovery of biogeochemical and biological factors (including increased sediment, phosphorus and carbon export and increased primary productivity) observed in these wildfire affected watersheds (Emelko *et al.* 2016; Silins *et al.* 2016). Previous reports on duration of wildfire impacts to water quality and stream biology have focused on shorter timescales (2-3 years) than those described here (Moody and Martin

2001; Robson *et al.* 2018). Results of the present study demonstrate that the effects of both wildfire and post-fire salvage-logging on macroinvertebrate assemblages (these latter effects have not been previously described) can be long lasting (Figure 2.7) and these effects are strongly associated with the persistence of fire effects on the chemical and biological stream environments. In particular, dissolved organic carbon (DOC), total dissolved solids (TDS), stream discharge (Q), and periphyton productivity (AFDM) were closely associated with variation in invertebrate assemblage structure among disturbance categories. DOC and AFDM continue to be influenced by wildfire related changes to runoff and water quality (Emelko *et al.* 2016; Silins *et al.* 2016), whereas stream discharge and total dissolved solids are governed by watershed characteristics (precipitation regime, groundwater contribution and surficial geology) unrelated to the wildfire. It is important to recognize that multiple stream water quality and physical variables after wildfire were strongly correlated, thus while redundancy analysis identified DOC and AFDM as the dominant fire associated variables, sediment, phosphorus, carbon, and periphyton productivity are all likely key drivers regulating the persistence of wildfire effects. The glacial history of these research watersheds contributes to long lasting wildfire effects compared to mountain ecosystems in the western United States (e.g., Yellowstone National Park - Minshall *et al.*1997) due to presence of highly erodible glacial-fluvial deposits that provide a source of bioavailable phosphorus (Emelko *et al.* 2016).

The differences in ecological response (Figure 2.6) of the macroinvertebrate assemblages in the burned and burned & salvage-logged watersheds were unexpected (Table 2.2). Sediment export, phosphorous and dissolved organic carbon concentrations (biogeochemical) and periphyton productivity (biological) consistently follow the pattern burned & salvage-logged > burned > reference. Accordingly, it would be expected that the response of macroinvertebrate assemblages in burned and burned & salvage-logged watersheds would follow the same pattern. Notably, macroinvertebrate abundance was 2x greater in burned watersheds while abundance in burned & salvage-logged watersheds did not differ significantly from reference assemblages (Figure 2.5). Ordination of macroinvertebrate taxa also demonstrated differences in assemblage structure between burned and burned & salvage-logged watersheds. Chironomidae and Baetidae were dominant in burned watersheds while Tipulidae and Elmidae were indicative of burned & salvage-logged systems (Table 2.4; Figure 2.7). The unique assemblage structure and macroinvertebrate abundance between disturbance categories suggest that different mechanisms are driving the ecological response in wildfire affected watersheds.

Wildfire can affect macroinvertebrate assemblages through two main biophysical mechanisms. The first is a resource limitation mechanism in which macroinvertebrates respond to changes in the availability (quantity and quality) of both allochthonous (terrestrial) and autochthonous (instream) food resources (Minshall *et al.* 1989; Spencer *et al.* 2003; Mihuc and Minshall 2005). The River Continuum Concept (Vannote *et al.* 1980) predicts that food webs in undisturbed forested headwater streams will be supported primarily by allochthonous sources of energy as low nutrient concentrations and shading from the riparian canopy prevent significant instream primary productivity. Unburned research watersheds consistently fit this pattern with low primary productivity compared to nearby disturbed, both burned (Emelko *et al.* 2016) and harvested (Hawthorn 2014) watersheds. The second mechanism is related to physical habitat limitations, where increases in runoff, erosion, sediment and nutrient loading alter both habitat availability and suitability (Hauer and Spencer 1998; Shakesby and Doerr 2006). Considering the reference and burned disturbance categories, both periphyton productivity and macroinvertebrate abundance were greater in the burned watersheds suggesting that resource availability was likely the primary mechanism regulating macroinvertebrate assemblage response. However, the burned & salvage-logged watersheds (influenced by two consecutive disturbances) consistently showed disturbance metrics (suspended sediment, DOC, phosphorous and periphyton productivity) higher than watersheds affected by the wildfire only (Table 2.2). The unique invertebrate assemblage structure in the burned & salvage-logged watersheds, and the pattern of high primary productivity but low macroinvertebrate abundance suggests that habitat quality limitations, not resource availability, were the dominant driver of the ecological response in these systems. The increased sediment loading and more variable flow regime in the burned & salvage-logged watersheds likely reduced habitat quality to the point that few taxa were able to take advantage of the increased productivity. These observations are consistent with a previous study that reported differential effects of wildfire on invertebrate assemblages in low and high severity burns (Malison and Baxter 2010b), these differences were not interpreted in the context of broader ecological limitations proposed here.

The macroinvertebrate assemblage of the reference watersheds was consistent with streams with the high water quality and a more stable flow regime. Taxa known to be sensitive to environmental perturbation including stoneflies (Plecoptera) and flatheaded mayflies (Ephemeroptera: Heptageniidae) (Barbour *et al.* 1999; Voshell 2002) were relatively abundant in the reference watersheds (Table 2.4; Figure 2.7). Stoneflies are particularly sensitive to sedimentation and excess periphyton (Zwick 1992; Barbour *et al.* 1999; Voshell 2002). Diversity and evenness were moderately higher in reference watersheds, likely due to greater stability of the flow regime and high-quality habitat compared to burned and burned & salvage-logged watersheds.

Macroinvertebrate assemblages in the burned watersheds included greater abundance of disturbance-adapted taxa as well as taxa adapted to capitalize on increased food availability. Invertebrate families in burned watersheds included the true flies Chironomidae and Psychodidae and the mayfly family Baetidae (Figure 2.7). Many species within Chironomidae and Baetidae are widely considered to be disturbance-adapted taxa and increase in abundance following wildfire as they have short generation times and can reproduce quickly (Richards and Minshall 1992; Malison and Baxter 2010b). The family Baetidae contains several genera specialized for consuming periphyton (Minshall *et al.* 2001b); their high abundance suggests that individuals were able to capitalize on increased periphyton productivity in the burned watersheds. The abundance of a given taxon will be greatest in the area that provides the most suitable habitat (Brittain and Eikeland 1988); the wildfire alone did not compromise habitat quality to the point that invertebrate taxa were unable to take advantage of the excess periphyton resources.

In contrast, it appears that salvage-logging deteriorated water quality and stream habitat to a greater extent than in watersheds impacted by the fire alone, preventing invertebrates from utilizing the additional periphyton productivity. Streamflow (Q) was very responsive to rainfall and snowmelt events resulting in higher peak streamflows than in reference watersheds (Figure 2.2). Suspended sediment and turbidity were consistently higher during these periods of high flows and considerable amounts of fine sediment were deposited on and intruded into gravel interstices in the streambed. The reduced invertebrate abundance observed in these watersheds is consistent with the observations of Wood & Armitage (1997) and Bjornn *et al*. (1977), who showed that increased fine sediment reduced invertebrate density and abundance. While sediment is an important natural component of stream ecosystems, excess fine sediment can fill pore spaces and reduce oxygen availability in gravel bed streams, compromising habitat and food resources and altering macroinvertebrate behavior including foraging, respiration and drift (Bjornn *et al.* 1977; Brittain and Eikeland 1988; Wood and Armitage 1997; Jones *et al.* 2012). Crane flies (Diptera: Tipulidae) and riffle beetles (Coleoptera: Elmidae) were strongly associated with burned & salvage-logged watersheds (Figure 2.7). Crane flies have a burrowing lifestyle and are well adapted to high sediment environments (Giller and Malmqvist 1998; Voshell 2002). As well riffle beetle larvae can grip substrate during high flows and protect themselves from sediment abrasion by withdrawing their gills (Bjornn *et al.* 1977; Brown 1987; Voshell 2002; Yee and Kehl 2015). Fine sediment deposition likely contributed to the low abundance of caddisflies (Trichoptera) as some taxa require clean substrate to attach their cases and retreats (Bjornn *et al.* 1977; Voshell 2002). The low abundance of baetid mayflies in the burned & salvage-logged watersheds is further evidence of the habitat limitation mechanism overriding the resource mechanism. Many genera of Baetidae are disturbance-adapted scrapers (consume periphyton) and do well in post-fire environments with high periphyton productivity (Vieira *et al.* 2004; Malison and Baxter 2010b). High suspended sediment loads however can be detrimental as many genera are also clingers (Bjornn *et al.* 1977), impact from moving sediment dislodges individuals from rocks, causing injury and reducing abundance (Naman *et al.* 2016).

2.5 Conclusion

The clear differences in macroinvertebrate assemblage structure between reference, burned and burned & salvage-logged watersheds eight years after the Lost Creek wildfire indicate that the effects of wildfire on aquatic communities in this northern Rocky Mountain ecosystem are persistent. However, despite clear differences in the relative abundance of taxa between disturbance categories, taxonomic richness and diversity did not vary strongly. Only 2 of 29 taxa were missing from one or more disturbance categories, both these families

(Hygrobatidae and Torrenticolidae) were locally rare across disturbance categories. It is clear that despite the legacy effects observed in this study, fire-affected watersheds still support sensitive taxa and functional macroinvertebrate assemblages eight years after severe wildfire. Nevertheless, care should be used when making post-wildfire management decisions related to salvage-logging. Burned & salvage-logged watersheds had poorer water quality and higher sediment loads than burned watersheds, best practices should be followed to minimize sediment inputs to sensitive watersheds (Wagenbrenner *et al.* 2016). As macroinvertebrates provide the primary energy sources for salmonids (Rinne 1996; Malison and Baxter 2010b), ensuring healthy assemblage structure is vital on Alberta's eastern slopes. These watersheds provide critical habitat for Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*) and Bull Trout (*Salvelinus confluentus*), both currently listed as threatened or endangered in North America (Alberta Environment and Parks 2014; US Fish and Wildlife Service 2017).

Tables and Figures

Table 2.1 Characteristics of Southern Rockies Watershed Project research watersheds.

Watershed	Watershed Area (km^2)	Area Burned (km^2)	Area Salvage-Logged (km^2)	Elevation (m)	Slope (%)	Aspect
Reference (Unburned)						
Star	10.59	0 (0%)	0	1479-2627	45	North East
North York	8.29	0.02 (0.2%)	0	1562-2633	48.8	North East
Burned						
South York	3.59	1.91 (53.2%)	0	1691-2635	42.1	North East
Lynx	8.21	5.53 (67.4%)	0	1632-2629	43.3	North East
Drum	7.13	7.12 (99.9%)	0	1432-2156	47.5	North East
Burned & Salvage-logged						
Lyons East	13.15	10.72 (81.5%)	2.62	1441-2027	31.8	North
Lyons West	7.07	4.13 (58.4%)	2.38	1449-2059	24.8	North East

Table 2.2 Environmental predictors (mean ± standard error) included in the redundancy analysis (RDA).

Watershed	Stream Discharge	Stream Temperature	Periphyton Productivity	Alkalinity (as CaCO3)	Dissolved Organic Carbon	Dissolved Inorganic Carbon	Soluble Reactive Phosphorous	Total Dissolved Solids	Total Inorganic Nitrogen	Total Suspended Solids
	Q ($m^3 s^{-1}$)	AVDT (°C)	AFDM (mg cm^{-2})	ALK (mg L^{-1})	DOC (mg L^{-1})	DIC (mg L^{-1})	SRP (µg L^{-1})	TDS (mg L^{-1})	TIN (µg L-1)	TSS (mg L-1)
Reference (Unburned)										
Star	0.32 ± 0.02	4.00 ± 0.17	0.06 ± 0.02	158.13 ± 4.67	1.89 ± 0.58	34.53 ± 1.35	2.58 ± 0.24	173.13 ± 7.02	118.39 ± 6.42	0.83 ± 0.46
North York	0.40 ± 0.03	3.15 ± 0.13	0.12 ± 0.06	120.84 ± 4.19	1.07 ± 0.17	26.67 ± 1.10	2.42 ± 0.19	133.48 ± 5.29	100.42 ± 7.96	0.47 ± 0.12
Burned										
South York	0.18 ± 0.01	4.04 ± 0.21	0.19 ± 0.08	108.67 ± 4.81	1.68 ± 0.28	24.19 ± 1.41	2.67 ± 0.33	116.08 ± 7.37	77.63 ± 17.56	5.63 ± 2.83
Lynx	0.51 ± 0.05	4.39 ± 0.19	0.24 ± 0.13	127.64 ± 3.46	1.65 ± 0.32	29.17 ± 0.85	2.63 ± 0.25	135.63 ± 4.85	105.75 ± 11.67	1.24 ± 0.35
Drum	0.20 ± 0.02	5.49 ± 0.14	0.18 ± 0.05	148.67 ± 10.35	2.03 ± 0.41	32.20 ± 2.64	5.08 ± 0.56	165.5 ± 9.89	87.25 ± 16.74	4.27 ± 2.01
Burned & Salvage-logged										
Lyons East	0.41 ± 0.06	7.11 ± 0.36	0.40 ± 0.13	100.16 ± 12.12	3.69 ± 0.56	22.26 ± 2.78	8.42 ± 0.91	124.00 ± 10.32	24.83 ± 9.79	8.49 ± 4.74
Lyons West	0.30 ± 0.02	5.90 ± 0.31	0.17 ± 0.06	104.46 ± 10.33	3.61 ± 0.68	23.26 ± 2.34	6.25 ± 0.68	127.58 ± 8.89	26.54 ± 8.90	12.08 ± 6.07

Table 2.3 Macroinvertebrate counts and relative abundances by class and order (relative abundance shown in brackets).

Taxon	Reference	Burned	Burned & Salvage-logged	Total
Class: Insecta	3575 (94%)	12763 (94.33%)	3982 (97.69%)	20320 (94.91%)
Order: Diptera	447 (11.75%)	2972 (21.67%)	452 (11.09%)	3871 (18.08%)
Order: Ephemeroptera	1197 (31.48%)	6091 (45.02%)	1200 (29.44%)	8488 (39.65%)
Order: Plecoptera	1595 (41.94%)	1764 (13.04%)	988 (24.24%)	4347 (20.30%)
Order: Trichoptera	307 (8.07%)	1393 (10.30%)	175 (4.29%)	1875 (8.76%)
Order: Coleoptera	29 (0.76%)	543 (4.01%)	1167 (28.63%)	1739 (8.12%)
Class Turbellaria	45 (1.18%)	126 (0.93%)	28 (0.69%)	199 (0.93%)
Class: Arachnida	113 (2.97%)	160 (1.18%)	64 (1.57%)	337 (1.57%)
Class: Crustacea	70 (1.84%)	481 (3.56%)	2 (0.05%)	553 (2.58%)
Total:	3803	13530	4076	21409

Table 2.4 Macroinvertebrate counts and relative abundances by family (relative abundance shown in brackets).

Abbreviations are shown in brackets for taxa included in the NMDS ordination (Figure 2.7).

Taxon		Reference	Burned	Burned & Salvage-logged	Total
Arachnida: Trombinifomes	Hydryphantidae	17 (0.45%)	3 (0.02%)	3 (0.07%)	23 (0.11%)
	Hygrobatidae	5 (0.13%)	2 (0.01%)	0 (0%)	7 (0.03%)
	Lebertiidae	5 (0.13%)	20 (0.15%)	15 (0.37%)	40 (0.19%)
	Sperchontidae	18 (0.47%)	101 (0.75%)	5 (0.12%)	124 (0.58%)
	Torrenticolidae	0 (0%)	0 (0%)	5 (0.12%)	5 (0.02%)
Crustacea	Ostracoda	113 (2.97%)	160 (1.18%)	64 (1.57%)	337 (1.57%)
Insecta: Coleoptera	Elmidae (ELMI)	29 (0.76%)	543 (4.01%)	1167 (28.63%)	1739 (8.12%)
Insecta: Diptera	Ceratopogonidae	3 (0.08%)	37 (0.27%)	6 (0.15%)	46 (0.21%)
	Chironomidae (CHIRO)	418 (10.99%)	2253 (16.65%)	346 (8.49%)	3017 (14.09%)
	Empididae	4 (0.11%)	59 (0.44%)	3 (0.07%)	66 (0.31%)
	Psychodidae (PSYCH)	12 (0.32%)	561 (4.15%)	31 (0.76%)	604 (2.82%)
	Tipulidae (TIPUL)	5 (0.13%)	40 (0.30%)	65 (1.59%)	110 (0.51%)
	Other Diptera	5 (0.13%)	22 (0.16%)	1 (0.02%)	28 (0.13%)
Insecta: Emphemeroptera	Baetidae (BAET)	22 (0.58%)	1239 (9.16%)	73 (1.79%)	1334 (6.23%)
	Ephemerellidae	16 (0.42%)	205 (1.52%)	129 (3.16%)	350 (1.63%)
	Heptageniidae (HEPTA)	195 (5.13%)	76 (0.56%)	1 (0.02%)	272 (1.27%)
	Siphlonuridae (SIPHL)	78 (2.05%)	31 (0.23%)	51 (1.25%)	160 (0.75%)
	Other Ephemeroptera	886 (23.3%)	4540 (33.56%)	946 (23.21%)	6372 (29.76%)
Insecta: Plecoptera	Capniidae+Leuctridae (CA_LE)	158 (4.15%)	97 (0.72%)	19 (0.47%)	274 (1.28%)
	Chloroperlidae (CHLOR)	367 (9.65%)	416 (3.07%)	453 (11.11%)	1236 (5.77%)
	Peltoperlidae (PELTO)	50 (1.31%)	255 (1.88%)	5 (0.12%)	310 (1.45%)
	Perlidae	42 (1.1%)	18 (0.13%)	74 (1.82%)	134 (0.63%)
	Perlodidae	19 (0.5%)	58 (0.43%)	14 (0.34%)	91 (0.43%)
	Other Plecoptera	959 (25.22%)	920 (6.8%)	423 (10.38%)	2302 (10.75%)
Insecta: Trichoptera	Brachycentridae (BRAC)	151 (3.97%)	769 (5.68%)	34 (0.83%)	954 (4.46%)
	Hydropsychidae	14 (0.37%)	41 (0.3%)	2 (0.05%)	57 (0.27%)
	Rhyacophilidae	88 (2.31%)	508 (3.75%)	67 (1.64%)	663 (3.1%)
	Other Trichoptera	54 (1.42%)	75 (0.55%)	72 (1.77%)	201 (0.94%)
Platyhelminthes	Turbellaria (TURB)	70 (1.84%)	481 (3.56%)	2 (0.05%)	553 (2.58%)
Total:		3803	13530	4076	21409

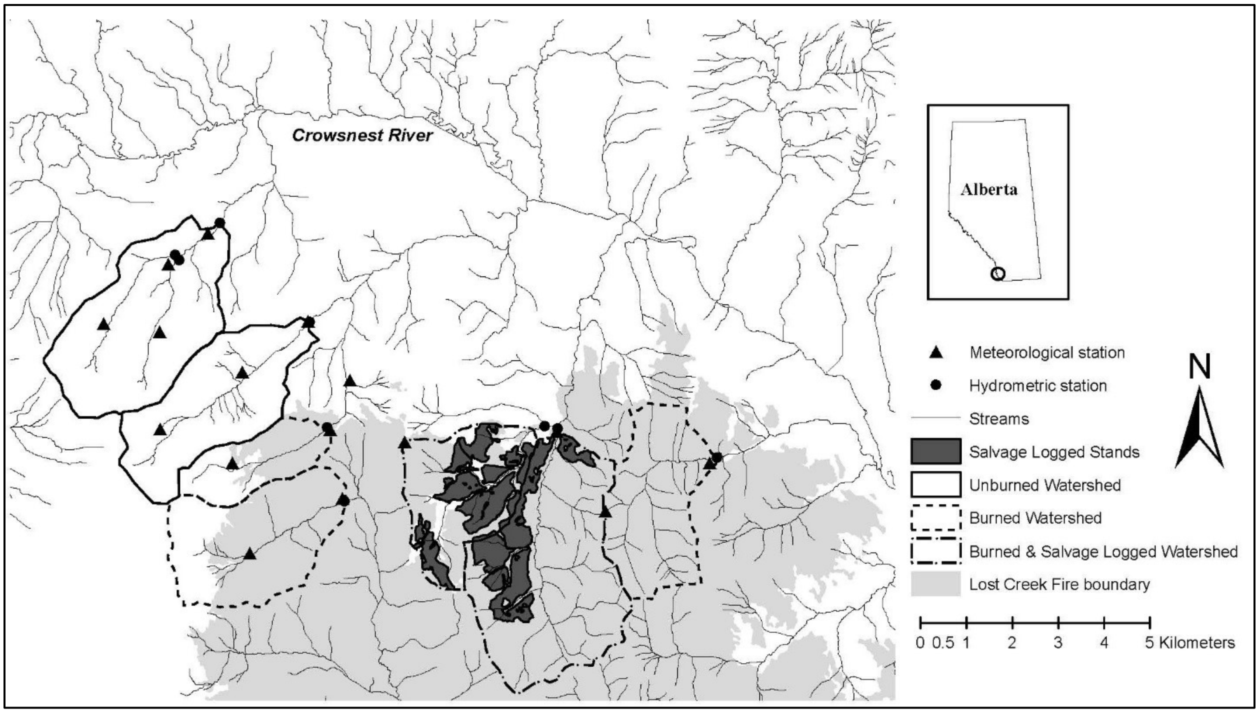


Figure 2.1 Southern Rockies Watershed Project research watersheds.

West to east: Star Creek, North York Creek, South York Creek, Lynx Creek, Lyons West Creek, Lyons East Creek and Drum Creek. Lines indicate watershed boundaries; solid = reference, dash = burned, dot-dash = burned & salvage-logged. Shading indicates forest disturbance: light grey = burned area, dark grey = burned & salvage-logged area.

