

**LINKING STREAM ECOSYSTEM INTEGRITY TO CATCHMENT AND REACH CONDITIONS IN AN
INTENSIVELY-MANAGED FOREST LANDSCAPE**

by

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ABSTRACT

Forests are vital to maintain headwater stream integrity in forested biomes, which in turn ensures the delivery of aquatic ecosystem services downstream. Forest harvesting, however, can alter land-water linkages and compromise stream integrity. Although the main effects of forestry on streams have been documented, most studies have focused on short-term, post-harvest effects and used only a few (mainly abiotic) indicators. To address this, I investigated the effects of varying forest management intensities (FMIs) on different components of stream ecosystems in a holistic two-year study. In 12 catchments ranging in FMI, I measured a suite of abiotic and biotic indicators of stream ecosystem integrity to determine which explanatory catchment and reach variables were driving the observed differences. Most indicators detected the gradient in FMI, with abiotic indicators responding most strongly: streams in catchments with highest FMI tended to have higher fine inorganic sediment deposition and entrainment, water cations and carbon, DOM aromaticity and humification, and water temperature. These abiotic differences were associated with higher biofilm biomass and shredder densities, but lower leaf decomposition and contribution of algae to stream macroinvertebrate diets. Therefore, higher FMIs promoted the delivery of terrestrial water-borne materials to streams, which were incorporated into food webs. However, there were hardly signs of impaired biological communities in these 12 streams compared to data from 3 reference streams.

Fixed-width riparian buffers are used to protect stream ecosystems from forestry, but this fails to acknowledge areas with strong hydrological connectivity (variable source areas – VSAs) that may warrant special protection due to being vegetation and biogeochemical hotspots. To assess whether these hotspots have an effect on the receiving waters, I compared

stream ecosystem integrity between VSA and non-VSA stream reaches in a paired study.

Although I detected some differences (higher understory vegetation density, deposited organic matter, % gatherers, lower % riffles, DOC, algal biomass), I found little evidence that inputs from VSAs had significant effects on stream communities and functions.

Overall, this study demonstrates the advantages of assessing several indicators for a more holistic understanding of the linkages between forestry and streams, it shows that current management practices do not fully protect against an increased delivery of terrestrial materials derived from high FMI to streams, and calls for more studies assessing the ecological implications of VSAs.

DEDICATION

To all my tiny stream buddies that sacrificed their lives for this project

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1. General introduction

1.1. Forest-stream linkages

Headwater streams are an integral component of river networks, and they constitute from 65 to more than 80% of the total stream and river channel length worldwide (Leopold et al. 1964; Sidle et al. 2000). Small streams have an immediate and intimate connection with the surrounding land due to their high edge to volume ratio, making them the primary interface between terrestrial and aquatic ecosystems. Because they represent the capillaries of the landscape and the main source of water and organic and inorganic materials in transport, their integrity is vital to that of the downstream river ecosystems (Meyer et al. 2007; Freeman et al. 2007). But the same characteristics that make headwater streams crucial for the integrity of river networks makes them particularly vulnerable to catchment disturbance because “the valley rules the stream” (Hynes 1975).

In forested catchments, the forests are key in controlling land-water linkages, maintaining the integrity of stream ecosystems and ensuring the provision of aquatic ecosystem services (AESs) (Sweeney et al. 2004). For example, forests filter pollutants before they reach waterbodies or stabilize soil and stream banks to mitigate erosion, and therefore can provide the AES of clean drinking water (Furniss et al. 2010). By controlling water fluxes (e.g. through rain interception, evapotranspiration and infiltration) and energy fluxes (e.g. by subsidizing stream food webs with leaf litter and terrestrial insects), forests are key at providing AESs such as fish, recreation and flood control (Wells et al. 2010). As human impact on ecosystems increases and resources such as clean drinking water become scarcer, AESs and the role of forests as AES providers are being increasingly recognized and valued. For instance, New York City chose to spend 1-1.5 billion USD to buy and conserve the undeveloped forest lands in

the Catskill mountains watershed to ensure the supply of clean source water to the city, instead of spending 6-8 billion USD to build a new water filtration plant (Barbier and Heal 2006).

1.2. Forestry and its effects on stream ecosystems

In addition to the role forests play in providing clean drinking water, fish and other aquatic wildlife, society relies on forests for the provision of every-day materials, such as timber for construction, fiber for pulp and paper, and biomass for bioenergy production. Forest harvesting is still an important economic activity in Canada despite a decreased demand for Canadian wood products over the past decade. The forest industry employed 201,645 people (including 9,500 in indigenous communities), contributing \$22.1 billion to the GDP and accounting for 7% of all Canadian exports in 2015. In fact, Canada has the largest positive forest product trade balance in the world (NRCan 2016). The province of New Brunswick has the largest forestry industry in the country (in terms of % of the overall GDP coming from the forest industry) and the highest forest use intensity (in terms of harvest volumes as % of annual productive capacity) (NFD 2017; CBC 2017), which employs 11,992 workers and contributes and creates a total revenue of \$3.3 billion (NRCan 2016). However, because harvesting activities alter forest condition (structure and composition), this can compromise the ability of forests to maintain the integrity of aquatic ecosystems, which leads to conflicts between different aspects of the ecosystem valued by humans (e.g. clean drinking water vs. wood products) and has detrimental implications for all the species that rely on these aquatic ecosystems besides humans.

The effects of forest harvesting on streams have been well established over the past few decades and include changes to both the abiotic and biotic environment. For example, tree

removal is followed by lower interception, evapotranspiration and infiltration rates of water, which results in more water being delivered to streams after rain events, in a shorter lag time between the rain event and the rise of stream water levels, and in reduced groundwater recharge (Moore and Wondzell 2005; Buttle et al. 2009), which can compromise the AES of flood control. This increased water flow can lead to more water-borne dissolved and suspended materials being delivered to water bodies after harvesting, which is exacerbated by roads, soil disturbance by machinery, reduced soil stability (due to vegetation removal) and enhanced biogeochemical processes in soils. This can result in more sediments, nutrients (e.g. P and N) and cations (e.g. Ca) being delivered to streams (Feller 2005; Croke and Hairsine 2006; Kreutzweiser et al. 2008b; Richardson and Béraud 2014; Webster et al. 2015), potentially compromising another important AES – the provision of clean water. In addition, stream water temperature and thermal diel fluctuations tend to increase after forest harvesting due to more sunlight reaching streams after canopy removal (Moore et al. 2005). Canopy removal has also been shown to reduce the input of organic matter and woody debris to streams, which can alter food web dynamics and habitat availability (Bilby and Ward 1991; England and Rosemond 2004; Santiago et al. 2011; Burton et al. 2016). All of these well-documented abiotic changes may lead to direct and/or indirect changes in stream biota. For example, biofilm and algal biomass can either increase or decrease in response to forest harvesting (e.g. Danehy et al. 2007; Wilkerson et al. 2010), BMI richness and density can decrease and increase, respectively (e.g. Martel et al. 2007; Kreutzweiser et al. 2008a; Medhurst et al. 2010), the relative abundances of BMI functional feeding groups can change (e.g. increased or decreased shredder densities, Richardson and Béraud 2014), and salmonid fish incidence can decline and density increase (Deschênes et al. 2007; Mellina and Hinch 2009). Ecosystem functions such as leaf litter decomposition and primary production can also be affected by forest harvesting, with

both post-harvest increases and decreases being documented (Kiffney et al. 2003; Mckie and Malmqvist 2009; Kreutzweiser et al. 2010; Yeung et al. 2017). These structural and functional biological changes, in turn, can affect the delivery of AESs such as fishing or C cycling (Balvanera et al. 2006; Woodward 2009).

To mitigate such impacts, the forest industry has designed and implemented numerous best management practices (BMPs), including the application of riparian buffer zones (RBZs, i.e. streamside no-harvest forest reserves) and guidelines for stream crossings and road construction (Schilling 2009; McDermott et al. 2010). RBZs are widely applied worldwide, but the design varies among countries and even states or provinces. For example, buffer width guidelines typically range between 15 and 30 m across USA and Canada (Lee et al. 2004), and between 0 and 500 m across the globe depending on the type of stream (McDermott et al. 2007). Previous studies have assessed the effectiveness of RBZs, and fixed-width RBZs of 30 m have been suggested to provide a good balance between stream protection and timber production (Broadmeadow and Nisbet 2004). However, most of these studies have 1) focused on short-term post-harvest effects, 2) used only a few indicators, with a focus on abiotic ones, and 3) only considered fixed-width buffers, without considering the hydrological and biogeochemical implications of riparian forest heterogeneity. This could limit our understanding of the effects of forest harvesting on the integrity of stream ecosystems, and thus, will be explored in more detail in the following paragraphs.

1.3. Knowledge gaps

1.3.1. Intensive forest management and its cumulative effects

Natural and anthropogenic disturbances can happen anywhere in the catchment, at multiple times and, in the case of forestry, with different harvesting techniques (e.g. a forest stand far from the stream is harvested one year by clearcutting, and a second stand closer to the stream is harvested the following year by commercial thinning), and these harvesting impacts may be compounded by the effects of roads and other operational activities such as soil preparation and herbicide application. This means that the effects of forestry activities on stream ecosystems will be the result of multiple, interacting stressors, resulting in a high potential for cumulative impacts (Kreutzweiser et al. 2013; Webster et al. 2015). This is especially true in the case of intensive forestry, where forests are managed to maximize timber yield in the shortest time possible by subjecting stands to site preparation, planting, and various aspects of tending including the application of fertilizers, herbicides and insecticides, and/or thinning (pre-commercial and commercial). In extensively managed forests, on the other hand, stands are usually entered once during a rotation and left free to grow more or less naturally, and the monetary investment per unit area is considerably lower (Grigal 2000). Therefore, intensive forestry results in more activities that can disturb stream ecosystems, in shorter rotation times (which results in more frequent harvesting disturbances), and in more frequent visits to the catchment (which results in greater road traffic). However, little is known about the cumulative effects of intensive forest management on stream ecosystems, with most studies to date looking at effects after single harvesting events (e.g. Jackson et al. 2007; Medhurst et al. 2010; De Wit et al. 2014; Klimesh et al. 2015; Witt et al. 2016; Yeung et al. 2017). The need for studies on the effects of intensive forest management is becoming

increasingly important due to the predicted intensification of forestry in some parts of the world. In the 2014 New York Declaration on Forests, governments, companies and NGOs committed to reducing global deforestation by half by 2020 and ending it by 2030, but the demand for wood products is expected to grow as the global population continues to grow; thus, the only way to meet the global demand for wood products will be to intensify timber production on lands that have already been allocated for forestry (Creed et al. 2016). Therefore, based on this future scenario (i.e. increased intensive forest management) and on the importance of AESs from forested catchments, it is necessary to understand whether existing BMPs are effective at protecting the ecological integrity of streams and their associated AESs under the cumulative effects that may result from intensive forest management practices. In other words, studies are needed that assess the actual disturbances that stream ecosystems are exposed to under intensive forest management, and their responses to those disturbances.

1.3.2. Need for multi-indicator studies

Each component of stream ecosystems responds to catchment disturbance differently and over different spatial and temporal scales. For example, water chemistry tends to change rapidly after disturbance and can reflect punctual changes in catchment processes, whereas biotic communities tend to integrate the changes over a longer period of time, and thus, reflect the averaged condition of the system. In addition, different ecosystem components may interact in unpredictable ways (e.g., synergistic/antagonistically) (Piggott et al. 2015; Nöges et al. 2016). For example, an increased input of nutrients after harvesting would be expected to enhance algal growth, but a simultaneous increase in sediments could reduce the amount of suitable habitat for algal growth, interfere with photosynthesis and reduce nutrient uptake,

resulting in non-detectable changes in algal biomass. To understand the often complex interactions and responses of stream systems to forest harvesting, integrative approaches that incorporate multiple indicators representing different physical, chemical and biological (e.g., structure vs. function) components of the ecosystem are needed (Gessner and Chauvet 2002; Parr et al. 2016). However, most studies to date have generally focused on a few indicators (e.g., Janisch et al. 2012; Klimesh et al. 2015; Oliveira et al. 2016; Witt et al. 2016), with most measuring abiotic parameters (namely water quality and temperature). Fewer studies have investigated effects on stream communities (e.g., microbial, algal or invertebrate communities) in the context of abiotic changes, and even fewer studies have addressed stream ecosystem functioning and food web dynamics (Cristan et al. 2016).

The paucity of studies assessing the effects of forest management on stream food web dynamics is surprising considering that it is a good candidate: food webs can be sensitive to disturbance (forest harvesting changes the input of materials from the catchment to the stream, affecting the availability of food sources – England and Rosemond 2004; Kreutzweiser et al. 2008b; Wilkerson et al. 2010), and are extremely relevant ecologically (changes in the source of energy to food webs can affect, for example, BMI and fish growth and productivity – Müller-Navarra et al. 2000; Gladyshev et al. 2011), with implications for AESs such as fishing. Therefore, to gain a better understanding of the linkages between catchment disturbance and effects, more holistic studies that go beyond the assessment of one or a few (especially abiotic) indicators and that address the implications of forest management for stream food web dynamics are necessary. This knowledge will help regulatory and industrial forest managers to better assess the overall condition of stream ecosystems in relation to their practices, and to identify which guidelines need refinement.

1.3.3. Incorporating riparian heterogeneity into guidelines

Riparian zones along streams are important groundwater discharge areas, but because groundwater does not flow uniformly across riparian zones (it is controlled by heterogeneous local topography and soil types), these landscapes differ in hydrological and biogeochemical importance (Buttle 2002; Grabs et al. 2012). Variable source areas (VSAs) or groundwater discharge areas are riparian areas where topography leads the water to flow into this area and to converge and accumulate before being delivered to the receiving waters; thus, they are areas of strong hydrological connectivity with the surrounding land. Such conditions have been shown to create biogeochemical and ecological riparian hotspots, with these areas often having greater vegetation diversity and cover (Jansson et al. 2007; Kuglerová et al. 2014b), being critical areas for the cycling of carbon, nitrogen and phosphorus (Mengistu et al. 2014), and exerting an important influence on the chemistry of the streams to which they are hydrologically connected (Zimmer et al. 2013; Ledesma et al. 2015). It has been suggested that the implementation of fixed-width RBZs fails to recognize this spatial heterogeneity in riparian zones, which could result in failing to meet the conservation goals of these streamside protection areas; this is because VSAs can be wider than the conventional 30-m riparian buffer zones, and in these circumstances VSAs would be harvested and disturbed (Creed et al. 2011; Kuglerová et al. 2014a). Thus, RBZ designs that reflect the heterogeneous nature of the hydrological connectivity with the surrounding land have been proposed, i.e., wider RBZs around VSAs and narrower RBZs along less hydrologically-connected stream reaches (Creed et al. 2008; Kuglerová et al. 2014a; Laudon et al. 2016). However, the biological implications of these VSAs for the receiving stream ecosystems are not clear. Water chemistry has been shown to differ in areas where groundwater is discharged into streams, delivering more organic

carbon, Na, Si, Ca (Grabs et al. 2012; Zimmer et al. 2013; Ledesma et al. 2015), but very few studies have assessed whether these differences translate into biological changes; the studies that have considered biological endpoints reported differences in the benthic macroinvertebrate community (Hunt et al. 2006; LeCraw and Mackereth 2010). Therefore, before modifying riparian buffer guidelines (in fact, some guidelines have already been revised to incorporate hydrological connectivity, e.g., OMNR 2010), it is important to conduct holistic studies that look at both the abiotic and biotic implications of these VSAs for stream ecosystems, as well as studies that compare the response of VSA and non-VSA stream reaches to disturbance.

1.4. Thesis objectives

In this PhD thesis, I address the above-described limitations by: 1) investigating the effects of varying intensities of forest management on different components of stream ecosystems (represented by a suite of indicators of stream ecosystem integrity) in a holistic two-year study – Chapter 2; 2) studying the effects of intensive forest management on headwater stream food web dynamics – Chapter 3; and 3) comparing stream ecosystem condition (assessed by measuring a suite of abiotic and biotic indicators) between VSA and non-VSA stream reaches – Chapter 4.

1.5. Approach

1.5.1. Study area

This study was conducted in the Black Brook (BB) forestry district located in the eastern Canadian province of New Brunswick, the province with the highest forestry intensity in Canada (CBC 2017). The 190,000 ha BB district, owned by J.D. Irving, Ltd. (JDI), is considered one of the

most intensively managed forests in the country, yet it is third-party certified as sustainably managed under the Sustainable Forestry Initiative (SFI) (Etheridge et al. 2005). Some of the water-related BMPs implemented in BB, which contribute to it being SFI certified, include the application of RBZs, no machine traffic within 3 m of the water's edge, skid trails on slopes running parallel to stream channels, approved culvert installations and road crossings, and sediment abatement efforts such as swales (D.P. Kreuzweiser, personal communication). BB is part of the Sisson Ecodistrict in the Central Uplands Ecoregion, which is composed mainly of Ordovician–Devonian sedimentary rocks (Zelazny 2007). The district is composed of shade-tolerant, high-quality hardwood stands (25%), mixedwood (18%), softwood-cedar (15%) and softwood (42%) forests. Eighty-eight percent of the softwood forest was comprised of plantations in 2002, including 56% black spruce (*Picea mariana*), 30% white spruce, 9% Norway spruce (*Picea abies*) and 3% pine (*Pinus sp.*). Within these plantations, stands are thinned (pre-commercial and commercial) prior to harvesting. State-of-the science forest characterization and harvest data obtained from high-resolution LiDAR and other advanced remote sensing and GIS techniques are available for BB. These tools enable a more refined characterization of landscape and forest characteristics, and allow for a more precise quantification of structural attributes that are key determinants of the ecological function of forests (Wulder et al. 2008). Catchments were delineated using an Arc-GIS flow accumulation grid based on the LiDAR-derived digital elevation model (DEM). Detailed characterization of each catchment was achieved using LiDAR-derived forest structural metrics (e.g., canopy height, canopy cover, vertical complexity index), photo-interpreted composition data from high-resolution digital stereo imagery (e.g., area weighted proportion of conifer, deciduous and mixed wood stand types, overstory species composition as a percent of catchment area), and topographic information derived from the LiDAR-based DEM (e.g., catchment slope, roughness, stream

gradient). Therefore, working in BB allowed me to study the effects of intensive forest management on the integrity of aquatic ecosystems, and to take advantage of innovative forest inventory tools to assess these impacts. To assess how BB stream ecosystem condition compared to the condition of undisturbed streams, and to get a sense of the range of natural variability for stream indicators, three reference streams were selected in the nearby Mount Carleton provincial park where there is no active forest management.

1.5.2. Stream indicators

The selection of stream indicators for this study was done to represent different abiotic and biotic components of stream ecosystems, and these indicators needed to be potentially sensitive to disturbance and ecologically relevant. Three of the selected abiotic indicators (sediment deposition, water chemistry and temperature) have often been reported to respond to forest management (Moore et al. 2005; Croke and Hairsine 2006; Kreuzweiser et al. 2008b), are important determinants of habitat suitability for stream organisms, and can reflect the capacity of the system to provide the AES of clean drinking water. One component of water quality – quantity of dissolved organic matter (DOM) – is often included in the suite of parameters that are measured, but the interest in its quality (i.e., chemical composition and structure of DOM molecules) is more recent and few studies have assessed the relationship between DOM quality and forest harvesting (Yamashita et al. 2011; Cawley et al. 2014). DOM quality controls its reactivity with different elements such as trace metals (Findlay and Sinsabaugh 2003), influences ecosystem functions such as leaf decomposition (Emilsson et al. 2017), and affects its incorporation into microbial food webs (Berggren et al. 2014, Wiegner et al 2015). Recent studies indicate that catchment disturbance influences DOM composition

(Yamashita et al. 2011; Burrows et al. 2013; Lu et al. 2014), therefore, this endpoint was included as a potential indicator of stream integrity.

As described below, the biotic indicators in this study were selected based on stream ecology theory, and they represent critical structural and functional characteristics of stream ecosystems that are sensitive to catchment disturbance. Headwater streams are known to be strongly influenced by the riparian vegetation, which reduces autotrophic production by shading and contributes large amounts of leaf litter (Vanote et al. 1980). This terrestrial organic matter is considered a key food source for stream benthic macroinvertebrates (BMIs) (Wallace et al. 1997), and its decomposition by microbes and BMIs is a critical stream ecosystem function that has implications for C cycling (Gessner and Chauvet 2002). Therefore, I selected leaf decomposition as one of my biotic indicators, and characterized the associated BMI community, as both are considered to be good indicators of stream ecosystem integrity and are commonly used to detect impacts (Gessner and Chauvet 2002; Macadam and Stockan 2015). Although terrestrial organic matter is considered to be the main energy source for headwater stream food webs, recent research demonstrates that aquatic production (algae) may be a disproportionately important source due to its higher nutritional value relative to detritus (Finlay 2001; McNeely et al. 2007; Hayden et al. 2016). The reliance of stream consumers on one source or the other can have strong ecological implications (e.g., it can affect BMI growth due to different nutritional qualities, and consequently fish growth), so a good understanding of these energy dynamics is important when assessing stream condition (Brett et al. 2017). The effect of forest harvesting on these dynamics was studied by quantifying biofilm and algal biomass (i.e., food availability), as well as the diets of BMIs. BMI diets were estimated by measuring carbon, nitrogen and hydrogen stable isotopes in BMIs and their potential food sources. These stable isotopes provide a time-integrated measure of energy flow and trophic

interactions in food webs, since the stable isotope composition of consumers tends to reflect that of the food they have assimilated over time (Peterson and Fry 1987; Fry 2006; Vander Zanden et al. 2016).

1.6. Hypotheses

I hypothesized that: 1) abiotic indicators would detect the gradient in forest management intensity, with the prediction that higher sediment deposition and nitrogen, phosphorus and DOC concentrations would occur in streams with greater forest management intensity, but that the magnitude of change would be small due to RBZs mitigating most of the forestry-related abiotic effects; temperature would not be related to management intensity since all the streams were covered by riparian forest; 2) differences in biotic indicators (i.e., changes in biofilm and algal biomass, BMI community structure, leaf decomposition and carbon source to stream food webs) across BB streams would be subtle, since RBZs would mitigate most of the effects; 3) VSAs would affect instream biofilm and algal biomass, with the prediction of higher biomass at VSA than non-VSA sites as a result of a greater delivery of nutrients and DOM through VSAs, and this would result in higher BMI richness and abundance at VSA sites.

1.7. Management implications

By improving the understanding of how intensive forest management and VSAs affect instream indicators, I hope to inform Black Brook forest managers on the effects of their management practices on stream ecosystem integrity and on the effectiveness of their BMPs (such as the above-mentioned 30-m wide riparian buffer zones, approved culvert installations and diversion swales). Processes and outcomes evaluated in my study in BB can be applied to

assessing ecosystem integrity in other intensive forest management settings, particularly in similar, temperate forest regions. This information is important to regulatory and industrial forest managers because forest sector competitiveness, the social license to operate, third party certifications and forest product market access are all increasingly being tied to environmental performance. Finally, my results will contribute to answering the important question of whether current best management practices are effective at protecting stream ecosystem integrity and associated AESs from intensive forest management, i.e., the predicted forestry of the future.

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2. How do abiotic and biotic indicators of stream ecosystem integrity change with forest management intensity?

2.1. Introduction

Among the many ecosystem services provided by forests, aquatic ecosystem services (AESs) are some of the most valuable. For example, forests filter pollutants before they reach waterbodies and stabilize soil and stream banks to mitigate erosion (Furniss et al. 2010). AESs such as food provision, recreation and hydrologic control (e.g., flood control) are also determined by the control forests exert on energy and water fluxes, such as subsidization of stream food webs, or rain interception, evapotranspiration and infiltration (Wells et al. 2010). However, because aquatic systems are ecologically linked to their surrounding land (Hynes 1975), disturbances to the surrounding forest such as harvesting may interfere with some ecological functions that may jeopardize these important AESs. For example, forest harvesting can result in greater hydrological variability characterized by higher peak flows and lower baseflows due to lower infiltration rates (Moore and Wondzell 2005; Buttle et al. 2009), affecting the AES of flood control. Studies have also shown that forest harvesting can increase suspended solids and key elements such as nitrates (Croke and Hairsine 2006; Kreutzweiser et al. 2008b; Richardson and Béraud 2014; Webster et al. 2015), potentially compromising another important service – the provision of clean water. In addition, stream water temperature and thermal diel fluctuations tend to increase after forest harvesting (Moore et al. 2005), and the input of organic matter and woody debris to streams may decrease (Bilby and Ward 1991; England and Rosemond 2004; Santiago et al. 2011; Burton et al. 2016). All this may lead to direct and/or indirect changes in stream biota such as biofilms and benthic algal community composition, benthic macroinvertebrate (BMI) abundance and diversity, and fish population structure (Mellina and Hinch 2009; Kreutzweiser et al. 2013; Richardson and Béraud

2014), as well as altered ecosystem functions such as leaf litter decomposition and primary production (Kiffney et al. 2003; Mckie and Malmqvist 2009; Kreutzweiser et al. 2010; Yeung et al. 2017), which can in turn affect the delivery of AESs (Balvanera et al. 2006; Woodward 2009).

To mitigate impacts, the forest industry has designed and implemented numerous best management practices (BMPs), including the application of riparian buffer zones (i.e., streamside no-harvest forest reserves) and guidelines for stream crossings and road construction (Schilling 2009; McDermott et al. 2010; OMNR 2010). Previous studies have assessed the effects of harvesting on particular aspects of aquatic ecosystems (Richardson and Béraud 2014; Webster et al. 2015) and the effectiveness of BMPs (Broadmeadow and Nisbet 2004; Cristan et al. 2016), although most have focused on short-term, post-harvest effects, using only a few indicators (e.g., Janisch et al. 2012; Klimesh et al. 2015; Oliveira et al. 2016; Witt et al. 2016), and mainly addressing effects on water chemistry, sediments and temperature rather than on stream ecosystem structure and function (Cristan et al. 2016). Because different components of stream ecosystems respond to disturbance differently and over different spatial and temporal scales, and because they may interact in often unpredictable ways (e.g., synergistic/ antagonistically) (Piggott et al. 2015; Nöges et al. 2016), it is important to look at multiple indicators representing different physical, chemical and biological (e.g., structure vs. function) components of the ecosystem simultaneously (Gessner and Chauvet 2002; Parr et al. 2016). Therefore, to gain a better understanding of the linkages between disturbance and effects, more holistic studies that go beyond the assessment of one or a few indicators are necessary.

Natural and anthropogenic disturbances can happen anywhere in the catchment, at multiple times and, in the case of forestry, with different harvesting techniques (e.g., a forest stand far from the stream is harvested one year by clearcutting, and a second stand closer to

the stream is harvested the following year by commercial thinning), and these harvesting impacts are often compounded by the effects of roads and other operational activities (e.g., soil preparation, herbicide application, winter salting); this results in a high potential for cumulative impacts of forest management activities on aquatic ecosystems (Kreutzweiser et al. 2013; Webster et al. 2015). However, little is known on the cumulative effects of intensive forest management on stream ecosystems, with most studies to date looking at post-harvest effects of single harvesting events (e.g., Jackson et al. 2007; Medhurst et al. 2010; De Wit et al. 2014; Klimesh et al. 2015; Witt et al. 2016; Yeung et al. 2017). The need for studies looking at the effects of intensive forest management is becoming increasingly important due to the predicted intensification of forestry. In the 2014 New York Declaration on Forests, governments, companies and NGOs committed to reducing global deforestation by half by 2020 and ending it by 2030, but the demand for wood products is expected to grow as the global population continues to grow; thus, the only way to meet the global demand for wood products will be to intensify timber production on lands that have already been allocated for forestry (Creed et al. 2016). Therefore, based on this future scenario (i.e., increased intensive forest management) and on the importance of AESs, it is necessary to understand whether existing BMPs are effective in protecting the ecological integrity of streams and the associated AESs under the cumulative effects that may result from intensive forest management practices.