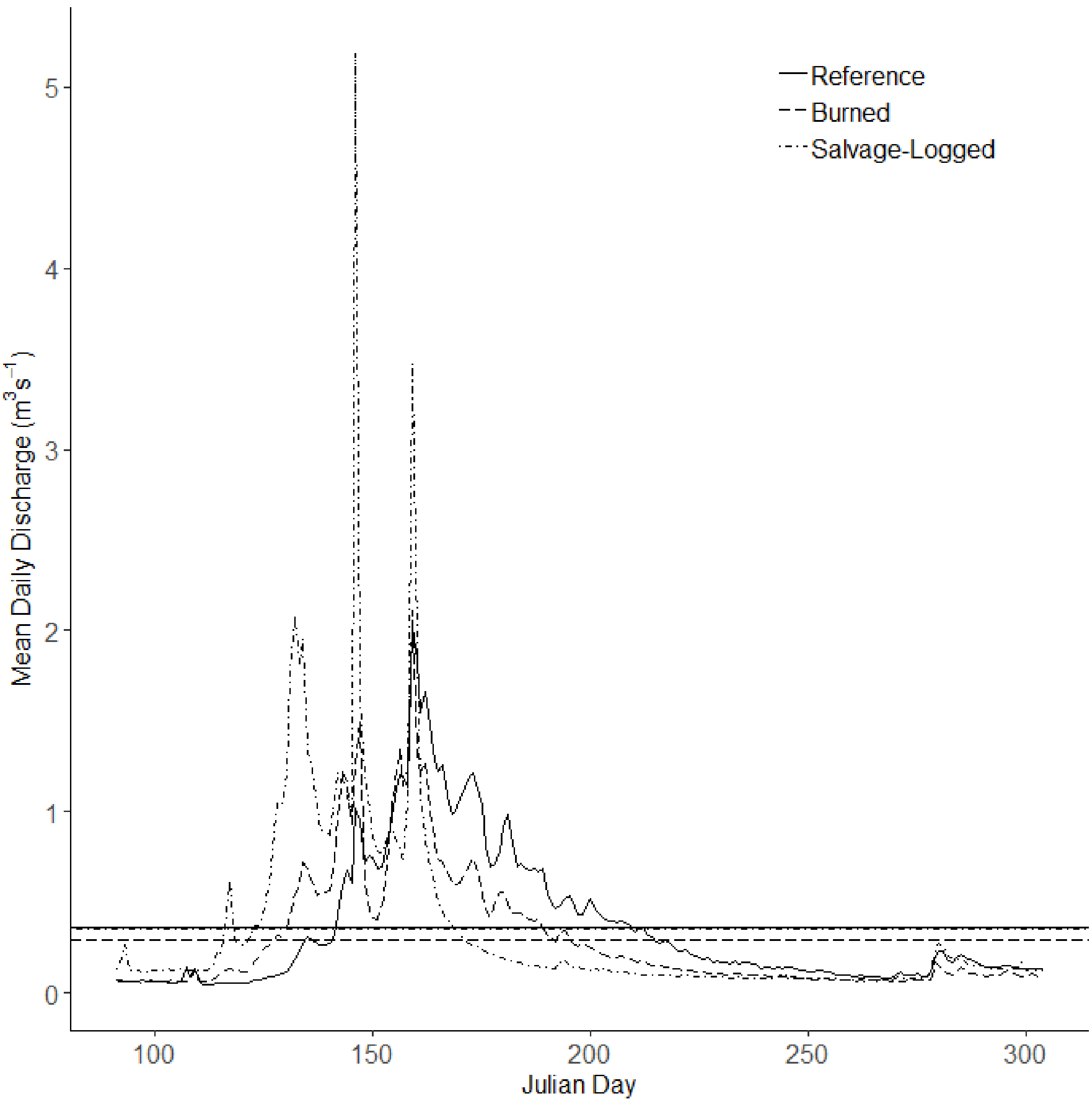


Figure 2.2 Mean daily discharge (m^3 s^{-1}) in reference, burned and burned & salvage-logged watersheds in 2011.

Horizontal lines indicate mean daily discharge for the ice-free period (April to October 2011); solid = reference, dash = burned, dot-dash = burned & salvage-logged.

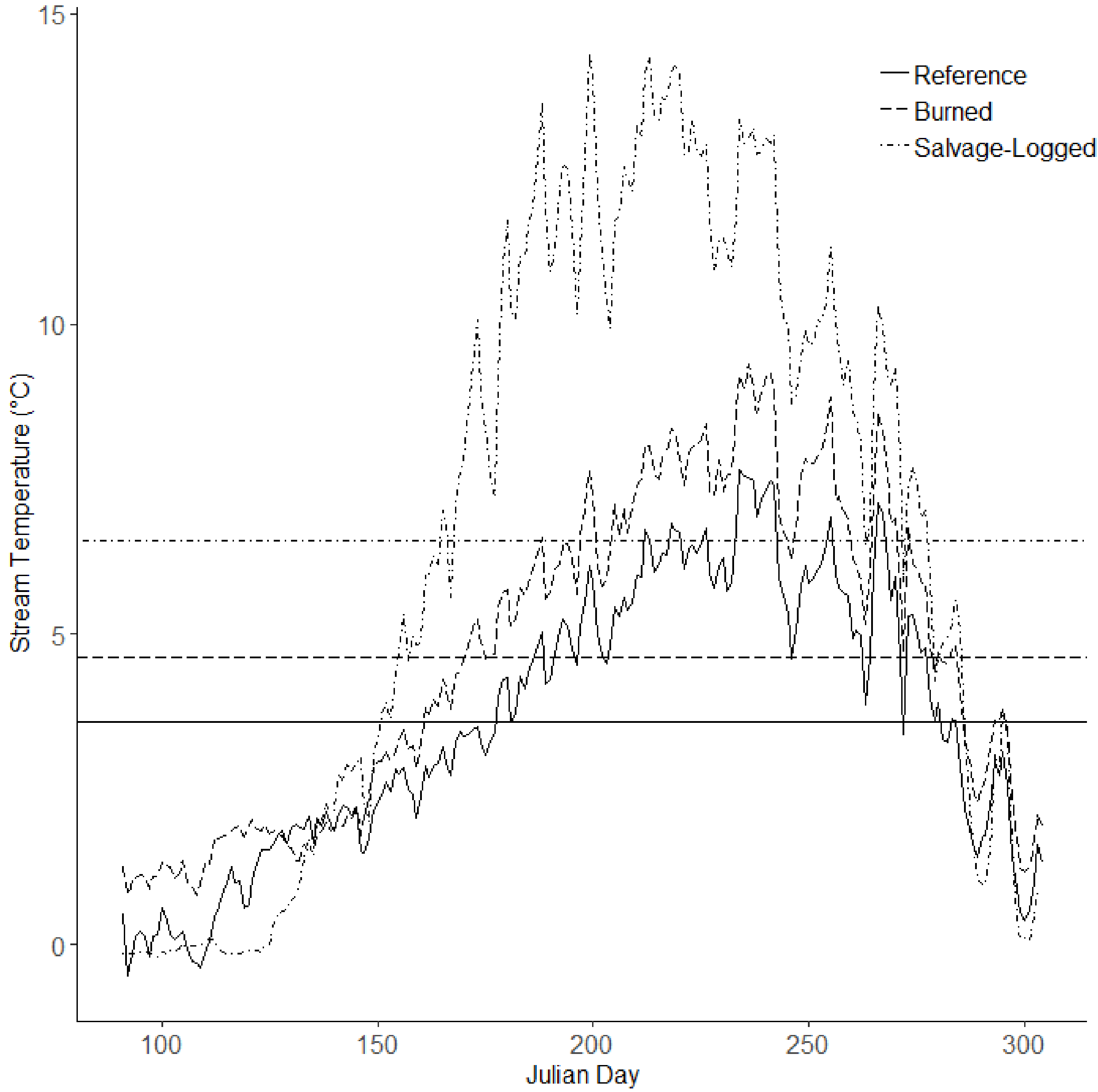


Figure 2.3 Mean daily stream temperature (°C) in reference, burned and burned & salvage-logged watersheds in 2011.

Horizontal lines indicate mean daily stream temperature for the ice-free period (April - October 2011); solid = reference, dash = burned, dot-dash = burned & salvage-logged.

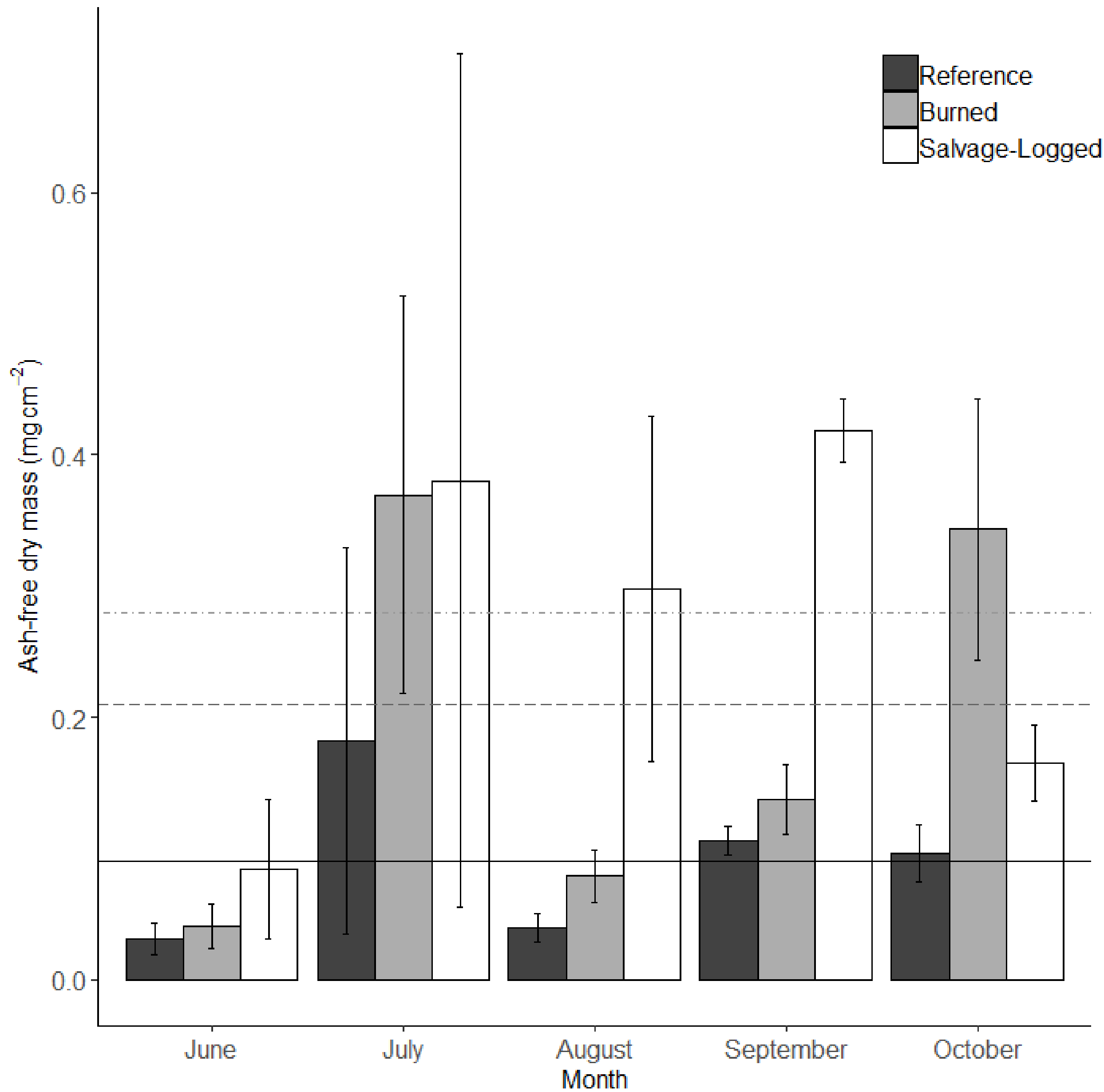


Figure 2.4 Mean monthly ash-free dry mass (mg cm^{-2}).

Bars show mean monthly ash-free dry mass (AFDM), error bars show standard error; black = reference, gray = burned, white= burned & salvage-logged. Horizontal lines indicate mean AFDM for 2011; solid = reference, dash = burned, dot-dash = burned & salvage-logged.

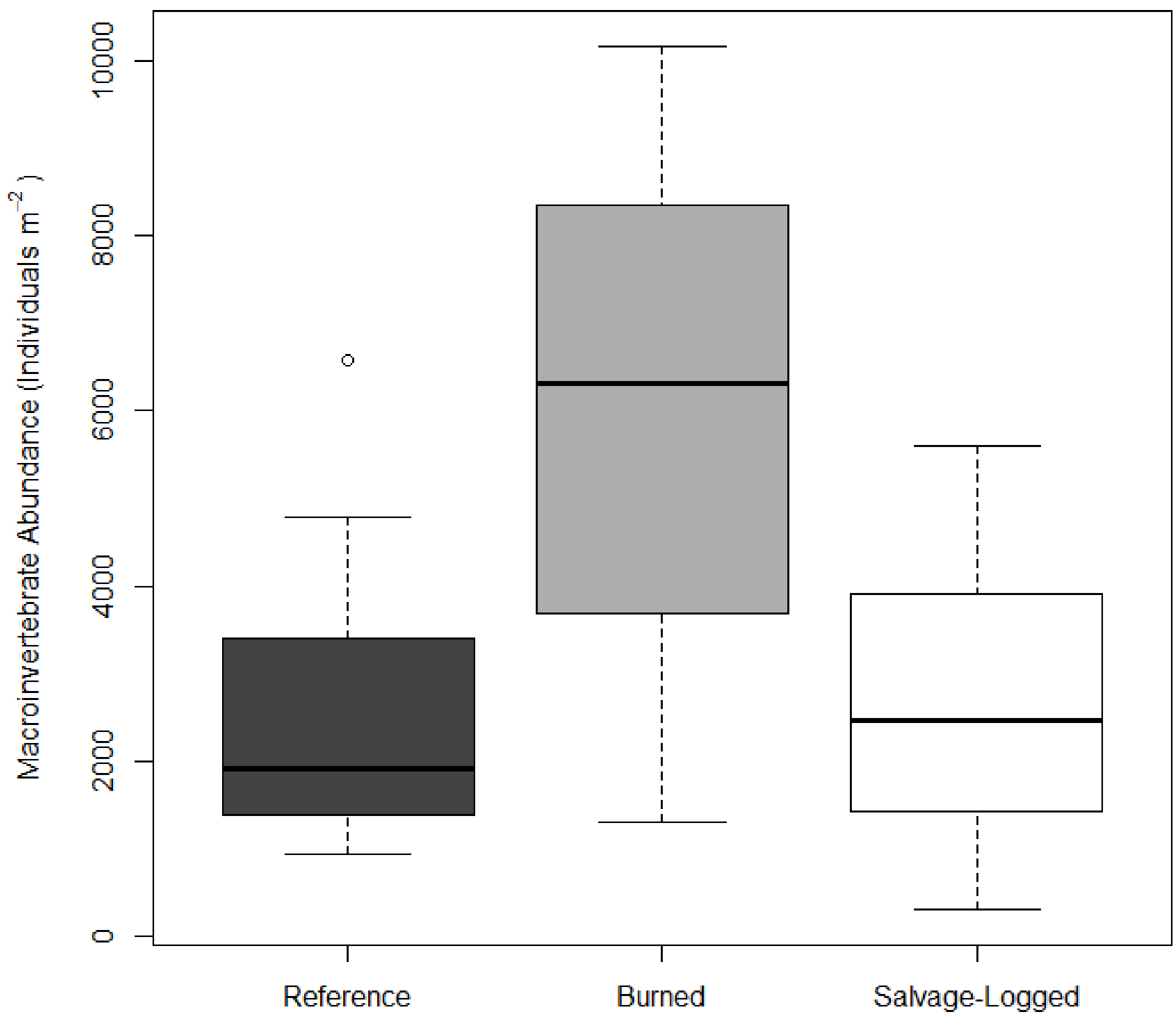


Figure 2.5 Macroinvertebrate abundance (individuals m^{-2}).

Black = reference, gray = burned, white = burned & salvage-logged.

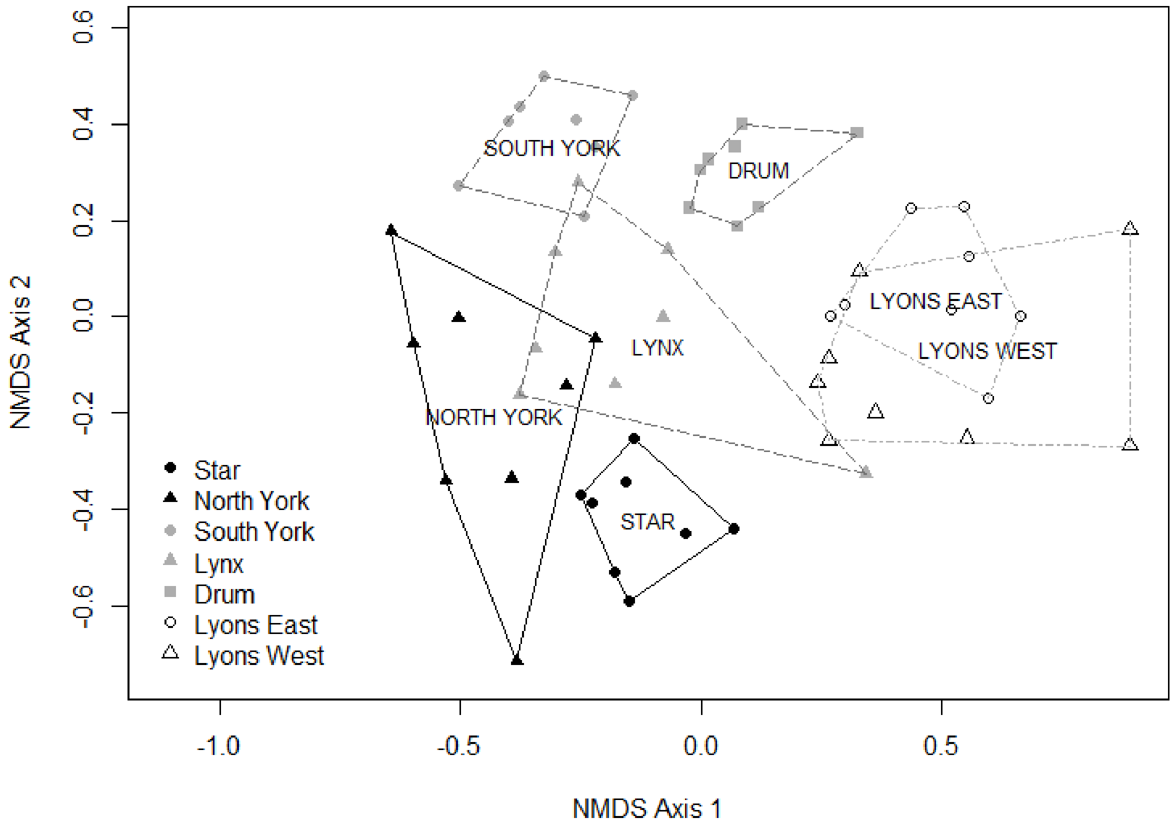


Figure 2.6 Bi-plot of non-metric multidimensional scaling results - site scores.

Ordination performed using a Bray Curtis Dissimilarity matrix calculated with taxon counts. Black = reference, grey = burned, white = burned & salvage-logged. Lines form a polygon encompassing all site scores for a given watershed (solid = reference, dash = burned, dot-dash = burned & salvage-logged).

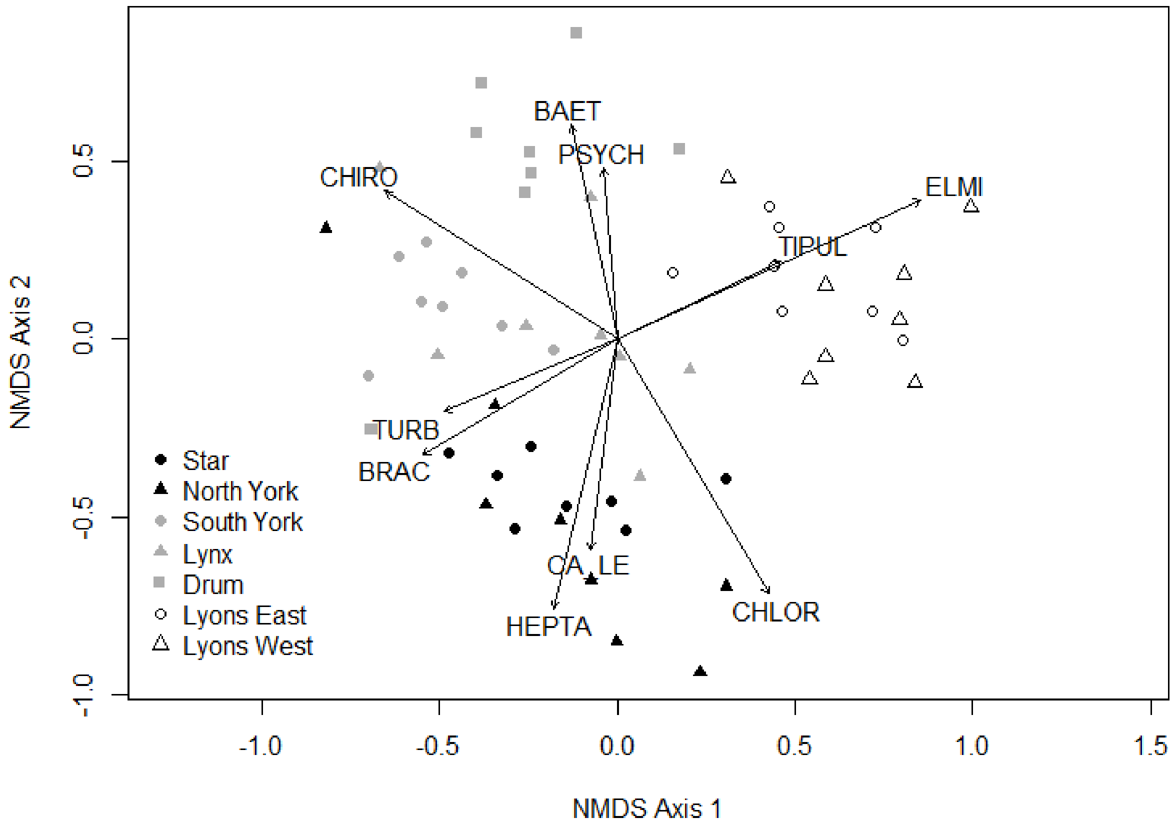


Figure 2.7 Bi-plot of non-metric multidimensional scaling - taxon vectors.

Ordination performed using a Bray-Curtis dissimilarity matrix calculated with relative abundances. Points show site scores and vectors show highly correlated taxa ($P \leq 0.0005$); taxon abbreviations are explained in Table 2.3. Black = reference, grey = burned, white = burned & salvage-logged.

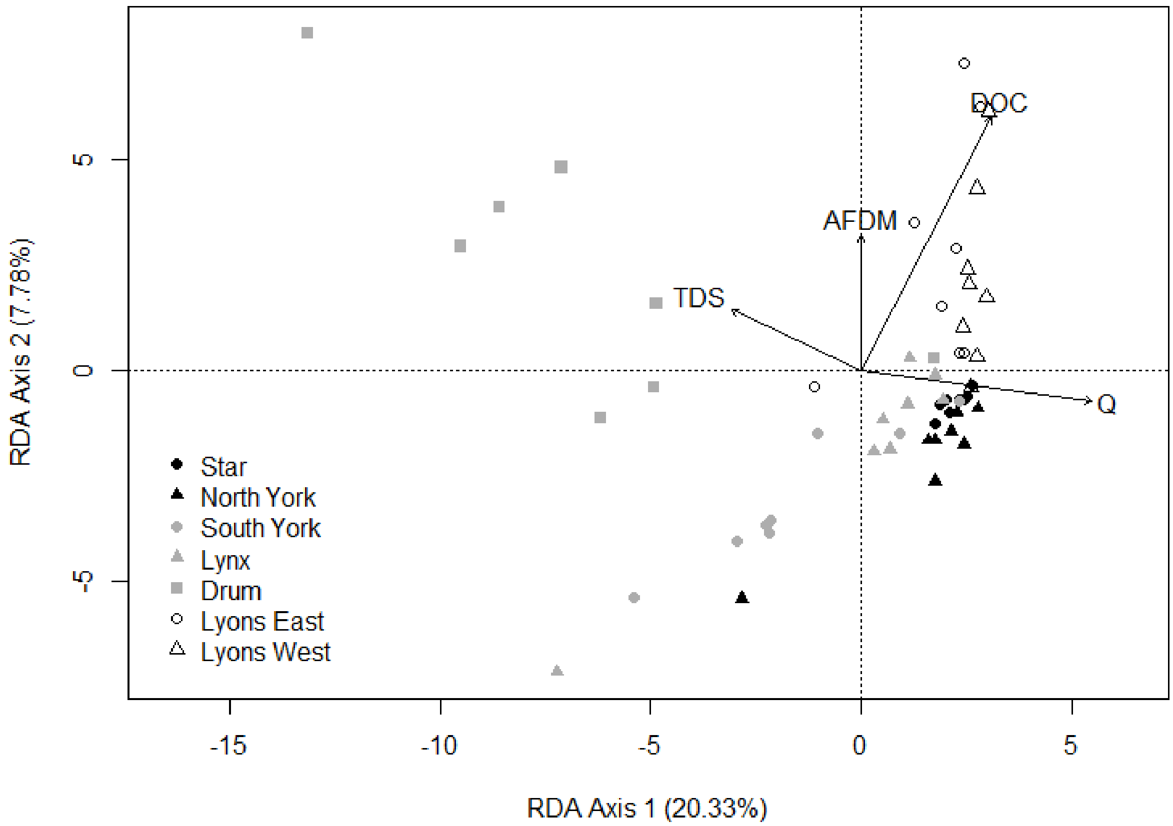


Figure 2.8 Bi-plot of redundancy analysis (RDA) results.

Points show site scores, vectors show environmental parameters significantly correlated with macroinvertebrate assemblages. Parameter abbreviations are explained in Table 2.2. Black = reference, grey = burned, white = burned & salvage-logged.

Literature Cited

Alberta Environment and Parks (2014) 'Alberta Species at Risk.' Available at http:// aep .alberta.ca/fish-wildlife/species-at-risk/documents/SpeciesAssessedConservation-2014a.pdf [Accessed 4-14-17].

Aloi J (1990) A critical review of recent freshwater periphyton field methods. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 656-670.

Bailey RC, Norris RH, Reynoldson TB (2001) Taxonomic resolution of benthic macroinvertebrate communities in bioassessments. *Journal of the North American Benthological Society* **20**, 280-286.

Barbour MT, Snyder BD, Stribling JB, 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, D.C.

Bixby R, Cooper S, Gresswell R, Brown L, Dahm C, Dwire K (2015) Fire effects on aquatic ecosystems: an assessment of the current state of the science. *Freshwater Science* **34**, 1340-1350.

Bjornn T, Brusven M, Molnau M, Milligan J, Klamt R, Cach, E, Schaye C (1977) Transport of granitic sediment in streams and its effects on insects and fish. *Idaho Forest Wildfire and Range Experiment Station Bulletin* **17**, 11-20.

Borcard D, Gillet F, Legendre P (2011) 'Numerical Ecology with R.' (Springer: New York, NY, United States)

Bowman M, Bailey R (1997) Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macroinvertebrate communities? *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1802-1807.

Brittain J, Eikeland T (1988) Invertebrate drift - A review. *Hydrobiologia* **166**, 77-93.

Brown, H (1987) Biology of riffle beetles. *Annual Review of Entomology* **32**, 253-273.

Clifford HF, 1991. Aquatic invertebrates of Alberta an illustrated guide. University of Alberta Press, Edmonton, AB.

Emelko M, Silins U, Bladon K, Stone M (2011) Implications of land disturbance on drinking water treatability in a changing climate: Demonstrating the need for "source water supply and protection" strategies. *Water Research* **45**, 461-472.

Emelko MB, Stone M, Silins U, Allin D, Collins AL, Williams CHS, Martens AM, Bladon KD (2016) Sediment-phosphorus dynamics can shift aquatic ecology and cause downstream legacy effects after wildfire in large river systems. *Global Change Biology* **22**, 1168-1184.

Flannigan M, Logan K, Amiro B, Skinner W, Stocks B (2005) Future area burned in Canada. *Climatic Change* **72**, 1-16.

Frazer GW, Canham CD, Lertzman KP. Gap Light Analyzer (GLA), version 2.0: *Imaging Software to extract canopy structure and gap light transmission indices from true-colour fisheye* *photographs, user manual and program documenation.* Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.

Giller P, Malmqvist B (1998) 'The Biology of Streams and Rivers.' (Oxford University Press: New York, NY)

Gresswell R (1999) Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* **128**, 193-221.

Hauer F, Locke H, Dreitz V, Hebblewhite M, Lowe W, Muhlfeld C, Nelson C, Proctor M, Rood S (2016) Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes. *Science Advances* **2**, e1600026.

Hauer FR, Spencer CN (1998) Phosphorus and nitrogen dynamics in streams associated with wildfire: A study of immediate and longterm effects. *International Journal of Wildland Fire* **8**, 183-198.

Hauer FR, Stanford JA, Lorang MS (2007) Pattern and process in Northern Rocky Mountain headwaters: Ecological linkages in the headwaters of the Crown of the Continent. *Journal of the American Water Resources Association* **43**, 104-117.

Hawthorn K (2014) The role of fine sediment in phosphorus dynamics and stream productivity in Rocky Mountain headwater streams: Possible long-term effects of extensive logging. MSc thesis, University of Alberta.

Hynes HBN (1975) The stream and its valley. *Proceedings of the International Association of Theoretical and Applied Limnology* **19**, 1-15.

Isaak DJ, Young, M Luce C, Hostetler S, Wenger S, Peterson E, Hoef J, Groce M, Horan D, Nagel D (2016) Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 4374-4379.

Jones J, Murphy J, Collins A, Sear D, Naden P, Armitage P (2012) The impact of fine sediment on macro-invertebrates. *River Research and Applications* **28**, 1055-1071.

Kelly E, Schindler D, St Louis V, Donald D, Vlaclicka K (2006) Forest fire increases mercury accumulation by fishes via food web restructuring and increased mercury inputs. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 19380-19385.

Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* **129**, 271-280.

Malison R, Baxter CV (2010a) The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 570-579.

Malison RL, Baxter CV (2010b) Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. *Journal of the North American Benthological Society* **29**, 1324-1338.

Mihuc TB, Minshall GW (2005) The trophic basis of reference and post-fire stream food webs 10 years after wildfire in Yellowstone National Park. *Aquatic Sciences* **67**, 541-548.

Mihuc TB, Minshall GW, Robinson CT (1996) Response of benthic macroinvertebrate populations in Cache Creek, Yellowstone National 60 Park to the 1988 wildfires. In 'The ecological implications of fire in Greater Yellowstone: proceedings on the second biennial Conference on the Greater Yellowstone Ecosystem', 19–21 September 1993, Yellowstone National Park, WY, USA. (Ed JM Greenlee) International Association of Wildland Fire, pp. 83–94. (Fairfield, WA, USA).

Minshall GW (2003) Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management* **178**, 155-161.

Minshall GW, Brock JT, Andrews DA, Robinson CT (2001a) Water quality, substratum and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek fire. *International Journal of Wildland Fire* **10**, 185-199.

Minshall GW, Brock JT, Varley JD (1989) Wildfires and Yellowstone stream ecosystems. *Bioscience* **39**, 707-715.

Minshall GW, Robinson CT, Lawrence, DE (1997) Postfire responses of lotic ecosystems in Yellowstone National Park, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2509-2525.

Minshall GW, Robinson CT, Lawrence DE, Andrews DA, Brock JT (2001b) Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbance by wildfire. *International Journal of Wildland Fire* **10**, 201-213.

Moody J, Martin D (2001) Initial hydrologic and geomorphic response following a wildfire in the Colorado Front Range. *Earth Surface Processes and Landforms* **26**, 1049-1070.

Morris E, Caruso T, Buscot F, Fischer M, Hancock C, Maier T, Meiners T, Muller C, Obermaier E, Prati D, Socher S, Sonnemann I, Waschke N, Wubet T, Wurst S, Rillig M (2014) Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution* **4**, 3514-3524.

Naman S, Rosenfeld J, Richardson J (2016) Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1292-1305.

Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E and Wagner H (2019). vegan: Community Ecology Package. R package version 2.5-4. https://CRAN.R-project.org/package=vegan

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reid D, Quinn J, Wright-Stow A (2010) Responses of stream macroinvertebrate communities to progressive forest harvesting: Influences of harvest intensity, stream size and riparian buffers. *Forest Ecology and Management* **260**, 1804-1815.

Richards C, Minshall GW (1992) Spatial and temporal trends is stream macroinvertebrate communities - the influence of catchment disturbance. *Hydrobiologia* **241**, 173-184.

Rice EW (2012) Standard methods for the examination of water and wastewater. American Public Health Association: Washington, D.C.

Rinne JN (1996) Management briefs: short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *North American Journal of Fisheries Management* **16**, 653-658.

Robson B, Chester E, Matthews T, Johnston K (2018) Post-wildfire recovery of invertebrate diversity in drought-affected headwater streams. *Aquatic Sciences* **80**, 21.

Roby KB, 1989. Watershed response and recovery from the Will Fire: ten years of observation. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-109: 131-136. (Berkeley, CA, USA).

Romme WH, Boyce MS, Gresswell R, Merrill EH, Minshall GW, Whitlock C, Turner MG (2011) Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. *Ecosystems* **14**, 1196-1215.

Rugenski AT, Minshall GW (2014) Climate-moderated responses to wildfire by macroinvertebrates and basal food resources in montane wilderness streams. *Ecosphere* **5**, 25.

Schoennagel T, Veblen T, Romme W (2004) The interaction of fire, fuels, and climate across rocky mountain forests. *Bioscience* **54**, 661-676.

Shakesby R, Doerr S (2006) Wildfire as a hydrological and geomorphological agent. *Earth-Science Reviews* **74**, 269-307.

Silins U, Anderson A, Bladon KD, Emelko MB, Stone M, Spencer SA, Williams CHS, Wagner MJ, Martens AM, Hawthorn K (2016) Southern Rockies Watershed Project. *Forestry Chronicle* **92**, 39-42.

Silins U, Bladon K, Kelly E, Esch E, Spence J, Stone M, Emelko M, Boon S, Wagner M, Williams C, Tichkowsky I (2014) Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. *Ecohydrology* **7**, 1508-1523.

Silins U, Stone M, Emelko MB, Bladon KD (2009) Sediment production following severe wildfire and post-fire salvage logging in the Rocky Mountain headwaters of the Oldman River Basin, Alberta. *Catena* **79**, 189-197.

Spencer C, Gabel K, Hauer F (2003) Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management* **178**, 141-153.

Thorp J, Covich A (2009) 'Ecology and Classification of North American Freshwater Invertebrates Third Edition.' (Academic Press: London, UK).

US EPA (2012). Selected analystical methods for environmental remediation and recovery (SAM) 2012. U.S. Environmental Protection Agency, Wahstington, DC. EPA/600/R-12/555.

US Fish and Wildlife Service (2017) 'Environmental Conservation Online System.' Available at https://ecos.fws.gov/ecp0/pub/SpeciesReport.do?groups=E&listingType=L&mapstatus=1 [Accessed 4-14-17].

Vannote R, Minshall G, Cummins K, Sedell J, Cushing C (1980) River continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130-137.

Verkaik I, Vila-Escale M, Rieradevall M, Baxter CV, Lake PS, Minshall GW, Reich P, Prat N (2015) Stream macroinvertebrate community responses to fire: are they the same in different fire-prone biogeographic regions? *Freshwater Science* **34**, 1527-1541.

Vieira N, Clements W, Guevara L, Jacobs,B (2004) Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology* **49**, 1243-1259.

Voshell JR (2002) 'A Guide to Common Freshwater Invertebrates of North America.' (The McDonald and Woodward Publishing Company: Blacksburg, Virginia)

Wagenbrenner J, Robichaud P, Brown R (2016) Rill erosion in burned and salvage logged western montane forests: Effects of logging equipment type, traffic level, and slash treatment. *Journal of Hydrology* **541**, 889-901.

Wagner MJ, Bladon KD, Silins U, Williams CHS, Martens AM, Boon S, MacDonald RJ, Stone M, Emelko MB, Anderson A (2014) Catchment-scale stream temperature response to land disturbance by wildfire governed by surface-subsurface energy exchange and atmospheric controls. *Journal of Hydrology* **517**, 328-338.

Westerling A, Hidalgo H, Cayan D, Swetnam T (2006) Warming and earlier spring increase western US forest wildfire activity. *Science* **313**, 940-943.

Wood P, Armitage P (1997) Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**, 203-217.

Writer J, McCleske, R, Murphy S, Stone M, Collins A, Thoms M (2012) Effects of wildfire on source-water quality and aquatic ecosystems, Colorado Front Range. *Wildfire and Water Quality: Processes, Impacts and Challenges* **354**, 117-122.

Yee D, Kehl S (2015) Order Coleoptera. In 'Thorp and Covich's Freshwater Invertebrates (Fourth Edition).' (Eds J Thorp, D Rogers.) pp. 1003-1042. (Academic Press: Cambridge, MA, USA).

Zwick P (1992) Stream habitat fragmentation - a threat to Biodiversity. *Biodiversity and Conservation* **1**, 80-97.

Chapter 3 Analysis of Food Web Structure in Rocky Mountain Aquatic Ecosystems Following Severe Wildfire in Southern Alberta

3.1 Introduction

Wildfire is a significant disturbance in North American forested watersheds (Gresswell 1999) that can strongly influence aquatic ecology (Minshall 2003; Spencer *et al.* 2003; Malison and Baxter 2010b). Rocky Mountain forests in North America are facing increased severity, frequency and duration of wildfires in response to a warming climate (Westerling *et al.* 2006), and the area burned in Canada is predicted to increase by 74 – 118 % by the end of the 21st century (Flannigan *et al.* 2005). Forested watersheds provide important habitat for aquatic fauna including benthic macroinvertebrates and fish (Rinne 1996; Isaak *et al.* 2016). The eastern slopes of Alberta's Rocky Mountains support two salmonid species at risk, Westslope Cutthroat Trout (*Oncorhynchus clarkii lewisi*) and Bull Trout (*Salvelinus confluentus*) (Alberta Environment and Parks 2014; US Fish and Wildlife Service 2017). As aquatic ecosystems and the terrestrial landscape are inextricably linked (Hynes 1975), increased wildfire activity will have impacts on aquatic ecosystems.

Wildfire influences aquatic energy dynamics by altering the availability and quality of primary energy resources. Primary producers form the base of freshwater food webs and can be broadly divided into two categories: autochthonous resources, consisting of instream periphyton and macrophytes, and allochthonous resources, consisting of terrestrial vegetation and detritus. Low order, headwater streams in Rocky Mountain watersheds are primarily supported by allochthonous carbon (Cummins 1974; Vannote *et al.* 1980). Wildfire can shift the primary support of freshwater ecosystems from allochthonous to autochthonous (Spencer *et al.* 2003; Silins *et al.* 2014). Terrestrial sources of energy are depleted when riparian vegetation burns and instream primary productivity is stimulated by the post-wildfire increases in nutrient loading, stream temperature and light availability (Spencer *et al.* 2003; Mihuc and Minshall 2005). As different macroinvertebrate taxa are specialized for consuming different food sources (Cummins 1973), changes in resource availability can lead to changes in biological communities (Minshall 2003). Generally it is expected that a reduction in terrestrial vegetation entering the stream will contribute to declines in consumers specialized for feeding on detritus (e.g., shredders) while increases in periphyton productivity can lead to increases in taxa that consume periphyton (e.g., scrapers) (Mihuc *et al.* 1996; Minshall *et al.* 1997). Abundance of macroinvertebrates has been shown to both increase (Malison and Baxter 2010b) and decrease (Rinne 1996) following wildfire. As macroinvertebrates are an important food resource for some vertebrates, these changes can have important consequences for higher trophic levels. Silins *et al.* (2014) and Koetsier *et al.* (2007) both observed that trout from burned watersheds had greater lengths and weights compared to those from unburned watersheds. As well, Malison and Baxter (2010a) observed greater numbers of terrestrial consumers (bats and spiders) in riparian zones five years after a severe wildfire in Idaho.

Quantifying aquatic energy dynamics and food web pathways in freshwater systems is challenging. Macroinvertebrate consumers are small and camouflaged within gravel beds and leaf packs in stream habitats (Voshell 2002). Behavioral observations and gut content analysis for the determination of food web structure is challenging due to the difficulty distinguishing between detritus, periphyton and tissue (Rounick *et al.* 1982; Pinnegar and Polunin 1999). As well, many macroinvertebrates are omnivorous (consume both plant and animal tissue) and will consume a wide range of food types (algae, vascular vegetation, detritus and other macroinvertebrates) (Cummins 1973; Mihuc and Minshall 1995). They do not fit well within observational food webs made up of discrete trophic levels (e.g., primary producer, primary consumer, secondary consumer etc.). Stable isotope ratios can be used to define food webs and are better able to account for omnivory than traditional methods (Anderson and Cabana 2007). Carbon and nitrogen both have two stable isotopes: ^{12}C and ^{14}N are the lighter isotopes, ^{13}C and ^{15}N are the heavier isotopes. The ratios of light and heavy isotopes can be measured in plant and animal tissue using a mass spectrometer. Ratios are referenced to known standards (Vienna Pee Dee Belemite for carbon and air for nitrogen) and reported as the ratio of the heavy isotope to the light isotope in units of "‰" or "per mil" meaning parts per thousand (*see section 3.3.3*). Metabolic activities cause a change in the relative abundance of heavy and light isotopes called fractionation (Fry 2006; Resco *et al.* 2011). Lighter isotopes are preferentially metabolized resulting in products more depleted in heavy isotopes than the source pool (Resco *et al.* 2011). Heavy isotopes build up in the tissue of consumers and are passed on to the next trophic level. This particularly true for nitrogen; consumers are enriched in the heavy isotope of nitrogen relative to their food by 3-4 ‰ (Minagawa and Wada 1984). In contrast carbon shows relatively low enrichment between trophic levels (0-1 ‰), making it a better tool for determining which sources of organic carbon contribute to consumer diets (Deniro and Epstein 1978; Rounick *et al.* 1982; Fry 1991; Post 2002). Isotope ratios of food web constituents can be used in linear mixing models to determine the relative contribution of potential food sources to a consumers diet (Szepanski *et al.* 1999). Stable isotope studies have been widely applied to gain insight into food web structure and energy structure in freshwater ecosystems (Rounick *et al.* 1982; Fry 1991; Spencer *et al.* 2003).