To try to address these two knowledge gaps, I investigated the effects of intensive forest management on different components of stream ecosystems to capture a range of structural and functional aspects by conducting a holistic two-year study in the Black Brook (BB) forestry district located in the eastern Canadian province of New Brunswick, which has the greatest relative forestry activity in Canada (CBC 2017). BB is considered one of the most intensively managed forests in the country, yet it is third-party certified as sustainably managed under the

Sustainable Forestry Initiative (Etheridge et al. 2005). In addition, state-of-the science forest characterization and harvest data obtained from high-resolution LiDAR and other advanced remote sensing and GIS techniques are available for BB, enabling a more refined characterization of landscape and forest characteristics. The condition of 15 streams with catchments ranging in forest management intensity was assessed by measuring indicators describing the physical environment (water chemistry, water temperature and sediment deposition), ecosystem structure (algae and BMI communities) and function (leaf litter decomposition), and food web dynamics. In this chapter, water chemistry, temperature, sediment deposition, biofilm, and leaf litter decomposition and the associated BMI communities are presented. The objective of this chapter was to understand how different forest catchment conditions that arise from varying intensities of forest management affect stream ecosystem integrity. This was done by assessing how a suite of in-stream indicators of different ecosystem attributes (physical environment, water quality, ecosystem structure and function) are associated with intensive forest management and the derived catchment and reach variables characterized by high-quality forest inventory tools. I hypothesized that abiotic indicators would detect the gradient in forest management intensity, with higher sediment deposition and N, P and DOC concentrations in streams with higher forest management intensity. However, the magnitude of these changes would be low, resulting in only subtle biological changes and with riparian buffer zones mitigating most biotic effects; hence, I hypothesized that current BMPs are effective at protective streams from intensive forest management.

2.2. Methods

2.2.1. Site selection and characterization

The study was conducted at two locations in northwestern New Brunswick, Canada. The 190,000 ha Black Brook District (BB), owned by J.D. Irving, Ltd. (JDI), is one of the most intensively managed forest lands in Canada (Etheridge et al. 2005). Mount Carleton (MC), the reference area, is a Provincial Park ~100 km east of the Black Brook District with no harvesting history (Figure 2-1). BB and MC are part of the Atlantic Maritime ecozone. BB is part of the Sisson Ecodistrict in the Central Uplands Ecoregion, and it is composed mainly of Ordovician–Devonian sedimentary rocks, and deep, loamy soils in areas of low relief and less fertile, shallow, stony soils in higher terrain (Zelazny 2007a). The vegetation in these fertile soils originally consisted of a mixture of hardwood and coniferous tree species such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*), although commercial forestry has favoured the distribution of spruce (Zelazny 2007a). BB, more specifically, is composed of shade-tolerant, high-quality hardwood stands (25%), mixedwood (18%), softwood-cedar (15%) and softwood (42%) forests. Eighty-eight percent of the softwood forest was comprised of plantations in 2002 including 56% black spruce (*Picea mariana*), 30% white spruce, 9% Norway spruce (*Picea abies*) and 3% pine (*Pinus sp.*) (Etheridge et al. 2006). MC is part of the Ganong Ecodistrict in the Highlands Ecoregion, and it is underlain by Devonian felsic volcanic and metasedimentary rocks. Felsic volcanic rocks result in coarse-textured, poor soils, but are accompanied by fine-textured particles derived from metasedimentary rocks (Zelazny 2007b). Balsam fir and black spruce dominate the vegetation in this ecodistrict, but in mid-slopes white spruce, white birch (*B. papyrifera*) and yellow birch and red maple (*A. rubrum*) are common as well (Zelazny 2007b).

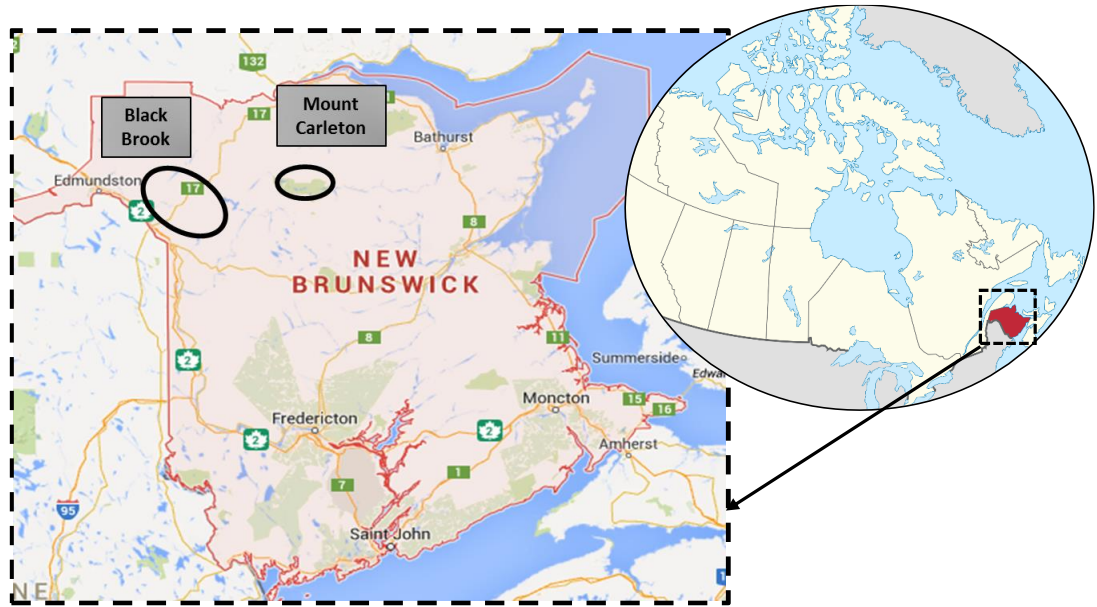


Figure 2-1: Map of Canada showing the location of New Brunswick (in red), and map of New Brunswick (red outline around the province) showing the location of Black Brook and Mount Carleton. (Adapted from: https://en.wikipedia.org/wiki/List_of_municipalities_in_New_Brunswick and <https://www.google.com/maps>).

Twelve low order streams (1st-3rd) were selected in the northern end of BB (Figure 2-2) to capture a range in forest condition (including forest structure – i.e., the vertical and horizontal arrangement of the vegetation, and vegetation species composition) and in the proportion of catchment harvested. My main interest was in assessing the indicators across a gradient of forest condition and harvesting intensity, but I also selected three reference streams in MC to determine a regional range of natural variation in the indicators for forest catchments that had not been managed. The reason why MC was selected as the reference area in spite of this being part of a different ecoregion (which mainly differs in geology: felsic in MC vs. sedimentary in BB) was the absence of unmanaged catchments closer to BB. Because catchment geology is known to influence stream ecosystems by, for example, controlling water chemistry and flowpaths (Hynes 1975), reference streams were not included in the regression models (see section 2.2.4. for further details), but they were used to compare the stream indicator values in

BB to those in nearby unmanaged systems. The reference stream MC2 had a beaver dam ~1 km upstream of the sampling reach, which presented a good opportunity to compare anthropogenic (harvesting in BB) to natural (beaver dam in MC2) disturbance. Catchments in BB were delineated using an Arc-GIS flow accumulation grid based on the high resolution (1 m) LiDAR derived digital elevation model (DEM) obtained from JDI (1-m DEM was converted into a 5-m DEM to facilitate computation), whereas catchments in MC were delineated by using the provincial DEM (20-m resolution). Detailed characterization of each BB catchment was achieved using LiDAR-derived forest structural metrics, photo-interpreted composition data from high-resolution digital stereo imagery (known as forest resource inventory or FRI), and topographic information derived from the LiDAR-based DEM (see section 2.2.3 for more details). Such a detailed catchment characterization could not be done for MC due to the lack of high-resolution LiDAR and FRI data (see Appendix I Table A1 for the list variables available for BB and MC). The BB catchments ranged not only in harvesting intensity (18-100 % of the catchment harvested in the last 10 years), but also in road density (21-89 m of road per ha), stream crossings (0-4), catchment size (77-389 ha), and forest composition (deciduous/mixed/coniferous dominated) (Table 2-1).

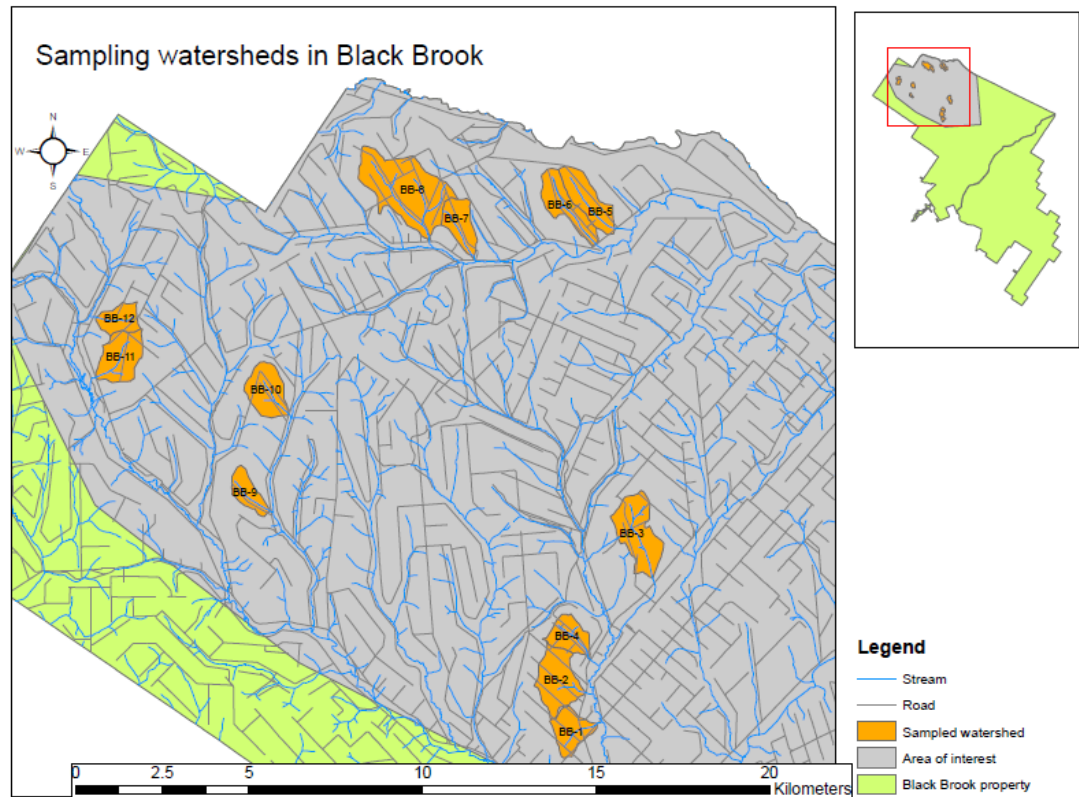


Figure 2-2: Map showing the 12 catchments selected for this study (in orange) in the Black Brook Forestry District (in green). Roads (gray lines) and streams (blue lines) are presented too.

Sixty-meter long stream reaches were selected for sampling immediately upstream of road crossings. However, in 8 out of 15 streams, roads intersected stream channels further upstream of the sampling reach (at least 300 m upstream). Thus, with this design I ensured that I was not measuring the direct effects of stream crossings on downstream stream ecosystems (since this could overwhelm the effects of other drivers of stream ecosystem condition in the catchment that I was interested in), but that I incorporated road crossings as potential stressors contributing to the cumulative effects from forest management practices as this another stressor related to forest management. Therefore, stream crossing density was included as an explanatory catchment characteristic in subsequent analyses (see section 2.2.3.2).

Table 2-1: Coordinates, catchment size, harvesting intensity, number of stream crossings, road density, % coniferous (CON) and % deciduous (DEC) for each BB and MC stream.

Stream	Latitude	Longitude	Area (ha)	% harvested (last 10 years)	Stream crossings (per stream km)	Road density (road m per ha)	CON	DEC
BB01	47°27'24.7"N	67°48'56.3"W	100	40.9	1.63	89	92	0
BB02	47°27'53"N	67°49'11.9"W	147	87.6	0.40	45	81	19
BB03	47°29'36.3"N	67°47'41.4"W	205	50.8	0.64	28	8	88
BB04	47°28'23.9"N	67°49'07.5"W	97	100.0	1.74	68	63	34
BB05	47°35'07"N	67°48'42.6"W	140	43.5	0	34	71	28
BB06	47°34'52"N	67°49'10.1"W	144	34.2	0.36	39	66	26
BB07	47°34'34.9"N	67°51'55.6"W	115	47.3	0	32	14	63
BB08	47°34'52.6"N	67° 53'0.2"W	392	51.6	0.56	42	49	36
BB09	47°30'37.5"N	67°56'31.3"W	66	18.1	0	21	17	68
BB10	47°32'07.8"N	67°56'08.7"W	138	35.1	0.44	34	48	48
BB11	47°32'39.3"N	68°00'36"W	141	19.5	0.91	23	53	22
BB12	47°33'35.4"N	68°00'39.7"W	72	64.4	0	33	16	77
MC2	47°23'31.6"N	66°54'39.4"W	196	0	0	0	-	-
MC3	47°21'40.8"N	66°54'56.3"W	308	0	0	0	-	-
MC4	47°21'09.1"N	66°54'07"W	192	0	0	0	-	-

2.2.2. Measurement of response variables

2.2.2.1. Sediment deposition

To estimate the amount of fine sediments deposited to the stream bottom, seven sediment traps were deployed along the 60-m reach. Centrifuge tubes (50-ml polypropylene tubes) were placed in bricks, and the bricks were placed on the stream bottom of depositional areas (Kreutzweiser et al. 2009). After pushing the tube down as much as possible and without disturbing the sediments, the caps were removed. After 23-24 days in 2014 (October-November) and 25-30 days in 2015 (September-October), caps were replaced, and tubes withdrawn and kept frozen until further analysis in the lab.

Contents of the thawed tube were poured into a 250 μm sieve and the filtrate retained. The filtrate was filtered through pre-ashed 1.2 μm GF/C Whatman filters, and the filters were oven-dried for 48 h at 60 $^{\circ}\text{C}$, left to cool in a desiccator and weighed. Then, filters were ashed in a muffle furnace at 500 $^{\circ}\text{C}$ for 2 h, left to cool in a desiccator, and weighed to calculate ash-free dry mass (AFDM). The size-class used for this study (1.2-250 μm) is representative of clay and silt particles, which are known to be transported from roads or harvested sites as well as the most biologically problematic size-class (e.g., clogging gills) (Waters 1995).

2.2.2.2. Water chemistry and DOM quality

Water samples were collected at the downstream end of each sampling reach in September, October and November of 2014 and in August, September and October of 2015. Water samples were kept refrigerated until analysis. Water quality parameters were analyzed at the Great Lakes Forestry Centre (Sault Ste. Marie, ON, Canada) following standard methods (Hazlett et al. 2008), and included pH, conductivity, alkalinity, water cations and anions (Ca, K, Mg, Na, SO_4 , Cl, SiO_2), nutrients (NO_2+NO_3 , NH_4 , total N, dissolved organic carbon – DOC, dissolved inorganic carbon – DIC, reactive P, total P) and metals (Al, Fe, Mn, Zn, Cd, Cu, Ni, Pb). Dissolved organic matter (DOM) was characterized at Laurentian University (Sudbury, ON, Canada) using Cary Eclipse and Cary 60 UV-Vis spectrophotometers; three-dimensional fluorescence scans were run at 5 nm excitation steps from 250 to 450 nm, and emissions were read at 2 nm steps from 300 to 600 nm. The generated excitation-emission matrices were then corrected and adjusted, and variables describing optical properties of DOM (e.g., humification index, fluorescence index, specific UV absorbance at 254 nm or SUVA) were calculated. PCA was conducted with the mean value (averaged across three months within each year) of water chemistry (WC) variables and DOM characterization variables for each year, and the first and

second principal components (hereafter WC_PC1 and WC_PC2, and DOM_PC1 and DOM_PC2) were used to represent the collective water chemistry variables and DOM characteristics in subsequent statistical analyses (see section 2.3.2. for PCA results). Note that in 2014, results were below detection for 5 out of 7 variables describing optical properties of DOM; therefore, the DOM PCA was conducted only in 2015.

2.2.2.3. Water temperature

Water temperature was continuously measured every 30 (in 2014) and 60 (in 2015) minutes during the sampling season (July 31st – November 10th in 2014; June 15th – October 22nd in 2015) with water temperature and level data loggers (Onset HOBO Data Loggers), and daily maximum, minimum and mean temperatures were calculated. The daily values were averaged for different periods of time (monthly average, summer average and fall average). The relative trends across streams were comparable for different temperature variables (e.g., the stream with the highest daily maximum in summer was also the stream with the highest mean temperature in autumn), so only two variables are presented herein (which overlapped in 2014 and 2015): averaged daily average fall temperature (AFT) extending between September 1st and October 19th, and averaged daily maximum August temperature (MAT) extending between August 1st-31st.

2.2.2.4. Leaf decomposition and benthic macroinvertebrate communities

Senescent speckled alder leaves (*Alnus incana* ((L.) Moench)) were collected in Saint John (New Brunswick, Canada) just before abscission in the fall before the study, and air-dried. The leaves were pre-leached by keeping them in slowly flowing water for 48 hours, and dried in the oven at 30 °C for 48 h. Leaves were weighed into 4.0 ± 0.1 g groups and placed in mesh bags with a 5 mm x 10 mm mesh size (to ensure that BMI could access the leaves) and a 15-cm

diameter metal wire frame inserted to maintain the shape and minimize leaf clumping. Leaf packs were tied to bricks placed on the stream bottom or tied to rebar driven into the substrate where water levels were too low to use bricks. In September 2014, six leaf packs were distributed within each 60-m reach at each site and incubated in the streams for 31-33 days. Leaf packs had to be discarded from one of the streams (BB05) upon retrieval due to low water levels during the incubation period. In September 2015, a second set of six leaf packs was deployed within each reach and incubated for 33-35 days. In both years, leaf packs were retrieved and the contents emptied into 400-ml plastic containers filled with stream water and then preserved in 37% formaldehyde (ca. 10% of the volume).

In the lab, samples were dyed with Phloxine B at least 24 h prior to processing to facilitate detection of invertebrates among the leaves and debris. Containers were emptied into 1 mm and 250 μ m sieves under the fume hood and then leaves were washed individually with distilled water. Using a dissecting microscope, invertebrates were picked from the material collected in the sieves and stored in 70% ethanol. They were then identified to genus (with the exception of *Chironomidae* and *Ceratopogonidae* as well as non-Insecta taxa – all identified to family) and then classified according to their functional feeding group (FFG) using Merritt et al. (2008). These data were used to calculate abundance, richness, Margalef's richness, Shannon's diversity index, % EPT (Ephemeroptera + Plecoptera + Trichoptera), % *Chironomidae* and the percentage of each FFG. Residual leaf material was dried in the oven at 60 °C for 48 h, cooled in a desiccator and weighed. Dried leaves were finally ashed in a muffle furnace at 500 °C for 2 h, cooled in a desiccator, and ash-free dry mass (AFDM) calculated by subtracting ash mass from dry mass. Percent AFDM lost was calculated by subtracting the AFDM at the end of the incubation period from the starting AFDM (which was calculated to be 95.2% of the starting dry mass during a preliminary study). Finally, % lost AFDM per degree-day

was calculated by dividing % lost AFDM by accumulated degree-days during the incubation period. Ash mass, i.e., the leaf inorganic mass (LIM), was used as an indicator of the degree of very fine sediment entrainment in biofilms on leaf material.

2.2.2.5. Biofilm and algal biomass on tiles

To estimate the biomass of periphyton communities and total biofilm (algae, bacteria, fungal biomass) on rock surfaces in streams, one row of 10 unglazed clay tiles (4.7 x 4.7 cm) was deployed in each of three different riffles within the 60-m reach. The 10 tiles were glued to a duct tape band, and the band was secured to the streambed using rebar. Half of the tiles (five) in each row were used to measure total biofilm biomass, and the other half to quantify chlorophyll a content (periphyton or algal biomass). In 2014, the incubation started at the end of July/beginning of August and lasted 48-51 days. In 2015, tiles were deployed in mid-July and incubated for 24-25 days. The incubation was modified in 2015 because in 2014 many grazers (notably *Glossosoma*) were found on some of the tiles; therefore, in 2015 the deployment period was shortened to ensure sufficient time for biofilm growth, but less time for grazers to colonize the tiles (personal observation). Upon retrieval, tiles were scraped with scalpels and the slurry washed with stream water into Whirl-pak bags. The slurry from five tiles was pooled into a single sample (five tiles for total biomass and five tiles for chlorophyll a). Samples were kept in the dark and refrigerated in the field, and frozen at the end of the day.

In the lab, samples were thawed and filtered through pre-combusted and preweighed GF/C Whatman filters. Filters for chlorophyll a analysis were frozen, and filters for total biofilm biomass were oven-dried for 48 h at 60 °C, left to cool in a desiccator and weighed. Then, dried filters were ashed in a muffle furnace at 500 °C for 2 h, left to cool in a desiccator, and ash mass was weighed to calculate ash-free dry mass (AFDM). Ash mass, i.e., the biofilm inorganic mass

(BIM), was used as an indicator of the degree of very fine sediment entrainment in biofilms of rock surfaces. Chlorophyll a was extracted by submerging the filters in 90% ethanol in glass tubes placed in an 80 °C water bath for 7 minutes. After cooling, chlorophyll a concentration of the extract was measured using a Trilogy fluorometer (Turner Designs, Sunnyvale, CA, USA). An autotrophic index was calculated by dividing chlorophyll a concentration (algal biomass) by total biofilm biomass.

2.2.3. *Catchment and reach-level explanatory variables*

Explanatory variables were classified into five groups under two main categories: catchment variables and reach variables. Catchment variables included those related to harvest, catchment forest condition and landscape characteristics; reach variables included those related to riparian forest condition and stream morphology. In addition to being used as indicator variables, abiotic endpoints (sediment loading, water chemistry, DOM quality and water temperature) were treated as explanatory variables for a separate set of models in the analyses of biotic indicators (leaf decomposition, BMI community and biofilm). All the variables within each category are shown in Appendix I Table A1.

2.2.3.1. Harvest levels in catchments

Harvest variables were calculated from the GIS layers provided by JDI and that contained information on the stands harvested each year since 1986. From this data, the area of each catchment harvested each year using different harvesting methods was calculated. This data was summarized into categories related to time since harvesting and harvesting method. For time since harvesting, the cumulative area harvested in the last 5, 10, 20 and 30 years was used. Harvesting method was either clearcut (CC) harvesting or partial harvesting (PH) in which trees were selectively harvested (usually 35-50% of the trees removed) as is typically

conducted in commercial thinning of spruce plantations or selection cuts in deciduous stands. Total cumulative harvest area was the sum of clearcut and partial harvests over each of the 4 time periods. As a result, there were 12 harvest variables in total describing the percentage of the catchment harvested during a period of time and with a given harvesting method (CC_5 y, CC_10 y, ..., PH_5 y, PH_10 y, ..., total_30 y). Because 6 of the 12 BB catchments underwent some sort of harvesting between the sampling in 2014 and 2015, the values of harvesting variables differ between years.

2.2.3.2. Landscape features

Landscape features that could potentially affect stream ecosystems were selected, and they were calculated from several data sources. Catchment area (upstream of the sampling sites) was obtained in ArcGIS following watershed delineation from the 5-m DEM and using a flow accumulation threshold of 0.1 ha. Stream length and density (unit length/watershed area) were calculated from the stream shapefile provided by JDI. Road variables were calculated from the road shapefile provided by JDI, with road crossing frequency obtained by dividing the number of road crossings upstream of the sampling reach by total stream length upstream of the sampling reach, and road density by adding the length of all the roads in the catchment and dividing this by the area of the catchment (upstream of the sampling sites). Note that roads in BB are dirt roads, and that salt or dust settlers are not used. Mean elevation of the catchment and slope $[(\text{maximum elevation} - \text{minimum elevation})/\text{distance between maximum and minimum elevation}]$ were calculated from the LiDAR derived 5 m DEM. Effective Variable Source Area (effVSA, which describes the hydrological connectivity between the catchment and the stream, and thus, has implications for stream ecosystems) was calculated on a hydrologically conditioned DEM, where the D8 algorithm was used to calculate contributing

areas and the stream network (a contributing area of 0.25 ha was used as the channelization threshold) by following the method used by Mengistu et al. (2014). Briefly, topographic wetness index (TWI), which is an indicator of topographically driven soil wetness, was calculated following the equation $TWI = \ln(\alpha/\tan \beta)$, where α is the upslope contributing area of a given grid cell based on a flow accumulation map calculated using the D-infinity algorithm, and β is the slope of that grid cell. To allow comparisons among catchments, TWI maps were normalized. The VSAs were calculated from these maps by starting at the stream and recursively moving to lower TWI values until there is a breakpoint where values start increasing again. EffVSA was calculated by selecting grid cells with TWI values greater than the 75th percentile of the TWI values within the VSA, and finally % effVSA was calculated by dividing the effVSA area by catchment area (Mengistu et al. 2014). % effVSA was available for only BB catchments, but the other landscape variables were available for both BB and MC.

2.2.3.3. Catchment forest condition

Variables describing catchment forest condition were obtained from two GIS data sources provided by JDI, with forest composition (species assemblages) variables being derived from the Forest Resource Inventory (FRI, photo-interpreted composition data from high-resolution digital stereo imagery) and forest structural (age, height) metrics being derived from LiDAR returns captured from 6 pulses m⁻². From the FRI tree species composition, a percent of total catchment area was calculated for the overstory (>2m) and understory (<2m) layers, resulting in 34 variables (each tree species is a variable). Forest stands were classified as deciduous, coniferous or mixed forest depending on which overstory and understory tree species predominated. Several forest structure metrics were calculated from LiDAR for each catchment by averaging the structural metric values based on pulse returns from each 5x5 m

cell in each catchment: P90 – the height of the 90th LiDAR percentile; CrC2 – percent crown closure at 2 m from the ground; CrC10 – percent crown closure at 10 m from the ground; S2 – percentage of LiDAR returns within the 0-2 m above ground height bin (which represents the understory or young plantation); S10 – percentage of returns within the 8-10 m bin (which represents tall trees, thereby older stands); Vertical Complexity Index (VCI) – a value between 0-1, with 1 meaning that all height bins have equal numbers of LiDAR returns and decreasing values meaning that the distribution of returns per height bin is more uneven. All these variables were available for only BB catchments (as previously stated, due to a lack of high-resolution LiDAR and FRI data available for MC).

2.2.3.4. Riparian forest condition

Riparian forest composition and structure were characterized by using GIS data provided by JDI (for the entire catchment) and by ground based vegetation surveys (only for the sampling reach). From the GIS data, % deciduous/coniferous/mixed forest (calculated from the FRI data) and riparian height (% of the riparian forest with P90 >5 m; calculated from LiDAR) were obtained for a 30-m wide band along each side of the stream. For a more detailed characterization of the riparian forest within the sampling reach, the woody understory vegetation (<5 cm DBH) was surveyed along 80-m long transects parallel to the stream and located one meter from the stream edge on both sides of the stream. This was done by recording which species were present and at which height class within 50-cm radius plots at 2 m intervals along the transect. The percent and category (moss/ fern/ non-woody seed plants) of the herbaceous ground cover was also recorded in each plot. The overstory composition and structure were recorded by identifying and measuring the DBH of every tree (>5 cm DBH) within a belt transect 3 m wide starting from the stream edge and 80 m long. The relative

abundance of each woody plant species was calculated by counting the number of plots in which that species was recorded and dividing it by the total number of plots (2 transects of 41 plots per stream, i.e., 82 plots). Overstory, understory and total richness were calculated from this data. Finally, canopy cover was measured by taking pictures of the canopy from the stream every 10 m within the 80-m sampling reach with a Canon EOS 50D camera with a 185° SuperFisheye (5.6mm F/5.6) lens and a self-leveling mount on a tripod (Régent Instruments Inc. Ville de Quebec, QC). The pictures were processed using WinSCANOPY 2009a for Canopy Analysis (Régent Instruments Inc.). Variables derived from the GIS data provided by JDI were available for only BB sites, whereas variables derived from the vegetation surveys and canopy pictures were available for both BB and MC.

2.2.3.5. Stream morphology

Stream morphology was characterized by visually surveying eight 10 m long sections and then averaging results for the entire 80-m reach for flow structure (% riffle/ run/ pool), substrate composition (% bedrock/ boulder/ cobble/ gravel/ sand/ silt/ clay), width and averaged depth, and number of large woody debris (LWD > 10 cm diameter) structures. All these variables were available for both BB and MC.

2.2.4. *Statistical analysis*

Each stream indicator was plotted in a Box plot to look for differences among streams and between years, followed by a linear mixed model ANOVA testing for between-year differences (year was treated as a fixed factor and stream as random). Log-transformation was performed when necessary to meet the assumptions of normality and homogeneity of variance. The inter-annual congruence of each stream indicator was further assessed by conducting a Pearson's product-moment correlation analysis between 2014 and 2015 results.

For model selection purposes, only BB streams were included because 1) several variables derived from high quality forest and landscape characterization data were only available for BB (Appendix I Table A1) and I wanted to include these variables in the models, the reason being that a refined catchment characterization may allow a better separation of the effects of harvesting from the effects of forest condition or landscape characteristics; and 2) the geological and topographical differences between BB and MC resulting from these areas being part of different ecoregions could confound the comparison between reference and harvested sites.