The Lost Creek Wildfire (2003) was one of the more severe fires in recent decades on the eastern slopes of Alberta's Rocky Mountains and provided an opportunity to assess the long-term impacts of wildfire. The Southern Rockies Watershed Project (SRWP) was established to document the effects of the wildfire on hydrology, biogeochemistry and aquatic ecology. Eleven years of continuous monitoring have shown the effects of wildfire on water quality and biogeochemistry to be persistent (Emelko *et al.* 2016; Silins *et al.* 2016), nutrient export and primary productivity remained elevated in wildfire affected watersheds. Given the persistent increase in instream primary productivity in wildfire affected watersheds, primary producers (instream and terrestrial), macroinvertebrates and fish were sampled eight years after the wildfire to assess the long-term impacts on energy use and food web structure. The objectives of this study were to:

1) quantify the stable isotope signature of a range of primary producers, as well as primary, secondary and tertiary consumers from both unburned (reference), burned, and burned & salvage-logged watersheds;
2) quantify the relative proportion of terrestrial and instream organic carbon in the diets of different consumers;
3) evaluate the effects of changes in the base of the aquatic food web on the growth (length:age and weight:age ratios) of a tertiary consumer, Cutthroat Trout (Oncorhynchus clarkii).

3.2 Methods

3.2.1 Site Description

The 2003 Lost Creek wildfire burned 211.63 km^2 of forest in the Crowsnest and Castle River watersheds, and was one of the most severe wildfire on the eastern slopes of Alberta's Rocky Mountains in recent decades. After the fire, five watersheds were instrumented as part of the Southern Rockies Watershed Project, including three burned watersheds (South York, Lynx and Drum Creeks) and two reference (unburned) catchments (Star and North York Creeks) (Figure 3.1). In the winters of 2004 and 2005 portions of the burned regions of the Lyons Creek valley were salvage-logged and Lyons East and Lyons West Creeks (2.62 and 2.38 km^2 harvested respectively) were instrumented to assess the additional disturbance from post-wildfire salvage-logging. All watersheds except Lynx Creek are tributaries of the Crowsnest River; Lynx Creek is a tributary of the Castle River.

The hydrologic regime of these watersheds is snowmelt dominated with the highest flows occurring in late May to early June, corresponding with the peak of spring snowmelt. Mean annual precipitation (2004-2014) in the reference, burned and burned & salvage-logged catchments was 1087 mm (898-1398 mm), 1146 mm (950-1431 mm) and 775 mm (582-971 mm) respectively. Mean annual area-weighted discharge in the reference, burned and burned & salvage-logged catchments for the same time period was 744 mm (483-1080 mm), 871 mm (571-1091 mm) and 592 mm (373-887 mm), respectively. Forest cover prior to the fire consisted predominantly of Lodgepole Pine (*Pinus contorta* var. *latifolia*) at lower elevations, Englemann Spruce *(Picea engelmanii*) and Subalpine Fir (*Abies lasiocarpa*) at mid elevations, and alpine meadow vegetation and bare rock at higher elevations. Watershed characteristics are summarized in Table 3.1. No pre-disturbance hydrologic, water quality or aquatic ecological data existed for the study watersheds prior to the wildfire. Replication of undisturbed (reference) and disturbed (burned and burned & salvage-logged) watersheds with similar physical and environmental characteristics have been used to support broader inferences on wildfire and salvage logging impacts (Spencer *et al.* 2003; Reid *et al.* 2010), based on the assumption that disturbed watersheds would behave in a similar way to reference catchments had the wildfire not occurred.

3.2.2 Food Web Constituents

3.2.2.1 Primary Producers

Terrestrial vegetation was collected from the streambed in October 2011 using a Surber sampler (500 μm mesh; 0.96 m^2) during macroinvertebrate sampling and preserved in 95% ethanol. These samples are representative of the post-fire conditioned vegetation available to primary consumers. In the lab, vegetation was rinsed with 95% ethanol and sorted into broad categories: willow catkins, grass, leaves, needles, conifer cones, seeds, wood and particulate organic matter (POM) using a dissecting microscope (Table 3.2). POM consisted of any material too small or decomposed to be readily identified. Samples were lyophilized (freeze-dried), ground to a fine powder with a mortar and pestle and stored in sealed glass vials at room temperature for approximately 1 week prior to stable isotope analysis.

Periphyton samples were collected using unglazed ceramic tiles (155 cm^2) anchored to the streambed in each study catchment. Tiles were scrubbed clean in running stream water prior to deployment in September 2011, then periphyton was allowed to colonize naturally for 31 – 36 days. Samples were collected in October 2011 by scraping and rinsing periphyton from the tile surface into acid washed (10% HCl) HDPE Nalgene sample bottles. Samples were frozen prior to preparation for stable isotope analysis. Sediments containing inorganic carbon (calcium carbonate - $CaCO_3$) such as limestone and clay deposited within periphyton biomass can inflate the $\delta^{13}C$ signature of periphyton samples (Kennedy *et al.* 2005; Brodie *et al.* 2011b). In the lab periphyton samples were lyophilized and examined under a dissecting microscope; visible sediment was removed from the samples with forceps. A subset of periphyton was acid washed (5% HCl) to remove any remaining inorganic carbon using the rinse method (Brodie *et al.* 2011b). Acidified samples were rinsed in deionized (DI) water, dried at 50 °C and ground to a fine powder. As acid washing confounds measurements of $\delta^{15}N$, a separate periphyton sample was analyzed without acid treatment to accurately determine nitrogen isotope ratios (Brodie *et al.* 2011a).

3.2.2.2 Macroinvertebrates

Benthic macroinvertebrate sampling was also conducted in October 2011. Invertebrates were collected using a Surber sampler (500 µm mesh, 0.096 m^2), from eight randomly chosen riffle sections along a 100 m transect upstream of each established gauging station. The sampler was placed on the streambed facing upstream; large rocks within the sampling area were rubbed clean and removed, then the bed material was vigorously disturbed for 2 minutes. Sampler contents were placed in a white plastic basin and large debris (e.g., whole leaves, twigs and rocks) were rinsed and removed. Water was removed using a 500 µm sieve and the remaining contents (macroinvertebrates, plant material and detritus) were transferred to an HDPE Nalgene sample bottle and preserved with 95% ethanol. Macroinvertebrates were sorted, enumerated and identified to the lowest practical taxonomic unit (usually family) using a dissecting microscope and keys in Clifford (1991) and Thorp and Covich (2009). Sorted samples were preserved in 95% ethanol prior to preparation for stable isotope analysis.

The 500 µm mesh of the Surber sampler permitted the collection of larger bodied water mites and later insect instars. Smaller individuals would have been able to pass through the mesh. A subset of 11 abundant insect taxa (Ephemeroptera: Baetidae and Heptageniidae; Plecoptera: Peltoperlidae, Perlodidae, Perlidae and Capniidae & Leuctridae; Trichoptera: Hydropsychidae and Rhyacophilidae; Diptera: Psychodidae and Tipulidae and Coleoptera: Elmidae) were selected for stable isotope analysis (Table 3.3). As macroinvertebrate mass was not sufficient to run unique duplicate samples for $\delta^{13}C$ and $\delta^{15}N$, samples were not acid pre-treated prior to analysis. Carbonates in macroinvertebrate exoskeletons can increase the $\delta^{13}C$ signatures due to the presence of inorganic (non-dietary) carbon in certain taxa including molluscs and crustaceans (Jacob *et al.* 2005; Jaschinski *et al.* 2011), but neither of these groups were sampled as part of this study. No acid pretreatment is consistent with other studies of freshwater invertebrates low in carbonates (e.g., Zah *et al.* 2001; Post 2002). Since all invertebrate samples received the same preparation methods, comparisons between watersheds are valid. Individual macroinvertebrates of the same taxa from each Surber sample were combined to provide enough material for stable isotope analysis. Macroinvertebrates were freeze-dried whole and ground to a fine powder with a mortar and pestle.

3.2.2.3 Fish

Cutthroat Trout were the only fish species sampled for this study as they were present in both burned and reference watersheds. The additional effects of salvage logging on fish populations was not assessed. Not all sampling locations used for collection of algae, terrestrial vegetation and macroinvertebrate samples supported resident trout populations due to fish barriers (waterfalls) and small size; therefore, ampling was mainly conducted in nearby reference and burned watersheds (Figure 3.2). Lynx Creek was the only watershed sampled for both fish, invertebrates and primary producers; however, fish sampling took place downstream of macroinvertebrate and algae sampling due to road-access requirements. Prior sampling (Silins *et al*., 2014) indicated that local salmonid species Cutthroat Trout (*Oncorhynchus clarkii*) and Rainbow Trout (*Oncorhynchus mykiss*) did not occur consistently across watersheds in all disturbance categories.

Fish were sampled by backpack electrofishing in October 2011. Twenty (20) individuals with fork lengths between 100 and 250 mm were collected from each watershed. Fresh weight and fork length were recorded. Fish were then euthanized by a stunning blow the head. All collection, handling and euthanasia of fish was conducted under the direct supervision of Alberta Fish and Wildlife biologists (Fish Research License #11-2663 FR). Otoliths (inner ear bones) removed to determine age. Otoliths were soaked in glycerin to allow visual determination of fish age using a dissecting microscope. Fish were frozen whole prior to extraction of muscle tissue for stable isotope analysis. Fish in the 2 and 3 year age classes were sampled consistently across watersheds; fish in the 1 and 4+ year age classes were excluded from growth rate analysis due to insufficient replication. Fish growth rate was calculated using two metrics, the ratio of fresh weight (g) to age (years) and fork length (mm) to age (years). In the lab, fish were thawed, and a sample of muscle tissue dissected from the left side of the body (US Environmental Protection Agency 2000). As lipids are depleted in $\delta^{13}C$ relative to other tissues (Deniro and Epstein 1977) they were extracted from tissue samples prior to carbon stable isotope analysis using chloroform and methanol (Bligh and Dyer 1959). Lipid extraction can compromise the detection of an accurate $\delta^{15}N$ signature (Sotiropoulos *et al.* 2004), a paired untreated tissue sample was analyzed for $\delta^{15}N$.

3.2.3 Stable Isotope Analysis

Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the Biogeochemical Analytical Service Laboratory (BASL) at the University of Alberta (Edmonton, Alberta). Homogenized samples were weighed into tin (Sn) capsules using a microbalance. Isotopic composition was determined using a EuroVector EuroEA3028-HT elemental analyzer coupled to a GV Instruments IsoPrime continuous-flow isotope ratio mass spectrometer. $\delta^{13}C$ and $\delta^{15}N$ ratios (‰) were determined using Equation 3.1 (Resco *et al.* 2011).

$$\delta X(‰) = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1000 \qquad (3.1)$$

where R_{sample} was the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ in the sample, and $R_{standard}$ is referenced to Vienna Pee Dee Belemite (VPDB) and air for ^{13}C or ^{15}N respectively. Higher values indicate greater amounts of the heavier isotope (^{13}C or ^{15}N). National Institute of Standards and Technologies (NIST) 8415 whole egg powder Standard Reference Material (SRM) was used as an in-house ^{13}C and ^{15}N QA/QC check throughout analyses with standard deviation of 0.2 ‰ and 0.1 ‰ respectively.

3.2.4 Data Analysis

Statistical analyses were conducted using R (R Core Team, 2018). One-way analysis of variance (ANOVA) was used to determine the effect of disturbance category (reference, burned, and burned & salvage-logged) on carbon and nitrogen isotope ratios. T-tests were used to determine the effect of disturbance category (reference and burned) on the growth rate metrics and isotope ratios of Cutthroat Trout. Where data did not meet the assumptions of parametric tests a $\log_{10}$ transformation was applied or non-parametric Wilcoxon or Kruskal-Wallace rank sum tests were used.

The relative contribution of instream and terrestrial organic material to consumer diets was calculated using a two-source linear mixing model (Phillips and Gregg 2001; Equations 3.2 and 3.3)

$$\bar{\delta}_M = f_A \bar{\delta}_A + f_B \bar{\delta}_B \tag{3.2}$$

$$1 = f_A + f_A \tag{3.3}$$

where $\bar{\delta}_M$, $\bar{\delta}_A$ and $\bar{\delta}_B$ are the mean $\delta^{13}C$ signatures of the consumer (M) and sources A and B, and f_A and f_B are the proportions of source A and B in M. Carbon stable isotopes were used in the model as carbon shows relatively little trophic fractionation compared to nitrogen (Deniro and Epstein 1978).

3.3 Results

All data are reported as mean ± standard error ($\sigma_{\bar{x}}$) unless otherwise specified.

3.3.1 Primary Producers

Terrestrial vegetation had similar $\delta^{13}C$ in reference, burned and burned & salvage-logged watersheds ($\delta^{13}C$ = -27.17 ‰ ± 0.16, -26.79 ‰ ± 0.17 and -27.04 ‰ ± 0.20 respectively; *P* = 0.288). $\delta^{13}C$ varied by category (leaf, wood, needle etc.) but the ranges were similar across treatments; no consistent pattern was evident between disturbance categories (Table 3.2; Figure 3.3a). $\delta^{15}N$ in terrestrial vegetation followed the pattern burned > burned & salvage-logged > reference ($\delta^{15}N$= -2.25 ‰ ± 0.09, -1.03 ‰ ± 0.13 and -1.54 ‰ ± 0.16 in the reference, burned and burned & salvage-logged watersheds respectively; *P* < 0.001). $\delta^{15}N$ showed greater variability in the burned` and burned & salvage-logged watersheds (Table 3.2; Figure 3.3b).

No significant differences in periphyton $\delta^{13}C$ were evident between disturbance categories ($\delta^{13}C$ = -33.61 ‰ ± 1.04, -34.42 ‰ ± 1.54 and -30.40 ‰ ± 0.17 in the reference, burned and burned & salvage-logged watersheds respectively, *P* = 0.441) (Table 3.2; Figure 3.3a). Periphyton was depleted in $\delta^{13}C$ relative to terrestrial vegetation. $\delta^{15}N$ was elevated in the burned and burned & salvage-logged watersheds ($\delta^{15}N$ = -0.76 ‰ ± 0.14, 0.66 ‰ ± 0.35 and 0.71‰ ± 0.18 in the reference, burned and burned & salvage-logged watersheds respectively, $P < 0.01$) (Table 3.2; Figure 3.3b). Periphyton was enriched in $\delta^{15}N$ relative to terrestrial vegetation.

3.3.2 Macroinvertebrates

Macroinvertebrate isotope signatures varied by family. Mean $\delta^{13}C$ for all invertebrates was lowest in the burned and similar in the reference and burned & salvage-logged watersheds (mean $\delta^{13}C$ = -30.76 ‰ ± 0.38, -32.48 ‰ ± 0.29 and -30.03 ‰ ± 0.24 in the reference, burned and burned & salvage-logged watersheds respectively; $P < 0.001$) (Table 3.3; Figure 3.4a). Invertebrates from burned and burned & salvage-logged streams were enriched in $\delta^{15}N$ relative to reference invertebrates ($\delta^{15}N$ = 0.34 ‰ ± 0.26, 2.12 ‰ ± 0.19 and 2.36 ‰ ± 0.22 in the reference, burned and burned & salvage-logged watersheds respectively; $P < 0.001$) (Table 3.3; Figure 3.4b).

3.3.3 Fish

Fish from burned watersheds were slightly depleted in $\delta^{13}C$ relative to fish from reference watersheds ($\delta^{13}C$ = -28.06 ‰ ± 0.16, -28.63 ‰ ± 0.17 in the reference and burned watersheds respectively; $P < 0.05$) (Table 3.3; Figure 3.5a). Fish $\delta^{15}N$ did not differ between treatments ($\delta^{15}N$ = 6.80 ‰ ± 0.10, 6.80 ‰ ± 0.06 in the reference and burned watersheds respectively; P = 0.50) (Table 3.3; Figure 3.5b).

Fish in the 2 and 3 year age classes had slightly higher (not significant at $\alpha = 0.05$) weight:age ratios in reference compared to burned watersheds (weight:age = 18.95 g yr^{-1} ± 1.71, 16.48 g yr^{-1} ± 1.73 in the reference and burned watersheds respectively; $P = 0.09$) (Figure 3.6a). Fork length:age ratios did not differ between fish from reference or burned watersheds (fork length:age = 56.48 mm yr^{-1} ± 1.81, 52.99 mm yr^{-1} ± 1.67 in the reference and burned watersheds respectively; $P = 0.13$) (Figure 3.6b).

3.3.4 Source Partitioning – Linear Mixing Model

The linear mixing model showed high variability between taxa in the proportion of autochthonous (instream) organic carbon contributing to their diets. The standard error of the estimates was quite large due to small sample sizes and variability in isotopic discrimination among sampled taxa and potential food sources; results should be interpreted cautiously. The relative contribution of instream and terrestrial carbon could not be calculated for all taxa indicating that not all dietary carbon sources had been accounted for in this study. Invertebrates from reference watersheds had the lowest proportion of autochthonous carbon in their diets while invertebrates from salvage-logged watersheds had the highest proportion (C_{auto} = 46.6% ± 14.4, 60.5 % ± 12.9 and 75.5 % ± 18.2). Of the taxa in wildfire-affected catchments for which carbon contributions could be calculated with a corresponding estimate for the reference watersheds, 6 of 7 burned and 4 of 5 burned & salvage-logged showed higher proportions of instream carbon relative to the same taxa in reference watersheds. Caddisflies of the family Rhyacophilidae in the burned watersheds had a similar proportion of instream carbon to reference watersheds while rhyacophilids in burned & salvage-logged watersheds showed a smaller proportion (Table 3.4).

3.4 Discussion

Carbon isotopes ratios of primary producers, macroinvertebrates and fish were not affected by the wildfire (Figure 3.7a). The carbon isotope ratios of biota have been reported to both increase (Mihuc and Minshall 2005; Silins *et al.* 2014) and decrease (Spencer *et al.* 2003) following wildfire suggesting either a complex or no direct relationship between wildfire and carbon isotopes. The long time since fire (8 years) may also have contributed to the weak fire signal in carbon isotopes. Instream and terrestrial vegetation had distinct $\delta^{13}C$ signatures in all disturbance categories; terrestrial material was enriched in $\delta^{13}C$ by 3.36 to 7.63 ‰ relative to periphyton. Mihuc and Minshall (2005) also observed distinct $\delta^{13}C$ signatures however they observed terrestrial material to be depleted in $\delta^{13}C$ relative to periphyton. Mixing model analysis suggested that instream organic carbon was an important energy source for macroinvertebrates in all disturbance categories (reference, burned and burned & salvage-logged; Table 3.4). While not all components of consumer diets have been accounted for, in general instream and terrestrial food sources contributed approximately equally to macroinvertebrate diets in reference watersheds. Instream carbon made up a greater portion of invertebrate diets in burned and burned & salvage-logged watersheds (Table 3.4). Increased periphyton use in the burned watersheds was consistent with the increased availability of periphyton; mean annual ash-free dry mass (2005-2011) was between 1.7 and 16.2x and 2.3 and 29.5x higher in the burned and burned & salvage-logged watersheds respectively compared to reference catchments (Silins *et al.*- *unpublished data*). Increased periphyton use following wildfire is consistent with the theoretical basis of the River Continuum Concept (RCC) (Vannote *et al.* 1980). The RCC predicts that terrestrial vegetation is the primary source of energy in headwater streams and when this source of energy is removed, instream primary productivity becomes the most important source. This has been shown in wildfire studies by Spencer *et al.* (2003) and Mihuc and Minshall (2005). Many invertebrates are generalists in their feeding strategies and will indiscriminately consume the most available and accessible food source (Mihuc and Minshall 1995); the increased availability of autochthonous energy in the form of periphyton is reflected in the isotopic signature and relative proportion of that carbon in the invertebrate tissue.

The enrichment in $\delta^{15}N$ in consumers from wildfire affected watersheds (Figure 3.7b) supported the inferences from the mixing model analysis that suggested macroinvertebrates in burned watersheds were consuming more instream food resources (periphyton). Enrichment in $\delta^{15}N$ was observed in both aquatic and terrestrial primary consumers, suggesting that other changes to the nitrogen cycle were occurring as result of the wildfire. Macroinvertebrates from burned and burned & salvage-logged watersheds were enriched in $\delta^{15}N$ by 1.80 and 2.04 ‰ respectively (Table 3.3). The increase in $\delta^{15}N$ of consumers following wildfire is consistent with other wildfire studies (e.g., Spencer *et al.* 2003; Silins *et al.* 2014). The proposed mechanism for this enrichment is increased periphyton consumption. Periphyton has been shown in this and other studies to have a higher $\delta^{15}N$ signature than terrestrial material (Spencer *et al.* 2003; Mihuc and Minshall 2005). Increased periphyton consumption is reflected in the enrichment of $\delta^{15}N$ in macroinvertebrates from wildfire affected watersheds and is consistent with interpretations from the carbon isotope mixing model discussed previously. However, increased consumption of autochthonous energy sources was likely not the only mechanism influencing the $\delta^{15}N$ of the macroinvertebrate consumers. The $\delta^{15}N$ of the terrestrial primary producers in wildfire affected catchments was also enriched in $\delta^{15}N$ by 0.71 to 1.57‰ (Table 3.2). This increase would also have contributed to the increased $\delta^{15}N$ in macroinvertebrates regardless of a change in the proportion of instream and terrestrial material consumed.

Removal of terrestrial vegetation associated with large landscape disturbances such as wildfire and forest harvest have been shown to influence the nitrogen dynamics of both aquatic and terrestrial ecosystems (Pardo *et al.* 2002; Bladon *et al.* 2008). Nitrogen is most available immediately following disturbance due to an increase in microbial nitrification and becomes limiting as succession progresses (Vitousek and Reiners 1975; Pardo *et al.* 2002; Hyodo *et al.* 2013). This pattern was observed in our study watersheds with nitrogen exports increasing in burned watersheds and returning to baseline conditions within 4-5 years (Bladon *et al.* 2008; Silins *et al.* 2016). Nitrogen export has subsequently declined below baseline conditions due to significant uptake by regenerating forests in burned and burned & salvage-logged watersheds (Silins *et al.*- *unpublished data*). Nitrification is the process in which ammonium (NH_4^+) is sequentially oxidized from nitrite (NO_2^-) to nitrate (NO_3^-) by microbes; in this process the microbes discriminate against the heavier isotope of nitrogen resulting in pools of ammonium enriched in ^{15}N and nitrate depleted in ^{15}N (Pardo *et al.* 2002). Ammonium is available for direct uptake by vegetation resulting in foliage more enriched in $\delta^{15}N$ (Hobbie *et al.* 1999; Pardo *et al.* 2002). This pattern was evident in primary producers from wildfire-affected watersheds (Figure 3.3b). As nitrification decreases and nitrogen becomes limiting, plants rely more heavily on mycorrhizal fungi as a source of nitrogen. Fractionation occurs within the fungi and nutrients depleted in $\delta^{15}N$ are passed on to the hosts resulting in foliage depleted in $\delta^{15}N$ (Hobbie et al. 1999; Hyodo et al. 2013) as observed in the reference watersheds. Caution should be used interpreting changes in consumer nitrogen isotope ratios in situations where the isotope ratios of primary producers have not been quantified.

Cutthroat Trout showed no significant differences in nitrogen isotope ratios despite the increased $\delta^{15}N$ observed in macroinvertebrates from burned watersheds. Trout have been shown to have highly variable life history responses to variation in food webs associated with different environments (Juncos *et al.* 2011) suggesting they are well able to adjust to food web changes associated with wildfire. Trout were not sampled in the same watersheds as primary producers and macroinvertebrate consumers, which may also be a factor in this finding. The watersheds selected for electrofishing were larger and had a lower proportion of area burned than the core research watersheds making them less influenced by the effects of wildfire (Gresswell 1999). Cutthroat Trout did not have significant differences in growth rates (length:age and weight:age ratios) between burned and reference watersheds. This is in contrast to the increased growth rates observed in fish from wildfire affected catchments in 2005 (2 years post-fire, Silins *et al.* 2014). There are several possible explanations for the lack of a long-term wildfire effect on the growth of Cutthroat Trout. Macroinvertebrate abundance was higher in burned watersheds in both 2007 (Silins *et al.* 2014) and 2011 (reported in Chapter 2) however abundance is not a reliable indicator of biomass (Llopis-Belenguer *et al.* 2018) and macroinvertebrate biomass was not quantified in this study. It is also likely the diets of fish from unburned watersheds were supplemented by terrestrial invertebrates. Rosenberger *et al.* (2011) found that Rainbow trout (*Oncorhynchus mykiss*) in unburned watersheds contained a higher proportion of terrestrial insects comparted to the diets of fish form burned watersheds. Water temperature is also an important determinant of fish growth; stream temperature was not measured in the watersheds from which fish were sampled. It is likely the differences in fish growth observed in earlier sampling were driven by differences in stream temperature following the wildfire.

3.5 Conclusion

The differences in stable isotope signatures of macroinvertebrate consumers from different disturbance categories (reference, burned and burned & salvage-logged) suggest that instream (autochthonous) primary productivity continues to be an important food resource in wildfire affected watersheds. An additional effect of salvage logging could not be distinguished, as fewer than half of the taxa for which the proportion of instream carbon contribution could be calculated had a corresponding measure from the reference watersheds. While our inferences are limited by a single round of sampling, effects on invertebrate assemblages and fish studied here reflect the longer term effects of physical, chemical, and biological factors produced by wildfire and are consistent with the elevated primary productivity observed over the eight year study. Increased use of autochthonous resources is consistent with observations following wildfire in Montana (Spencer *et al.* 2003) and Yellowstone National Park (Mihuc and Minshall 2005). The resource use (instream vs terrestrial) and growth metrics of a tertiary aquatic consumer (Cutthroat Trout) were not different between reference and wildfire affected watersheds suggesting a muted wildfire influence. Fish are more mobile than many macroinvertebrates and can select the most suitable habitat within a watershed. Forested watersheds are important habitat for Cutthroat Trout and Bull Trout. Resilience to wildfire disturbance will provide an advantage to threatened species already under pressure from sedimentation (Hauer *et al.* 2007), increasing temperatures (Isaak *et al.* 2010) and whirling disease (Nehring and Walker 1996; Cahill *et al.* 2018).

Tables and Figures

Table 3.1 Characteristics of Southern Rockies Watershed Project research watersheds.

Watershed	Watershed Area (km^2)	Area Burned (km^2)	Area Salvage-logged (km^2)	Elevation (m)	Slope (%)	Aspect
Reference (Unburned)						
Star	10.59	0 (0%)	0	1479-2627	45	North East
North York	8.29	0.02 (0.2%)	0	1562-2633	48.8	North East
Burned						
South York	3.59	1.91 (53.2%)	0	1691-2635	42.1	North East
Lynx	8.21	5.53 (67.4%)	0	1632-2629	43.3	North East
Drum	7.13	7.12 (99.9%)	0	1432-2156	47.5	North East
Burned & Salvage-logged						
Lyons East	13.15	10.72 (81.5%)	2.62	1441-2027	31.8	North
Lyons West	7.07	4.13 (58.4%)	2.38	1449-2059	24.8	North East

Table 3.2 Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$; mean ± standard error) for primary producers.

Differences indicated the difference in mean $\delta^{13}C$ or $\delta^{15}N$ shown between primary producers of the same category in reference and wildfire affected (burned or burned & salvage-logged) watersheds.

Primary Producer	Reference		Burned				Burned & Salvage-logged			
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	Difference	$\delta^{15}N$ (‰)	Difference	$\delta^{13}C$ (‰)	Difference	$\delta^{15}N$ (‰)	Difference
Algae	-33.61 ± 1.04	-0.84 ± 0.14	-34.42 ± 1.54	-0.8	0.73 ± 0.40	1.57	-30.4 ± 0.17	3.21	0.50 ± 0.26	1.34
Terrestrial Vegetation	-27.17 ± 0.16	-2.25 ± 0.09	-26.79 ± 0.17	0.38	-1.03 ± 0.13	1.22	-27.04 ± 0.20	0.13	-1.54 ± 0.16	0.71
Catkins	-26.97 ± 0.22	-2.01 ± 0.17	--	--	--	--	-27.64 ± 0.38	-0.67	-1.28 ± 0.25	0.73
Grass	-26.74	-3.04	-26.23 ± 2.39	0.51	0.87 ± 1.78	3.91	-29.32 ± 2	-2.58	1.6 ± 1.03	4.64
Leaves	-29.1 ± 0.18	-2.11 ± 0.12	-28.09 ± 0.19	1.01	-1.31 ± 0.19	0.81	-28.79 ± 0.3	0.31	-1.5 ± 0.33	0.61
Needles	-27.15 ± 0.04	-4.08 ± 0.17	-26.32 ± 0.01	0.83	-3.36 ± 0.18	0.72	-25.71 ± 0.01	1.44	-3.59 ± 0.22	0.49
Other	-26.89 ± 0.1	-2.27 ± 0.12	-26.16 ± 0.2	0.73	-0.47 ± 0.2	1.8	-26.72 ± 0.18	0.17	-1.24 ± 0.16	1.03
Cones	-27.96	-3.04	-25.79	2.17	-2.18	0.86	-24.89 ± 0.09	3.07	-1.9 ± 1.2	1.14
Seeds	--	--	-28.34 ± 0.66	0	0.17 ± 0.22	0	-27.78 ± 0.9	0	-1.91 ± 1.07	0
Wood	-25.82 ± 0.25	-2.18 ± 0.22	-26 ± 0.26	-0.2	-1.52 ± 0.18	0.66	-26.28 ± 0.32	-0.46	-1.81 ± 0.23	0.37

Table 3.3 Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$; mean ± standard error) for aquatic consumers (macroinvertebrates and Cutthroat Trout).

Differences indicated the difference in mean $\delta^{13}C$ or $\delta^{15}N$ shown between consumers of the same taxa in reference and wildfire affected (burned or burned & salvage-logged) watersheds.

	Reference		Burned				Burned & Salvage-logged			
Taxa	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**$\delta^{13}C$ (‰)**	**Difference**	**$\delta^{15}N$ (‰)**	**Difference**	**$\delta^{13}C$ (‰)**	**Difference**	**$\delta^{15}N$ (‰)**	**Difference**
Elmidae	-36.9	-3.06	-35.06 ± 0.59	1.84	-0.12 ± 0.51	2.94	-31.49 ± 0.18	5.41	0.16 ± 0.14	3.22
Heptageniidae	-33.12 ± 0.52	-1.67 ± 0.12	-33.86 ± 0.75	-0.74	0.35 ± 0.68	2.02	-29.8	3.32	1.95	3.62
Baetidae	-34	0.52	-33.03 ± 0.71	0.97	2.46 ± 0.39	1.94	-30.45 ± 0.55	3.55	2.42 ± 0.14	1.9
Capniidae-Leuctridae	-26.47 ± 0.11	0.74 ± 0.11	-27.27 ± 0.4	-0.8	2.66 ± 0.5	1.92	-26.05 ± 0.25	0.42	3.53 ± 0.2	2.79
Peltoperlidae	-30.85 ± 0.21	-1.79 ± 0.23	-32.06 ± 0.9	-1.21	0.74 ± 0.46	2.53	-29.7 ±	1.15	1.87 ±	3.66
Tipulidae	-26.9	3.25	-30.53 ± 1.62	-3.63	3.98 ± 0.77	0.73	-28.54 ± 0.41	-1.64	2.65 ± 0.51	-0.6
Hydropsychidae	-30.11 ± 0.32	1.74 ± 0.49	-32.33 ± 0.83	-2.22	2.95 ± 0.66	1.21	-31.7	-1.59	2.12	0.39
Psychodidae	-27.5	1.34	-30.79 ± 0.74	-3.29	3.64 ± 0.33	2.3	-27.45 ± 0.95	0.05	3.64 ± 0.34	2.3
Perlidae	-32.2 ± 0.84	1.71 ± 0.35	-33.2	-1	4.49	2.79	-30.84 ± 0.35	1.36	3.9 ± 0.21	2.2
Perlodidae	-30.78 ± 0.37	1.34 ± 0.43	-32.68 ± 0.72	-1.9	2.64 ± 0.52	1.29	-31.98 ± 0.34	-1.2	2.23 ± 0.15	0.89
Rhyacophilidae	-28.75 ± 0.72	2.31 ± 0.43	-33.11 ± 0.63	-4.36	2.67 ± 0.33	0.36	-29.13 ± 0.36	-0.38	3.75 ± 0.3	1.44
Invertebrate Average	-30.76 ± 0.38	0.34 ± 0.26	-32.78 ± 0.29	-2.02	2.12 ± 0.19	1.8	-30.03 ± 0.24	0.73	2.36 ± 0.22	2.04
Salmonidae	-28.46 ± 0.15	6.8 ± 0.10	-29.12 ± 0.18	-0.66	6.81 ± 0.06	-1	–	–	–	–

Table 3.4 Estimated proportion (± standard error) of instream organic carbon contribution to the diets of aquatic consumers (macroinvertebrates and Cutthroat Trout).

Bold type indicates that instream carbon contributes greater than 50%.

	Reference	**Burned**		**Burned & Salvage-Logged**	
Taxa	**% Instream C**	**% Instream C**	**Difference**	**% Instream C**	**Difference**
Baetidae	*> 100 %*	**61.0 % ± 14.1**	--	**81.4 % ± 21.1**	--
Capniidae-Leuctridae	*< 0 %*	5.6 % ± 18.1	--	*< 0 %*	--
Elmidae	*> 100 %*	**76.0 % ± 16.1**	--	*> 100 %*	--
Heptageniidae	45.6 % ± 6.8	**78.1 % ± 17.5**	32.6 %	**78.2 % ± 22.8**	32.6 %
Hydropsychidae	**50.6 % ± 7.8**	**67.0 % ± 8.7**	16.3 %	*> 100 %*	--
Peltoperlidae	40.9 % ± 3.0	**76.6 % ± 6.6**	35.8 %	**75.0 % ± 22.8**	34.1 %
Perlidae	22.8 % ± 12.3	**58.9 % ± 7.7**	36.1 %	**86.6 % ± 12.3**	63.8 %
Perlodidae	**55.1 % ± 16.3**	**64.9 % ± 9.6**	9.8 %	*> 100 %*	--
Psychodidae	11.5 % ± 28.1	34.2 % ± 16.2	22.8 %	47.4 % ± 21.0	35.9 %
Rhyacophilidae	**76.1 % ± 14.5**	**75.7 % ± 10.8**	-0.4 %	**69.2 % ± 18.1**	6.9 %
Tipulidae	*< 0 %*	**55.2 % ± 16.9**	--	**88.0 % ± 11.6**	--
Invertebrate Average	46.6 %	**60.5 %**	19.0 %	**75.5 %**	33.0 %
Salmonidae	14.0 % ±4	24.0 % ± 4 %	10.0 %	--	--

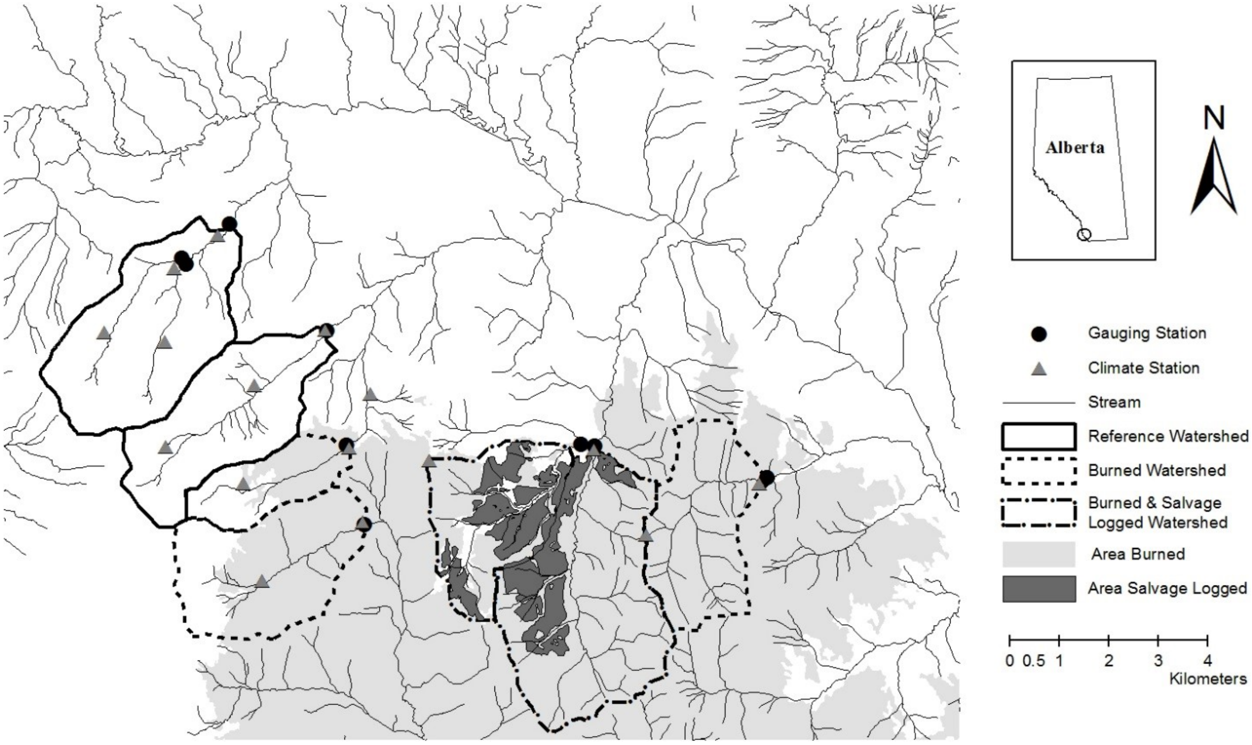


Figure 3.1 Southern Rockies Watershed Project research watersheds.

West to east: Star Creek, North York Creek, South York Creek, Lynx Creek, Lyons West Creek, Lyons East Creek and Drum Creek). Lines indicate watershed boundaries; solid = reference, dash = burned, dot-dash = burned & salvage-logged. Shading indicates forest disturbance: light grey = burned area, dark grey = burned & salvage-logged area.

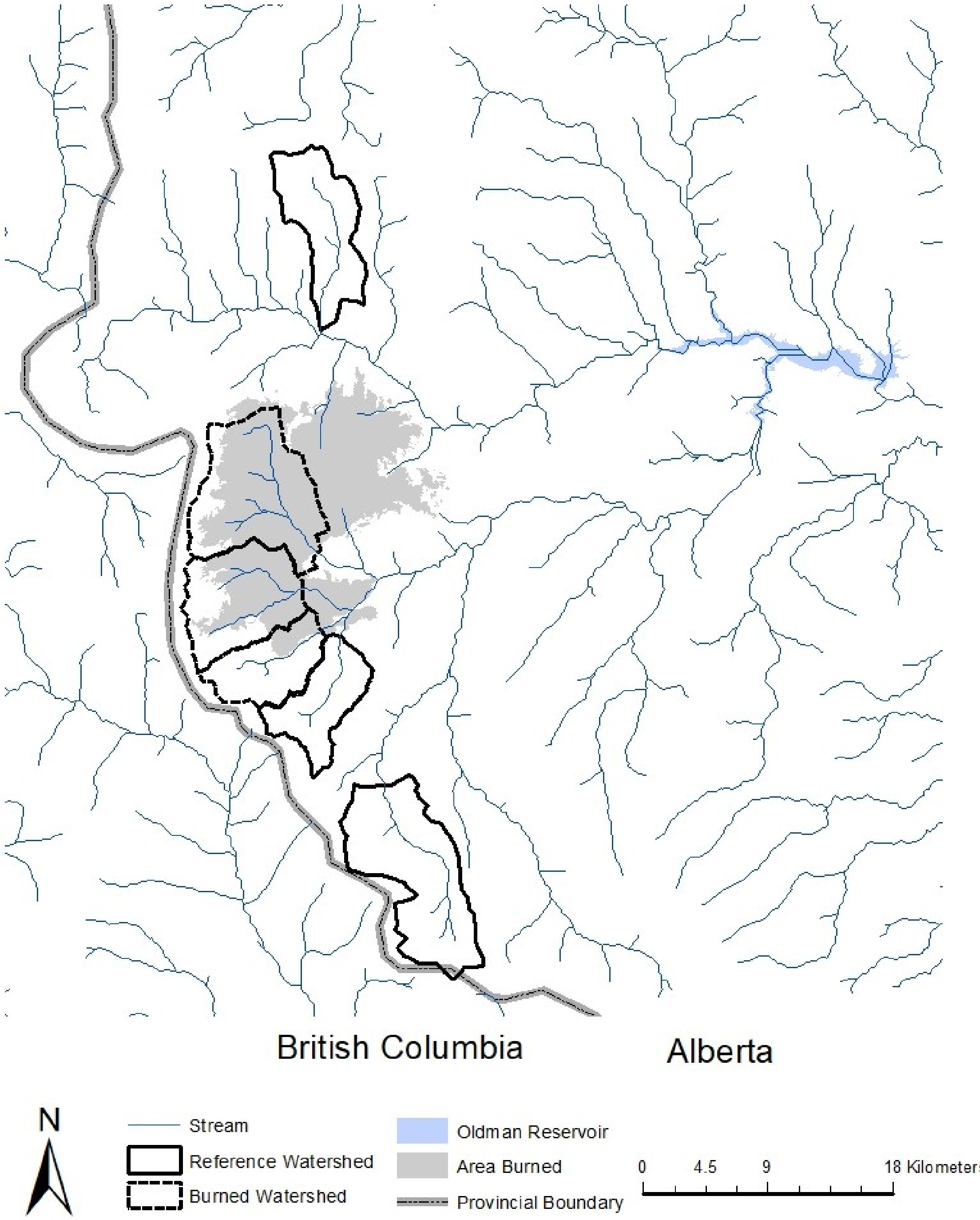
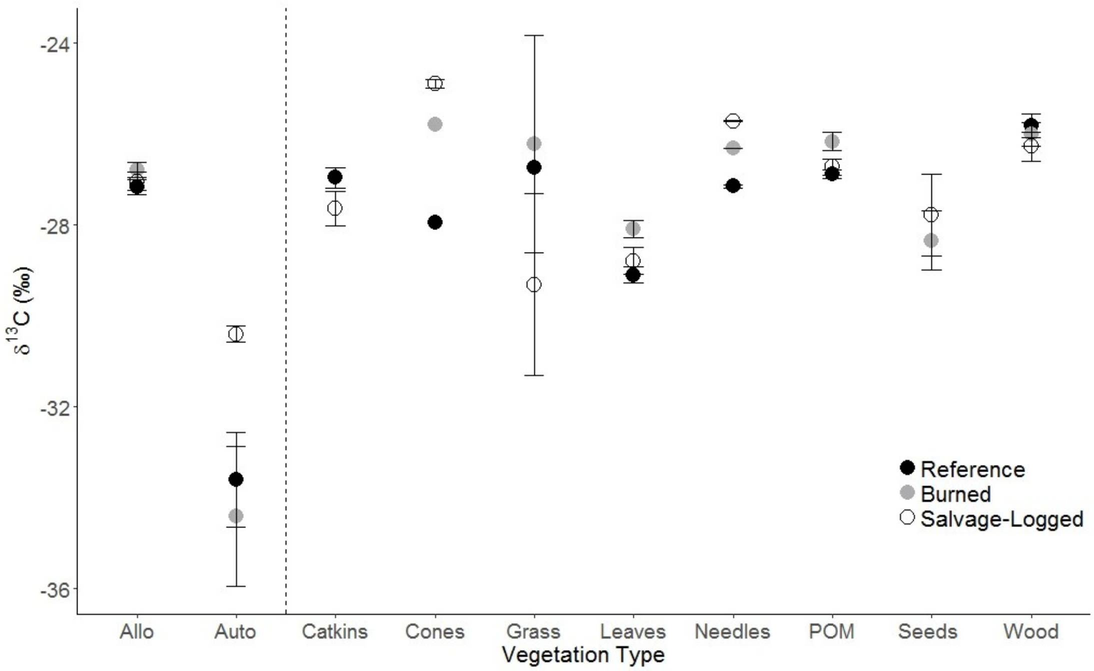


Figure 3.2 Regional fish sampling watersheds.