Linear regression models were built with stream indicators as response variables (RVs) and catchment and reach variables as explanatory variables (EVs) (Table 2-2). But, because all the EVs could not be included in the regression models, a subset of EVs was selected prior to regression analyses. As a first step during variable selection, a Pearson's correlation analysis was conducted among EVs within a category (Figure 2-3) (see Appendix I Table A1 for variables considered within each category). When several variables within a category of EVs were correlated among each other (which was the case for harvest, catchment forest condition and stream morphology categories), a Principal Components Analysis (PCAs) was performed for each category (on centered and scaled data) and the PCs that captured the main gradients within the category were selected for regression analyses. In the case of harvest, two separate PCAs had to be conducted with 2014 and 2015 data because some harvesting occurred in some of the catchments between years. The variance explained by each PC as well as the variables correlated with the selected PCs are summarized in Table 2-2; briefly, in 2014 harvest PC1 (45.5% of the variance explained) was positively related to partial harvest and negatively to recent clearcut, whereas harvest PC2 (22.5%) was positively related to cumulative harvest (mainly clearcut) over the past 30 years (see Appendix I Table A2 for correlation matrix among

harvest variables and Figure A1 for PCA results). In 2015, harvest PC1 (45.5%) was positively related to partial and total harvest, whereas harvest PC2 (25.3%) was negatively related to clearcut (mainly recent, <5-10 years) (see Appendix I Table A3 for correlation matrix among harvest variables and Figure A2 for PCA results). Forest condition PC1 (FC_PC1, 64%) was positively related to deciduous, mature (high-canopy) forests and negatively to young, conifer plantations, whereas FC_PC2 (27.7%) was positively related to mixed forests and negatively to coniferous forests (see Appendix I Table A4 and Figure A3). Stream morphology PC1 (44.0%) was positively related to % riffle, % cobble and width, and negatively related to % run, % silt, % sand and large woody debris; SM_PC2 was not selected because it did not capture a clear gradient (and because I could not select more than 9 variables for hierarchical partitioning, see below) (see Appendix I Table A5 and Figure A4). Landscape variables did not show strong correlations among each other and the PCA did not identify strong gradients (see Appendix I Table A6 and Figure A5), so the two variables that were most related to my research questions and that can potentially influence stream condition by influencing the delivery of terrestrial materials to streams were selected: road density (which was correlated with number of stream crossings) and % effective VSA (% effVSA). The riparian forest condition PCA also did not identify clear gradients (see Appendix I Table A7 and Figure A6), so two variables were selected based on their potential to influence stream condition: % riparian conifer (negatively correlated with % riparian mixed and % deciduous forest) and canopy openness. The category of stream morphology was not included in the regression analyses for water chemistry, DOM quality and water temperature, since there needed to be reasons based on ecological principles to hypothesize that a category of EVs could be influencing a given RV. All the RVs and EVs considered for regression analyses are shown in Table 2-2.

Table 2-2: Response and explanatory variables included in regression analyses. For principal components (PCs), the variance explained by each PC, the short form, as well as the variables positively (+) and negatively (-) correlated with each PC, have been specified.

Indicators (response variables)		Explanatory variables			
		Category	Variable	Description	
Abiotic	Sediment deposition	Catchment	2014	PC1 (46%)	+: Partial harvest (<10, 20, 30 y) -: Recent clearcut (<5, 10 y)
	Water chemistry			PC2 (23%)	+: Cumulative clearcut (<20, 30 y) & harvest (30 y)
	DOM quality		2015	PC1 (46%)	+: Partial (<5, 10, 20, 30 y) & total harvest (<10, 20, 30 y)
	Temperature			PC2 (25%)	-: Clearcut (<5, 10, 20 y)
Biotic	Leaf decomposition	Landscape	Road density % effective VSA (% effVSA)		
	BMI community	Forest condition	PC1 (64%; FC_PC1)	+: % deciduous, VCI, P90, CrC2, CrC10, S10 -: % coniferous, S2	
	Biofilm and algal biomass		PC2 (28%; FC_PC2)	+: % mixed, S2 -: % coniferous, CrC2	
Biotic	Riparian forest	Reach	% riparian conifer Canopy openness		
	Stream morphology**		PC1 (44%; SM_PC1)	+: % riffle, % cobble, width -: % run, % silt, % sand, LWD	
Abiotic *	Sediments	Abiotic *	LIM		Leaf Inorganic Mass (related to deposition of fine inorganic sediments)
	Water chemistry		PC1 (54%; WC_PC1)	+: Cations (Ca, Mg), C, conductivity, pH	
			PC2 (20% WC_PC2)	+: DOC, Fe, Al, Cl	
	DOM quality		SUVA		Indicator of DOM aromaticity (related to DOM humification too)
Temperature	MAT		Maximum August Temperature (related to other temperature variables such as average fall temperature)		

* Abiotic stream indicators were treated as explanatory variables only in the case of regression models explaining biotic indicators.

** Stream morphology was not included as an explanatory variable in the regression models explaining water chemistry, DOM quality and water temperature.

For the biotic indicators, because I was also interested in understanding how abiotic indicators were influencing biotic endpoints, a second set of regression models was built using 5 of the abiotic endpoints presented in this chapter (Table 2-2): leaf inorganic mass (LIM, representing fine inorganic sediments as described in section 2.3.1.), water chemistry PC1 (WC_PC1, representing cation/carbon concentrations as described in section 2.3.2.), water chemistry PC2 (WC_PC2, representing dissolved organic carbon and metals as described in section 2.3.2.), SUVA (representing the aromaticity and humification of DOM as described in

section 2.3.2.) and maximum August temperature (MAT, representing water temperature as described in section 2.3.3.).

Model selection was conducted using ordinary least-squares regression and Akaike Information Criterion adjusted for small sample sizes (AICc) (*MuMIn* package in R version 1.15.6, Bartón 2016) (Figure 2-3). All the potential regression models constructed from the subset of 9 catchment and reach EVs (and a second set of regression models constructed from the 5 abiotic stream EVs for the biotic indicators) as well as the null model were included in the analysis, and the four best models (lowest AICc score) were selected for each RV. To evaluate the relative importance of each model, ΔAICc and Akaike weights (ω_i) were calculated to assess and identify the best supported model (Anderson 2008). The R^2 of the four best regression models was also calculated to assess the proportion of the variance explained by these models.

Regression analyses were complimented with Hierarchical Partitioning analysis (HP) (*hier.part* package in R version 1.0-4, Walsh and Mac Nally 2013), which allowed me to determine the relative importance of each of the 9 EVs and to separate the independent and joint contribution of each EV to the variability of the RV (Chevan and Sutherland 1991) (Figure 2-3). To calculate the amount of variance in each RV explained by each EV, as well as the direction and significance of the relationship, simple linear regressions were performed and the coefficient of determination values (R^2) and slope coefficients (only in the cases where regression models were statistically significant at $\alpha = 0.1$) were recorded. For the biotic indicators, analyses (HP and linear regressions) were conducted twice, first with the 9 catchment and reach variables and then with the 5 abiotic indicators.

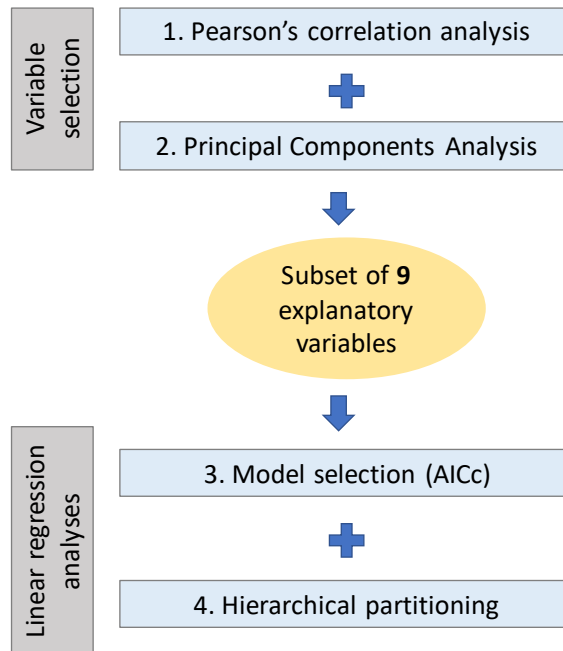


Figure 2-3: Flow chart describing the statistical tests conducted to assess the relationships between the indicators and the catchment and reach explanatory variables (EVs).

Although PCAs are very helpful for variable reduction purposes and to describe the main gradients in the data, they do not contain the same information as each individual EV. In addition, there were several EVs that were not captured by the first and second PCs or that were not included in the models. Therefore, to understand how each individual EV related to the stream RVs, Pearson's correlation analyses were conducted between all the EVs and RVs and these correlations were used to compliment and inform the interpretation of the results obtained from regression analyses. Correlation tables for each indicator can be found in Appendix I Tables A8 to A13.

To assess whether the relationships between catchment/reach variables and stream indicators identified in BB could be extended to MC streams, BB (correlation analysis with only the 12 BB streams) and BB+MC (correlation analysis including 12 BB and 3 MC streams) correlation coefficients between EVs and RVs were compared for the EVs that were available for all 15 streams (see Appendix I Table A1). Explanatory variables with correlation coefficients

$> |0.5|$ were selected and the difference between the BB and the BB+MC correlation coefficients ($\Delta r = r_{BB} - r_{BB+MC}$) was computed. If $\Delta r > 0.1$, I concluded that the relation between that given EV and RV weakened when including MC sites, whereas if $\Delta r < 0.1$ I concluded that the relationship strengthened when including MC sites.

Note that some EVs (namely harvesting variables) differed between 2014 and 2015; hence, statistical analyses were conducted separately for each year instead of combining the 2014 and 2015 data for each RV.

2.3. Results

2.3.1. Sediment deposition

Deposition of fine inorganic sediments ($< 250 \mu\text{m}$) differed significantly between 2014 and 2015 ($F_{1,174} = 154.3$, $p < 0.001$), with sediment traps collecting 0.24 g less in 2015 than in 2014, on average (Figure 2-4); in 2014, mean deposition values ranged between 0.021 (MC3) and 0.684 g (BB04), whereas in 2015 they ranged between 0.023 (MC3) and 0.176 g (BB01). Streams with low sediment deposition values (reference streams and BB05), however, showed very small inter-annual differences. 2014 and 2015 values showed a correlation of 0.63.

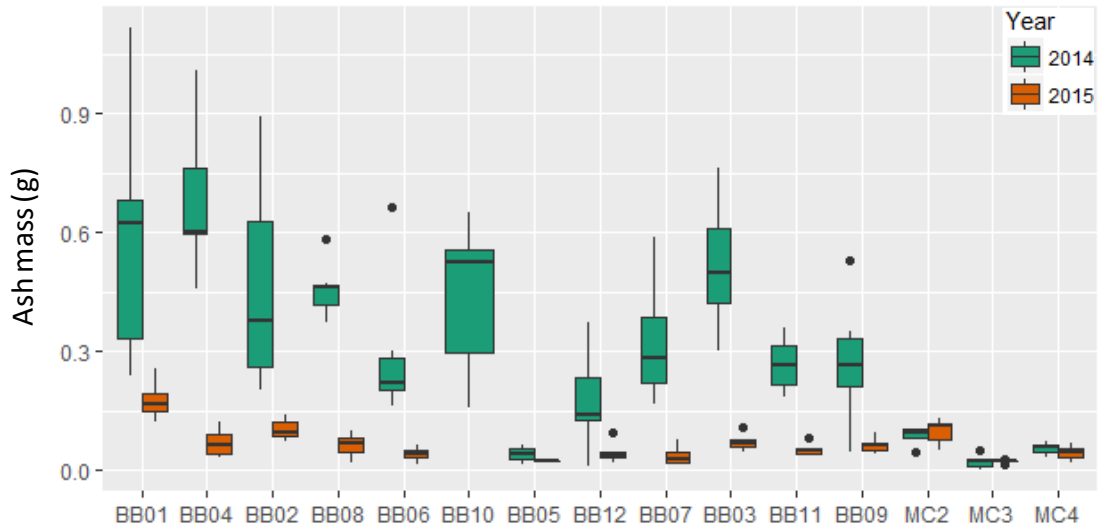


Figure 2-4: Box plot showing the dry mass of fine inorganic sediments (<0.25 mm) collected in the sediment traps ($n = 7$) in 2014 (green) and 2015 (orange) in each stream (Black Brook [BB] harvested streams are sorted according to road density – from highest to lowest; Mount Carleton [MC] are the reference streams) (The upper and lower hinges of each box correspond to the upper and lower quartiles, and the line in between to the median; the whiskers correspond to values higher or lower than the third and first quartiles; dots represent outliers or values that are higher or lower than 1.5 times the interquartile range).

The trend in organic/inorganic ratios in fine sediments across streams was more consistent interannually ($r = 0.91$ between 2014 and 2015) and differed less between years (Figure 2-5) than the trend and values for the absolute mass of the inorganic fraction, suggesting that the ratio is characteristic of each stream. Although interannual differences seemed small, the organic/inorganic ratio was significantly lower in 2014 - by 3% on average ($F_{1,177} = 19.8, p < 0.001$) - than that of 2015, meaning that the inorganic fraction was greater the year in which fine inorganic deposition was greater. The organic percentage ranged from ~20% (BB01 in both years) to ~64% (MC3 in both years) and reference streams, overall, had a greater proportion of organic fine sediments than BB streams (except BB05 and BB07, which had comparable proportions to reference streams).

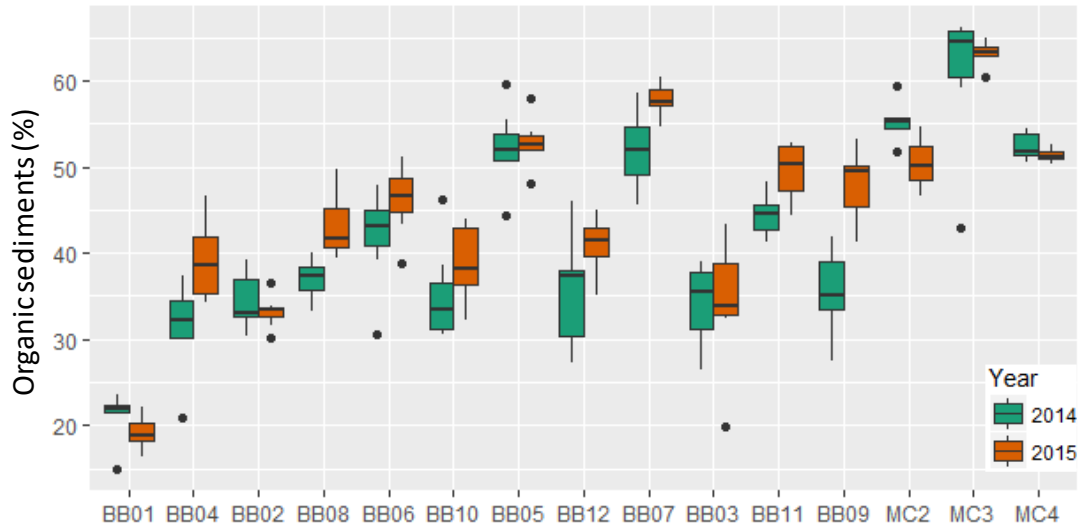


Figure 2-5: Box plot showing the proportion of organic fine sediments (<0.25 mm) collected in the sediment traps ($n = 7$) in 2014 (green) and 2015 (orange) in each stream (Black Brook [BB] harvested streams are sorted according to road density – from highest to lowest; Mount Carleton [MC] are the reference streams) (see Figure 2-4 for box plot description).

All three indicators of inorganic sediment load in the streams (fine sediment entrainment in leaves and in biofilms, and collection in sediment traps) were highly correlated. The fine sediment accumulation (inorganic mass) on leaf pack samples (LIM) was strongly correlated with fine inorganic sediments (FIS, <250 μm) collected in sediment traps in both years ($r = 0.82$ in 2014 and 0.94 in 2015), as well as with total fine sediments collected in traps (TFS, inorganic and organic <250 μm sediments) ($r = 0.67$ in 2014 and 0.0.88 in 2015) (Table 2-3). The inorganic mass of biofilm samples (BIM) followed the same trends as LIM in terms of correlations with sediment trap measures, but the correlation coefficients tended to be lower than those for LIM. Finally, LIM and BIM were also correlated ($r = 0.64$ in 2014 and 0.78 in 2015), thus, model selection was conducted with only one out of those two RVs (LIM). When considering the reference streams as well as the harvested sites, correlation coefficients tended to become slightly stronger for LIM in 2014, whereas they became slightly weaker for LIM and BIM in 2015.

Table 2-3: Table showing correlation coefficients among indicators of sediment loading for harvested (BB) and all (BB+MC) streams for 2014 and 2015. In bold are correlation coefficients >0.5. (LIM = Leaf pack inorganic mass, BIM = Biofilm inorganic mass, FIS = Fine inorganic sediments (<0.25 mm) collected in sediment traps, TFS = Total fine sediments (inorganic + organic, <0.25 mm) collected in sediment traps).

		BB				BB + MC			
		2014		2015		2014		2015	
		LIM	BIM	LIM	BIM	LIM	BIM	LIM	BIM
Sediment traps	FIS	0.82	0.68	0.94	0.71	0.87	0.66	0.91	0.64
	TFS	0.67	0.60	0.88	0.69	0.79	0.60	0.77	0.49
	BIM	0.64	-	0.78	-	0.67	-	0.77	-

According to AICc model selection, models containing only road density were the best models explaining LIM in both years ($\omega_i = 25.4$ in 2014 and 12.7 in 2015, $R^2 = 0.74$ in both years) and FIS in 2015 ($\omega_i = 18.7$, $R^2 = 0.59$), with the sign of the coefficient of road density in the regression models being positive (herein + and – signs are used to indicate positive and negative coefficients of a given EV in the regression model, respectively) (Table 2-4). However, models including stream morphology PC1 (-, which is positively related to % riffle, % cobble), % riparian coniferous (+) and/or % effVSA (+) in addition to roads closely followed the best model for both years and both sediment indicators. Note that the variance explained by the best models was lower for FIS in 2015 than in 2014, as well as than for LIM in both years, which was probably related to the lower precipitation and subsequent sediment deposition during sediment trap deployment in 2015.

Table 2-4: Summary of AICc model selection for fine inorganic sediments (FIS) collected in traps and inorganic mass collected in leaf packs (referred to as leaf inorganic mass or LIM) for 2014 and 2015 in 12 Black Brook streams (NB, Canada). The catchment and reach explanatory variables included in the four best regression models are presented, as well as their corresponding $\Delta AICc$, weight (%) and R^2 (R^2 for simple regression models and adjusted R^2 for multiple regression models). The symbol at the end of each variable indicates the sign of the coefficient for that variable within that regression model. In bold are the best models (lowest AICc value).

		Catchment	Reach	$\Delta AICc$	ω_j	R^2
FIS (traps)	2014	Road density (+) & % effVSA (-)	Stream morphology PC1 (-)	0	57	0.88
		% effVSA (-)	Stream morphology PC1 (-)	3.59	9.4	0.75
			Stream morphology PC1 (-)	4.15	7.2	0.69
		Road density (+)	Stream morphology PC1 (-)	5.14	4.3	0.72
	2015	Road density (+)		0	18.7	0.59
		Road density (+)	Stream morphology PC1 (-)	0.41	15.2	0.65
		Road density (+) & % effVSA (+)		0.81	12.5	0.64
		Road density (+) & % effVSA (+)	Stream morphology PC1 (-)	2.95	4.3	0.71
LIM	2014	Road density (+)		0	25.4	0.74
			% rip. conifer (+)	1.65	11.1	0.7
		Road density (+) & FC_PC1 (+)		1.69	10.9	0.77
		Road density (+)	% rip. conifer (+)	1.72	10.7	0.77
	2015	Road density (+)		0	12.7	0.73
		Road density (+) & Harvest PC2 (+)	Stream morphology PC1 (-)	0.05	12.4	0.85
		Road density (+) & % effVSA (+)		0.21	11.4	0.78
		Road density (+)	Stream morphology PC1 (-)	0.35	10.7	0.77

Of all 9 variables considered for the multiple regression, road density was the variable with the highest independent effect on FIS in 2015 ($I = 35.2\%$) and on LIM in 2014 and 2015 ($I = 27.2$ and 36.6% , respectively) according to hierarchical partitioning (HP), as well as the variable explaining the highest proportion of the variance according to linear regression (LR) ($R^2 = 0.54$, 0.74 and 0.73 , respectively); this effect was positive (herein + and – signs are used to indicate positive and negative relationships between the indicator and EVs, respectively) (Figure 2-6). Stream morphology PC1 (-) had the highest R^2 ($R^2 = 0.69$) and independent effect on FIS in 2014 ($I = 38.0\%$), and the second highest I (19.4%) and R^2 (0.46) in 2015. For LIM, however, % riparian conifer had a stronger independent effect and explained more of the variance than stream morphology.

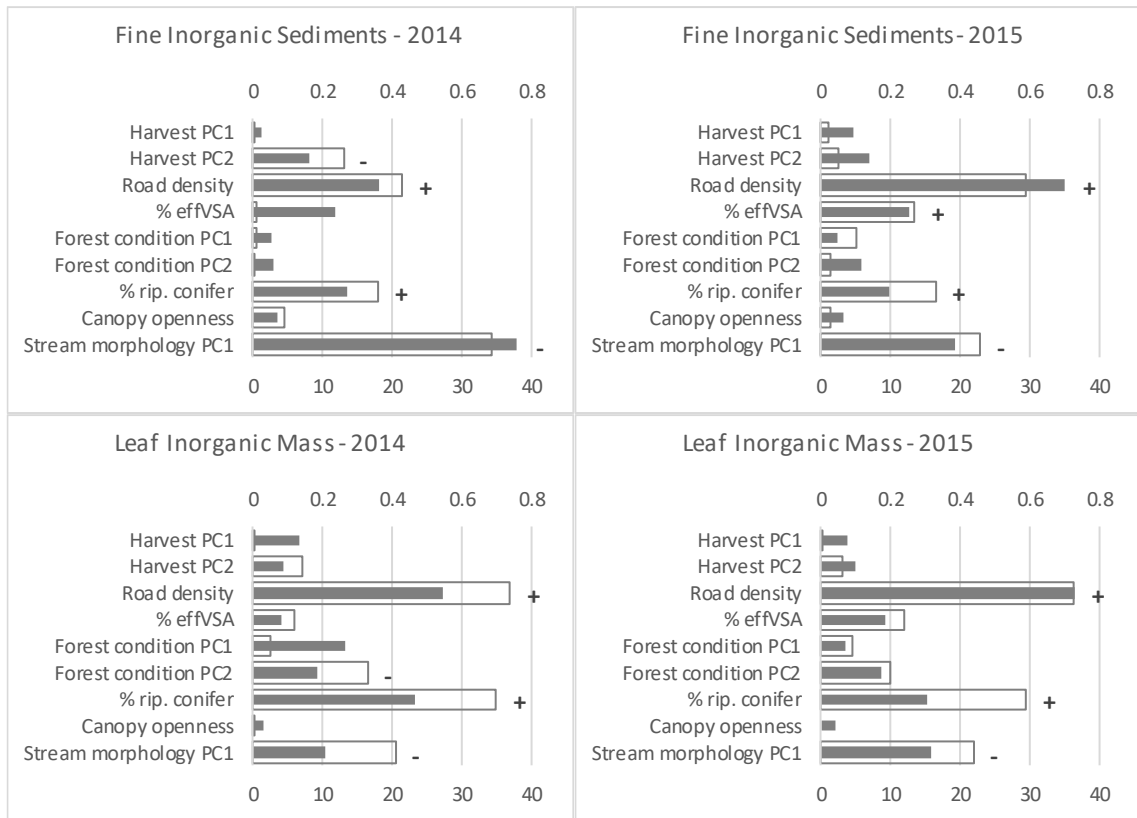


Figure 2-6: Distribution of the percentage of independent effect of each reach and catchment explanatory variable on the variation of fine inorganic sediments (<0.25 mm) collected in sediment traps and inorganic mass of leaf packs in 2014 and 2015 (dark bars, bottom X axis) in 12 Black Brook streams (NB, Canada). The wider white bars and the top X axis represent the R^2 of the simple linear regression between that explanatory variable and the response variable; the + or – signs correspond to the slope of significant univariate regression models at $\alpha = 0.1$.

2.3.2. Water chemistry and DOM quality

The first water chemistry PC (WC_PC1) captured 54 and 55% of the variability in 2014 and 2015, respectively (Figure 2-7), and WC_PC1s for both years were strongly and positively related to pH, conductivity, alkalinity, Ca and DIC (Pearson's $r > 0.95$), positively but less strongly related to K, Mg, DOC ($r > 0.6$), strongly and negatively related to SiO_2 ($r < -0.97$), and negatively but less strongly related to Na and total P ($r < -0.6$) in both years; hence, WC_PC1 represented cation and carbon dynamics. The second PC (WC_PC2), capturing about 21% of the variability, was positively related to DOC, Cl, Al and Fe ($r = 0.68, 0.77, 0.80$ and 0.82 , respectively) and represented DOC and associated metal dynamics.

Both the PCA loadings for each water chemistry variable and the scores for each stream remained similar between years; in fact, PC1 and PC2 scores for each stream were strongly correlated between 2014 and 2015 ($r = 0.99$ and 0.97 , respectively), suggesting that the trends in water chemistry across streams remained relatively constant between years. Moreover, including or excluding reference streams in the PCA yielded very similar results, suggesting that the relationships among variables were very similar between BB and MC sites. BB01, BB02 and BB04 were the streams with the highest PC1 (i.e., cation/carbon) scores, whereas the reference streams had the lowest values. Regarding PC2, BB01 had the highest score due to its high DOC, Fe and Al concentrations, whereas BB02 and BB04 had the lowest scores.

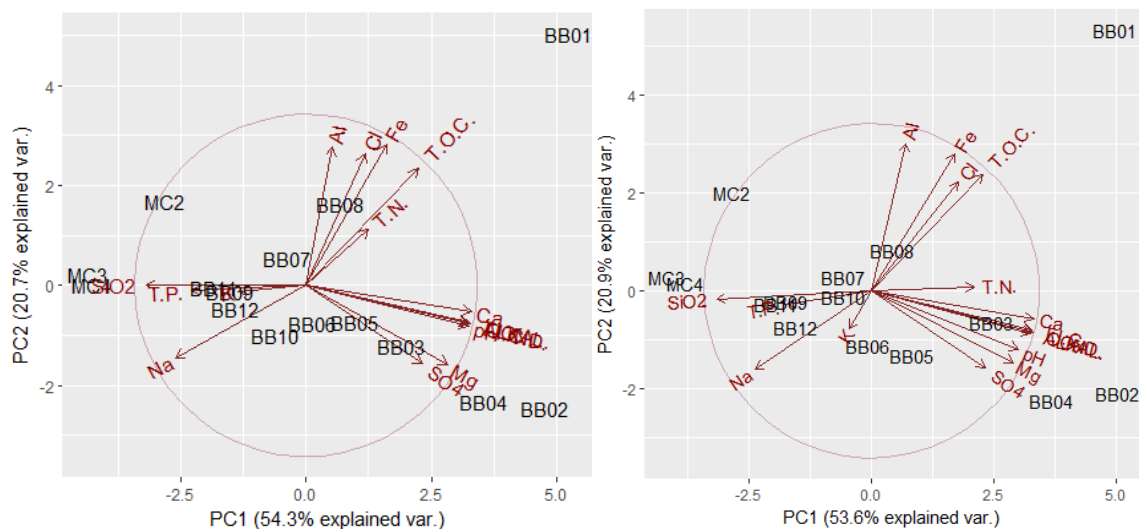


Figure 2-7: Principal component analysis of the water chemistry parameters (indicated by red arrows) for Black Brook (BB) and Mount Carleton (MC) streams (in black) in a) 2014 (average of September, October and November water samples) and b) 2015 (average of August, September and October water samples).

To evaluate potential influences of forest management on the quality of DOM in streams, a PCA was conducted with the measured optical properties of DOM in 2015. The first PC (DOM_PC1) captured 65.6 % of the variability and was strongly and negatively related to variables describing the aromaticity and extent of humification of DOM (e.g., HIX, SUVA, E2E3)

(see Appendix I Figure A7). BB01 had a very low score for DOM_PC1, which means that the DOM in this stream was high in aromatic and humic C molecules. DOM_PC2 captured 14.5% of the variability and was strongly and negatively correlated with the fluorescence index (which is related to the source of DOM being microbial vs. terrestrial). Because SUVA (an indicator of the DOM aromaticity) was strongly correlated with DOM_PC1, and because this variable was available in both 2014 and 2015, SUVA will be presented in the modeling results below as a representative of DOM_PC1 (i.e., the aromaticity and humification of DOM). SUVA was strongly correlated across sites between 2014 and 2015 ($r = 0.98$).