North to south: Blairmore Creek, Lynx Creek, Lost Creek, Carbondale River, Gardiner Creek and the West Castle River. Lines encompass watershed boundaries: solid = reference, dash = burned. The grey and black dashed line represents the British Columbia - Alberta provincial boundary.

a)



b)

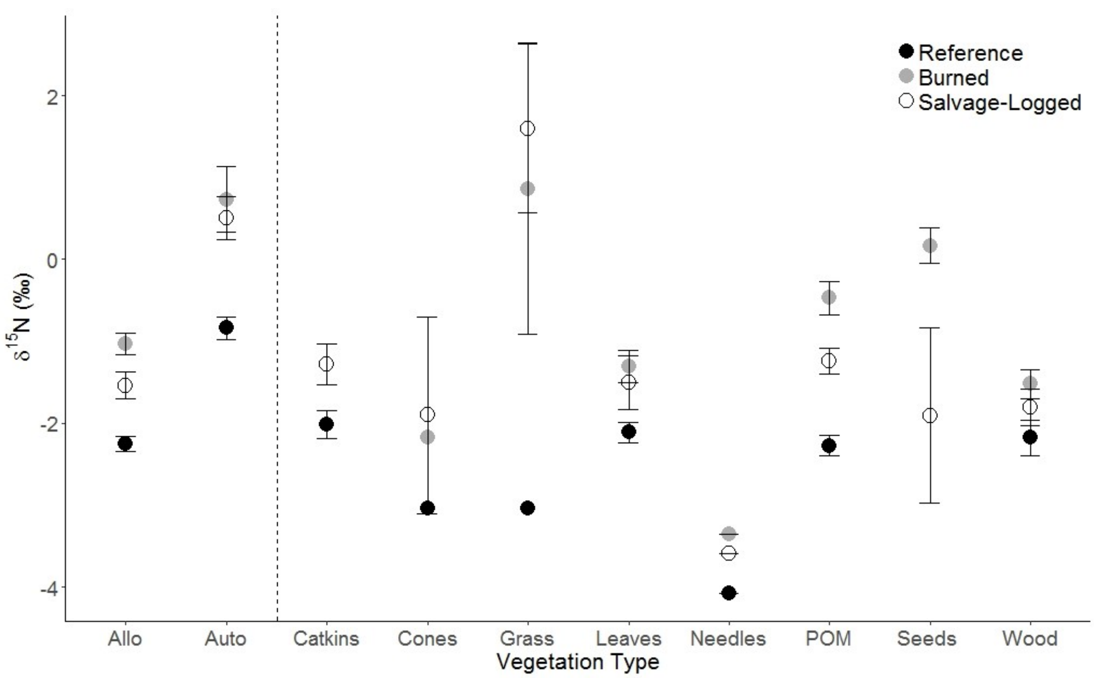


Figure 3.3 Stable isotope ratios for eight primary producer categories (right), and total combined allochthonous (allo) and autochthonous (auto) sources (left).

Error bars show standard error; black = reference, gray = burned, white = burned & salvage-logged.

a)

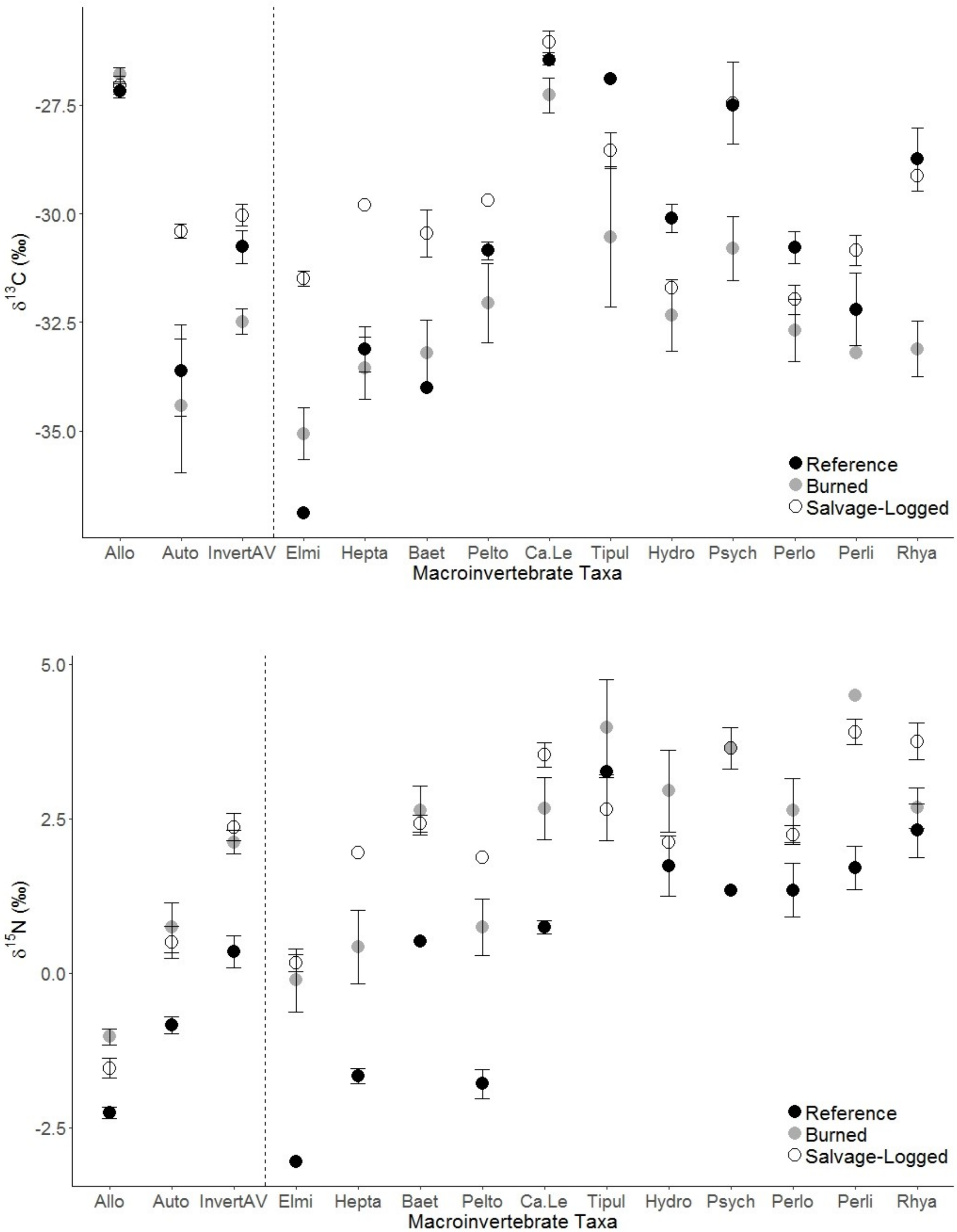


Figure 3.4 Stable isotope ratios for eleven macroinvertebrate families (right), and total combined macroinvertebrates (InvertAv).

Error bars show standard error; black = reference, gray = burned, white = burned & salvage-logged. Total allochthonous (allo) and autochthonous (auto) primary producers (from Figure 3.3) shown for comparison.

a) b)

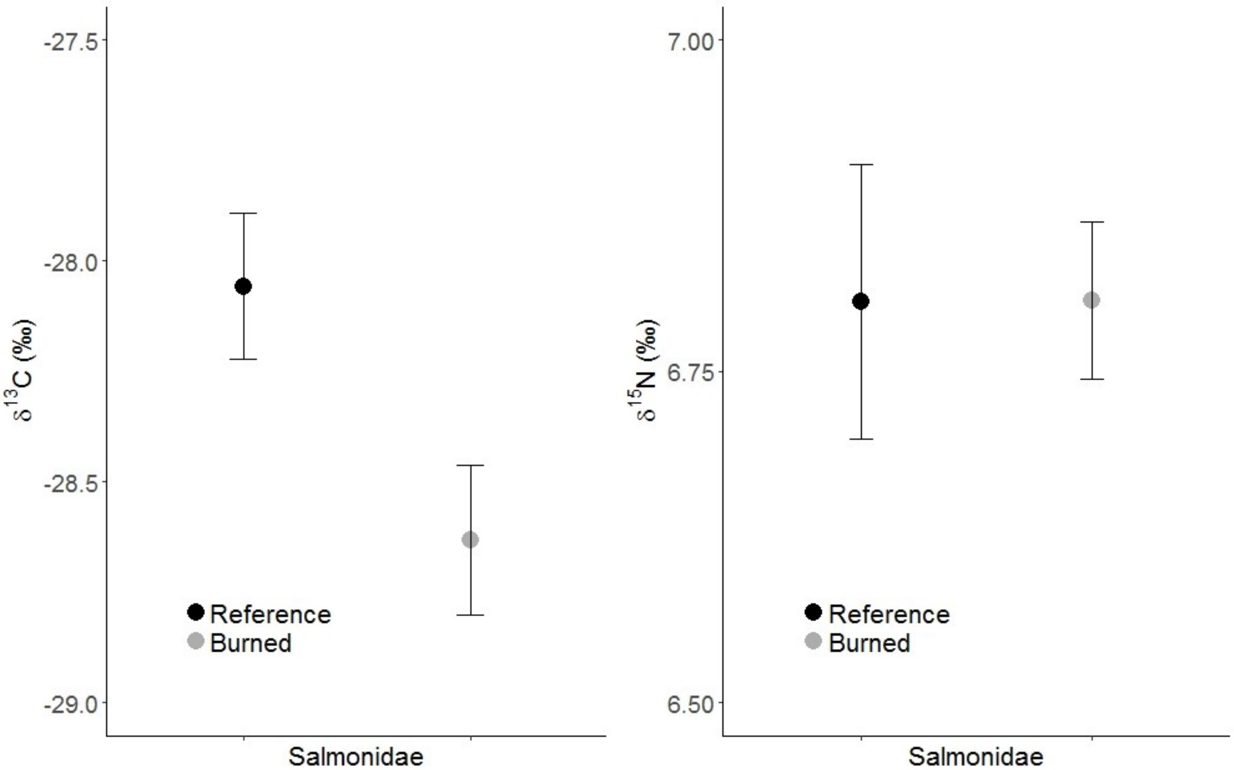


Figure 3.5 Stable isotope ratios of Cutthroat Trout (family Salmonidae).

Error bars show standard error; black = reference, gray = burned.

a) b)

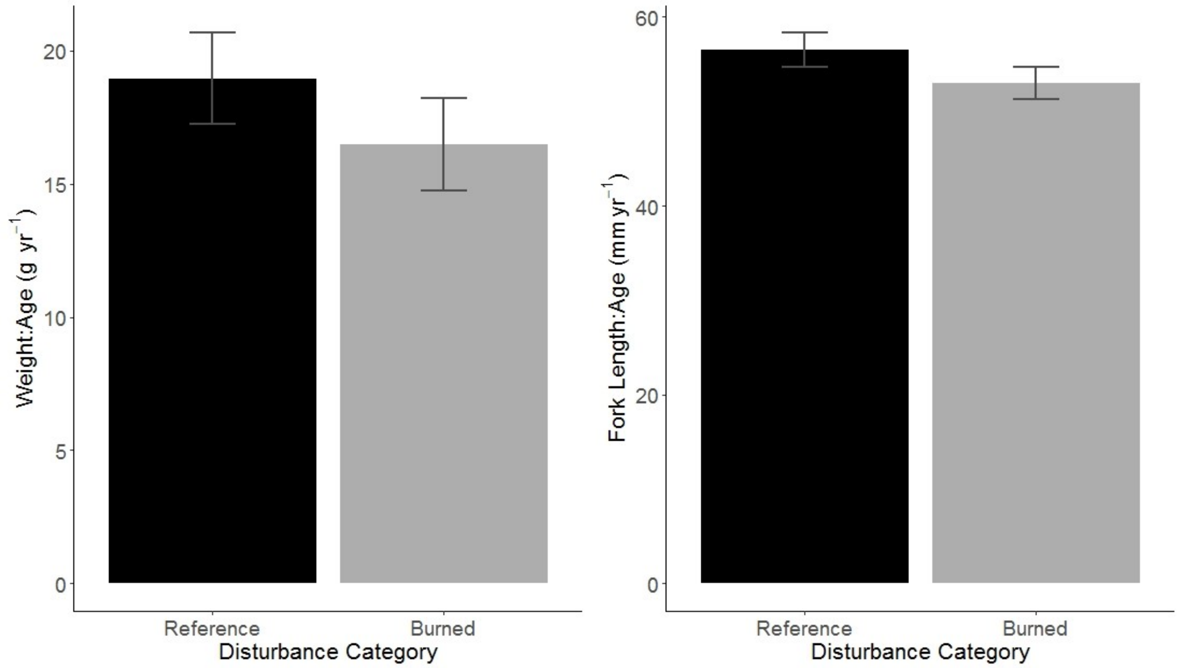
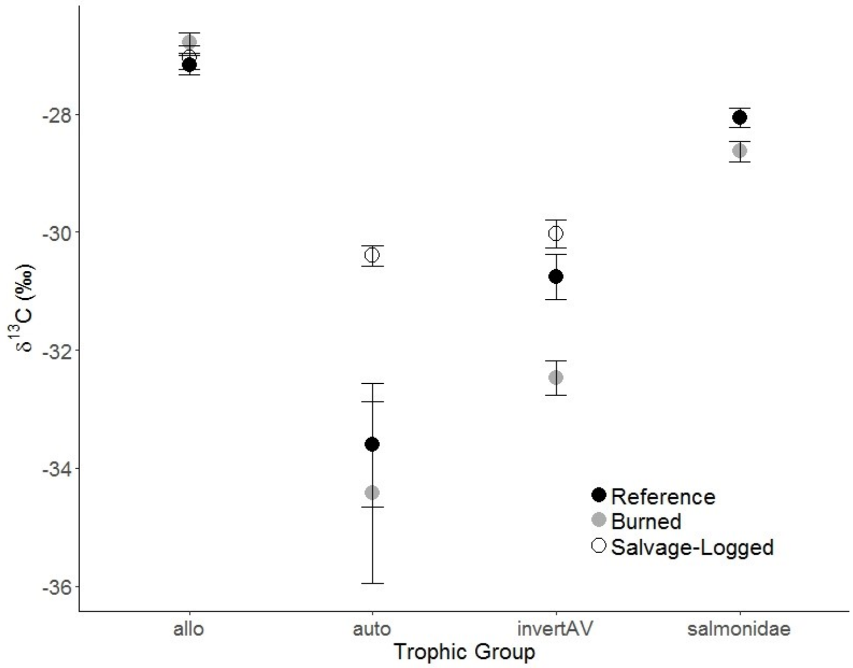


Figure 3.6 Weight:age and length:age ratios (proxies for growth rates) for Cutthroat Trout. Black = reference, grey = burned.

a)



b)

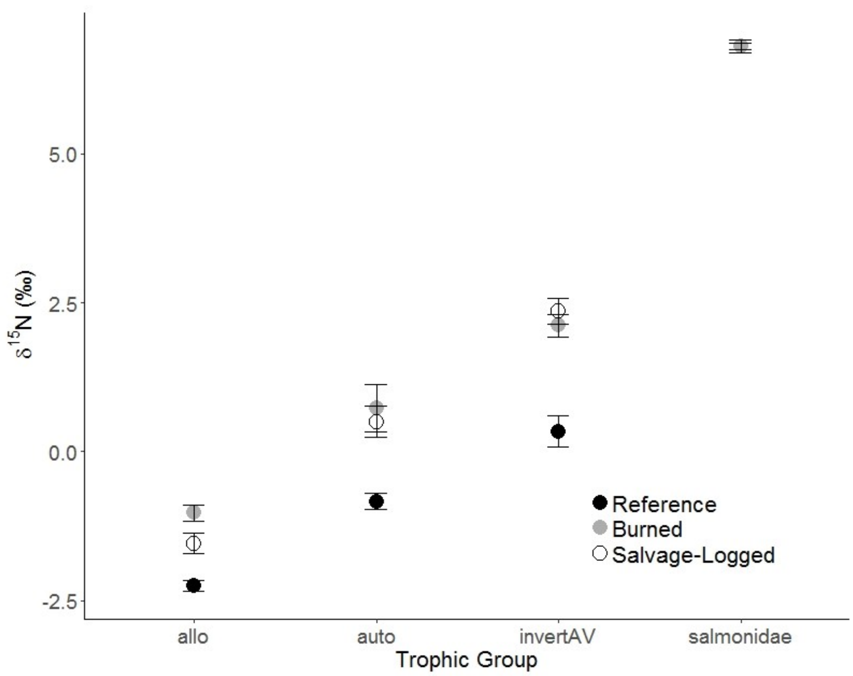


Figure 3.7 Stable isotope ratios of the major trophic levels comprising the food webs of reference, burned, and burned & salvaged-logged watersheds.

Literature Cited

Alberta Environment and Parks (2014) 'Alberta Species at Risk.' Available at http:// aep .alberta.ca/fish-wildlife/species-at-risk/documents/SpeciesAssessedConservation-2014a.pdf [Accessed 4-14-17].

Anderson C, Cabana G (2007) Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. *Journal of the North American Benthological Society* **26**, 273-285.

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

Bligh E, Dyer W (1959) A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology* **37**, 911-917.

Brodie C, Heaton T, Leng M, Kendrick C, Casford J, Lloyd J (2011a) Evidence for bias in measured delta N-15 values of terrestrial and aquatic organic materials due to pre-analysis acid treatment methods. *Rapid Communications in Mass Spectrometry* **25**, 1089-1099.

Brodie C, Leng M, Casford J, Kendrick C, Lloyd J, Zong Y, Bird M (2011b) Evidence for bias in C and N concentrations and delta C-13 composition of terrestrial and aquatic organic materials due to pre-analysis acid preparation methods. *Chemical Geology* **282**, 67-83.

Cahll CL, Mogensen S, Wilson KL, Cantin A, Sinnatamby RN, Paul AJ, Christensen P, Reilly JR, Winkel L, Farineau A, Post JR (2018) Multiple challenges confront a high-effort inland recreational fishery in decline. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 1357-1368.

Clifford HF, 1991. Aquatic invertebrates of Alberta an illustrated guide. University of Alberta Press, Edmonton, AB.

Cummins K (1973) Trophic relations of aquatic insects. *Annual Review of Entomology* **18**, 183-206.

Cummins K (1974) Structure and function of stream ecosystems. *Bioscience* **24**, 631-641.

Deniro M, Epstein S (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* **197**, 261-263.

Deniro M, Epstein S (1978) Influence of diet on distribution of carbon isotopes in animals. *Geochimica Et Cosmochimica Acta* **42**, 495-506.

Emelko MB, Stone M, Silins U, Allin D, Collins AL, Williams CHS, Martens AM, Bladon KD (2016) Sediment-phosphorus dynamics can shift aquatic ecology and cause downstream legacy effects after wildfire in large river systems. *Global Change Biology* **22**, 1168-1184.

Flanniga, M, Logan K, Amiro B, Skinner W, Stocks B (2005) Future area burned in Canada. *Climatic Change* **72**, 1-16.

Fry B (1991) Stable isotope diagrams of freshwater food webs. *Ecology* **72**, 2293-2297.

Fry B (2006) 'Stable Isotope Ecology.' (Springer: New York, NY, USA).

Gresswell R (1999) Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* **128**, 193-221.

Hauer FR, Stanford, JA, Lorang, MS (2007) Pattern and process in Northern Rocky Mountain headwaters: Ecological linkages in the headwaters of the Crown of the Continent. *Journal of the American Water Resources Association* **43**, 104-117.

Hobbie E, Macko S, Shugart H (1999) Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* **118**, 353-360.

Hynes HBN (1975) The stream and its valley. *Proceedings of the International Association of Theoretical and Applied Limnology* **19**, 1-15.

Hyodo F, Kusaka S, Wardle D, Nilsson M (2013) Changes in stable nitrogen and carbon isotope ratios of plants and soil across a boreal forest fire chronosequence. *Plant and Soil* **367**, 111-119.

Isaak DJ, Young M, Luce C, Hostetler S, Wenger S, Peterson E, Hoef J, Groce M, Horan D, Nagel D (2016) Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 4374-4379.

Isaak DJ, Luce CH, Rieman BE, Nagel DE, Peterson EE, Horan DL, Parkes S, Chandler GL (2010) Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* **20**, 1350-1371.

Jacob U, Mintenbeck K, Brey T, Knust R, Beyer K (2005) Stable isotope food web studies: a case for standardized sample treatment. *Marine Ecology Progress Series* **287**, 251-253.

Jaschinski S, Brepohl DC, Sommer U (2011) The trophic importance of epiphytic algae in a freshwater macrophyte system (Potamogeton perfoliatus L.): stable isotope and fatty acid analyses. *Aquatic Sciences* **73**, 91-101.

Juncos R, Milano D, Macchi PJ, Alonso MF, Vigliano PH (2011) Response of rainbow trout to different food web structures in northern Patagonia: implications for growth, bioenergetics, and invasiveness. *Transactions of the American Fisheries Society* **140**, 415-428.

Kennedy P, Kennedy H, Papadimitriou S (2005) The effect of acidification on the determination of organic carbon, total nitrogen and their stable isotopic composition in algae and marine sediment. *Rapid Communications in Mass Spectrometry* **19**, 1063-1068.

Koetsier P, Tuckett Q, White J (2007) Present effects of past wildfires on the diets of stream fish. *Western North American Naturalist* **67**, 429-438.

Llopis-Belenguer C, Blasco-Costa I, Balbuena JA (2018) Evaluation of three methods for biomass estimation in small invertebrates, using three large disparate parasite species as model organisms (vol 8, 3897, 2018). *Scientific Reports* **8**,

Malison R, Baxter CV (2010a) The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 570-579.

Malison RL, Baxter CV (2010b) Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. *Journal of the North American Benthological Society* **29**, 1324-1338.

Mihuc T, Minshall G (1995) Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. *Ecology* **76**, 2361-2372.

Mihuc TB, Minshall GW (2005) The trophic basis of reference and post-fire stream food webs 10 years after wildfire in Yellowstone National Park. *Aquatic Sciences* **67**, 541-548.

Mihuc TB, Minshall GW, Robinson CT (1996) Response of benthic macroinvertebrate populations in Cache Creek, Yellowstone National 60 Park to the 1988 wildfires. In 'The ecological implications of fire in Greater Yellowstone: proceedings on the second biennial Conference on the Greater Yellowstone Ecosystem', 19–21 September 1993, Yellowstone National Park, WY, USA. (Ed JM Greenlee) International Association of Wildland Fire, pp. 83–94. (Fairfield, WA, USA).

Minagawa M, Wada E (1984) Stepwise enrichment of N15 along food chains - further evidence and the relation between delta N15 and animal age. *Geochimica Et Cosmochimica Acta* **48**, 1135-1140.

Minshall GW (2003) Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management* **178**, 155-161.

Minshall GW, Robinson CT, Lawrence DE (1997) Postfire responses of lotic ecosystems in Yellowstone National Park, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2509-2525.

Nehring R, Walker P (1996) Whirling disease in the wild: The new reality in the intermountain West. *Fisheries* **21**, 28-30.

Pardo L, Hemond H, Montoya J, Fahey T, Siccama T (2002) Response of the natural abundance of N-15 in forest soils and foliage to high nitrate loss following clear-cutting. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **32**, 1126-1136.

Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. *Oecologia* **127**, 171-179.

Pinnegar J, Polunin N (1999) Differential fractionation of delta C-13 and delta N-15 among fish tissues: implications for the study of trophic interactions. *Functional Ecology* **13**, 225-231.

Post DM (2002) Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **83**, 703-718.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reid, D, Quinn, J, Wright-Stow, A (2010) Responses of stream macroinvertebrate communities to progressive forest harvesting: Influences of harvest intensity, stream size and riparian buffers. *Forest Ecology and Management* **260**, 1804-1815.

Resco V, Ferrio J, Carreira J, Calvo L, Casals P, Ferrero-Serrano A, Marcos E, Moreno J, Ramirez D, Sebastie M, Valladares F, Williams D (2011) The stable isotope ecology of terrestrial plant succession. *Plant Ecology & Diversity* **4**, 117-130.

Rinne JN (1996) Management briefs: short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *North American Journal of Fisheries Management* **16**, 653-658.

Rosenberger AE, Dunham JB, Buffington JM, Wipfli MS (2011) Persistent Effects of Wildfire and Debris Flows on the Invertebrate Prey Base of Rainbow Trout in Idaho Streams. *Northwest Science* **85**, 55-63.

Rounick JS, Winterbourn MJ, Lyon GL (1982) Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New-Zealand streams - A Stable Carbon Isotope Study. *Oikos* **39**, 191-198.

Silins U, Anderson A, Bladon KD, Emelko MB, Stone M, Spencer SA, Williams CHS, Wagner MJ, Martens, AM, Hawthorn, K (2016) Southern Rockies Watershed Project. *Forestry Chronicle* **92**, 39-42.

Silins U, Bladon K, Kelly E, Esch E, Spence J, Stone M, Emelko M, Boon S, Wagner M, Williams C, Tichkowsky I (2014) Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. *Ecohydrology* **7**, 1508-1523.

Sotiropoulos M, Tonn W, Wassenaar L (2004) Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecology of Freshwater Fish* **13**, 155-160.

Spencer C, Gabel K, Hauer F (2003) Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management* **178**, 141-153.

Szepanski MM, Ben-David,M, Van Ballenberghe V (1999) Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia* **120**, 327-335.

Thorp J, Covich A (2009) 'Ecology and Classification of North American Freshwater Invertebrates Third Edition.' (Academic Press: London, UK)

US EPA (2000). Guidance for assessing chemical contaminant data for use in fish advisories. Washington, DC. 1: 485.

US Fish and Wildlife Service (2017) 'Environmental Conservation Online System.' Available at https://ecos.fws.gov/ecp0/pub/SpeciesReport.do?groups=E&listingType=L&mapstatus=1 [Accessed 4-14-17].

Vannote R, Minshall G, Cummins K, Sedell J, Cushing C (1980) River continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130-137.

Vitousek P, Reiners W (1975) Ecosystem succession and nutrient retention: A Hypothesis. *Bioscience* **25**, 376-381.

Voshell, JR (2002) 'A Guide to Common Freshwater Invertebrates of North America.' (The McDonald and Woodward Publishing Company: Blacksburg, Virginia)

Westerling A, Hidalgo H, Cayan D, Swetnam T (2006) Warming and earlier spring increase western US forest wildfire activity. *Science* **313**, 940-943.

Zah R, Burgherr, P Bernasconi S, Uehlinger U (2001) Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology* **46**, 871-882.

Chapter 4 Synthesis

The broad objectives of my study were to determine if the longer-term changes in water quality, rainfall-runoff dynamics and biogeochemistry 8 years after the Lost Creek wildfire and post-wildfire salvage-logging produced measurable effects on the aquatic fauna (benthic macroinvertebrates and fish) in Rocky Mountain headwater streams. Chapter 2 reported on differences in macroinvertebrate assemblage structure between reference (unburned), burned and burned & salvage-logged watersheds. In addition I analyzed ecological traits of abundant and rare taxa to infer the mechanism behind differences in assemblage structure. In Chapter 3 I reported on differences in food web structure including differences in primary productivity between disturbance categories where stable isotope analysis (carbon and nitrogen) was used to determine the relative contribution of instream and terrestrial primary productivity to the diets of aquatic consumers.

Clear differences in macroinvertebrate assemblages were observed between disturbance categories (Chapter 2). Legacy effects of the Lost Creek wildfire on macroinvertebrate assemblages was expected given the severity of the wildfire. The landscape immediately after the fire was striking where the majority of forest canopy and forest floor organic matter had been consumed leaving exposed mineral soil (Figure 4.1). The wildfire had persistent effects on water quality; parameters such as total suspended solids, turbidity, phosphorous and dissolved organic carbon showed no sign of recovery after 11 years of continuous monitoring (Emelko *et al.* 2016; Silins *et al.* 2016). The additional effect of salvage-logging was apparent as the burned and salvage-logged watersheds experienced greater impacts to water-quality compared to watersheds affected only by wildfire. However, unexpectedly, the differences in macroinvertebrate assemblage structure did not follow the same pattern as the abiotic effects. Instead each of the reference, burned and burned & salvage-logged watersheds supported a unique assemblage of macroinvertebrates, suggesting that there were different mechanisms influencing the macroinvertebrate responses to wildfire and to post-fire salvage logging. While habitat and food resources are both important factors that can influence assemblage structure, the strength of influence depends on the severity of the wildfire or post-fire salvage logging disturbances and their effect on water quality and aquatic primary productivity.

Periphyton productivity was highest in the burned & salvage-logged watersheds and lowest in the reference watersheds. The abundance of macroinvertebrates in the burned watersheds was more than 2x higher compared to both the reference and burned & salvage-logged watersheds, suggesting that resource availability was likely the major mechanism driving assemblage structure in the burned watersheds. Macroinvertebrates were able to take advantage of the extra food availability because the water quality had not deteriorated to the point that the habitat was no longer suitable. In contrast, macroinvertebrates in the burned & salvage-logged watersheds were likely more affected by habitat degradation. The lower water quality and more extreme rainfall runoff dynamics observed in the burned & salvage-logged watersheds produced poor water quality that reduced habitat quality. The sediment loading and associated sediment intrusion into streambeds of salvage-logged streams limited habitat for several macroinvertebrate taxa including baetid mayflies (Ephemeroptera: Baetidae). This taxon has been reported to be tolerant to disturbance (e.g., Malison and Baxter 2010) and were observed in high abundance in the burned watersheds. As well very few caddisflies (Trichoptera) were observed in the burned & salvage-logged watersheds. Many caddisfly taxa are known to be sensitive to fine sediment deposition (Bjornn *et al.* 1977; Voshell 2002). Taxa tolerant of high sediment environments including crane flies (Diptera: Tipulidae) and riffle beetles (Coleoptera: Elmidae) (Bjornn *et al*

1977; Brown 1987; Giller and Malmqvist 1998; Voshell 2002)were abundant in burned & salvage-logged watersheds. Habitat limitation was the primary driver of assemblage structure in the burned & salvage-logged watersheds. Taxa that could tolerate the poor water quality and sediment loading were able to take advantage of the increased primary productivity.

Stable isotope analysis of food wed structure showed that instream food resources (periphyton) were an important source of energy for consumers in all disturbance categories (Chapter 3). Periphyton made up a larger proportion of the diets of macroinvertebrate consumers in both burned and burned & salvage-logged watersheds compared to unburned watersheds. Increased use of instream food resources is consistent with the increased availability of periphyton as well as observations of increased macroinvertebrate abundance in burned watersheds (Chapter 2). However, an additional effect of salvage-logging on the diet of macroinvertebrate consumers could not be detected.

Carbon isotope ratios of primary producers (terrestrial and aquatic), as well as consumers (macroinvertebrates and fish) did not appear to be affected by the wildfire. In contrast, nitrogen isotope ratios showed clear long-term responses to wildfire (Chapter 3) where primary producers and macroinvertebrate consumers were consistently enriched in $\delta^{15}N$ (the heavy isotope of nitrogen) in wildfire affected watersheds. Both primary producers and macroinvertebrate consumers showed this enrichment, indicating that food web structure is not the sole mechanism behind the enrichment. Increased $\delta^{15}N$ observed in aquatic consumers has been attributed to increased consumption of periphyton (Beaudoin *et al.* 2001; Spencer *et al.* 2003) however isotopic changes in terrestrial ecosystems must also be accounted for. The increase in $\delta^{15}N$ observed in both terrestrial and aquatic primary producers highlights the tight link between aquatic and terrestrial ecosystems. The loss of terrestrial vegetation caused by large landscape disturbances (e.g., wildfire and forest harvest) has been shown to affect the nitrogen dynamics of both aquatic and terrestrial systems (Pardo *et al.* 2002; Bladon *et al.* 2008). Strongly elevated nitrogen (both nitrate and ammonium) was evident for at least 3-4 years immediately following the Lost Creek wildfire (Bladon *et al.* 2008). Accordingly, it is likely that post-fire nitrification produced ammonium (NH_4^+) enriched in $\delta^{15}N$ which, when taken up by the rapidly regenerating vegetation produced foliage enriched in $\delta^{15}N$ (Hobbie *et al.* 1999; Hyodo *et al.* 2013). When that organic material entered the stream, it was broken down and contributed enriched $\delta^{15}N$ to the aquatic nitrogen cycle where it was taken up by aquatic primary producers (periphyton) as well as macroinvertebrate consumers.

Cutthroat trout (*Oncorhynchus clarkii*) did not show meaningful differences in isotope ratios (carbon and nitrogen) or growth metrics (length:age and weight:age ratios) between reference and burned watersheds. This is in contrast to the greater size and growth rates observed in Cutthroat Trout sampled in the same burned watersheds 2 years after the fire (Silins *et al.* 2014). A similar species, Rainbow Trout (*Oncorhynchus mykiss*) has been shown to adopt different feeding strategies in different environments (Juncos *et al.* 2011), this plasticity has facilitated their success across a range of ecosystems. Rieman *et al.* (1997) found that both Redband (interior Rainbow Trout – *Oncorhynchus mykiss*) and Bull Trout (*Salvelinus confluentus*) populations recovered within 3 years following intense wildfires in the Boise River basin in Idaho. Salmonids are, however, sensitive to warm water temperatures (Isaak *et al.* 2010) and sedimentation (Rinne 1996; Sear *et al.* 2016). The additive effects of climate warming (Isaak *et al.* 2016) and other sediment contributing landscape disturbances such as forest harvest and roads (Ripley *et al.* 2005) must be included when considering how wildfire will impact fish.

The salvage harvest conducted in the Lyons Creek valley had an additive effect on the severity of the wildfire disturbance. Sediment transport and deposition were greater in the burned & salvage-logged watersheds compared to the watersheds affected by wildfire alone (Silins *et al.* 2009; Emelko *et al.* 2016). The persistent effects on water quality had long lasting impacts on the macroinvertebrate assemblages in affected watersheds (Chapter 2). This additive effect highlights the need to consider cumulative impacts before moving forward with post-wildfire management. While recouping economic loses or reducing fuel loads can be important management goals, the consequences to aquatic ecosystems can be long-lasting. Eight years after the Lost Creek wildfire macroinvertebrate assemblages in burned & salvage-logged watersheds were quite different from those in the unburned reference watersheds and characterized by taxa tolerant of high sediment loads. While this study focused only on aquatic habitats, salvage-logging can also have consequences for terrestrial plant and animal species by reducing habitat for cavity nesting bird species, compacting soil, increasing erosion and reducing recovery of native vegetation (Beschta *et al.* 1995). In watersheds that supply drinking water to communities or habitat for rare, sensitive or threatened species, post-wildfire salvage-logging should be avoided unless sufficient best management practices are employed to reduced sediment transport into streams and rivers (Wagenbrenner *et al.* 2016).

Together with previous studies on abiotic variables, my research demonstrates that the effects of wildfire can be persistent but not devastating to aquatic ecosystems in mountain streams. While macroinvertebrate assemblage structure varied between disturbance categories, sensitive taxa were present in all watersheds. Macroinvertebrates and fish were able to use both instream and terrestrial food resources despite changes in water quality. The additional impacts of salvage-logging observed reinforce the need for informed, science-based management that balances public safety, economics and ecology.

4.1 Future Research

Long-term studies of the effects of wildfire on aquatic communities remain relatively few in the literature, highlighting the importance of maintaining long-term research projects such as the Southern Rockies Watershed Project (established 2004), the Experimental Lakes Area (established 1968), and the Hubbard Brook Ecosystem Study (established 1955) (Silins *et al.* 2016; Tetzlaff *et al.* 2017; Emmerton *et al.* 2019). While this study provided insight into the long-term impacts of wildfire, important knowledge gaps remain. In particular the additional effects of salvage-logging and long-term impacts of wildfire on salmonid fish could be better understood in northern Rocky Mountain ecosystems. Research efforts that would improve our understanding of wildfire impacts on aquatic ecosystems include:

1. More robust monitoring of wildfire impacts on salmonid fish

Only Cutthroat Trout were examined for this study as this was the only salmonid species detected in both reference and burned watersheds during sampling. Increasing sampling efforts including sampling at several intervals throughout the ice-free period would create more opportunities to detect other species (e.g., Rainbow Trout) across all disturbance categories (reference, burned and burned & salvage-logged). Since an additional effect of salvage-logging on trout could not be evaluated in this study, future research efforts should focus on addressing this knowledge gap. As well, no estimates were made during this study of trout population dynamics (abundance or age class structure). Regular monitoring of abundance and recruitment would provide insight into how difference in instream primary productivity and macroinvertebrate abundance may influence trout populations.

2. Continued monitoring of wildfire affected watersheds

This research showed that the impacts of the Lost Creek wildfire remained apparent in aquatic ecosystems 8 years post-fire. While continuous monitoring of the burned and burned & salvage-logged research watersheds was discontinued in 2014 (11 years post-fire), monitoring has continued in reference watersheds. It would be valuable to revisit the burned watersheds at regular time intervals (e.g., 15 and 20 years post-fire) to gain insight into even longer-term trends. Complete recovery of watersheds following wildfire disturbance is linked to recovery of the forest and forest canopy which in cool, montaine ecosystems can take upwards of 100 years (Romme 1982).

Figures

Figure 4.1 Photographs of Southern Rockies Research Project streams taken in the first spring following the Lost Creek wildfire (April 2004).

Photo credit: Southern Rockies Watershed Project.

Literature Cited

Beaudoin C, Prepas E, Tonn W, Wassenaar L, Kotak B (2001) A stable carbon and nitrogen isotope study of lake food webs in Canada's Boreal Plain. *Freshwater Biology* **46**, 465-477.

Beschta RL, Frissell CA, Gresswell RE, Hauer FR, Karr JR, Minshall GW, Perry DA, Rhodes JJ (1995) Wildfire and salvage logging: recommendations for ecologically sound post-fire salvage logging adn other post-fire treatments on Federal lands in the west., Oregon State University, Corvallis OR.

Bjornn T, Brusven M, Molnau M, Milligan J, Klamt R, Cacho E, Schaye C (1977) Transport of granitic sediment in streams and its effects on insects and fish. *Idaho Forest Wildfire and Range Experiment Station Bulletin* **17**, 11-20.

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

Brown H (1987) Biology of Riffle Beetles. *Annual Review of Entomology* **32**, 253-273.

Emelko MB, Stone M, Silins U, Allin D, Collins AL, Williams CHS, Martens AM, Bladon KD (2016) Sediment-phosphorus dynamics can shift aquatic ecology and cause downstream legacy effects after wildfire in large river systems. *Global Change Biology* **22**, 1168-1184.

Emmerton CA, Beaty KG, Casson NJ, Graydon JA, Hesslein RH, Higgins, SN, Osman H, Paterson MJ, Park A, Tardif JC (2019) Long-term responses of nutrient budgets to concurrent climate-related stressors in a boreal watershed. *Ecosystems* **22**, 363-378.

Giller P, Malmqvist B (1998) 'The Biology of Streams and Rivers.' (Oxford University Press: New York, NY)

Hobbie E, Macko S, Shugart H (1999) Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* **118**, 353-360.

Hyodo F, Kusaka S, Wardle D, Nilsson M (2013) Changes in stable nitrogen and carbon isotope ratios of plants and soil across a boreal forest fire chronosequence. *Plant and Soil* **367**, 111-119.

Isaak DJ, Young M, Luce C, Hostetler S, Wenger S, Peterson E, Hoef J, Groce M, Horan D, Nagel D (2016) Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 4374-4379.

Isaak DJ, Luce CH, Rieman BE, Nagel DE, Peterson EE, Horan DL, Parkes S, Chandler GL (2010) Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* **20**, 1350-1371.

Juncos R, Milano D, Macchi PJ, Alonso MF, Vigliano PH (2011) Response of rainbow trout to different food web structures in northern Patagonia: implications for growth, bioenergetics, and invasiveness. *Transactions of the American Fisheries Society* **140**, 415-428.

Malison RL, Baxter CV (2010) Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. *Journal of the North American Benthological Society* **29**, 1324-1338.

Mihuc TB (1997) The functional trophic role of lotic primary consumers: Generalist versus specialist strategies. *Freshwater Biology* **37**, 455-462.

Pardo L, Hemond H, Montoya J, Fahey T, Siccama T (2002) Response of the natural abundance of N-15 in forest soils and foliage to high nitrate loss following clear-cutting. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **32**, 1126-1136.

Rieman B, Lee D, Chandler G, Meyers D, J Greenlee (Ed.) (1997) 'Does wildfire threaten extinction for salmonids? Responses of redband trout and bull trout following recent large fires on the Boise National Forest, Fire Effects on Rare and Endangered Species and Habitats Conference.' Coeur d'Alene, Idaho. (International Association of Wildland Fire:

Rinne JN (1996) Management briefs: short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *North American Journal of Fisheries Management* **16**, 653-658.

Ripley T, Scrimgeour G, Boyce MS (2005) Bull trout (*Salvelinus confluentus*) occurrence and abundance influenced by cumulative industrial developments in a Canadian boreal forest watershed. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2431-2442.

Romme W (1982) Fire and Landscape Diversity in Subalpine Forests of Yellowstone National Park. *Ecological Monographs* **52**, 199-221.

Sear D, Jones J, Collins A, Hulin A, Burke N, Bateman S, Pattison I, Naden P (2016) Does fine sediment source as well as quantity affect salmonid embryo mortality and development? *Science of the Total Environment* **541**, 957-968.

Silins U, Anderson A, Bladon KD, Emelko MB, Stone M, Spencer SA, Williams CHS, Wagner MJ, Martens AM, Hawthorn K (2016) Southern Rockies Watershed Project. *Forestry Chronicle* **92**, 39-42.

Silins U, Bladon K, Kelly E, Esch E, Spence J, Stone M, Emelko M, Boon S, Wagner M, Williams C, Tichkowsky I (2014) Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. *Ecohydrology* **7**, 1508-1523.

Silins U, Stone M, Emelko MB, Bladon KD (2009) Sediment production following severe wildfire and post-fire salvage logging in the Rocky Mountain headwaters of the Oldman River Basin, Alberta. *Catena* **79**, 189-197.

Spencer C, Gabel K, Hauer F (2003) Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management* **178**, 141-153.

Tetzlaff D, Carey SK, McNamara JP, Laudon H, Soulsby C (2017) The essential value of long-term experimental data for hydrology and water management. *Water Resources Research* **53**, 2598-2604.