Among all the linear regression models built with the 9 EVs to explain the trends in WC_PC1 in BB, the model including harvest PC2 (-, related to cumulative harvest), % riparian conifer (+) and canopy openness (-) had the strongest support in 2014 according to AICc ($\omega_i = 41.4$, *adj. R*² = 0.96), but it was closely followed by the model excluding canopy openness ($\omega_i = 32.4$, *adj. R*² = 0.93) (Table 2-5). In 2015, the best supported model included forest condition PC1 (+, related to mature, deciduous forests), road density (+) and % riparian conifer (+) ($\omega_i = 27.8$, *adj. R*² = 0.87), followed by the model with % riparian coniferous as the only EV ($\omega_i = 19.3$, *R*² = 0.75). Among the 9 EVs considered, % riparian conifer (+) had the highest independent effect on WC_PC1 ($I = 38\%$) and explained the largest amount of variance (*R*² = 0.74) in 2014 according to HP and LR, respectively, followed by road density (+, $I = 17.0\%$; *R*² = 0.54), harvest PC2 (-, $I = 23.6\%$; *R*² = 0.36) and forest condition PC2 (-, $I = 8.1\%$; *R*² = 0.37; related to % mixed forest/S2) (Figure 2-8). In 2015, both % riparian conifer and road density had equally high independent effects on WC_PC1 ($I = 32.2$ and 30.9%) and *R*²s (0.75 and 0.63).

Table 2-5: Summary of AICc model selection for the first and second principal components for water chemistry (PC1 and PC2) and SUVA (indicator of DOM aromaticity) for 2014 and 2015 in 12 Black Brook streams (NB, Canada). The catchment and reach explanatory variables included in the four best regression models are presented, as well as their corresponding $\Delta AICc$, weight (%) and R^2 (R^2 for simple regression models and adjusted R^2 for multiple regression models). The symbol at the end of each variable indicates the sign of the coefficient for that variable within that regression model. In bold are the best models (lowest AICc value).

		Catchment	Reach	$\Delta AICc$	ω_i	R^2
Water chemistry PC1	2014	Harvest PC2 (-)	% rip. conifer (+) & Canopy open. (-)	0	41.4	0.96
		Harvest PC2 (-)	% rip. conifer (+)	0.49	32.4	0.93
		Harvest PC2 (-) & % effVSA (+)	% rip. conifer (+)	3.34	7.8	0.94
		Harvest PC2 (-) & Harvest PC1 (+)	% rip. conifer (+)	4.76	3.8	0.93
	2015	FC_PC1 (+) & Road density (+)	% rip. conifer (+)	0	27.8	0.87
			% rip. conifer (+)	0.73	19.3	0.75
		FC_PC1 (+)	% rip. conifer (+)	2.08	9.8	0.77
	Road density (+)	% rip. conifer (+)	2.70	7.2	0.75	
Water chemistry PC2	2014	Road density (+) & Harvest PC1 (-)		0	28.3	0.67
		Harvest PC1 (-)		0.30	24.4	0.59
		Harvest PC1 (-)	Canopy openness (+)	3.90	4.0	0.54
		Harvest PC1 (-) & FC_PC2 (+)		4.24	3.4	0.53
	2015	Road density (+) & Harvest PC1 (-)		0	35.5	0.66
		Harvest PC1 (-)		2.65	9.4	0.49
		Road density (+) & Harvest PC1 (-) & Harvest PC2 (+)		3.33	6.7	0.71
	Road density (+) & Harvest PC1 (-)	Canopy openness (+)	4.35	4.0	0.68	
SUVA	2014	Road density (+) & Harvest PC1 (-)		0	24.3	0.68
		Road density (+)		0.50	18.9	0.60
		Road density (+) & Harvest PC1 (-) & % effVSA (+)		1.18	13.5	0.77
		Road density (+) & % effVSA (+)		1.82	9.8	0.63
	2015	Road density (+) & Harvest PC2 (+) & FC_PC2 (+)		0	42.0	0.73
		Road density (+) & Harvest PC1 (-)		2.32	13.2	0.67
		Road density (+)		2.69	11.0	0.59
	Road density (+) & Harvest PC1 (-) & Harvest PC2 (+)		4.94	3.5	0.73	

For WC_PC2, the model including road density (+) and harvest PC1 (-, positively related to partial harvest in both years and negatively to recent clearcut in 2014) was the likeliest one in both years ($\omega_i = 28.3$ and 35.5 , $adj. R^2 = 0.67$ and 0.66 in 2014 and 2015, respectively), but it was closely followed by the model with only harvest PC1 in 2014 ($\omega_i = 24.4$, $R^2 = 0.59$) (Table 2-5). This same variable had the highest independent effect on WC_PC2 in both years (-, $l = 34.9$

and 28.6%), followed by road density (+, $t = 20.7$ and 20.3%) and canopy openness (+, $t = 14.8$ and 22.8%) (Figure 2-8).

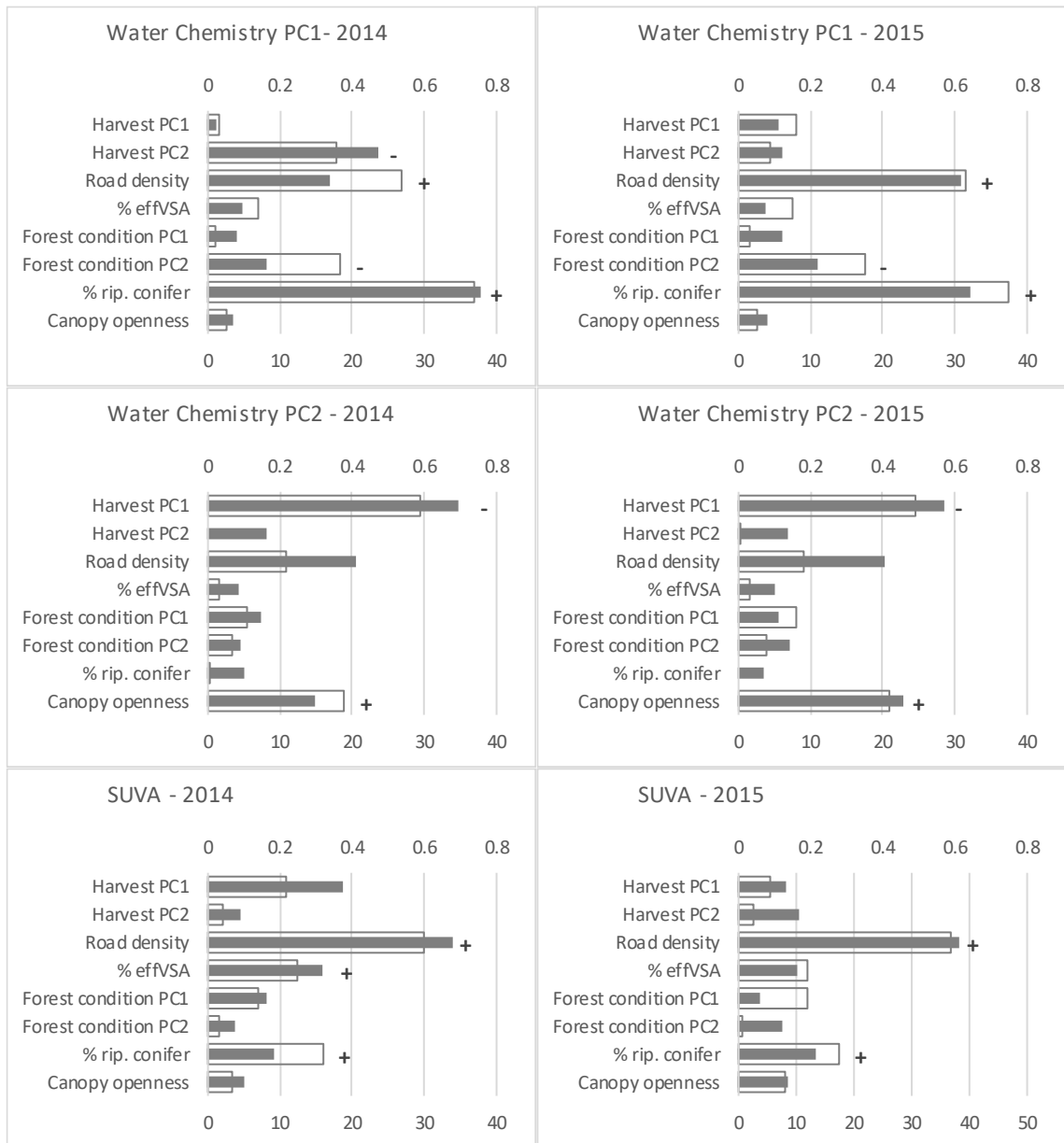


Figure 2-8: Distribution of the percentage of independent effect of each reach and catchment explanatory variable on the variation of water chemistry PC1, water chemistry PC2 and SUVA (Specific UV Absorbance at 254 nm) in 2014 and 2015 (dark bars, bottom X axis) in 12 Black Brook streams (NB, Canada). The wider white bars and the top X axis represent the R^2 of the simple linear regression between that explanatory variable and the response variable; the + or - signs correspond to the slope of significant univariate regression models at $\alpha = 0.1$.

Finally, the best model explaining SUVA in 2014 was the same as the best model explaining WC_PC2 (i.e., road density (+) and harvest PC1 (-), positively related to partial harvest, negatively to recent clearcut); $\omega_i = 24.3$, *adj. R*² = 0.68), but it was closely followed by the model with only road density ($\omega_i = 18.9$, *R*² = 0.60) or the model including % effVSA (+; $\omega_i = 13.5$, *adj. R*² = 0.77) (Table 2-5). In 2015, the model including road density (+), harvest PC2 (+, negatively related to clearcut) and forest condition PC2 (+, related to % mixed forest and S2) was considerably more likely than all the other regression models ($\omega_i = 42.0$, *adj. R*² = 0.73). In terms of independent effects on SUVA, road density had the highest in both years (*I* = 34.1 and 38.3%), as well as the highest *R*² (0.60 and 0.59), and it was followed by harvest PC1 (-, although LR was non-significant), % effVSA (+) and % riparian conifer in 2014 (+, *I* = 18.9, 15.9 and 9.2%, respectively), and by % riparian conifer (+) in 2015 (*I* = 13.3%) (Figure 2-8).

2.3.3. Water temperature

There was a difference of 3.2°C (in 2014) and 2.9°C (in 2015) between the streams with the lowest (7.4 °C in MC4 in 2014 and 7.5 °C in BB12 in 2015) and highest (10.6°C and 10.4°C in MC2 in 2014 and 2015, respectively) AFT (averaged fall temperature), and a difference of 5.9°C (in 2014) and 6.3°C (in 2015) between the streams with the lowest (9.0°C in MC4 and 8.9°C in BB12) and highest (14.9°C and 15.2°C in MC2) MAT (maximum August temperature) (Figure 2-9). The high temperatures recorded in MC2 were probably due to the beaver dam upstream of the sampling reach. When MC2 was excluded, the highest AFTs were recorded in BB08 (8.6°C in 2014) and BB01 (9.2°C in 2015), and the highest MATs in BB01 (13.5 and 13.8°C). Interannual temperature differences within streams were small (< 1 °C), with the largest AFT difference being 0.86°C in BB01 and the largest MAT difference being 1.3°C in MC3, and 2014 and 2015 temperatures were strongly correlated (*r* = 0.90 for AFT and 0.93 for MAT).

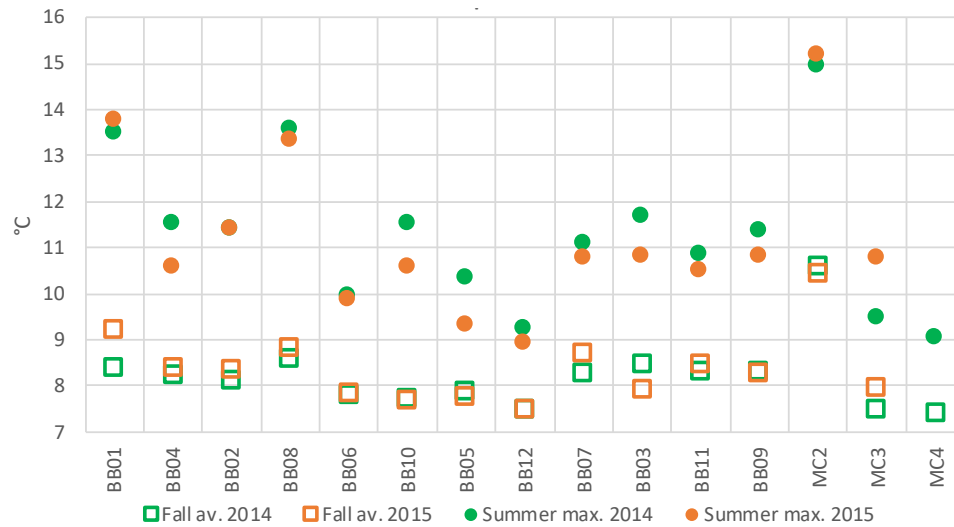


Figure 2-9: Averaged daily fall water temperatures (AFT, Sept 1 – Oct 19, open squares) for each stream in 2014 (green) and 2015 (orange), and averaged daily maximum August water temperatures (MAT, circles) for each stream in 2014 (green) and 2015 (orange) (Black Brook [BB] harvested streams are sorted according to road density – from highest to lowest; Mount Carleton [MC] are the reference streams).

Since regression analyses results were very similar for AFT and MAT, only the latter will be presented. The regression model including canopy openness (+) and % riparian conifer (+) was the best supported model in both years according to AICc ($\omega_i = 25.9$ and 21.7 , *adj. R*² = 0.59 and 0.55) (Table 2-6). This model was twice as likely as the second best supported models, which included % riparian conifer and harvest PC1 (-, positively related to partial harvest and negatively to clearcut) in 2014 ($\omega_i = 13.0$, *adj. R*² = 0.54), and canopy openness and road density (+) in 2015 ($\omega_i = 10.1$, *adj. R*² = 0.49). % riparian conifer had the highest independent effect on MAT in both years (*I* = 26.3 and 20.6%), but this value was very similar for canopy openness (+, *I* = 22.4%) and harvest PC1 (-, *I* = 23.8%) in 2014, and to canopy openness (*I* = 18.2%) and road density (+, *I* = 18.5%) in 2015 (Figure 2-10). However, % riparian conifer explained less variance than canopy openness or road density in both years according to linear regression.

Table 2-6: Summary of AICc model selection for maximum August water temperature (MAT) in 2014 and 2015 in 12 Black Brook streams (NB, Canada). The catchment and reach explanatory variables included in the four best regression models are presented, as well as their corresponding $\Delta AICc$, weight (ω_i) and R^2 (R^2 for simple regression models and adjusted R^2 for multiple regression models). The symbol at the end of each variable indicates the sign of the coefficient for that variable within that regression model. In bold are the best models (lowest AICc value).

	Catchment	Reach	$\Delta AICc$	ω_i	R^2
2014		Canopy openness (+) & % rip. conifer (+)	0	25.9	0.59
	Harvest PC1 (-)	% rip. conifer (+)	1.37	13.0	0.54
	Harvest PC1 (-)	Canopy openness (+) & % rip. conifer (+)	2.92	6.0	0.65
	Harvest PC1 (-)		3.54	4.4	0.33
2015		Canopy openness (+) & % rip. conifer (+)	0	21.7	0.55
	Road density (+)	Canopy openness (+)	1.54	10.1	0.49
		Canopy openness (+)	2.00	8.0	0.36
	Road density (+)		2.39	6.6	0.33

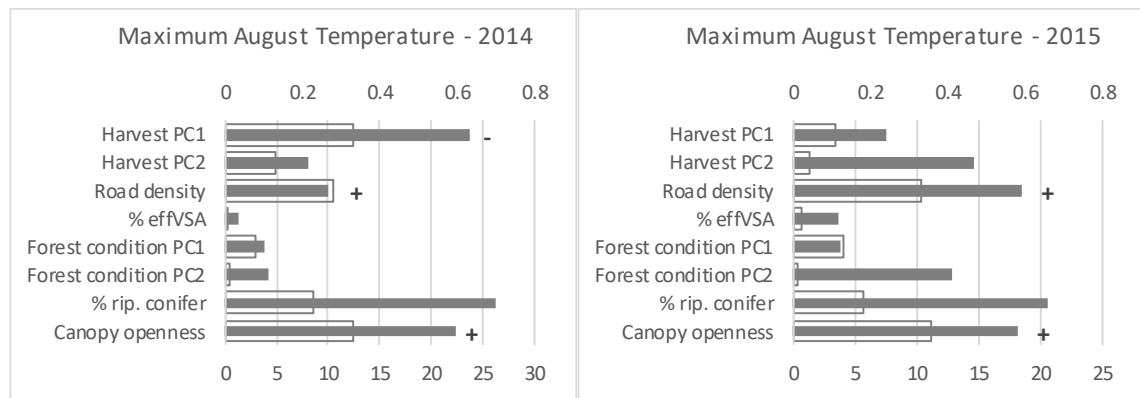


Figure 2-10: Distribution of the percentage of independent effect of each reach and catchment explanatory variable on the variability of averaged daily maximum August water temperature (MAT) in 2014 and 2015 (dark bars, bottom X axis) in 12 Black Brook streams (NB, Canada). The wider white bars and the top X axis represent the R^2 of the simple linear regression between that explanatory variable and the response variable; the + or – signs correspond to the slope of significant univariate regression models at $\alpha = 0.1$.

2.3.4. Leaf decomposition and benthic macroinvertebrate communities in leaf packs

2.3.4.1. Leaf decomposition

There was high variability in the values of leaf decomposition (% lost AFDM per degree-day) for leaf packs among streams, with mean values ranging between 0.057 (MC2 in 2014) and 0.149 (BB10 in 2015) (Figure 2-11). Two of the reference streams (MC3 and MC4) had

decomposition values between the lowest and highest values in BB, especially in 2015; whereas MC2 had values similar to the low end of the range in BB streams in both years, specifically BB01 and BB02. Average decomposition rate across sites was significantly greater in 2015 compared to 2014 by 0.007% per degree-day on average ($F_{1,157} = 4.3, p = 0.04$), but 2014 and 2015 decomposition values were quite strongly correlated across streams ($r = 0.70$).

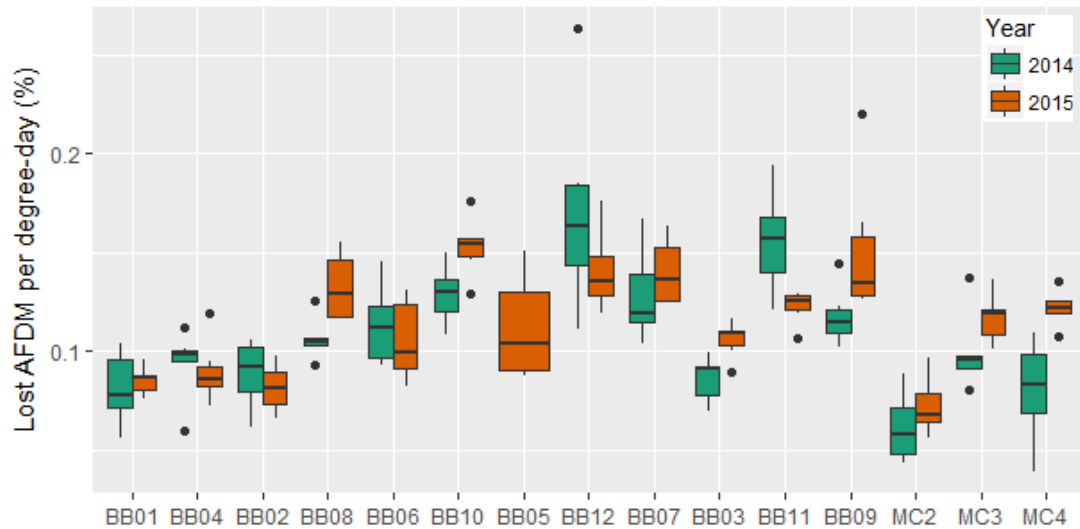


Figure 2-11: Box plot showing the percent organic mass (ash free dry mass) lost per degree-day in leaf pack samples ($n = 6$) in 2014 (green) and 2015 (orange) in each stream (Black Brook [BB] harvested streams are sorted according to road density – from highest to lowest; Mount Carleton [MC] are the reference streams) (see Figure 2-4 for box plot description).

The best model explaining leaf decomposition according to AICc included harvest PC2 (+, cumulative harvest) and % riparian conifer (-) in 2014 ($\omega_i = 30.3, adj. R^2 = 0.72$), and it was twice as likely as the second-best model, which included stream morphology PC1 (+, representing % riffle, % cobble and width) as the only EV ($\omega_i = 14.4, R^2 = 0.59$) (Table 2-7). In 2015, the best supported model included road density (-), canopy openness (+) and stream morphology PC1 (+) ($\omega_i = 31.9, adj. R^2 = 0.81$), and it was twice as likely as the model excluding stream morphology PC1 ($\omega_i = 16.5, adj. R^2 = 0.68$). Among the 9 EVs considered for multiple regression, stream morphology PC1 (+) was the EV with the highest independent effect on leaf

decomposition in both years (+, $I = 19.4$ and 21.3%), but it was closely followed by % riparian conifer (-, $I = 19.2\%$) and harvest PC2 (+, $I = 17.9\%$) in 2014, and by canopy openness (+, $I = 17.4\%$), % riparian conifer (-, $I = 16.0\%$) and road density (-, $I = 16.1\%$) in 2015 (Figure 2-12). Stream morphology PC1 was also the variable explaining more of the variance in 2014 ($R^2 = 0.59$ vs. 0.49 for % riparian conifer and 0.47 for harvest PC2), but road density and % riparian conifer explained more of the variance in 2015 ($R^2 = 0.43$ and 0.56 vs. 0.37 for stream morphology PC1).

Table 2-7: Summary of AICc model selection for leaf decomposition (% lost AFDM per degree-day), and benthic macroinvertebrate abundance, richness and proportion of shredders in leaf packs for 2014 and 2015 in 12 Black Brook streams (NB, Canada). The catchment and reach explanatory variables included in the four best regression models are presented, as well as their corresponding $\Delta AICc$, weight (%) and R^2 (R^2 for simple regression models and adjusted R^2 for multiple regression models). The symbol at the end of each variable indicates the sign of the coefficient for that variable within that regression model. In bold are the best models (lowest AICc value).

	Catchment	Reach	$\Delta AICc$	ω_i	R^2
2014	Harvest PC2 (+)	% rip. conifer (-)	0	30.3	0.72
		Stream morph. PC1 (+)	1.49	14.4	0.59
	FC_PC2 (+)	Stream morph. PC1 (+)	2.87	7.2	0.64
	Harvest PC2 (+)	Stream morph. PC1 (+)	3.46	5.4	0.62
2015	Road density (-)	Canopy openness (+) & SM_PC1 (+)	0	31.9	0.81
	Road density (-)	Canopy openness (+)	1.31	16.5	0.68
		% rip. conifer (-)	2.52	9.1	0.56
		Canopy openness (+) & % rip. conifer (-)	4.35	3.6	0.58

The most strongly supported regression model based on the 5 abiotic indicators as EVs explained as much of the variance as the most supported models built based on the 9 catchment and reach EVs (described in the previous paragraph), but it only included a single EV: water chemistry PC1 (-, $\omega_i = 40.5$ and 49.8 , $R^2 = 0.70$ and 0.77 in 2014 and 2015, respectively) (see Appendix I Table A15). WC_PC1 was also the variable with the highest independent effect on leaf decomposition based on HP (-, $I = 33.4$ and 52.1%) and it had the

highest R^2 , but it was closely followed by LIM (-, $t = 27.9$ and 25.6% , $R^2 = 0.63$ and 0.71) (see Appendix I Figure A9).

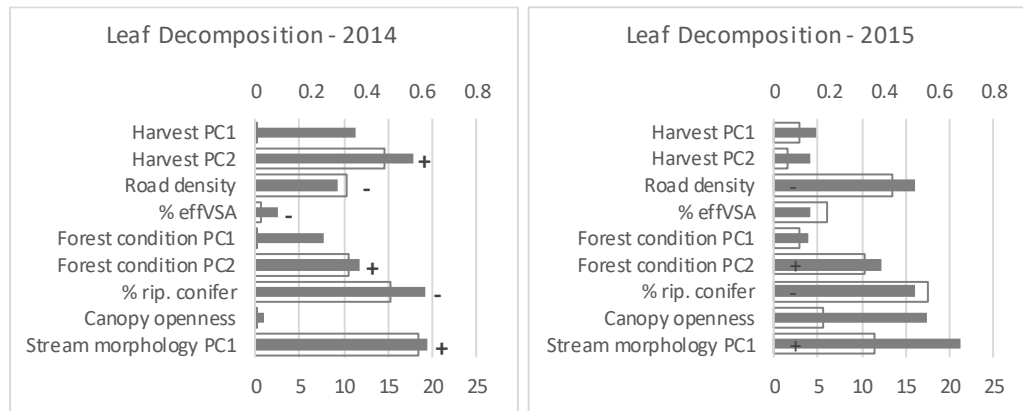


Figure 2-12: Distribution of the percentage of independent effect of each reach and catchment explanatory variable on the variability of leaf decomposition (% lost AFDM per degree-day) in 2014 and 2015 (dark bars, bottom X axis) in 12 Black Brook streams (NB, Canada). The wider white bars and the top X axis represent the R^2 of the simple linear regression between that explanatory variable and the response variable; the + or – signs correspond to the slope of significant univariate regression models at $\alpha = 0.1$.

2.3.4.2. Benthic macroinvertebrate community (BMI)

The abundance of BMI individuals ranged from 36 (BB12) to 309 individuals/leaf pack (BB08) in 2014 and from 118 (BB01) to 480 (BB07) in 2015; richness ranged from 9.7 (BB12) to 18.3 taxa/leaf pack (BB08) in 2014 and from 14.3 (BB09) to 23.3 (BB08) in 2015. Both abundance and richness were higher in 2015 ($F_{1,158} = 70.9$ and 22.4 , respectively, $p < 0.001$), but Margalef's richness did not differ significantly between years ($F_{1,161} = 0.9$, $p = 0.33$), with average values ranging from 6.2 (BB09) to 8.4 (BB08) in 2014 and from 5.5 (MC2) to 8.3 (BB01) in 2015. However, 2014 and 2015 Margalef's richness values were not correlated ($r = -0.05$); richness and especially abundance showed greater inter-annual congruence ($r = 0.30$ and 0.58 , respectively) than Margalef's richness. The proportion of EPT ranged from 22.3% (MC2) to 69.7% (BB01) in 2014 and from 19.2% (MC2) to 59.5% (BB10) in 2015; the proportion of chironomids ranged from 19.6% (BB01) to 65.8% (MC2) in 2014 and from 33% (BB03) to 74.7%

(MC2) in 2015. Regarding the proportion of functional feeding groups, it varied across streams and between years (see Appendix I Figure A8). In some streams, shredders were the most abundant group (e.g., BB01 and BB02 – ~70%, dominated by *Leuctra* and *Capniids*), whereas in other streams it was collector-gatherers (e.g., BB06 and BB08 – ~40-50%, dominated by *Baetis* and *Ephemerella*), scrapers (BB05 – 41%, dominated by *Epeorus*) or predators (BB04 in 2014 – 50%, dominated by *Dicranota* and *Rhyacophila*). Percent shredders was strongly correlated between 2014 and 2015 ($r = 0.90$). In reference streams, metrics describing the BMI community in the leaf packs tended to fall within the range of BB stream values, especially those for MC3 and MC4. MC2 had the lowest % EPT and highest % chironomids of all 15 streams, and % shredders at this site was closer to the upper range for BB sites. MC3 and MC4 were closer to the upper range for BB sites in abundance and % predators.

In 2014, the null model had more support ($\omega_i = 25.7$) than the next best supported model explaining BMI abundance on leaf packs (which included canopy openness as the only EV (+), $\omega_i = 10.9$, $R^2 = 0.18$) (Table 2-8); in 2015, however, the model with canopy openness was the most likely (+, $\omega_i = 22.4$, $R^2 = 0.52$), followed by those including harvest PC1 (+, mostly representing partial harvest) and road density (-) in addition to canopy openness ($\Delta AICc > 1.79$ though). In 2014, % effVSA had the highest independent effect on BMI abundance ($I = 28.7\%$), followed by forest condition PC1 ($I = 17.2\%$, related to mature, deciduous forests) and canopy openness ($I = 13.8\%$), although it is important to note that none of the simple linear regressions including each of these three EVs were significant (Figure 2-13). In 2015, canopy openness (+, $I = 52.7\%$) had a higher independent effect than % effVSA (-, $I = 13.1\%$). Regarding the regression models built based on the 5 abiotic indicators, the best model included MAT (+) and SUVA (-) in 2014 ($\omega_i = 49.8$, $R^2 = 0.64$), and MAT and LIM (-) in 2015 ($\omega_i = 32.2$, $R^2 = 0.45$) (see Appendix I Table

A15). MAT was the variable with the highest independent effect on BMI abundance in both years ($I = 70.4$ and 38.0%), but in 2015, unlike in 2014, the linear regression was non-significant and the R^2 as low as 0.09 (see Appendix I Figure A9).

Table 2-8: Summary of AICc model selection for leaf decomposition (% lost AFDM per degree-day), and benthic macroinvertebrate abundance, richness and proportion of shredders in leaf packs for 2014 and 2015 in 12 Black Brook streams (NB, Canada). The catchment and reach explanatory variables included in the four best regression models are presented, as well as their corresponding $\Delta AICc$, weight (%) and R^2 (R^2 for simple regression models and adjusted R^2 for multiple regression models). The symbol at the end of each variable indicates the sign of the coefficient for that variable within that regression model. In bold are the best models (lowest AICc value).

		Catchment	Reach	$\Delta AICc$	ω_i	R^2	
Abundance	2014			0	25.7	0	
			Canopy openness (+)	1.71	10.9	0.18	
		% effVSA (-)		1.78	10.6	0.18	
		Harvest PC2 (-)		2.74	6.5	0.03	
	2015		Canopy openness (+)		0	22.4	0.52
		Harvest PC1 (+)	Canopy openness (+)		1.79	9.1	0.54
Harvest PC1 (+) & Road density (-)		Canopy openness (+)		1.9	8.7	0.69	
FC_PC2 (-) & Road density (-)		Canopy openness (+)		1.92	8.6	0.69	
Richness	2014	Harvest PC1 (-)		0	22.2	0.4	
			Canopy openness (+)			1.01	13.4
				1.63	9.9	0	
		FC_PC1 (-)		2.64	5.9	0.23	
	2015		Canopy openness (+)			0	15.5
		Harvest PC1 (+)	Canopy openness (+)		0.87	10	0.45
		% effVSA (-)			1.53	7.2	0.29
% effVSA (-)		Canopy openness (+)		1.76	6.4	0.41	
% shredders	2014	% effVSA (+)	% rip. conifer (+)	0	28.6	0.74	
			% rip. conifer (+)		1.32	14.8	0.65
		% effVSA (+) & FC_PC1 (+)	% rip. conifer (+)		1.86	11.3	0.87
		% effVSA (+) & FC_PC2 (-)			3.32	5.4	0.72
	2015		Stream morph. PC1 (-)		0	43.7	0.63
		% effVSA (+)	Stream morph. PC1 (-)		3.27	8.5	0.6
			Stream morph. PC1 (-) & Canopy openness (+)		4.22	5.3	0.57
	Harvest PC1 (-)	Stream morph. PC1 (-)		4.29	5.1	0.56	

For the richness of BMI on leaf packs, only harvest PC1 (-, positively related to partial harvest and negatively to clearcut) was in the best model in 2014 ($\omega_i = 22.2$, $R^2 = 0.40$), followed by one including only canopy openness (+, $\omega_i = 13.4$, $R^2 = 0.34$); the latter EV was in

the best supported model in 2015 ($\omega_i = 15.5$, $R^2 = 0.38$), followed by the model including harvest PC1 (+, positively related to partial harvest) and canopy openness ($\omega_i = 10.0$, $adj. R^2 = 0.45$) or only % effVSA (-, $\omega_i = 7.2$, $R^2 = 0.29$) (Table 2-8). In 2014, harvest PC1 (-) had the highest independent effect on BMI richness ($I = 26.2\%$) and highest R^2 (0.40), followed closely by canopy openness ($I = 23.8\%$); in 2015, however, % effVSA had the highest I (32.8%), but canopy openness had a higher R^2 (0.38 vs. 0.29) (Figure 2-13). For the effects of abiotic indicators on BMI richness, MAT as the only EV was the most likely model in both years (although it was almost as likely as the null model in 2015), and this variable also had the highest independent effect on BMI richness ($I = 42.2$ and 71.0%) (see Appendix I Table A15 and Figure A9).

The proportion of shredder BMIs in leaf packs was best explained by % effVSA (+) and % riparian conifer (+) in 2014 ($\omega_i = 28.6$, $adj. R^2 = 0.74$), but the model with only stream morphology PC1 (-, representing % riffle, % cobble and width) had considerably more support than the remaining models in 2015 ($\omega_i = 43.7$, $R^2 = 0.63$) (Table 2-8). HP indicated that % effVSA (+) had the highest independent effect on the proportion of shredders in 2014 ($I = 24.3\%$), followed by % riparian conifer (+, $I = 21.3\%$), stream morphology (-, $I = 17.9\%$), forest condition PC2 (-, $I = 14.4$, related to % mixed forest and S2) and road density (+, $I = 6.4\%$) (Figure 2-13). In 2015, stream morphology had the highest I (36.5%), followed by % riparian conifer ($I = 21.1\%$); simple LR models in 2015 were only significant for these two variables. For the abiotic indicators, the model including SUVA (+) and WC_PC2 (-, related to DOC and metals) had the greatest support in 2014 ($\omega_i = 55.7$, $adj. R^2 = 0.76$); in 2015, this model was the second-best ($\omega_i = 13.9$, $adj. R^2 = 0.64$), with the model including only LIM being more likely ($\omega_i = 20.6$, $adj. R^2 = 0.50$) (see Appendix I Table A15). SUVA (+) had the highest independent effect on % shredder, but it was closely followed by the remaining abiotic indicators (especially in 2015); LIM explained the

largest portion of the variance, but it was also closely followed by the other variables (except WC_PC2, which had a considerably lower R^2) (see Appendix I Figure A9).

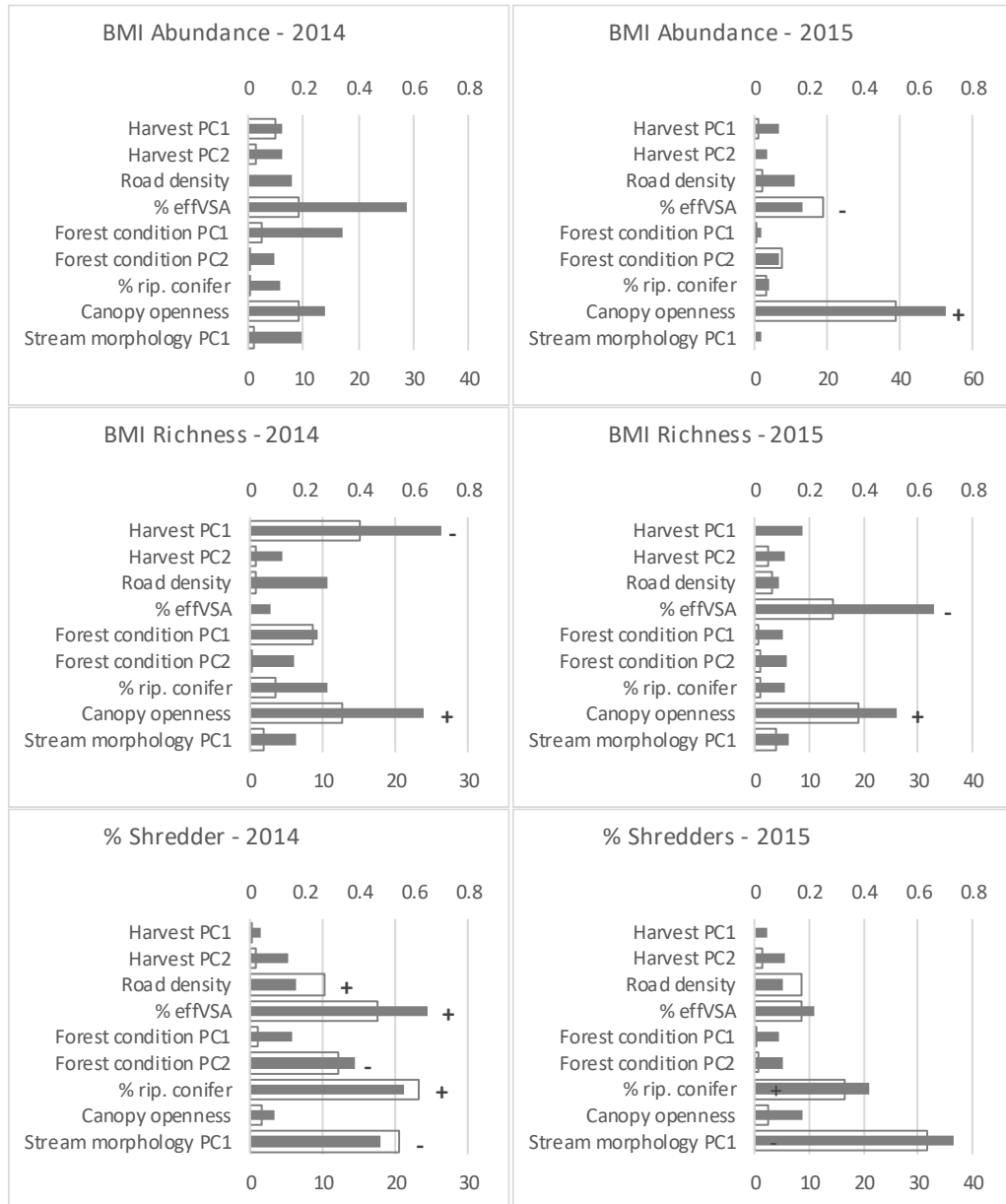


Figure 2-13: Distribution of the percentage of independent effect of each reach and catchment explanatory variable on the variability of benthic macroinvertebrate (BMI) abundance, richness and proportion of shredders collected on leaf packs in 2014 and 2015 (dark bars, bottom X axis) in 12 Black Brook streams (NB, Canada). The wider white bars and the top X axis represent the R^2 of the simple linear regression between that explanatory variable and the response variable; the + or - signs correspond to the slope of significant univariate regression models at $\alpha = 0.1$.

Finally, reference streams showed a distinct BMI community composition in leaf packs in both years relative to harvested sites, with differences being driven mainly by the presence of *Taenionema*, *Diplectrona* and *Isoperla* in reference streams (Figure 2-14). BB01 showed a quite distinct composition in comparison to all the other streams (especially in 2014); the distinct BB01 community was mainly driven by the presence of taxa such as *Sialis*, *Tipula* and *Procleon*.

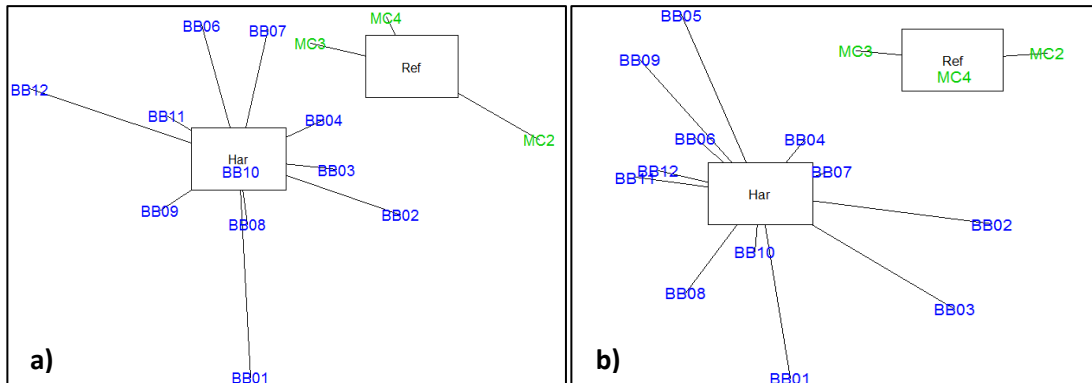


Figure 2-14: Non-metric multidimensional scaling analysis for 12 Black Brook harvested (Har) streams (in blue) and 3 Mount Carleton reference (Ref) streams (in green) based on leaf pack benthic macroinvertebrate communities in a) 2014 and b) 2015. Boxes represent group (harvested or reference streams) centroids.

Several of the EVs used for modeling were correlated with the NMDS ordination of streams based on their leaf pack BMI community (see Appendix I Table A9), but relationships were stronger with reach EVs (including the abiotic indicators presented in this chapter) than with catchment EVs. Harvest PC2 ($r^2 = 0.45$, positively related to partial harvest and negatively to clearcut) was the only catchment variable correlated with the BMI ordination in 2014, and road density ($r^2 = 0.39$) and forest condition PC1 ($r^2 = 0.47$, related to mature, deciduous forests) in 2015. Among reach variables, stream morphology PC1 ($r^2 = 0.78$ and 0.73 , related to % riffle, % cobble, width) showed the strongest correlations with the BMI ordination in both years, followed by MAT ($r^2 = 0.74$ and 0.60) and WC_PC1 ($r^2 = 0.70$ and 0.60), but LIM, WC_PC2 (only in 2014) and SUVA were also significantly correlated with the ordination in both years (r^2

= 0.38-0.58). With respect to the direction of these correlations between catchment/reach variables and the leaf pack BMI community NMDS, most variables identified a similar gradient with the ordination (Figure 2-15). At one end of the gradient were the BMI communities associated with streams with higher LIM, MAT, SUVA, WC_PC1 (cations/carbon), % run, % silt, % riparian conifer (only in 2014) and road density (only in 2015), and at the other end were the BMI communities associated with streams with lower values for these environmental variables.

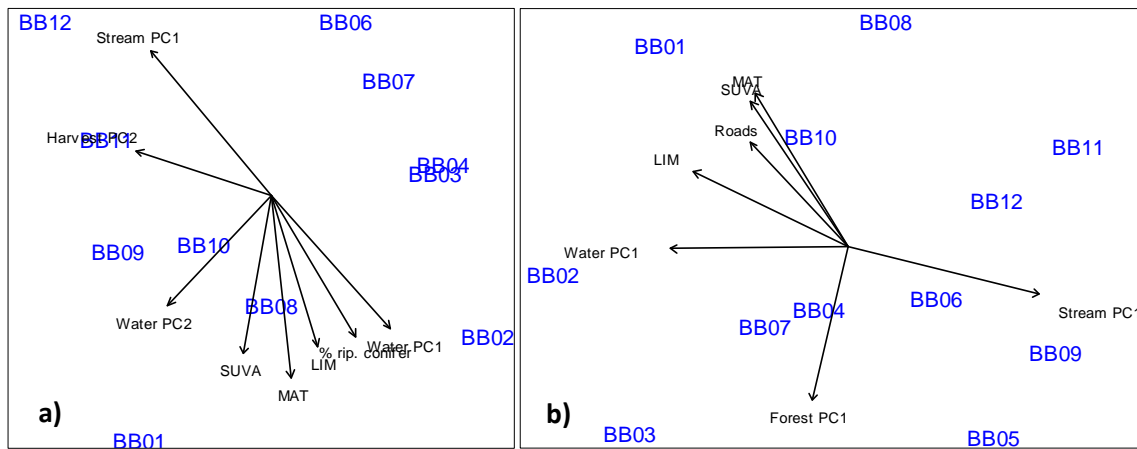


Figure 2-15: Two-dimensional NMDS ordination of 12 harvested Black streams (New Brunswick, Canada) based on their benthic macroinvertebrate community in a) 2014 and b) 2015. The arrows are catchment and reach variables significantly correlated ($p < 0.10$) with the ordination.

2.3.5. Biofilm and algal biomass on tiles

Mean total biofilm biomass values ranged from 0.18 (MC2 in 2014) to 2.0 g/m^2 (BB01 in both 2014 and 2015), with MC reference streams having mean values within the biomass range for BB sites (Figure 2-16). Values were significantly higher in 2015 than in 2014 by 0.37 g/m^2 , on average ($F_{1,43} = 6.7$, $p = 0.01$), and the inter-annual correlation coefficient was $r = 0.68$.

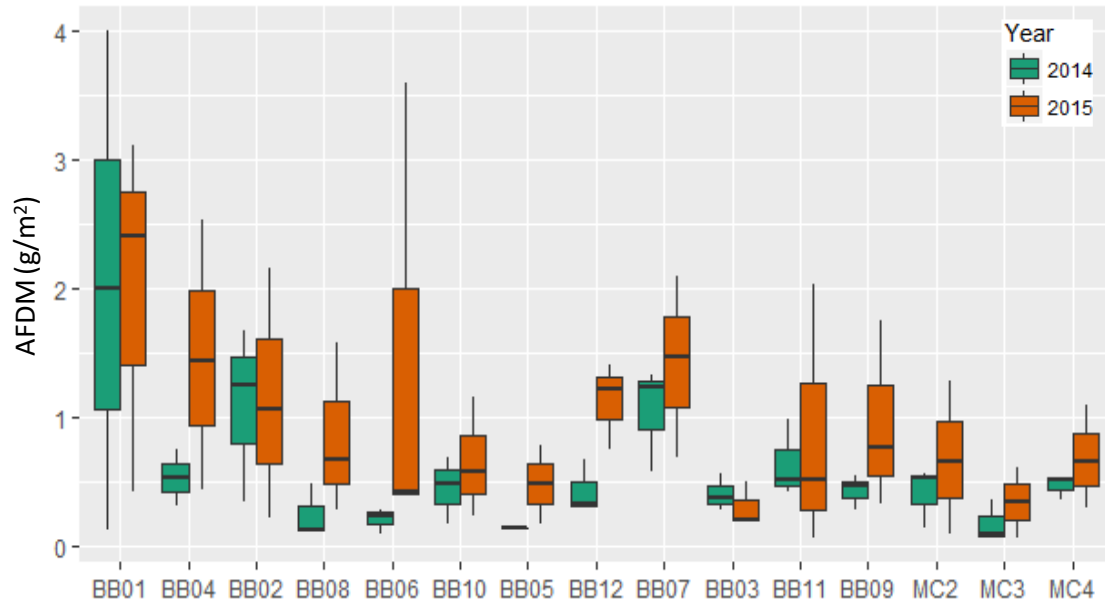


Figure 2-16: Box plot showing the total biofilm biomass (ash free dry mass) in samples scraped from tiles ($n = 3/\text{site}$) in 2014 (green) and 2015 (orange) in each stream (Black Brook [BB] harvested streams are sorted according to road density – from highest to lowest; Mount Carleton [MC] are the reference streams) (see Figure 2-4 for box plot description).

Algal biomass (chlorophyll-a content) values in BB07 were several times higher than in the other streams (25 and 13.5 mg/m² in 2014 and 2015 compared to an average of 3.8 and 3.5 mg/m² across all other streams) (Figure 2-17). Similarly, BB10 had high algal biomass values in 2014. The lowest algal biomass values tended to be in reference streams (lowest value overall was 0.26 mg/m² in MC2 in 2015), although some BB streams had similarly low values (e.g., BB05). There were no significant differences in algal biomass between years across sites ($F_{1,43} = 1.4, p = 0.24$), and 2014 and 2015 values showed a correlation of $r = 0.59$. Autotrophic index values followed similar trends as chlorophyll-a (data not shown), so only chlorophyll-a values are used in subsequent models as indicators of the autotrophic content of biofilm samples.

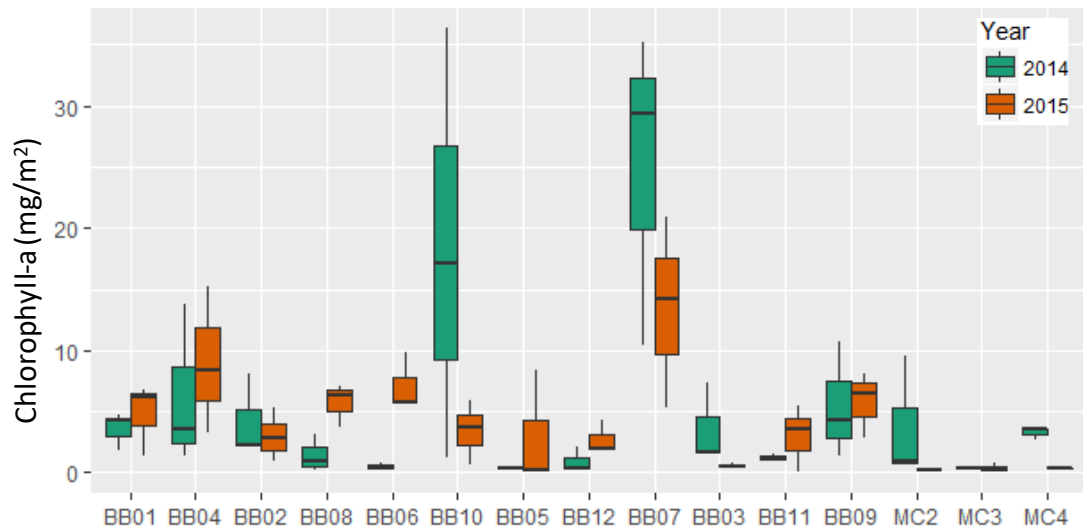


Figure 2-17: Box plot showing the algal biomass (chlorophyll-a content) in biofilm samples scraped from tiles ($n = 3/\text{year}$) in 2014 (green) and 2015 (orange) in each stream (Black Brook [BB] harvested streams are sorted according to road density – from highest to lowest; Mount Carleton [MC] are the reference streams) (see Figure 2-4 for box plot description).

Road density (+) was included in all but one of the 8 best models explaining biofilm biomass (Table 2-9). In addition to road density, the best model in 2014 included % effVSA (+) and canopy openness (+) ($\omega_i = 24.2\%$, $adj. R^2 = 0.76$), and the best model in 2015 included % riparian conifer (-) ($\omega_i = 42.8\%$, $adj. R^2 = 0.66$). In 2015, road density was also the variable with the highest R^2 (0.52) and independent effect ($I = 27.3\%$) on biofilm biomass of the 9 EVs considered, but % effVSA had a stronger independent effect (although a lower R^2) in 2014 ($I = 31.6$ vs. 22.7% , $R^2 = 0.36$ vs. 0.44 for % effVSA and road density, respectively) (Figure 2-18). The abiotic variable with the strongest independent effect on biofilm biomass was SUVA (+) in 2014 ($I = 45.7\%$), but LIM (+) in 2015 ($I = 32.3\%$); both these variables explained a similar proportion of the variance in both years (see Appendix I Figure A9). The model including only SUVA ($\omega_i = 69.9\%$, $R^2 = 0.76$) explained as much of the variance as the best model built based on the 9 catchment and reach EVs in 2014, but it explained considerably less variance in 2015 ($\omega_i =$

18.3%, $R^2 = 0.28$) and it was only slightly more likely than the null model (see Appendix I Table A15).

Table 2-9: Summary of AICc model selection for total biofilm biomass and algal biomass for 2014 and 2015 in 12 Black Brook streams (NB, Canada). The catchment and reach explanatory variables included in the four best regression models are presented, as well as their corresponding $\Delta AICc$, weight (%) and R^2 (R^2 for simple regression models and adjusted R^2 for multiple regression models). The symbol at the end of each variable indicates the sign of the coefficient for that variable within that regression model. In bold are the best models (lowest AICc value).

		Catchment	Reach	$\Delta AICc$	ω_i	R^2
Biofilm biomass	2014	Road density (+) & % effVSA (+)	Canopy openness (+)	0	24.2	0.76
		% effVSA (+)	Canopy openness (+)	1.33	12.4	0.6
		Road density (+) & % effVSA (+)		2.31	7.6	0.57
		Road density (+)		3.1	5.1	0.44
	2015	Road density (+)	% rip. conifer (-)	0	42.8	0.66
		Road density (+)		1.86	16.9	0.52
		Road density (+) & % effVSA (+)	% rip. conifer (-)	4.96	3.6	0.66
		Road density (+)	Canopy openness (+)	5.24	3.1	0.47
Algal biomass	2014	Harvest PC1 (+)	Canopy openness (+)	0	25.5	0.48
			Canopy openness (+)	1.21	13.9	0.3
				1.79	10.4	0
		FC_PC1 (+)	Canopy openness (+)	3.38	4.7	0.31
	2015		Canopy openness (+)	0	24.5	0.33
				1.09	14.2	0
		Harvest PC1 (+)	Canopy openness (+)	3.03	5.4	0.29
		% effVSA (-)		3.61	4	0.09

In 2014, the best model explaining algal biomass was the model with canopy openness (+) and harvest PC1 (+, positively related to partial harvest and negatively to clearcut) ($\omega_i = 25.5\%$, $adj. R^2 = 0.48$), and it was twice as likely as the model with only canopy openness ($\omega_i = 13.9\%$, $R^2 = 0.30$) (Table 2-9). In 2015, however, the model including the latter variable was the most likely one ($\omega_i = 24.5\%$, $R^2 = 0.33$), but it was only 10% more likely than the null model. Canopy openness (+) was the variable with the highest independent effect on algal biomass in both years ($I = 51.4$ and 39.7%), as well as the only variable producing a significant simple linear regression model (Figure 2-18). None of the models including abiotic variables were significant and the null model had a stronger support (see Appendix I Table A15 and Figure A9).

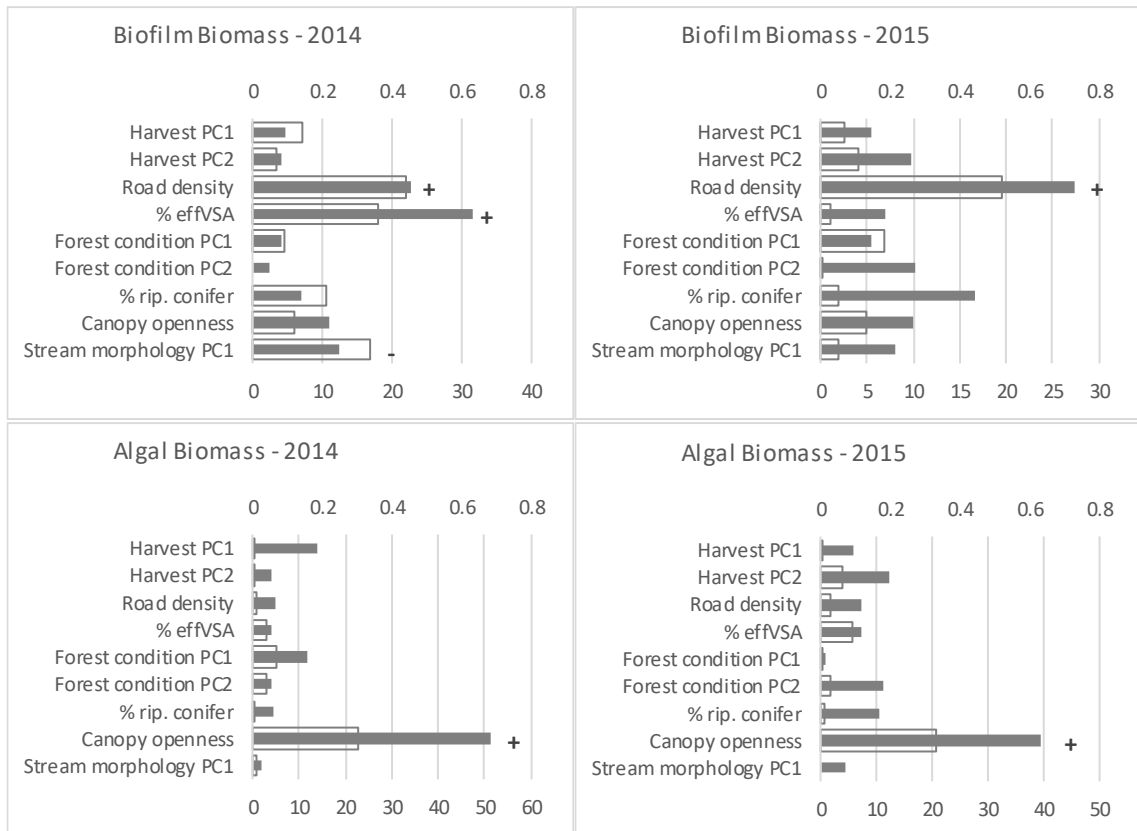


Figure 2-18: Distribution of the percentage of independent effect of each reach and catchment explanatory variable on the variability of total biofilm biomass and algal biomass in 2014 and 2015 (dark bars, bottom X axis) in 12 Black Brook streams (NB, Canada). The wider white bars and the top X axis represent the R^2 of the simple linear regression between that explanatory variable and the response variable; the + or – signs correspond to the slope of significant univariate regression models at $\alpha = 0.1$

2.3.6. Harvested (BB) vs. reference (MC)

Most of the correlations between explanatory variables and stream indicators remained more or less constant (i.e., a difference in r lower than 0.1) when reference streams were included in the correlation analyses (in addition to BB streams), but some of these correlations became stronger and others weaker depending on the EV and RV (Table 2-9). For example, correlations between algal biomass (unlike total biofilm biomass) and canopy openness became weaker, whereas correlations between algal biomass and recent clearcut (<5 y and <10 y) became stronger. All the correlations with leaf decomposition or % shredder became weaker

Table 2-10: Comparison of correlation coefficients from correlation analyses with only BB streams (r_{BB}) and with all 15 streams (r_{BB+MC}) in 2014 and 2015. Yellow cells indicate that the correlation between that catchment/reach variable (rows) and stream indicator (column) was 0.1 greater when only including BB streams ($r_{BB} - r_{BB+MC} > 0.1$), green cells indicate that the correlation was 0.1 greater when BB and MC sites were included ($r_{BB} - r_{BB+MC} < -0.1$), and blue cells indicate that differences between BB and BB + MC correlation coefficients was lower than 0.1 ($r_{BB} - r_{BB+MC} < |0.1|$).