Voshell JR (2002) 'A Guide to Common Freshwater Invertebrates of North America.' (The McDonald and Woodward Publishing Company: Blacksburg, Virginia)

Wagenbrenner J, Robichaud P, Brown R (2016) Rill erosion in burned and salvage logged western montane forests: Effects of logging equipment type, traffic level, and slash treatment. *Journal of Hydrology* **541**, 889-901.

Literature Cited

Alberta Agriculture and Forestry, 2019. Historical Wildfire Database - Alberta Wildfire Records.

Alberta Environment and Parks (2014) 'Alberta Species at Risk.' Available at http:// aep .alberta.ca/fish-wildlife/species-at-risk/documents/SpeciesAssessedConservation-2014a.pdf [Accessed 4-14-17].

Anderson C, Cabana G (2007) Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. *Journal of the North American Benthological Society* **26**, 273-285.

Bailey RC, Norris RH, Reynoldson TB (2001) Taxonomic resolution of benthic macroinvertebrate communities in bioassessments. *Journal of the North American Benthological Society* **20**, 280-286.

Barbour MT, Snyder BD, Stribling JB, 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, D.C.

Beaudoin C, Prepas E, Tonn W, Wassenaar L, Kotak B (2001) A stable carbon and nitrogen isotope study of lake food webs in Canada's Boreal Plain. *Freshwater Biology* **46**, 465-477.

Beschta RL, Frissell CA, Gresswell RE, Hauer FR, Karr JR, Minshall GW, Perry DA, Rhodes JJ (1995) Wildfire and salvage logging: recommendations for ecologically sound post-fire salvage logging adn other post-fire treatments on Federal lands in the west., Oregon State University, Corvallis OR.

Bisson PA, Rieman BE, Luce C, Hessburg PF, Lee DC, Kershner JL, Reeves GH, Gresswell RE (2003) Fire and aquatic ecosystems of the western USA: current knowledge and key questions. *Forest Ecology and Management* **178**, 213-229.

Bixby R, Cooper S, Gresswell R, Brown L, Dahm C, Dwire K (2015) Fire effects on aquatic ecosystems: an assessment of the current state of the science. *Freshwater Science* **34**, 1340-1350.

Bjornn T, Brusven M, Molnau M, Milligan J, Klamt R, Cacho E, Schaye C (1977) Transport of granitic sediment in streams and its effects on insects and fish. *Idaho Forest Wildfire and Range Experiment Station Bulletin* **17**, 11-20.

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

Bligh E, Dyer W (1959) A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology* **37**, 911-917.

Borcard D, Gillet F, Legendre P (2011) 'Numerical Ecology with R.' (Springer: New York, NY, United States)

Bowman M, Bailey R (1997) Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macroinvertebrate communities? *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1802-1807.

Brittain J, Eikeland T (1988) Invertebrate Drift - A Review. *Hydrobiologia* **166**, 77-93.

Brodie C, Heaton T, Leng M, Kendrick C, Casford J, Lloyd J (2011a) Evidence for bias in measured delta N-15 values of terrestrial and aquatic organic materials due to pre-analysis acid treatment methods. *Rapid Communications in Mass Spectrometry* **25**, 1089-1099.

Brodie C, Leng M, Casford J, Kendrick C, Lloyd J, Zong Y, Bird M (2011b) Evidence for bias in C and N concentrations and delta C-13 composition of terrestrial and aquatic organic materials due to pre-analysis acid preparation methods. *Chemical Geology* **282**, 67-83.

Brown H (1987) Biology of Riffle Beetles. *Annual Review of Entomology* **32**, 253-273.

Burles K, Boon S (2011) Snowmelt energy balance in a burned forest plot, Crowsnest Pass, Alberta, Canada. *Hydrological Processes* **25**, 3012-3029.

Cahill CL, Mogensen S, Wilson KL, Cantin A, Sinnatamby RN, Paul AJ, Christensen P, Reilly JR, Winkel L, Farineau A, Post JR (2018) Multiple challenges confront a high-effort inland recreational fishery in decline. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 1357-1368.

Clifford HF, 1991. Aquatic invertebrates of Alberta an illustrated guide. University of Alberta Press, Edmonton, AB.

Cooper S, Page H, Wiseman S, Klose K, Bennett D, Even T, Sadro S, Nelson C, Dudley T (2015) Physicochemical and biological responses of streams to wildfire severity in riparian zones. *Freshwater Biology* **60**, 2600-2619.

Covich A, Palmer M, Crowl T (1999) The role of benthic invertebrate species in freshwater ecosystems - Zoobenthic species influence energy flows and nutrient cycling. *Bioscience* **49**, 119-127.

Cummins K (1973) Trophic relations of aquatic insects. *Annual Review of Entomology* **18**, 183-206.

Cummins K (1974) Structure and function of stream ecosystems. *Bioscience* **24**, 631-641.

DeBano L (2000) The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology* **231**, 195-206.

Deniro M, Epstein S (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis *Science* **197**, 261-263.

Deniro M, Epstein S (1978) Influence of Diet on Distribution of Carbon Isotopes in Animals. *Geochimica Et Cosmochimica Acta* **42**, 495-506.

Emelko M, Silins U, Bladon K, Stone M (2011) Implications of land disturbance on drinking water treatability in a changing climate: Demonstrating the need for "source water supply and protection" strategies. *Water Research* **45**, 461-472.

Emelko MB, Stone M, Silins U, Allin D, Collins AL, Williams CHS, Martens AM, Bladon KD (2016) Sediment-phosphorus dynamics can shift aquatic ecology and cause downstream legacy effects after wildfire in large river systems. *Global Change Biology* **22**, 1168-1184.

Emmerton CA, Beaty KG, Casson NJ, Graydon JA, Hesslein RH, Higgins SN, Osman H, Paterson MJ, Park A, Tardif JC (2019) Long-term responses of nutrient budgets to concurrent climate-related stressors in a boreal watershed. *Ecosystems* **22**, 363-378.

Flannigan M, Logan K, Amiro B, Skinner W, Stocks B (2005) Future area burned in Canada. *Climatic Change* **72**, 1-16.

Frazer GW, Canham CD, Lertzman KP. Gap Light Analyzer (GLA), version 2.0: *Imaging Software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, user manual and program documenation.* Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.

Fry B (1991) Stable Isotope Diagrams of Freshwater Food Webs. *Ecology* **72**, 2293-2297.

Fry B (2006) 'Stable Isotope Ecology.' (Springer: New York, NY, USA)

Giller P, Malmqvist B (1998) 'The Biology of Streams and Rivers.' (Oxford University Press: New York, NY)

Gresswell R (1999) Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* **128**, 193-221.

Hauer F, Locke H, Dreitz V, Hebblewhite M, Lowe W, Muhlfeld C, Nelson C, Proctor M, Rood S (2016) Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes. *Science Advances* **2**, e1600026.

Hauer FR, Spencer CN (1998) Phosphorus and nitrogen dynamics in streams associated with wildfire: A study of immediate and longterm effects. *International Journal of Wildland Fire* **8**, 183-198.

Hauer FR, Stanford JA, Lorang MS (2007) Pattern and process in Northern Rocky Mountain headwaters: Ecological linkages in the headwaters of the Crown of the Continent. *Journal of the American Water Resources Association* **43**, 104-117.

Hawthorn K (2014) The role of fine sediment in phosphorus dynamics and stream productivity in Rocky Mountain headwater streams: Possible long-term effects of extensive logging. MSc thesis, University of Alberta.

Hobbie E, Macko S, Shugart H (1999) Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* **118**, 353-360.

Houghton J (2001) The science of global warming. *Interdisciplinary Science Reviews* **26**, 247-257.

Hynes HBN (1975) The stream and its valley. *Proceedings of the International Association of Theoretical and Applied Limnology* **19**, 1-15.

Hyodo F, Kusaka S, Wardle D, Nilsson M (2013) Changes in stable nitrogen and carbon isotope ratios of plants and soil across a boreal forest fire chronosequence. *Plant and Soil* **367**, 111-119.

Isaak D, Young M, Luce C, Hostetler S, Wenger S, Peterson E, Hoef J, Groce M, Horan D, Nagel D (2016) Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 4374-4379.

Isaak DJ, Luce CH, Rieman BE, Nagel DE, Peterson EE, Horan DL, Parkes S, Chandler GL (2010) Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* **20**, 1350-1371.

Jacob U, Mintenbeck K, Brey T, Knust R, Beyer K (2005) Stable isotope food web studies: a case for standardized sample treatment. *Marine Ecology Progress Series* **287**, 251-253.

Jaschinski S, Brepohl DC, Sommer U (2011) The trophic importance of epiphytic algae in a freshwater macrophyte system (*Potamogeton perfoliatus* L.): stable isotope and fatty acid analyses. *Aquatic Sciences* **73**, 91-101.

Jones J, Murphy J, Collins A, Sear D, Naden P, Armitage P (2012) The impact of fine sediment on macro-invertebrates. *River Research and Applications* **28**, 1055-1071.

Juncos R, Milano D, Macchi PJ, Alonso MF, Vigliano PH (2011) Response of rainbow trout to different food web structures in northern Patagonia: implications for growth, bioenergetics, and invasiveness. *Transactions of the American Fisheries Society* **140**, 415-428.

Kelly E, Schindler D, St Louis V, Donald D, Vlaclicka K (2006) Forest fire increases mercury accumulation by fishes via food web restructuring and increased mercury inputs. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 19380-19385.

Kennedy P, Kennedy H, Papadimitriou S (2005) The effect of acidification on the determination of organic carbon, total nitrogen and their stable isotopic composition in algae and marine sediment. *Rapid Communications in Mass Spectrometry* **19**, 1063-1068.

Koetsier P, Tuckett Q, White J (2007) Present effects of past wildfires on the diets of stream fish. *Western North American Naturalist* **67**, 429-438.

Kunze M, Stednick J (2006) Streamflow and suspended sediment yield following the 2000 Bobcat Fire, Colorado. *Hydrological Processes* **20**, 1661-1681.

Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* **129**, 271-280.

Lindenmayer D, Foster D, Franklin J, Hunter M, Noss R, Schmiegelow F, Perry D (2004) Ecology - Salvage harvesting policies after natural disturbance. *Science* **303**, 1303-1303.

Llopis-Belenguer C, Blasco-Costa I, Balbuena JA (2018) Evaluation of three methods for biomass estimation in small invertebrates, using three large disparate parasite species as model organisms (vol 8, 3897, 2018). *Scientific Reports* **8**,

Malison RL, Baxter CV (2010a) The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 570-579.

Malison RL, Baxter CV (2010b) Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. *Journal of the North American Benthological Society* **29**, 1324-1338.

Martin D (2016) At the nexus of fire, water and society. *Philosophical Transactions of the Royal Society B-Biological Sciences* **371**,

Martin D, Moody J (2001) Comparison of soil infiltration rates in burned and unburned mountainous watersheds. *Hydrological Processes* **15**, 2893-2903.

Mihuc T, Minshall G (1995) Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. *Ecology* **76**, 2361-2372.

Mihuc TB (1997) The functional trophic role of lotic primary consumers: Generalist versus specialist strategies. *Freshwater Biology* **37**, 455-462.

Mihuc TB, Minshall GW (2005) The trophic basis of reference and post-fire stream food webs 10 years after wildfire in Yellowstone National Park. *Aquatic Sciences* **67**, 541-548.

Mihuc TB, Minshall GW, Robinson CT (1996) Response of benthic macroinvertebrate populations in Cache Creek, Yellowstone National 60 Park to the 1988 wildfires. In 'The ecological implications of fire in Greater Yellowstone: proceedings on the second biennial Conference on the Greater Yellowstone Ecosystem', 19–21 September 1993, Yellowstone National Park, WY, USA. (Ed JM Greenlee) International Association of Wildland Fire, pp. 83–94. (Fairfield, WA, USA).

Minagawa M, Wada E (1984) Stepwise Enrichment of N15 Along Food Chains - Further Evidence and the Relation Between Delta N15 and Animal Age. *Geochimica Et Cosmochimica Acta* **48**, 1135-1140.

Minshall GW (2003) Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management* **178**, 155-161.

Minshall, GW, Andrews, DA, Brock, JT, Robinson, CT, Lawrence, DE (1989) Changes in wild trout habitat following forest fire. In 'Wild Trout IV Symposium. Yellowstone National Park, Wyoming, USA', September 18-19, 1989.

Minshall GW, Brock JT, Andrews DA, Robinson CT (2001a) Water quality, substratum and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek fire. *International Journal of Wildland Fire* **10**, 185-199.

Minshall GW, Brock JT, Varley JD (1989) Wildfires and Yellowstone Stream Ecosystems. *Bioscience* **39**, 707-715.

Minshall GW, Robinson CT, Lawrence DE (1997) Postfire responses of lotic ecosystems in Yellowstone National Park, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2509-2525.

Minshall GW, Robinson CT, Lawrence DE, Andrews DA, Brock JT (2001b) Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbance by wildfire. *International Journal of Wildland Fire* **10**, 201-213.

Moody J, Martin D (2001) Initial hydrologic and geomorphic response following a wildfire in the Colorado Front Range. *Earth Surface Processes and Landforms* **26**, 1049-1070.

Morris E, Caruso T, Buscot F, Fischer M, Hancock C, Maier T, Meiners T, Muller C, Obermaier E, Prati D, Socher S, Sonnemann I, Waschke N, Wubet T, Wurst S, Rillig M (2014) Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution* **4**, 3514-3524.

Naman S, Rosenfeld J, Richardson J (2016) Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1292-1305.

Nehring R, Walker P (1996) Whirling disease in the wild: The new reality in the intermountain west. *Fisheries* **21**, 28-30.

Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H (2019). vegan: community ecology package. R package version 2.5-4. https://CRAN.R-project.org/package=vegan

Pardo L, Hemond H, Montoya J, Fahey T, Siccama T (2002) Response of the natural abundance of N-15 in forest soils and foliage to high nitrate loss following clear-cutting. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **32**, 1126-1136.

Parks Canada (2018) 'Kenow Wildfire.' Available at https://www.pc.gc.ca/en/pn-np/ab/waterton/securite-safety/feu-fire-kenow [Accessed March 10, 2019].

Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. *Oecologia* **127**, 171-179.

Pinnegar J, Polunin N (1999) Differential fractionation of delta C-13 and delta N-15 among fish tissues: implications for the study of trophic interactions. *Functional Ecology* **13**, 225-231.

Post DM (2002) Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **83**, 703-718.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reid D, Quinn J, Wright-Stow A (2010) Responses of stream macroinvertebrate communities to progressive forest harvesting: Influences of harvest intensity, stream size and riparian buffers. *Forest Ecology and Management* **260**, 1804-1815.

Resco V, Ferrio J, Carreira J, Calvo L, Casals P, Ferrero-Serrano A, Marcos E, Moreno J, Ramirez D, Sebastie M, Valladares F, Williams D (2011) The stable isotope ecology of terrestrial plant succession. *Plant Ecology & Diversity* **4**, 117-130.

Rice EW (2012) Standard methods for the examination of water and wastewater. American Public Health Association: Washington, D.C.

Richards C, Minshall GW (1992) Spatial and temporal trends is stream macroinvertebrate communities - the influence of catchment disturbance. *Hydrobiologia* **241**, 173-184.

Rieman B, Lee D, Chandler G, Meyers D, J Greenlee (Ed.) (1997) 'Does wildfire threaten extinction for salmonids? Responses of redband trout and bull trout following recent large fires on the Boise National Forest, Fire Effects on Rare and Endangered Species and Habitats Conference.' Coeur d'Alene, Idaho. (International Association of Wildland Fire).

Rinne JN (1996) Management briefs: short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *North American Journal of Fisheries Management* **16**, 653-658.

Ripley T, Scrimgeour G, Boyce MS (2005) Bull trout (*Salvelinus confluentus*) occurrence and abundance influenced by cumulative industrial developments in a Canadian boreal forest watershed. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2431-2442.

Robson B, Chester E, Matthews T, Johnston K (2018) Post-wildfire recovery of invertebrate diversity in drought-affected headwater streams. *Aquatic Sciences* **80**, 21.

Roby KB, 1989. Watershed response and recovery from the Will Fire: ten years of observation. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-109: 131-136. (Berkeley, CA, USA).

Romme W (1982) Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* **52**, 199-221.

Romme WH, Boyce MS, Gresswell R, Merrill EH, Minshall GW, Whitlock C, Turner MG (2011) Twenty years after the 1988 yellowstone fires: Lessons about disturbance and ecosystems. *Ecosystems* **14**, 1196-1215.

Rosenberger AE, Dunham JB, Buffington JM, Wipfli MS (2011) Persistent effects of wildfire and debris flows on the invertebrate prey base of rainbow trout in Idaho streams. *Northwest Science* **85**, 55-63.

Rounick JS, Winterbourn MJ, Lyon GL (1982 Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New-Zealand streams - A Stable Carbon Isotope Study. *Oikos* **39**, 191-198.

Rugenski AT, Minshall GW (2014) Climate-moderated responses to wildfire by macroinvertebrates and basal food resources in montane wilderness streams. *Ecosphere* **5**, 25.

Schoennagel T, Veblen T, Romme W (2004) The interaction of fire, fuels, and climate across rocky mountain forests. *Bioscience* **54**, 661-676.

Sear D, Jones J, Collins A, Hulin A, Burke N, Bateman S, Pattison I, Naden P (2016) Does fine sediment source as well as quantity affect salmonid embryo mortality and development? *Science of the Total Environment* **541**, 957-968.

Shakesby R, Doerr S (2006) Wildfire as a hydrological and geomorphological agent. *Earth-Science Reviews* **74**, 269-307.

Silins U, Anderson A, Bladon KD, Emelko MB, Stone M, Spencer SA, Williams CHS, Wagner MJ, Martens AM, Hawthorn K (2016) Southern Rockies Watershed Project. *Forestry Chronicle* **92**, 39-42.

Silins U, Bladon K, Kelly E, Esch E, Spence J, Stone M, Emelko M, Boon S, Wagner M, Williams C, Tichkowsky I (2014) Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. *Ecohydrology* **7**, 1508-1523.

Silins U, Stone M, Emelko MB, Bladon KD (2009) Sediment production following severe wildfire and post-fire salvage logging in the Rocky Mountain headwaters of the Oldman River Basin, Alberta. *Catena* **79**, 189-197.

Sotiropoulos M, Tonn W, Wassenaar L (2004) Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecology of Freshwater Fish* **13**, 155-160.

Spencer C, Gabel K, Hauer F (2003) Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management* **178**, 141-153.

Szepanski MM, Ben-David M, Van Ballenberghe V (1999) Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia* **120**, 327-335.

Tetzlaff D, Carey SK, McNamara JP, Laudon H, Soulsby C (2017) The essential value of long-term experimental data for hydrology and water management. *Water Resources Research* **53**, 2598-2604.

Thorp J, Covich A (2009) 'Ecology and Classification of North American Freshwater Invertebrates Third Edition.' (Academic Press: London, UK).

US Fish and Wildlife Service (2017) 'Environmental conservation online system.' Available at https://ecos.fws.gov/ecp0/pub/SpeciesReport.do?groups=E&listingType=L&mapstatus=1 [Accessed 4-14-17].

US EPA (2000). Guidance for assessing chemical contaminant data for use in fish advisories. Washington, DC. 1: 485.

US EPA (2012). Selected analytical methods for environmental remediation and recovery (SAM) 2012. U.S. Environmental Protection Agency, Wahstington, DC. EPA/600/R-12/555.

Vannote R, Minshall G, Cummins K, Sedell J, Cushing C (1980) River continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130-137.

Verkaik I, Vila-Escale M, Rieradevall M, Baxter CV, Lake PS, Minshall GW, Reich P, Prat N (2015) Stream macroinvertebrate community responses to fire: are they the same in different fire-prone biogeographic regions? *Freshwater Science* **34**, 1527-1541.

Vieira N, Clements W, Guevara L, Jacobs B (2004) Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology* **49**, 1243-1259.

Vitousek P, Reiners W (1975) Ecosystem succession and nutrient retention: A Hypothesis. *Bioscience* **25**, 376-381.

Voshell JR (2002) 'A Guide to Common Freshwater Invertebrates of North America.' (The McDonald and Woodward Publishing Company: Blacksburg, Virginia)

Wagenbrenner J, Robichaud P, Brown R (2016) Rill erosion in burned and salvage logged western montane forests: Effects of logging equipment type, traffic level, and slash treatment. *Journal of Hydrology* **541**, 889-901.

Wagner MJ, Bladon KD, Silins U, Williams CHS, Martens AM, Boon S, MacDonald RJ, Stone M, Emelko MB, Anderson A (2014) Catchment-scale stream temperature response to land disturbance by wildfire governed by surface-subsurface energy exchange and atmospheric controls. *Journal of Hydrology* **517**, 328-338.

Westerling A, Hidalgo H, Cayan D, Swetnam T (2006) Warming and earlier spring increase western US forest wildfire activity. *Science* **313**, 940-943.

Wood P, Armitage P (1997) Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**, 203-217.

Writer J, McCleskey R, Murphy S, Stone M, Collins A, Thoms M (2012) Effects of wildfire on source-water quality and aquatic ecosystems, Colorado Front Range. *Wildfire and Water Quality: Processes, Impacts and Challenges* **354**, 117-122.

Yee D, Kehl S (2015) Order Coleoptera. In 'Thorp and Covich's Freshwater Invertebrates (Fourth Edition).' (Eds J Thorp, D Rogers.) pp. 1003-1042. (Academic Press: Cambridge, MA, USA).

Zah R, Burgherr P, Bernasconi S, Uehlinger U (2001) Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology* **46**, 871-882.

Zwick P (1992) Stream habitat fragmentation - a threat to biodiversity. *Biodiversity and Conservation* **1**, 80-97.