		2014										2015															
		Δ FIS	Δ % org. fine sed'	Δ LIM	Δ BIM	Δ WC_PC1	Δ WC_PC2	Δ SUVA	Δ MAT	Δ leaf decomposition	Δ % shredders	Δ BMI NMDS	Δ biofilm biomass	Δ algal biomass	Δ FIS	Δ % org. fine sed'	Δ LIM	Δ BIM	Δ WC_PC1	Δ WC_PC2	Δ SUVA	Δ MAT	Δ leaf decomposition	Δ % shredders	Δ BMI NMDS	Δ biofilm biomass	Δ algal biomass
Harvest	Partial <10y																										
	Partial <5y																										
	Clearcut <10y																										
	Clearcut <5y																										
	Total <5y																										
	Total <10y																										
Landscape	Road crossings																										
	Road density																										
	Elevation																										
Riparian	Forest NMDS1																										
	Canopy openness																										
Stream morphology	PC1																										
	PC2																										
	Width																										
	% Riffle																										
	% Run																										
	% Silt																										
Sediments	FIS																										
	% organic																										
	LIM																										
	BIM																										
Water	Chemistry PC1																										
	Chemistry PC2																										
	DOM - SUVA																										
Temperature	Max. August																										
Leaf	% lost AFDM																										
	% shredders																										
	BMI NMDS																										
Biofilm	Total biomass																										
	Algal biomass																										

when MC sites were included, but this was affected by the low leaf decomposition and high % shredder values in MC2. In contrast, correlations between water chemistry variables (WC_PC1)

and harvesting, as well as between sediment variables and harvesting (especially in 2014) tended to become stronger when MC sites were included. All the correlations between temperature and catchment/reach variables became weaker when MC streams were included. However, these trends were strongly affected by MC2, which had temperatures 3°C higher than the other two reference streams; once MC2 was removed, all correlations between temperature and other EV and RVs were comparable when MC3 and MC4 reference sites were included or excluded.

2.4. Discussion

2.4.1. Sediment deposition

Elevated sediment levels are considered the main pollutant in streams from forest management (Croke and Hairsine 2006). The relative importance of different sources (harvesting vs. roads) continues to be an important research question with implications for forest managers (Croke and Hairsine 2006; Anderson and Lockaby 2011), and there is wide evidence demonstrating that both harvesting and roads are major sediment contributors (Reid and Dunne 1984; Kreuzweiser et al. 2005; Croke and Hairsine 2006; Kara et al. 2014; Webster et al. 2015; Davies et al. 2016; Al-chokhachy et al. 2016). In Black Brook, roads (which are gravel) were the main variable explaining the amount of fine inorganic sediments (FIS) deposited in sediment traps as well as entrained in leaves and biofilms, whereas the degree of harvesting had a considerably weaker effect than; this indicates that most sediment inputs were related to ground disturbances associated with roads and crossings and to the delivery of sediments released during harvesting, rather than to the release of sediments during forest harvesting. Regardless of the source, my results demonstrate that best management practices

in place are not enough to curb all the sediments coming from an intensive forest management setting. Based on a literature review, Sweeney and Newbold (2014) reported that 30-m buffers were 85% effective at trapping sediments, with mostly the finest particles reaching streams. Therefore, it seems that the fine sediment fraction that was not effectively intercepted by riparian buffers in BB (~15% according to Sweeney and Newbold 2014) reflected the gradient in forest management intensity (namely road density and stream crossings) in the catchment. This effect was observed even in 2015 where fine sediment deposition was much lower, an observation most likely related to the lower accumulated precipitation during the deployment of traps in that year (105 vs. 67 mm). This observation suggests that the effects of roads are dependent on hydrologic year, with rainier years resulting in greater sediment accumulation in streams.

Sediment deposition and entrainment tended to be greater in streams with more coniferous and lower canopy riparian forests, raising the question of whether these buffer zones were less effective at trapping sediments. Forests with open tree canopies that provide enough light to allow the growth of a vigorous understory and ground cover are considered more effective for retaining sediments (Phillips 1989; Broadmeadow and Nisbet 2004). Therefore, because coniferous forests tend to be more effective at intercepting PAR than deciduous ones, the former forests could be retaining less sediments due to less undergrowth. The large woody debris contributed by mature trees is also effective at retaining sediments (Montgomery 1997), so younger forests could be trapping less sediments due to a lower abundance of such structures. However, because young, coniferous riparian buffers tended to be located in catchments with higher forest management intensity, the observed relationship between riparian forest structure and composition and stream sediments could simply be a result of the higher catchment disturbance at these sites. In fact, hierarchical partitioning

showed that riparian forest variables shared a lot of the explained variance with other catchment variables (e.g., the joint effect of % riparian conifer tended to be greater than the independent effect), whereas road density had a higher independent effect on stream sediments.

Of the three indicators of fine inorganic sediments in BB streams, LIM (leaf inorganic mass) and BIM (biofilm inorganic mass) seemed to be better indicators than FIS (fine inorganic sediments in sediment traps) because the former: 1) showed a stronger correlation with roads, 2) detected effects of harvesting degree (significantly correlated with harvest variables in 2015, unlike FIS, see Appendix I Table A8), 3) were less affected by % riffle and % run, 4) trends across streams were more consistent interannually ($r = 0.94, 0.87$ and 0.63 for LIM, BIM and FIS, respectively), suggesting that they were less affected by annual differences in precipitation and runoff, 5) measured indirect biological implications, i.e., the reduced palatability of biofilm and leaves for consumers and consequent transfer of energy to food webs, and 6) facilitated measurement of other biological endpoints simultaneously (e.g., leaf decomposition or biofilm biomass). Therefore, I recommend incorporating the measurement of inorganic leaf mass, which includes fine sediments entrained in biofilms, as part of the standardized leaf pack method when looking at the effects of catchment disturbance on stream ecosystems. However, sediment traps allowed the measurement of the organic fraction in sediments, which was significantly and negatively correlated with road density and crossings, and which has implications for stream food webs. The organic/inorganic ratio decreased with increased roads, but the absolute organic value was not affected, meaning that the amount of food (fine particulate organic matter) delivered to streams was not affected by roads.

2.4.2. *Water chemistry and DOM quality*

The trends in water chemistry and DOM quality variables from occasional grab samples remained consistent within and between years in BB and MC (strong interannual correlation: $r > 0.97$), and were predicted by catchment characteristics. The first water chemistry PC (which was strongly related to conductivity, alkalinity, pH, Ca and DIC) was strongly and positively related to forest management intensity, namely to road density and recent harvest (<10 y). This agrees with previous studies that have shown increased conductivity and cations being delivered to streams from roads, as well as increased levels of cations after logging due to a reduction in plant uptake, increased decomposition and mineralization, elevated water fluxes, etc. (Danehy et al. 2007; Kreutzweiser et al. 2008b; Richardson and Béraud 2014; Webster et al. 2015). Fine inorganic sediments and water chemistry PC1 were strongly correlated, suggesting that in more intensively-managed catchments, there was a higher delivery of both water-borne fine and dissolved materials. As with sediments, % coniferous forest (especially in the riparian forest) was strongly and positively correlated with water chemistry PC1, which could be either due to these forests being less effective at intercepting water-borne materials, or because forest composition was correlated with forest management intensity (i.e., higher forest management intensity in conifer plantations than in deciduous/mixed forests).

DOC, nitrogen, Fe, Al and Cl in BB stream waters seemed to increase with recent clearcut (<5, <10 y) but not with partial harvesting, suggesting that complete removal of the trees triggers greater biogeochemical responses and fluxes into receiving waters than partial harvesting. In fact, WC_PC2 was negatively related to partial harvest, suggesting that the delivery of DOC, N, Fe and Al decreased with partial harvest. This agrees with previous studies that have observed an increase in nutrients and metals in streams after logging, and that

nutrient exports were ameliorated to some extent by partial or stem-only harvesting (Feller 2005; Kreuzweiser et al. 2008b). Fe and Al concentrations in BB streams were also strongly related to roads (and sediments), suggesting that these metals were probably delivered to streams attached to sediment particles through roads. Although elevated in some cases, all the water chemistry parameters were below levels deemed unsafe for aquatic life and drinking water (CCME 2014).

DOM quality in the streams in my study was strongly related to road density and forest composition. DOM tended to be of lower quality for microbial breakdown, i.e., more aromatic and humic (as indicated by higher SUVA and HIX) (Kalbitz et al. 1999; Weishaar et al. 2003), in streams with higher road density and associated fine sediment delivery. In addition, recent clearcut seemed to contribute to this increase in aromaticity and humification, whereas partial harvest did not. This contrasts with other studies that reported reduced contributions of aromatic DOM in harvested compared to reference catchments, which has been attributed to the reduced organic soil mass after harvesting (Yamashita et al. 2011; Burrows et al. 2013), or no significant differences (De Wit et al. 2014; Cawley et al. 2014). The different results in my study could be related to the increased hydrological connectivity resulting from the intensive management in some catchments. The streams with lowest DOM quality (BB01-BB03, BB08) were also the streams with larger quantities of fine sediments, DIC, DOC, Ca ..., suggesting that sites with high road density received more runoff, and consequently, larger quantities of water-borne materials, such as terrestrial DOM characterized by more humic, aromatic and complex compounds (McKnight et al. 2001). This hypothesis would be supported by the observations by Roiha et al. (2012), who measured a decrease in terrestrially originated carbon (lower SUVA) as runoff decreased. The fact that % effective VSA was also positively related to SUVA suggests that both anthropogenically (via roads) and naturally (via effective VSAs) enhanced hydrological

connectivity contributed to the delivery of more aromatic and humic terrestrial compounds. Optical properties of DOM were also related to forest (namely riparian forest) condition, with deciduous-dominated mature forests delivering higher quality DOM (lower SUVA and HIX values) than younger coniferous forests; this contrasts with studies that did not find differences in SUVA between conifer and deciduous-dominated catchments (Cawley et al. 2014). Higher quality DOM exported from deciduous-dominated riparian and catchment forests likely reflects DOM extracts from rich organic forest floor material composed of deciduous leaf litter. Because DOM quality has been shown to control its reactivity, influence ecosystem functions and affect microbial food webs (e.g., Weishaar et al. 2003; Docherty et al. 2006; Emilson et al. 2017), forest management related changes in DOM quality could have biological implications in these streams (see sections 2.4.4 and 2.4.5 in this chapter and Chapter 3).

2.4.3. Water temperature

Stream temperature was mainly related to riparian condition, namely to the riparian forest composition, height and canopy openness. The stronger independent effect of forest composition (% riparian conifer) than canopy openness suggests that temperature is not only affected by shading, but also by the actual riparian forest composition and identity of the species providing the shade, with some species absorbing less solar radiation or influencing longwave radiation differently (Macdonald et al. 2003; Moore et al. 2005). The positive relationship between % coniferous and water temperature was surprising considering that coniferous canopies are known to block solar radiation more efficiently than deciduous canopies. The structure of the riparian forest helps understand this counterintuitive relationship between forest composition and water temperature: water temperature was also strongly and negatively correlated with riparian canopy height (i.e., temperature was colder in

streams with higher riparian canopies). Therefore, it can be concluded that because the conifer dominated riparian forests tended to have a lower height, they were less effective at absorbing solar radiation.

Although riparian condition was the main factor explaining water temperature differences, there was also an effect of forest management. Riparian forest removal typically leads to increased and more variable water temperatures, especially in the summer (see review by Moore et al. 2005). The effects of upland harvesting on stream water temperature when riparian buffers are retained is more variable, with some studies suggesting that riparian buffers are effective at reducing harvesting impacts on stream temperature (e.g., Wilkerson et al. 2006; Clinton 2011), and others detecting increased temperatures despite riparian buffers (Kiffney et al. 2003; Witt et al. 2016). In this study, however, even though all the streams had a riparian buffer zone (usually about 30 m wide), % recent clearcut (<5 y and <10 y) was strongly and positively related (especially in 2014) to maximum summer temperature. Studies have shown that warming of groundwater in areas of upland clearing can increase stream water temperature (Moore et al. 2005), and although in this study I did not monitor groundwater temperature, my results support this hypothesis. This is further supported by the fact that only recent clearcut, and not partial harvesting, contributed to warmer stream temperatures, with the vegetation left after partial harvesting being sufficient to shade the soil and prevent the warming of shallow groundwater. My study also agrees with the 5-10-year post-logging recovery time for stream temperature proposed by Moore et al. (2005), since I only detected the effects of clearcut in the most recent 5- and 10-year harvest periods. Road density was positively related to water temperature as well (the independent effect of roads on temperature was as high as that of riparian variables in 2015), which could result from the bare roads promoting the warming of shallow groundwater.

Maximum temperatures in the Black Brook streams never exceeded 16 °C and were thus well below the threshold of 24°C set by the United States Environmental Protection Agency to protect coldwater fish species such as brook trout (EPA 1986). However, the observed temperature differences among streams (streams in catchments of recent clearcut had averaged daily maximum August water temperatures of about 4-5 °C higher than streams in catchments with no recent clearcut) could be affecting other organisms and/or ecosystem functions (Dodds et al. 2014; Griffiths and Tiegs 2016).

2.4.4. Leaf decomposition and benthic macroinvertebrate communities

2.4.4.1. Leaf decomposition (LD)

As the proportion of the catchment recently harvested increased, LD tended to decrease, and the more recent the harvesting, the stronger the negative relationship was in Black Brook. This agrees with studies that have shown that LD is affected by even moderate levels of harvesting, even when riparian buffer zones are retained (Kreutzweiser et al. 2008a; Lecerf and Richardson 2010). Yeung et al. (2017) proposed that the recovery time of this crucial ecosystem function ranges between 8-15 years; BB streams would fall within the range, since negative correlations between harvest and leaf decomposition were only significant for harvesting in the past 5 and 10 years. In fact, the accumulated harvesting over longer periods of time (<30 years) seemed to have a positive effect on leaf decomposition.

In addition to logging, part of the effects of forest management on LD was attributable to roads, with road density being negatively related to LD. The impact of roads on LD was probably mediated by the enhanced delivery of water-borne particulate and dissolved materials, a claim supported by the strong negative effect of water chemistry PC1 (i.e., high cation and carbon concentrations) and fine inorganic sediments on LD. Inundation of

submerged leaves by sediments has been shown to result in lower decomposition rates (Webster & Waide 1982; Lecerf & Richardson 2010); my leaf packs did not show signs of burial in sediments (personal observation), but fine sediments seemed to be entrained in leaves (as evidenced by the strong correlation between fine inorganic sediments in traps and leaf inorganic mass), which could result in reduced palatability of leaves and explain the observed decrease in LD. The negative relationship between conductivity/Ca values and LD observed in BB contrasts with other studies that showed a positive relationship between conductivity/calcium and LD, since calcium tends to be a limiting nutrient for decomposing microbes (Egglisshaw 1968; Lecerf and Richardson 2010). However, Emilson et al. (2017) observed that increased conductivity due to salts and dust coming from roads resulted in lower bacterial LD, which was explained by a change in the bacterial community and consequent decline in enzyme activity. McKie et al. (2006) showed that even though microbial activity was enhanced following liming, the shredder-mediated decomposition was reduced due to changes in benthic invertebrate communities. Therefore, the reduced LD following higher conductivity observed in BB could be a result of a) lower microbial activity as explained by Emilson et al. (2017), b) lower decomposition attributable to invertebrates as shown by McKie et al. (2006), and/or c) adverse effects of fine sediments (co-delivered to streams with Ca) override the benefits of higher calcium levels to microbial communities. Overall, leaf packs in streams with higher harvest and road density tended to have average LD approximately 15% lower than less intensively managed streams (~35% vs. 20% leaf biomass loss).

In addition to forest management intensity, several other catchment and reach variables were significantly related to LD. In fact, several of the EVs had a higher joint than independent effect on LD, meaning that most of the effect of these variables on LD was in combination with other EVs. LD tended to be slower in streams with more coniferous catchment and riparian

forests than in streams with more deciduous and mixed forests, which could be related to differences in quantity/quality of the DOM (more humic and aromatic DOM leaching from coniferous forests in the case of BB) leached from different forest types (Wong and Williams 2010; Cuss and Guéguen 2013) and affecting microbial decomposition. However, Emilson et al. (2017) found that the more humic DOM stimulated microbial decomposition, probably due to the adaptation of these communities to utilize the more complex allochthonous DOM. Effects of forest composition on LD are mixed, with some studies reporting higher rates (Kominoski et al. 2011) and others reporting no changes with increased deciduous cover (Chauvet et al. 2016). Stream morphology, in particular % riffle, was also strongly and positively related with LD in both years, suggesting that some of the observed LD may have resulted from physical breakdown (Webster and Benfield 1986). However, because I placed the leaf packs in comparable habitats across streams, this explanation seems unlikely to account for differences among streams.

2.4.4.2. Benthic macroinvertebrate (BMI) community

Although abiotic indicators revealed changes in habitat quality at the most intensively managed sites and these changes resulted in lower LD rates, the BMI communities in leaf packs did not indicate any impairment at these sites. In fact, the most abiotically-impacted streams (based on sediment deposition and water chemistry) had among the highest % EPT values, which is considered an indicator of good site quality. This contrasts with at least two studies that showed decreased richness and/or abundance in leaf pack BMIs after harvesting (Kreutzweiser et al. 2008a; Lecerf and Richardson 2010). In my study, higher abundance and richness were positively related to canopy openness and negatively to % effVSA. It could be hypothesized that an increased consumption of autochthonous food sources (due to a greater

algal production resulting from a more opened canopy) as opposed to terrestrial sources (delivered through effective VSAs), in combination with warmer water temperatures, may support greater BMI richness and abundance in these streams, but this hypothesis will be further explored in Chapter 3. This means that BMI abundance and richness were mainly related to factors that were not affected by forest management (canopy openness was not related to harvesting because all streams had no-harvest buffers), although richness was positively related to recent clearcut and negatively to partial harvest in 2014. However, the composition of BMI communities in leaf packs (as indicated by the NMDS ordination of streams based on their BMI communities) seemed to shift as the physicochemical habitat quality (namely stream morphology, sediments, DOM quality, water chemistry and temperature) changed across the forest management gradient, similar to the pattern found by Kreutzweiser et al. (2008b).

Relative shredder abundance on the leaf packs was surprisingly low in some streams (as low as 8%) considering that these are forested headwater streams (Vanote et al. 1980), reiterating that leaves are important both as a food source and habitat to non-shredder BMIs (Richardson 1992). Catchment variables did not have a strong direct effect on percent shredder, but the abiotic indicators related with forest management intensity had a strong positive effect on percent shredder, namely DOM humification/aromaticity and inorganic sediment deposition and entrainment in leaves; therefore, the highest values were recorded in two of the streams with the most intensively managed catchments (BB01 and BB02, ~70%). Increased percent shredder has been attributed to increased detrital resources after harvesting (Jackson et al. 2007; Medhurst et al. 2010), but trends in the opposite direction have also been reported (Smith et al. 2009; Richardson and Béraud 2014). In BB, it seems that shredders had a competitive advantage over the other FFGs in streams with highly managed catchments and

higher levels of fine inorganic sediments, with all the FFGs but shredders declining in relative abundance as sediments increased. As discussed below, this advantage likely stemmed from the increased delivery of terrestrial materials to streams and the resulting elevated heterotrophic biofilm biomass in streams with highly managed catchments (assuming that the biofilm biomass measured on tiles is representative of the biofilm growing on leaves). The positive relationship between % effective VSA and relative shredder abundance also suggests that shredders responded positively to an increased delivery of materials from the catchment to the stream (via the increased hydrological connectivity between the catchment and the stream promoted by effective VSAs). Finally, the strong negative effect of stream morphology PC1 on % shredder may indicate that this FFG preferred streams with more runs, silt and large woody debris in comparison to the other FFGs.

Increases in shredder abundance, however, did not translate into higher decomposition rates. In fact, relative and absolute shredder abundance were negatively correlated with LD in 2014 ($r = -0.64$ and -0.61) and relative abundance negatively in 2015 ($r = -0.37$). Riipinen et al. (2009) proposed that LD is mainly related to the size and biomass of those shredders. In the present study, therefore, the increase in shredder abundance in the most impacted streams may have been driven by the small-bodied stonefly shredders (Leuctridae, Nemouridae and Capniidae) that predominated at these sites and which are known for being less voracious feeders than the larger caddisfly shredders that were found at the less impacted streams (Dangles and Guerold 2001). In fact, LD positively correlated with the absolute abundance of >1 mm *Lepidostoma* caddisfly shredders in 2015 ($r = 0.49$), but not with <1 mm Capniids and Nemourids, and negatively with *Leuctra* ($r = -0.55$), supporting this hypothesis.

Overall, the LD and leaf pack BMI community analyses agree with studies concluding that ecosystem structure and function are not always linked (Mckie and Malmqvist 2009; Riipinen et

al. 2009). A change in structure can occur without a measurable change in function, and vice-versa. In the case of this study, function (leaf litter decomposition rates) detected the gradient in forest management intensity, while some structural characteristics such as BMI richness and abundance did not.

2.4.5. *Biofilm and algal biomass*

Total biofilm biomass in the BB stream responded positively to forest management intensity, agreeing with previous observations of elevated biofilm biomass in logged sites even when 30-m buffers were retained (Kiffney et al. 2003), as well as in thinned forests (Danehy et al. 2007). Within forest management intensity, roads had the strongest positive effect on biofilm biomass, but recent clearcut was also positively correlated with this stream indicator. The strong relationship of biofilm biomass with SUVA and WC_PC2 suggest that increased levels of DOC resulting from higher forest management favours the growth of biofilms. This apparent greater biofilm growth seemed to happen despite the less labile nature of this DOC (indicated by the more aromatic and humic nature of this DOM), probably due to microbial communities in forested headwater streams being highly adapted to efficiently assimilating the more humic and aromatic DOC originating from surrounding forests (Kreutzweiser and Capell 2003; Burrows et al. 2013; Emilson et al. 2017). These results would add evidence in favour of OM quantity overriding the importance of quality in terms of stimulating ecosystem productivity (Marcarelli et al. 2011; Roiha et al. 2012). Even though sediments are known to negatively impact biofilms (Izagirre et al. 2009; Jones et al. 2012), the increased food availability for heterotrophic biofilm microbes seemed to outweigh the negative impacts of sediments in these streams. In fact, this increase in total biofilm biomass was probably driven

by heterotrophic microbes, since algal biomass was not related to forest management intensity in this study and others (Davies et al. 2016).

Algal biomass was mainly related to canopy openness, suggesting that primary production is not nutrient but light limited in the BB streams. BB07 and BB10, the streams with the highest algal biomass values, had reaches of narrow buffer zones and sections that were affected by recent windthrow (personal observation), which resulted in more open canopies (22 and 18% canopy openness in BB07 and BB10, respectively, as opposed to 14% across all the other streams). This riparian buffer blowdown may have produced similar increases in algal biomass as has been observed before with riparian harvesting (Lecerf et al. 2012) and with decreased buffer width (Wilkerson et al. 2010). These two BB sites support the suggestion by Moore et al. (2005) that narrower buffers are more prone to blowdown, and can thus be less effective at retaining shade for stream reaches. Finally, the relative scraper abundance collected in leaf packs was not correlated with the algal biomass on tiles, as previously reported (Medhurst et al. 2010), but relative and absolute shredder abundance (in 2014) was positively correlated with total biofilm biomass, suggesting that this FFG was favoured by the increased amount of biofilm growing on leaves, despite the fine inorganic sediments entrained in the biofilm.

2.4.6. *Harvested (BB) vs. reference (MC)*

Mount Carleton reference streams differed from Black Brook harvested streams in sediment deposition (less inorganic sediments, lower spatial variability and a higher organic fraction in sediment traps) and water chemistry (higher SiO₂ and lower Ca, Mg, conductivity, alkalinity, DIC, SO₄ and nitrogen levels). These differences probably stemmed from the absence of soil disturbance (harvesting) and roads in the unmanaged MC catchments as opposed to the

managed BB ones. However, differences in water chemistry could also be attributed to the different geology underlying these areas: felsic volcanic rocks (characteristic from MC) are known to be rich in elements such as Si, Na and K, which would explain the higher levels of these elements in MC streams compared to BB streams; sedimentary rocks (characteristic from BB), on the other hand, tend to be richer in dolomites and calcium carbonates, which would explain the higher pH, Mg, Ca and C levels in BB streams (Feller 2005). However, these abiotic differences did not translate into significant biotic differences between harvested and reference streams. Reference streams had leaf decomposition values, BMI abundance and richness values, and total biofilm biomass values that fell within the range for harvested sites. Most relationships described for BB also applied for MC, meaning that the environmental factors influencing these stream indicators were comparable between the managed and unmanaged sites. The exceptions were leaf decomposition and water temperature; but the weaker relationships between explanatory variables and these indicators were mainly driven by the reference stream MC2. MC2 had more sediments and DOC, considerably warmer water and lower leaf decomposition values than the other two reference streams, which is probably a result of the beaver dam upstream of the sampling reach in MC2 (Naiman et al. 1986). Finally, the similarity between BB and MC relations seemed to be greater in 2014, suggesting that other factors (e.g., weather in a given year) may be affecting the relationships between catchment/reach variables and stream indicators differently in each area.

2.4.7. Conclusions and management implications

The suite of indicators measured in this study detected differences related to the gradient in forest management intensity in Black Brook District. As a general trend, streams in the most intensively managed catchments had higher fine sediment deposition and

entrainment, higher conductivity, alkalinity, DIC, etc. (WC_PC1), higher DOM aromaticity and humification, warmer water, more biofilm biomass, lower leaf decomposition, and higher shredder and lower grazer densities (Figure 2-19). The main challenge was to discern between causality and correlation among variables, since harvesting intensity and roads were correlated with other catchment and reach variables. Catchments in lower elevations tended to have more intensive forest management (i.e., degree of harvesting and road density), more coniferous plantations and less deciduous/mixed forests. The composition of the riparian forest was related to that of the catchment, so streams in lower elevations tended to have more coniferous and less deciduous/mixed riparian forests and a lower riffle/run ratio and were narrower (Figure 2-19). Despite these correlations, the observed differences in stream indicators appeared to be more related to forest management activity (namely road density) than to forest composition. This can be visualized by looking at Table 2-11, which shows that road density (and the associated increased fine inorganic sediment deposition) was the explanatory variable affecting the greatest number of stream indicators. This table also shows that biotic indicators were more directly influenced by reach than catchment variables; among the reach explanatory variables, factors both related (e.g., sediments and water chemistry) and unrelated (e.g., canopy openness) to forest management intensity seemed to be influencing the biotic indicators. In addition, the indicator responses (e.g., increased fine sediment deposition and conductivity) can be linked from previous literature to forest management impacts (Croke and Hairsine 2006; Kreutzweiser et al. 2008b; Richardson and Béraud 2014; Webster et al. 2015).

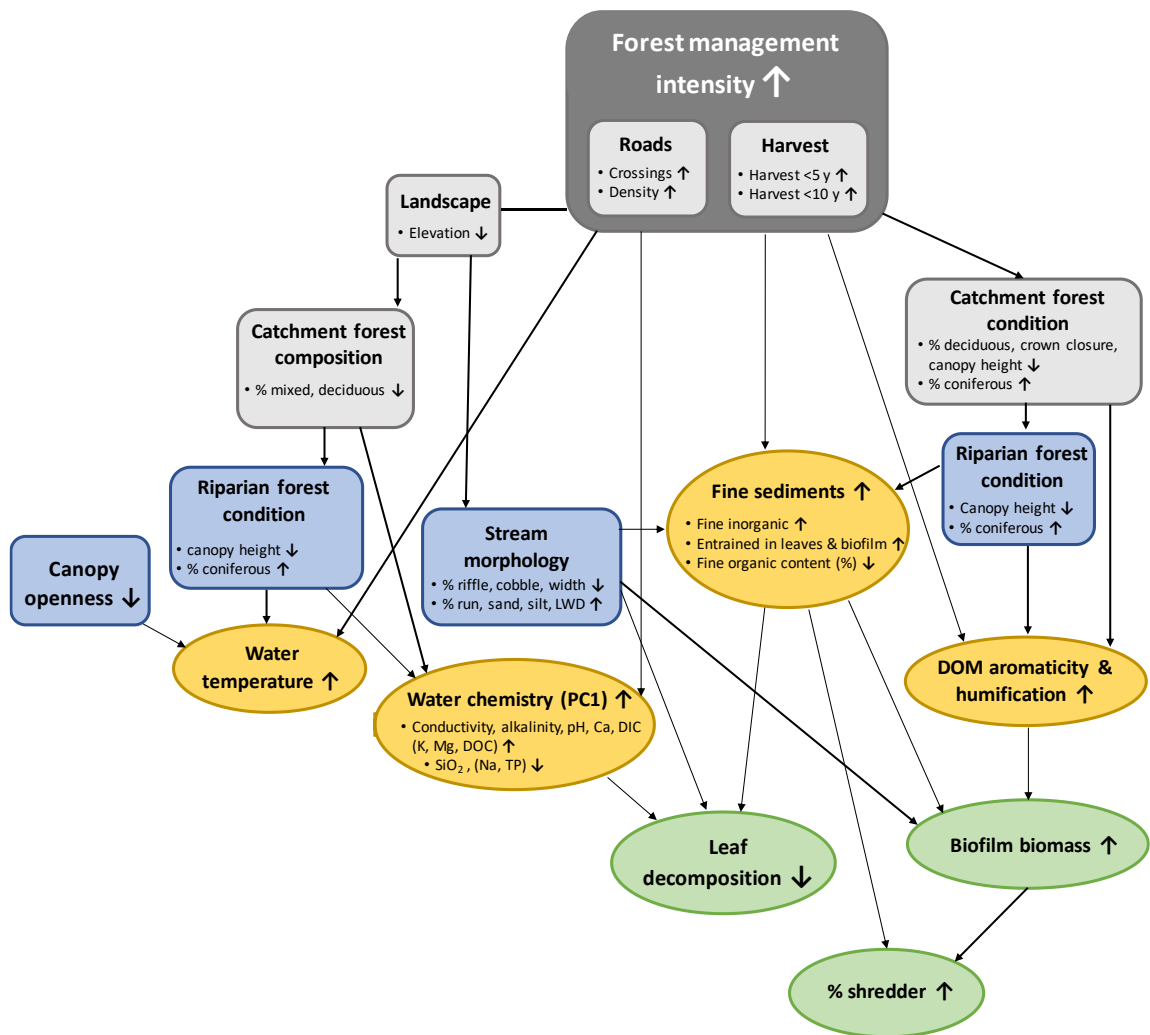


Figure 2-19: Diagram summarizing the relationships among catchment and reach explanatory variables (gray and blue boxes, respectively), and abiotic and biotic stream indicators (yellow and green circles, respectively). Arrows between box/circles indicate hypothesized relationships based on regression analyses, and the up/down arrows after variables indicate positive/negative relations.

Abiotic indicators, namely fine inorganic sediments and water chemistry, were strongly correlated to forest management intensity; sediments were more strongly related to roads, whereas water and DOM quality were related to harvesting intensity and forest composition in addition to roads. Therefore, it appears that the higher degree of harvesting in low elevation catchments (mainly conifer plantations) may have resulted in higher levels of ground disturbance overall, enhanced the biogeochemical processing in forest soils through

temperature (from canopy opening) and organic matter (from slash) increases, and promoted higher rates of water and water-borne material transport to streams (Kreutzweiser et al. 2008b). The delivery of these water-borne materials to streams was facilitated by the higher road density and stream crossings in these catchments, contributing to greater runoff volumes and peak flows carrying fine sediments, cations and DOC reaching the streams in the most intensively managed catchments. Forest composition may have also affected this delivery because different forest types may have variable effectiveness at intercepting these water-borne materials before reaching the stream, but it seems more likely that this relationship was mainly due to the correlation between forest composition and forest management intensity (i.e., higher forest management intensity in conifer plantations than in deciduous/mixed forests).

Despite measurable differences in habitat quality among streams related to intensity of forest management, these differences did not appear to translate into impaired biological communities: all sites contained rich and diverse BMI communities, with no indication of impairment in community structure compared to the MC stream BMI communities. However, at the more sediment-influenced sites, there tended to be reduced rates of LD, which is a critical ecological function in forested headwater streams (Gessner and Chauvet 2002). This underscores the importance of looking at both structural and functional biotic indicators to assess the effects of catchment disturbance on stream ecosystems (Christensen and Bartuska 1996; Giller 2005), and the importance of measuring a suite of abiotic indicators to better understand the biological responses. For example, contrasting conclusions could be drawn from this study when looking at indicators individually, ranging from forest management intensity resulting in site impairment (based on LD), to no effect (based on leaf pack BMI abundance and diversity), to forestry stimulating productivity (based on biofilm biomass). But

by looking at the system holistically, it can be said that the response of BMIs to the increased biofilm biomass due to forestry was potentially limited by the high inorganic sediment content in the biofilms; equally, the higher sediment content in biofilms may have made leaves less palatable, resulting in reduced decomposition rates. Therefore, based on these results, including a suite of indicators representing different components of the ecosystem is strongly recommended for future work trying to understand the linkages between disturbance and effects.

Table 2-11: Table showing the strength of the effect of 9 catchment and reach explanatory variables and 5 abiotic stream explanatory variables (columns) on 12 the stream abiotic and biotic indicators measured in this study (rows). Dark gray indicates that an explanatory variable showed the strongest independent effect on an indicator; light gray indicates that a variable was significantly related (based on simple linear regressions, $\alpha = 0.1$) to an indicator, but that the effect was less strong than that of the variable in dark gray. 14 or 15 indicates that the regression was statistically significant only in 2014 or 2015, respectively.

	Catchment						Reach			Abiotic				
	Harvest PC1	Harvest PC2	Roads	% effVSA	FC_PC1	FC_PC2	Canopy	% riparian conifer	SM_PC1	LIM	WC_PC1	WC_PC2	SUVA	MAT
Fine Inorganic Sediments		14		15										
Leaf Inorganic Mass														
WC_PC1 (Ca, C)		14												
WC_PC2 (DOC, Fe, Al)														
DOM quality (SUVA)				14										
Temperature (MAT)	14													
Leaf decomposition		14												14
BMI abundance				15			15							14
BMI richness	14			15										
% shredders			14	14		14								15
Biofilm biomass				14					14		14	14		
Algal biomass														

In summary, results indicate that even in an intensively managed forest landscape such as BB, the contemporary forest management practices are largely effective at retaining forest stream habitats and their communities at levels that are comparable to those in a nearby non-managed forest watershed or to within levels that do not indicate site impairment. Most of the harvesting-related effects were strongest for recent harvesting (< 10 years), suggesting that stream ecosystems in BB seemed to recover from the impacts of older harvesting. However, the changes in physicochemical habitat quality, especially the fine sediment deposition resulting from roads, and the reduced rates of leaf litter decomposition at the most intensively managed streams (mainly BB01 and BB02) warrant attention. Increased conservation efforts to protect streams and their ecosystem services should be directed at reducing ground disturbance and minimizing roads and sediment inputs in catchments with high degrees of management activity.

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3. Linking stream food web structure to catchment and reach conditions in an intensively-managed forest landscape

3.1. Introduction

The source of energy supporting headwater stream ecosystems has been a key question in freshwater ecology for decades. Because primary production tends to be limited by low light conditions in shaded headwater streams (Rosemond et al. 2000; Lesutiene et al. 2014; Collins et al. 2016) and because large quantities of allochthonous (i.e., imported into a stream ecosystem from outside of it, namely from terrestrial ecosystems) material enter these streams (Webster and Meyer 1997), allochthonous inputs have been considered the key energy source for these food webs (River Continuum Concept, Vanote et al. 1980). However, recent research demonstrates that autochthonous (in-stream) production may be disproportionately important for these food webs, with algae contributing more to animal tissue than expected based on its small standing biomass relative to detritus (Mayer and Likens 1987; Finlay 2001; Lau et al. 2009; Hayden et al. 2016; Jonsson and Stenroth 2016; Rosi-Marshall et al. 2016).

The reason for this mismatch likely stems from the need to consider resource quality in addition to resource quantity, with the latter being the main basis for the classical River Continuum Concept framework (Marcarelli et al. 2011; Rosi-Marshall et al. 2016). Algae are considered as a higher quality food source for stream benthic macroinvertebrates (BMIs) compared to allochthonous materials due to algae's lower C:N and C:P ratios and the presence of essential fatty acids upon which BMIs depend (Brett and Müller-Navarra 1997; Frost et al. 2002; Guo et al. 2016a). Colonization of leaf litter by bacteria and fungi improve the stoichiometry, and thus, the quality of leaf litter (Cross et al. 2005), but fungi and bacteria themselves are of lower nutritional quality than algae due to their lack of highly unsaturated fatty acids (HUFA) such as EPA and DHA (Guo et al. 2016a). But with evidence supporting the

importance of both aquatic (e.g., Mayer and Likens 1987; Lau et al. 2009; Carroll et al. 2016; Hayden et al. 2016) and terrestrial (Wallace et al. 1997; Reid et al. 2008) production as key basal resources for headwater stream food webs, debate over the relative importance of autochthonous vs. allochthonous contributions continues (Brett et al. 2017).

Understanding the relative importance of autochthonous/allochthonous resource use and its implications for headwater stream food webs is vital to predicting how catchment disturbances may affect the flow of energy from basal sources to top trophic levels, but current knowledge of the relationship between catchment disturbance and stream food web linkages is relatively rudimentary (Brett et al. 2017). Forest harvesting, a widespread anthropogenic catchment disturbance, has the potential to alter the relative contributions of terrestrial vs. aquatic energy sources that support stream food webs. For example, forest harvesting can increase aquatic primary production by increasing light availability and nutrient delivery (Kiffney et al. 2003; Lecerf et al. 2012), and it can also reduce the subsidization of terrestrial organic matter due to vegetation removal (England and Rosemond 2004; Santiago et al. 2011). However, few studies have directly studied the relationship between forest harvesting and stream food web structure. Most of these studies reported an increase in autochthonous contributions to BMI diets due to reduced canopy cover and input of terrestrial detritus to streams (Rounick et al. 1982b; England and Rosemond 2004; Göthe et al. 2009). Ishikawa et al. (2016), on the other hand, observed a decrease in autochthonous contribution after clearcutting, which may have resulted from post-clearcut landslides and debris flows suppressing primary production. In all these studies, forests were harvested up to the streambanks; nevertheless, such practices are uncommon since riparian buffer zones (RBZ) are typically left unharvested or with modified harvest in most forest management areas to protect mapped or noticeable streams from logging impacts (Schilling 2009; McDermott et al. 2010). Thus, most of

the above-mentioned impacts on stream food webs could be mitigated by the use of unharvested RBZs, since undisturbed riparian forest buffers would provide shading as well as leaf litter (Broadmeadow and Nisbet 2004).

Despite this, upland logging with RBZs has still the potential to alter stream food webs. Forest management changes biogeochemical processes and water flows in the catchment, often resulting in an increase in water-borne inorganic and organic nutrients delivered to the receiving waters (Kreutzweiser et al. 2008b). Therefore, even forest management incorporating best management practices could alter stream food webs by modifying the delivery of sediments, nutrients, DOC quantity and quality, etc. (Croke and Hairsine 2006; Kreutzweiser et al. 2008; Richardson and Béraud 2014; Webster et al. 2015). However, to my knowledge, no study has investigated how forest harvesting under best management practices (including RBZs) in an intensively managed landscape affects headwater stream food web structure.

Stable isotope analyses (SIA) have been increasingly and successfully used in food web ecology to trace energy pathways and trophic interactions because the isotopes of certain elements provide a time and space integrated measure of energy flow (Peterson and Fry 1987; Fry 2006). In freshwater ecology, stable isotopes of C ($\delta^{13}\text{C}$) have been used to identify the contribution of autochthonous and allochthonous food sources to consumers (e.g., Rosenfeld and Roff 1992; Junger and Planas 1994; Finlay 2001; McNeely et al. 2006). This approach relies on isotopic differences between potential food sources, which arise from aquatic and terrestrial plants having different inorganic C sources and fractionation processes during photosynthesis (Peterson and Fry 1987). Because there are only minor changes in $\delta^{13}\text{C}$ when food C is incorporated into consumers' tissues (Post 2002), the isotopic composition of consumers will reflect that of food sources, making $\delta^{13}\text{C}$ an effective dietary tracer (Vander Zanden and Rasmussen 2001). This effectiveness, however, is conditional upon the terrestrial

and aquatic food sources having distinct $\delta^{13}\text{C}$ values, a condition that is not always met in stream ecosystems and that may limit the usefulness of SIA (Finlay 2004; Singer et al. 2005; Finlay et al. 2010; Hayden et al. 2016). Adding more dietary tracers can increase the isotopic separation of food sources, thus enhancing the discriminatory power to detect the contribution of each food source. Nitrogen isotopes ($\delta^{15}\text{N}$) change more than $\delta^{13}\text{C}$ during each trophic transfer (fractionation of $\sim 2\text{-}4$ per mil; Post 2002; McCutchan et al. 2003), thereby they are often used to estimate the trophic position of consumers; but they can also be used as dietary tracers if this fractionation value is accounted for (e.g., Cole and Solomon 2012; Carroll et al. 2016). More recently, hydrogen stable isotopes ($\delta^2\text{H}$) were shown to diverge substantially between terrestrial and aquatic food sources (Doucett et al. 2007; Finlay et al. 2010), and since then, $\delta^2\text{H}$ has been increasingly used as an energy flow tracer in studies of freshwater food webs (Vander Zanden et al. 2016).

SIA and mixing models present several challenges and limitations when it comes to tracing consumers' diets (Phillips et al. 2014). More specifically, gut contents might bias the isotopic signature of consumers (Lancaster and Waldron 2001); variable fractionation values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and variable dietary water contributions to consumer $\delta^2\text{H}$ can be a source of error when fixed values are assumed in mixing models (Phillips et al. 2014; Vander Zanden et al. 2016); and, the difficulty in measuring the algal isotopic signature within biofilms can lead to erroneous estimates (Hamilton et al. 2005; Rasmussen 2010; Brett et al. 2017) (see section 3.2.3 and 3.2.4 for further detail). But when these sources of uncertainty are acknowledged and considered, SIA can be a powerful tool to elucidate the relative contribution of aquatic and terrestrial food sources to stream food webs. Therefore, studies addressing these sources of uncertainty are important to increase the applicability of SIA to food web studies.

To address the surprising paucity of studies looking at the effects of forest harvesting on headwater stream food webs, I examined the relationship between forest management intensity and the transfer of energy from aquatic/terrestrial sources to stream consumers by conducting a two-year study in the Black Brook (BB) forestry district (New Brunswick, Canada). BB is considered one of the most intensively managed forests in Canada, yet it was third-party certified as sustainably managed under the Sustainable Forestry Initiative (Etheridge et al. 2005). Considering that forestry has been predicted to intensify in the near future (Creed et al. 2016), but that the need to demonstrate the sustainability of forestry practices is also increasing (CCME 2016), BB provides an opportunity to assess how the likely “forestry of the future” may impact stream food webs and the associated aquatic ecosystem services. In addition, state-of-the science forest characterization and harvest data obtained from high-resolution LiDAR and other enhanced forest inventory tools and GIS-based terrain analyses are available for BB. These tools enable a more refined characterization of landscape and forest features, and allow for a more precise quantification of structural attributes than what is typically available for a forest management area and that are key determinants of ecological function of forests (Wulder et al. 2008). Therefore, working in BB allowed me to study the effects of intensive forest management on stream food webs by taking advantage of innovative forest inventory tools to characterize catchment condition.

Twelve streams ranging in forest management intensity were selected in BB, which differed in area of the catchment that had been harvested, time since harvesting, harvesting technique, road density and stream crossings, and forest condition (i.e., composition and structure). Food web structure was characterized by measuring the isotopic signature ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$ – the latter only in 2015) of food sources and consumers (benthic macroinvertebrates, BMIs) sampled in 2014 and 2015, and by applying Bayesian mixing models

to quantify the contribution of each food source to consumers' diets. Food web structure of streams in the intensively managed catchments was compared to three undisturbed (reference) streams of comparable catchment sizes in a nearby non-managed forest landscape. The dietary contributions were related to harvesting, forest condition, landscape, riparian and stream variables to understand the relative importance of the catchment and reach-scale variables on stream food webs. The objective of this chapter was 1) to quantify the relative contributions of autochthonous versus allochthonous sources of energy to headwater stream food webs, 2) to understand how different forest catchment conditions that arise from varying intensities of forest management under current best management practices affect the contribution of each food source, and 3) attempt to better characterize uncertainties and limitations associated with the use of SIA to characterize stream food webs.

3.2. Methods

3.2.1. Site selection and characterization

Site selection and characterization of the 15 stream reaches and catchments used in this study are described in detail in Chapter 2 – section 2.2.1. Briefly, 12 low-order streams (1st-3rd) were selected in the northern end of BB with the goal of capturing a range in forest condition (e.g., deciduous/mixed/coniferous dominated and canopy heights ranging between 7.8-16.9 m P90) and forest management intensity (e.g., 18-100 % of the catchment harvested in the last 10 years and road density ranging between 21-89 m of road per ha). I also selected three reference streams in Mount Carleton (MC) Provincial Park to determine a range of natural variation in stream food web structure for forest catchments of similar composition but that had not been managed.

Catchments were delineated using an Arc-GIS flow accumulation grid based on digital elevation models (DEM, 5-m LiDAR derived DEM for BB and 20-m DEM for MC). Detailed characterization of each BB catchment was achieved using LiDAR-derived forest structural metrics, photo-interpreted composition data from high-resolution digital stereo imagery (known as forest resource inventory or FRI), and topographic information derived from the LiDAR-based DEM (see section 3.2.5 below for more details). Such a detailed catchment characterization could not be done for MC due to the lack of high-resolution LiDAR and FRI data (see Table 3-1 for the list of variables available for BB and MC). Sixty-meter long stream reaches were selected for sampling immediately upstream of road crossings.

3.2.2. Sample collection

Food resources and consumers (benthic macroinvertebrates or BMIs) were collected in September 2014 and 2015 to match the timing of natural leaf fall. Senescent leaves were collected (1 collection per stream) from riparian trees (only in 2014; see below for explanation). Coarse particulate organic matter (CPOM), which mainly consists of terrestrial detritus, was sampled by collecting conditioned leaves from in-stream leaf accumulations at the start, middle and end of each 60-m reach, and treated as three replicates. Seston or suspended fine particulate organic matter (FPOM), i.e., detritus <1 mm, was sampled by filtering stream water through pre-combusted (500 °C for 2 h) GF/F Whatman® filters until the filters were saturated (only in 2014; see below for explanation). Benthic FPOM was collected by suctioning the top centimeter of the substrate from depositional areas using a turkey baster (1 collection per stream in 2014, 3 in 2015). Biofilm (OM attached to surfaces, which mainly consists of microscopic algae, bacteria, fungi, extracellular polymeric substances and detritus) was collected by scraping with scalpels the surface of artificial substrates (unglazed tiles), and

washing the slurry with stream water into Whirl-pak® bags. Tiles were deployed in streams 48-51 days and 37-40 days prior to sampling to allow biofilm to grow in 2014 and 2015, respectively. Tile incubations were conducted in three pools and three riffles in 2014 to account for the variability in biofilm isotopic signature across habitats (Ishikawa et al. 2012). Based on the low variability in biofilm isotope ratios between pools and riffles observed in 2014 (data not shown), tiles were incubated only in riffles (3 per stream) in 2015 (since consumers were collected in riffles). Dissolved organic matter (DOM) was collected in 2014 by filtering stream water through 0.45 µm metricel PALL® filters and collecting the filtrate in amber borosilicate vials. Leaves, CPOM, FPOM and biofilm samples were frozen until further analysis in the lab, and DOM samples were kept refrigerated and in the dark. Riparian leaf and seston samples were not collected in 2015 because 2014 results did not show significant differences in C and N isotope ratios between riparian leaves and CPOM samples, and between seston and benthic FPOM samples (data not shown). C isotope ratios measured in DOM did not differ significantly among streams and from other food sources (data not shown), so DOM was not collected in 2015, nor were the data included in the 2014 analysis.

BMIs were collected by electroshocking (the electro shocker was set for 250-350 V DC, 30 Hz and 4 ms pulse width) within a 25 cm wide and 100 cm long rectangle for one minute (3 passes of 20 seconds separated by 10-second breaks). Drifting invertebrates were collected with a 363 µm mesh size drift net placed on the downstream edge of the rectangle. The net was rinsed with stream water and the contents emptied into a white sorting tray. Five rocks within the rectangle were inspected to pick the BMIs that were attached to rocks. All the invertebrates were live-sorted into the lowest possible taxonomic level (usually family) in the field to avoid predation and each taxon stored in separate Whirl-pak® bags partially filled with stream water. Samples were kept in the dark and on ice in the field, and frozen at the end of

the day. This procedure was followed at 3 riffle spots per stream at the start, middle and end of each 60-m reach, and treated as three subsamples. For taxa without enough biomass, subsamples were pooled into a single sample, but when each subsample contained enough biomass, each was processed separately. A qualitative sample was collected by electroshocking different habitats within the reach to collect extra individuals from taxa that were less abundant in our three standard semi-quantitative samples (to make sure I had enough biomass for stable isotope analysis).

Water samples for H isotope analysis were collected in September 2015 from the rectangle used to collect BMIs just before the shocking started. Stream water was extracted with a syringe, filtered through a 0.2 µm PES filter, and poured into a vial (3 subsamples per stream).

3.2.3. *Stable Isotope Analyses*

CPOM samples were rinsed to remove unwanted particles (i.e., debris and BMIs), oven-dried for 48 h at 60°C, and ground to a fine powder with a mortar and pestle. In 2014, biofilm and FPOM samples were filtered through pre-combusted (500°C for 2 h) GF/C and GF/F Whatman filters, respectively, and then filters were oven-dried for 48 h at 60°C. In 2015, biofilm and FPOM samples were poured through a 0.5-mm sieve to remove small BMIs, and the filtrate was freeze-dried for 96 h. Processed CPOM, FPOM and biofilm powder was weighed into tin (3.00-3.20 mg for C and N isotopes) and silver (0.35-0.45 mg for H isotopes) capsules.

BMIs were identified to genus and classified according to their functional feeding group (FFG) using Merritt et al. (2008). The taxa that were most widely represented across streams and that captured all five FFGs were selected for SIA: scraper Heptageniidae (*Epeorus*, *Heptagenia*, *Rhithrogena*), collector-gatherer/scrapper Baetis, collector-gatherer *Ephemerella*,

shredder *Leuctra*, collector-filterers *Parapsyche* and Philopotamidae (*Dolophilodes* and *Wormaldia*), and predators *Diura* and *Sweltsa*. Two preliminary studies were conducted to evaluate how BMI samples should be processed (see sections 3.2.3.1 and 3.2.3.2 below). Finally, BMI samples were freeze-dried for 48 h, ground to a fine powder with a glass rod and weighed into tin (0.40-1.20 mg for C and N isotopes) and silver (0.20-0.30 mg for H isotopes) capsules.

Carbon and N stable isotope ratios and content were measured at the Stable Isotope in Nature Laboratory (SinLab; Fredericton, New Brunswick, Canada) using a NC2500 (Carlo Erba; Milan, Italy) or a 4010 (Costech; California, USA) Elemental Analyzer coupled with a Delta Plus with Conflo II or a Delta XP with Conflo III (Thermo Finnigan; Bremen, Germany) continuous flow isotope ratio mass spectrometer (CF-IRMS). Repeated analyses of several internal standards showed that the analytical precision of C and N isotope ratio measurements in organic samples was $\pm 0.10\text{‰}$ and 0.11‰ (SD) on average, respectively.

The H isotope ratios of solid samples were also measured at the SinLab by converting sample H to H₂ gas through pyrolysis using a High Temperature Conversion Elemental Analyzer, and by measuring the isotopic composition of H₂ gas using a Delta V Plus IRMS with Conflo IV (Thermo Finnigan; Bremen, Germany). Prior to analysis, samples and standards were left to exchange with local atmospheric H₂ to correct for exchangeable H (Wassenaar and Hobson 2003). Repeated analyses of several internal standards showed that H isotope ratios in organic samples were precise to within $\pm 2.2\text{‰}$ (SD) on average. Water samples were analysed for H isotope ratios at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University (Flagstaff, Arizona, USA) using a DLT-100 liquid-water isotope analyser (Los Gatos Research; California, USA). The analytical precision of internal water standards was $\pm 0.18\text{‰}$ on average.

Stable isotope measurements are expressed as delta (δ) parts per thousand (‰) relative to the international standards Vienna PeeDee Belemnite for C, air for N, and Vienna Standard Mean Ocean Water for H, according to the equation:

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000 ,$$

where X is ^{13}C , ^{15}N or ^2H , and R is the corresponding $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$ or $^2\text{H}/^1\text{H}$ ratios.

3.2.3.1. Acid treatment

Inorganic C in samples can alter the measurement of organic carbon $\delta^{13}\text{C}$. Acid treating samples can solve this problem by removing the inorganic C, but it can result in undesired effects such as altered nutrient content and isotopic signature (Brodie et al. 2011). To determine whether inorganic C could compromise the accuracy of $\delta^{13}\text{C}$ measurements in my samples, I acid treated a subset and assessed how the procedure affected C and N isotope ratios and content. This was done with 17 BMI samples representing five different families and functional feeding groups that were processed as described above (i.e., freeze-dried and ground to a fine powder prior to the treatment). Each BMI sample was separated into two glass vials, with one vial undergoing acid-treatment and the other not. The acid treatment was conducted by fuming the opened vials containing the samples with 37 % HCl in a desiccator for two hours. The 34 samples (17 acid treated + 17 non-acid treated) were then analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C and %N as previously described. Based on the results (see section 3.3.1.), the remaining samples were not acid treated and data from untreated samples were used for subsequent analyses.

3.2.3.2. Gut removal

Gut clearance or gut removal is sometimes performed prior to stable isotope analysis to ensure that gut contents do not affect stable isotope ratios of the invertebrates. However, keeping invertebrates in confinement to allow gut clearance may change isotope values (Kaehler and Pakhomov 2001) and gut removal is very labour intensive or impossible in small invertebrates. Jardine et al. (2005) showed that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of primary consumers is very similar to those of their gut content, but that the difference is larger in the case of $\delta^{15}\text{N}$ and predators, suggesting that gut removal may be unnecessary for primary consumers, but necessary for predators. To determine whether gut content was affecting $\delta^{15}\text{N}$ readings of predator samples, I compared the isotopic values (and nutrient content) of predators with and without guts in 2014 samples. This was done with three predator taxa: *Diura* (Perlodidae, 15 samples, 14-30 individuals/sample), *Sweltsa* (Chloroperlidae, 14 samples, 14-30 individuals/sample) and *Rhyacophila* (Rhyacophilidae, 7 samples, 2-8 individuals/sample). The individuals in each sample were separated into two vials, with only the individuals in one of the vials undergoing gut removal. Gut removal was conducted under the dissecting microscope by removing the cerci, pulling the head and attached gut away from the body, and finally cutting the gut from the head and discarding it. Samples were then processed and analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C and %N as described above. Based on the results (see section 3.3.2.), gut removal was not done in 2015 and whole-body data were subsequently used for statistical analyses.

3.2.3.3. Cage experiment

A consumer's tissue usually has higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than its diet due to discrimination against the lighter isotope during elemental assimilation and excretion. Traditionally, fixed values have been used in mixing models to correct for these differences: 3.4‰ for ^{15}N and

0.4‰ for ^{13}C (Post 2002). However, more recent studies have shown that these discrimination or fractionation factors (fractionation factors herein) vary depending on environmental and physiological factors, diet quality, etc. and that this is one of the biggest sources of uncertainty when using mixing models to study trophic relationships (Phillips et al. 2014). For $\delta^2\text{H}$, fractionation is considered negligible (Solomon et al. 2009), but the relative contribution of food vs. dietary water to the $\delta^2\text{H}$ of consumer is a source of uncertainty that needs to be taken into consideration when using mixing models. Different dietary water contribution values can be found in the scientific literature (Solomon et al. 2009; Wang et al. 2009; Wilkinson et al. 2015) and several factors (e.g., metabolic rate, water flux, evaporative losses, behaviour) have been shown to affect this contribution (Vander Zanden et al. 2016). Therefore, to decrease this source of uncertainty as much as possible, a feeding experiment was conducted in 2015 to calculate the fractionation factors for ^{13}C and ^{15}N as well as the dietary water contribution to use for these food webs.

The experiment was conducted with four different taxa: *Leuctra* (Leuctridae, Plecoptera; shredder), *Zapada* (Nemouridae, Plecoptera; shredder), *Epeorus* (Heptageniidae, Ephemeroptera; scraper), and *Glossosoma* (Glossosomatidae, Trichoptera; scraper). Two streams were selected for the experiment, and shredders were incubated in one (BB09) and scrapers in the other (BB10). Four cages per species were incubated in riffles for 14 days. The cages were translucent to allow biofilm to grow, and they had four holes covered with 250 μm mesh to allow stream water to flow through the cage. Cages holding shredders were filled with alder leaves that had been conditioned in eight fine-mesh bags in the stream for 34 days; cages holding scrapers were filled with four 4.7 x 4.7 cm unglazed tiles that had been incubated in the stream for 35 days to allow biofilm to grow. Subsamples of these food sources were sampled at the beginning of the experiment to measure their isotopic signature at time zero: three leaves

were collected from each leaf bag, and five biofilm samples were collected by scraping and pooling the biofilm from four tiles. These samples were frozen at the end of the day.

Shredders were collected by electroshocking, placing a drift net downstream of the shocking area, emptying the content of the net into a tray, and picking the living individuals from the target genera. Then, 16 and 14 individuals (*Leuctra* and *Zapada*, respectively) were transferred into each cage as carefully as possible to avoid harming them. Scrapers were collected by picking individuals from rocks with forceps and transferring them into cages (8 *Epeorus* and 14 *Glossosoma*). Some individuals were put in bags to measure the isotopic signature at the beginning of the experiment, i.e., time zero. Three samples per species were taken at time zero, and in each sample 12, 12, 14 and 4 (*Leuctra*, *Zapada*, *Glossosoma* and *Epeorus*, respectively) individuals were pooled. These samples were frozen at the end of the day.

The cages were tied to two bricks with bungee cords and placed in fast flowing riffles to ensure that the cages were well oxygenated. During the two weeks of deployment, cages were visited to clear any debris clogging the mesh in the cages. After the incubation period, individuals from each cage were picked and stored in Whirl-pak® bags partially filled with stream water. Three out of four *Epeorus* cages could not be used for the study, because individuals had metamorphosed from larvae to adults during the two-week experiment. One *Epeorus* individual remained in the larval stage by the end of the experiment, so this one cage and individual were used for the study. The remaining food in each cage (the biofilm on the tiles and leaves) was also collected, and all food and BMI samples were kept in the dark and on ice in the field, and frozen at the end of the day. Once in the lab, all the samples were processed as previously described.

3.2.4. *Mixing models*

The relative contribution of food sources to the diets of the 8 BMI taxa was estimated using a Bayesian 2-isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) 3-source mixing model (CN herein) in 2014 and 2015, and a Bayesian 3-isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) 3-source mixing model in 2015 (CNH herein) with MixSIAR (Stock and Semmens 2013) in R. These models allow one to incorporate uncertainty in food source isotopic values as well as in trophic fractionation values. Separate mixing models were performed for each stream and taxon. Convergence of the models on the posterior distributions was determined before accepting the MixSIAR results by using the diagnostic tests in MixSIAR (Gelman-Rubin and Geweke).

After plotting the isotope data for each stream on biplots, two issues regarding sources were identified that had to be addressed prior to running the mixing models: 1) some potential food sources were isotopically similar (source overlapping), and 2) some fractionation-corrected consumers (namely scrapers) fell outside the convex hull defined by food sources (mixing polygon), suggesting that a food source contributing to the diet of these consumers was missing (Phillips et al. 2014). To address the first issue, redundant sources were excluded: benthic and suspended FPOM overlapped in 2014, so only benthic FPOM was used (because only benthic FPOM was sampled in 2015), and riparian leaves and CPOM overlapped in 2014, so only CPOM was used (because only CPOM was sampled in 2015). Biofilm scraped from tiles was linked to both issues. Biofilm $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ overlapped with FPOM in 8 out of 15 streams, with CPOM in 3 streams, and it separated from both FPOM and CPOM in 4 streams. This meant that grouping biofilm with another source, or keeping biofilm as a separate source, was problematic. A new marker, $\delta^2\text{H}$, was included in 2015 to get a better source separation, but the overlap between biofilm and other sources remained. This variability in biofilm isotopic

values across streams and the overlap with allochthonous food sources likely reflected the heterogeneous nature of biofilms in headwater streams (i.e., they are a mix of different things), and suggests that heterotrophic organisms and terrestrial FPOM made up the bulk of biofilm biomass.

This lack of isotopic source separation was tied to the second issue, i.e., scrapers had considerably more negative $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values than biofilms and they fell outside the mixing polygon. This suggested that biofilms were not reflecting the isotopic signature of aquatic primary producers (microscopic algae in biofilms) and that scrapers were selectively ingesting or assimilating this component of the biofilms. This phenomenon has previously been observed in headwater streams, in which heterotrophic organisms (bacteria, fungi) and terrestrial OM can make up the bulk of biofilm biomass on rock surfaces (epilithon) (Mayer and Likens 1987; McCutchan and Lewis 2002; McNeely et al. 2007; Chessman et al. 2009). To address this, algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was estimated from *Glossosoma* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (by subtracting trophic fractionation values, see below), since this genus 1) had consistently the most negative $\delta^{13}\text{C}$ values, 2) was present in every stream, and 3) is known to feed selectively on microscopic algae on biofilms (Oemke 1984; McNeely et al. 2006; Katano and Doi 2014). $\delta^2\text{H}$ values of algae were estimated by subtracting $170 \pm 15\text{‰}$ from stream water $\delta^2\text{H}$, based on studies showing that primary producers fractionate against ^2H during photosynthesis, resulting in 160-170‰ more negative values than environmental water (Yakir and DeNiro 1990; Solomon et al. 2011; Hondula et al. 2014). Therefore, since biofilms poorly reflected aquatic primary production, and tended to overlap with other food sources (mainly FPOM and sometimes CPOM), they were excluded from mixing models; hence, I ended up including three sources in mixing models: algae (autochthonous source; calculated), FPOM (allochthonous source, capturing both FPOM

and biofilms in most streams; measured) and CPOM (allochthonous source, mainly representing leaves; measured).

Trophic fractionation values for $\delta^{13}\text{C}$ ($0.4 \pm 1.20\text{‰}$) and $\delta^{15}\text{N}$ ($2.3 \pm 1.61\text{‰}$) were selected based on published data (McCutchan et al. 2003) and the cage experiment in this study. Fractionation for $\delta^2\text{H}$ was assumed to be 0 (Solomon et al. 2009). But because a fraction of an organism's ^2H comes from dietary water rather than assimilated food, this was accounted for by incorporating in the mixing models the dietary water contribution ($\delta^2\text{H}_{\text{WC}}$), which was calculated according to:

$$\delta^2\text{H}_{\text{WC}} = \delta^2\text{H}_{\text{cons}} - (\delta^2\text{H}_{\text{cons}} - \omega_{\text{tot}} * \delta^2\text{H}_{\text{water}}) / (1 - \omega_{\text{tot}}) ,$$

where $\delta^2\text{H}_{\text{water}}$ is the $\delta^2\text{H}$ of stream water, and ω_{tot} is the total contribution of dietary water to consumer $\delta^2\text{H}$ ($\delta^2\text{H}_{\text{cons}}$), calculated according to:

$$\omega_{\text{tot}} = 1 - (1 - \omega)^\tau ,$$

where ω is the per-trophic-level contribution of dietary water to consumers and τ is the trophic level ($\tau = 1$ for primary consumers and 2 for predators). A ω of 0.20 ± 0.1 was assumed based on values from Solomon et al. (2009), Wang et al. (2009) and Wilkinson et al. (2015), and backed by the cage experiment in this study.

3.2.5. *Catchment and reach explanatory variables*

Explanatory variables were classified into nine categories under two main groupings: catchment variables and reach variables. Catchment variables included those related to harvest, forest condition and landscape characteristics; reach variables included those related to riparian forest composition, stream morphology, sediments, water chemistry, DOM quality and biofilms. All the variables considered within each category are described in Table 3-1, but the detailed description of how these variables were measured can be found in Chapter 2.

3.2.6. Statistical analysis

Linear mixed models of ANOVA were used to analyse the influence of acid-treating samples and gut removal (explanatory variables) on $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C, %N and C:N (response variables). The acid treatment was treated as a binary fixed factor and sample (17 samples) as a random factor. Gut removal was treated as a binary fixed factor and stream as a random factor; these linear mixed models were conducted for all taxa together (3 taxa), in which taxon was included as a fixed factor and the acid treatment * taxon interaction was tested, as well as for each taxon individually. Linear mixed models of ANOVA were also used to assess the influence of adding a third isotope ($\delta^2\text{H}$, CNH) to 2-isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, CN) mixing models on the calculation of the contribution of each food source to BMI diets: mixing model type (CNH/CN) was treated as a fixed factor and stream as a random factor; linear mixed models were conducted for all taxa together (5 taxa), in which taxon was included as a fixed factor in the models and the mixing model type * taxon interaction was tested, as well as for each taxon individually. Mixed models were run using the *lme4* package (Bates et al. 2017) and the significance of the differences were tested using the *lmerTest* package, with the degrees of freedom calculated based on Satterthwaite's approximation (Kuznetsova et al. 2016). Linear mixed models were complimented with linear regression analyses and assessing the position of data-points in relation to the 1:1 line. This allowed me to visually interpret how acid-treatment and gut removal influenced the isotope and nutrient content of BMIs, as well as how introducing a third isotope influenced the calculations of dietary contributions.

Relationships between the contribution of algae (ΦA), CPOM (ΦC) and FPOM (ΦF) to each taxon (calculated using MixSIAR) and catchment and reach variables were evaluated using Pearson's correlation analysis. Only BB streams were included in this analysis, because 1)

several variables derived from high quality forest and landscape characterization data were only available for BB (Table 3-1) and I wanted to include these variables in the models, the reason being that a refined catchment characterization may allow a better separation of the effects of harvesting from the effects of forest condition or landscape characteristics; and 2) the geological and topographical differences between BB and MC resulting from these areas being part of different ecoregions could confound the comparison between reference and harvested sites.

To further explore the links between dietary contributions and EVs, redundancy analysis (RDA) was conducted with a subset of EVs. To be selected, EVs had to be significantly correlated with dietary contributions for at least three taxa, and correlation coefficients (r) had to be > 0.80 . Six variables fulfilled these conditions in 2014 (algal biomass, biofilm biomass, water chemistry PC1, DOM SUVA, fine inorganic sediments and % organic sediments) and 2015 (algal biomass, biofilm biomass, water chemistry PC1, DOM quality PC1, fine inorganic sediments and stream depth). Because some sites missed one of the five taxonomic groups considered for this analysis (*Baetis* missing in 2 streams in 2014 and in 3 streams in 2015; *Leuctra* missing in 1 stream in 2014 and 3 streams in 2015), and because RDA could not handle missing data, each missing dietary contribution value was replaced with the predicted value from the best models predicting dietary contributions. Model selection for the contribution of each food source to a given taxon was conducted using ordinary least-squares regression and Akaike Information Criterion adjusted for small sample sizes (AICc) (*MuMIn* package in R version 1.15.6, Bartón 2016). The best supported model was then used to estimate the missing dietary contribution values, which were then incorporated into the dataset used to run RDAs. The significance of the relationship between the subset of explanatory variables and dietary

contributions was assessed by testing the significance of the RDA model and axes using the built-in permutation tests in *vegan* (Oksanen et al. 2017). All statistical analyses were performed in R 3.0.1 (R Core Team 2013).

Table 3-1: Description of the explanatory catchment and reach variables for Black Brook and Mount Carleton sites. Variables shown in gray were only available for Black Brook (not for Mount Carleton).

		Variable	Description
Catchment	Management	PH_5y	Cumulative proportion of the catchment partially harvested (trees selectively harvested, usually 35-50% of the trees removed) over the past 5, 10, 20 and 30 years. Data: Yearly harvest GIS layers from JDI.
		PH_10y	
		PH_20y	
		PH_30y	
		CC_5y	Cumulative proportion of the catchment clearcut over the past 5, 10, 20 and 30 years. Data: Yearly harvest GIS layers from JDI.
		CC_10y	
		CC_20y	
		CC_30y	
		Tot_5y	The sum of clearcut and partial harvests over the past 5, 10, 20 and 30 years. Data: Yearly harvest GIS layers from JDI.
		Tot_10y	
		Tot_20y	
		Tot_30y	
		Stream crossings	Number of road stream crossings upstream the sampling reach.
		Road density	Length of roads in the catchment divided by catchment area.
	Forest	% coniferous	Proportion of the catchment with stands predominated by coniferous, deciduous or mixed (coniferous and deciduous tree species) forest. Data: JDI forest resource inventory.
		% deciduous	
		% mixed	
P90		Canopy height metric (height of the 90 th LiDAR percentile). Data: JDI LiDAR.	
S2		Understory predominance (% of LiDAR returns within 0-2 m). Data: JDI LiDAR.	
Landscape	Elevation	Mean elevation of the catchment. Data: LiDAR derived DEM.	
	Catchment area	Delineated in ArcGIS based on LiDAR-DEM.	
	Stream length	Stream length upstream the sampling reach. Data: JDI stream GIS layer.	
	% effVSA	Proportion of the catchment classified as effective VSA; indicates soil wetness based on the topographic index. Data: LiDAR-DEM.	
Reach	Riparian	% canopy openness	Measured by taking pictures of the canopy from the stream.
		% P90 > 5m	% of the 30-m riparian forest with canopy height (P90) >5 m. Data: LiDAR-DEM.
		% coniferous	% of the 30-m riparian forest classified as coniferous, deciduous or mixed (coniferous and deciduous together). Data: JDI forest resource inventory.
		% deciduous	
		% mixed	
	Stream	Width & depth	Measured every 10 m and then averaged for the entire 80-m reach.
		%Riffle/run/pool	Flow structure visually surveyed for 10-m sections, averaged across the 80-m reach.
		%Boulder/cobble/gravel/sand/silt	Substrate composition surveyed for 10-m sections, averaged across the 80-m reach.
		LWD	Number of large woody debris (LWD > 10 cm diameter) structures.
	Sediments	Biofilm IN	Inorganic mass of biofilms on tiles and leaf packs (indicators of fine inorganic sediments entrained in biofilms and leaves, respectively).
		Leaf IN	
		Fine IN	Fine (< 250 µm) inorganic and total (inorganic + organic) sediments in sediment traps.
		Fine IN+OR	
		Fine % OR	Proportion of organic fine sediments in sediment traps.
Water	WC_PC1	Positively related to pH, conductivity, alkalinity, Ca, K, Mg, DIC, DOC; negatively to SiO ₂ .	

		WC_PC2	Positively related to DOC, Cl, Al and Fe.
	DOM	DOM_PC1	Negatively related to the aromaticity and humification of DOM (HIX, SUVA...) (2015).
		SUVA	Variable describing the aromaticity of DOM (only DOM variable measured in 2014).
Reach	Biofilm	Biomass	Biomass of biofilms growing on tiles.
		Algal biomass	Algal biomass in biofilms growing on tiles (chl-a concentration).
		AI	Autotrophic Index measured by dividing algal biomass by total biofilm biomass.
		% OR	Organic fraction of biofilms on tiles.

3.3. Results

3.3.1. Acid treatment

C and N content in the BMIs decreased significantly, by 2.27 and 0.42% respectively, after acid treating the samples (ANOVA, $F_{1,16} = 194.0$ and 31.4 , $p < 0.001$). However, this decrease in nutrients did not significantly alter the isotopic values or C:N ratios (ANOVA, $F_{1,16} = 0.2$, 0.002 and 1.6 , $p = 0.66$, 0.97 and 0.22 , for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N, respectively) (Figure 3-1).

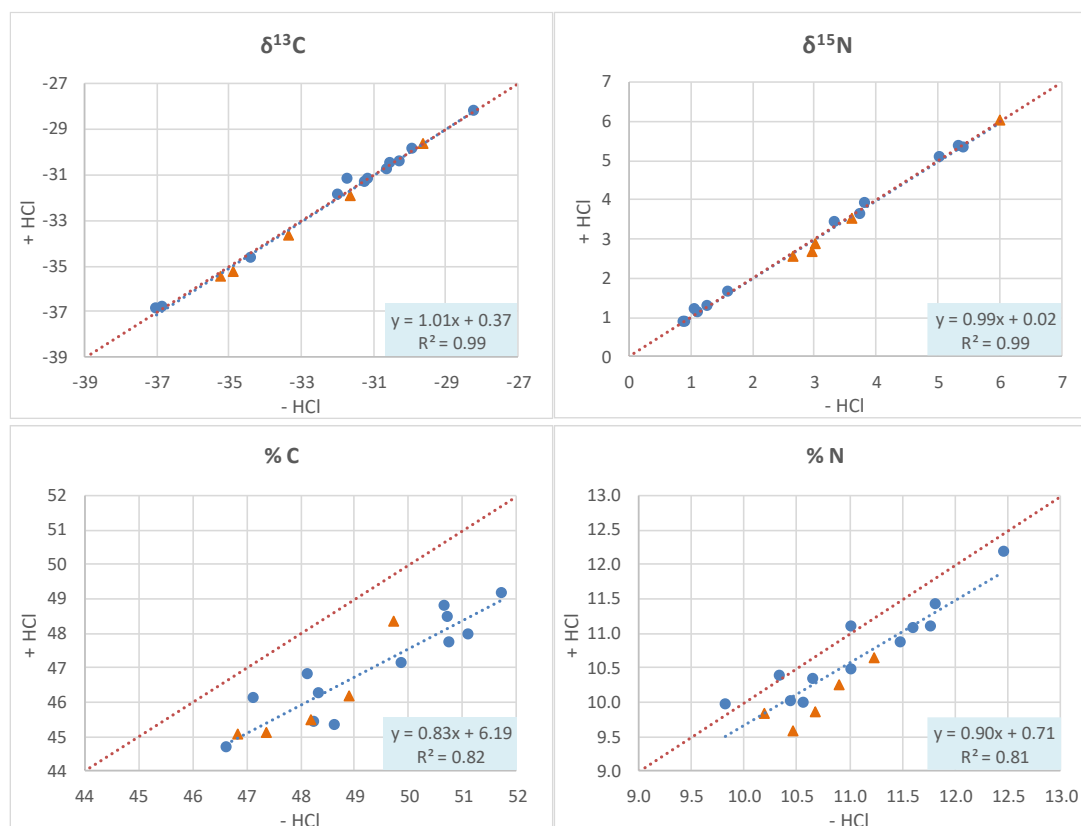


Figure 3-1: Relationships between acid-treated (+ HCl, Y axis) and non-acid-treated fractions (- HCl, X axis) of benthic macroinvertebrate samples (collected in 6 Black Brook – blue circles, and

3 Mount Carleton streams – orange triangles, in 2014, New Brunswick, Canada) for C and N isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and content (% C and % N). In blue is the fitted linear regression line, and in red the 1:1 line.

3.3.2. Gut removal

There were no significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between predators with and without guts (Figure 3-2; see Appendix II Table A16 for ANOVA results). However, both C and N contents were significantly lower in predators with guts than in predators without guts, by 1.50% and 0.78%, respectively on average (ANOVA, $F_{1,50} = 29.9$ and 19.6 , $p < 0.001$). The interaction between gut removal and taxon was significant for models predicting %N (ANOVA, $F_{1,51} = 14.0$, $p < 0.001$) and C:N (ANOVA, $F_{1,51} = 7.2$, $p = 0.002$), and marginally significant in the case of %C (ANOVA, $F_{1,51} = 2.4$, $p = 0.1$), so the effect of gut removal on these dependent variables was assessed for each taxon individually. The differences in C and N content were greatest for the chloroperlid *Sweltsa* (2.88% less C and 1.12% less N) followed by the perlotid *Diura* (1.50% less C and 0.79% less N), whereas the caddisfly *Rhyacophila* did not show significant differences in nutrient content between samples with and without gut contents. C:N ratios were significantly higher in *Sweltsa* and *Diura* stoneflies that retained their guts than in their gut-less counterparts, whereas C:N ratio was lower in *Rhyacophila* caddisflies with retained guts than in the ones with guts removed.

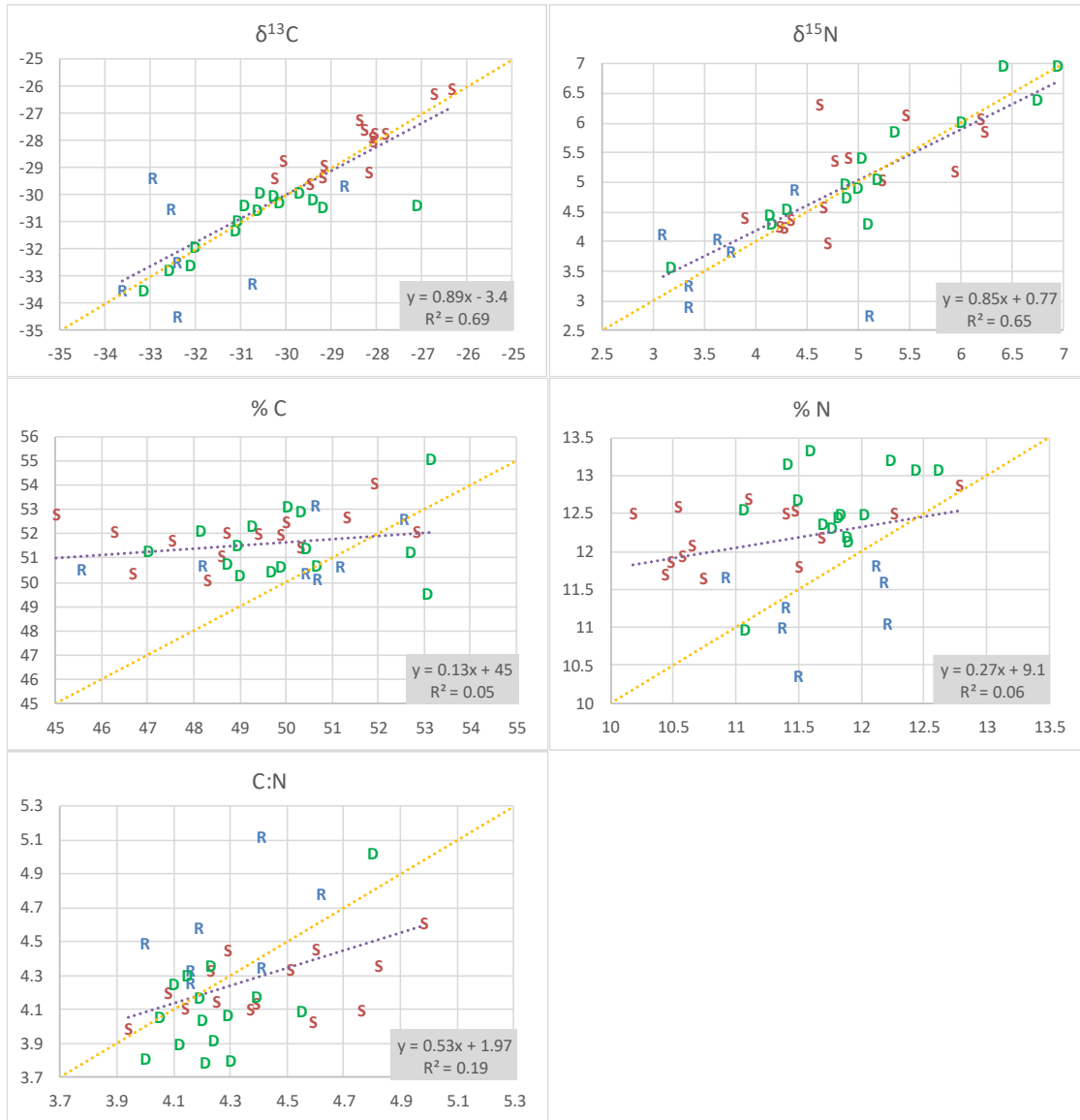


Figure 3-2: Relationships between predators with guts (X axis) and without guts (Y axis) for C and N isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), content (% C and % N) and C:N ratio. Green D's correspond to *Diura* (Perlodidae, $n = 15$ samples), red S's to *Sweltsa* (Chloroperlidae, $n = 14$) and blue R's to *Rhyacophila* (Rhyacophilidae, $n = 7$), collected in 12 Black Brook and 3 Mount Carleton streams in 2014, New Brunswick, Canada. In purple is the fitted linear regression line, and in yellow the 1:1 line.

3.3.3. Estimation of fractionation and water contribution values

Overall, $\delta^2\text{H}$ changed little in consumers over the duration of the cage experiment.

Leuctra and *Zapada* shredders became enriched in ^2H by $4.3 \pm 1.0\%$ and $10.3 \pm 1.9\%$, respectively, whereas *Glossosoma* scraper became depleted by $5.0 \pm 5.3\%$. Regarding the food

sources, leaf $\delta^2\text{H}$ remained almost constant ($0.29 \pm 1.8\text{‰}$ more positive on average), but biofilm $\delta^2\text{H}$ increased by $18.9 \pm 8.1\text{‰}$ on average. This difference in biofilm $\delta^2\text{H}$ between t_1 and t_0 was smaller than the variability among t_0 replicates ($\text{SD} = 26.3\text{‰}$); the variability among replicates decreased by the end of the experiment, i.e., at t_1 ($\text{SD} = 8.1\text{‰}$). The contribution from dietary water to shredder tissue $\delta^2\text{H}$ (ω) calculated at the end of this experiment was 0.27 ± 0.01 for *Leuctra* and 0.17 ± 0.04 for *Zapada* (Table 3-2). In the case of scrapers, because their $\delta^2\text{H}$ was considerably more negative than the $\delta^2\text{H}$ of their food source (i.e., biofilm on tiles), estimated algae $\delta^2\text{H}$ values (algae_{-170‰}) were used and ω was 0.17 ± 0.03 for *Glossosoma* and 0.21 for *Epeorus*. The difference between water $\delta^2\text{H}$ and scrapers $\delta^2\text{H}$ (corrected for dietary water by using $\omega = 0.20$) was $-174 \pm 9.7\text{‰}$ when averaging across all the scraper cages, and $-172.3 \pm 5.5\text{‰}$ when focusing only on *Glossosoma*. Changing ω to calculate scrapers $\delta^2\text{H}$ in turn changed the difference between water and scrapers, ranging from $168 \pm 9.4\text{‰}$ (when using $\omega = 0.17$) to $191.1 \pm 10.6\text{‰}$ ($\omega = 0.27$). Therefore, as described during the methods section, and based on these results and on the literature, I used $\omega = 0.20 \pm 0.1$ to correct for the dietary water contribution to consumers in my mixing models, and algae $\delta^2\text{H}$ was calculated by subtracting $170 \pm 15\text{‰}$ from water $\delta^2\text{H}$. These estimates agree with the values observed in the feeding experiment.

Table 3-2: Trophic fractionation values (mean \pm SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and dietary water contribution to consumer $\delta^2\text{H}$ calculated during the cage experiment for *Leuctra*, *Zapada*, *Glossosoma* and *Epeorus* ($n = 4$ cages/taxon). The experiment was conducted during two weeks in September 2015 in two Black Brook streams (New Brunswick, Canada).

	Fractionation		Water contribution (ω)
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^2\text{H}$
<i>Leuctra</i> (shredder)	0.23 ± 0.66	3.88 ± 0.20	0.27 ± 0.01
<i>Zapada</i> (shredder)	-2.01 ± 1.01	1.93 ± 0.15	0.17 ± 0.04
<i>Glossosoma</i> (scraper)	NA	NA	0.17 ± 0.03 *
<i>Epeorus</i> (scraper)	NA	NA	0.21 *^

Note: * Food source calculated by subtracting 170‰ from $\delta^2\text{H}$ water, since scrapers $\delta^2\text{H}$ was more negative than biofilm $\delta^2\text{H}$.
^ no replication, single cage.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of either food sources or consumers changed only slightly during the experiment. $\delta^{13}\text{C}$ became slightly more negative in leaves ($-0.27 \pm 0.5\text{‰}$ on average) and *Glossosoma* ($-1.3 \pm 1.3\text{‰}$), and more positive in biofilm ($0.52 \pm 0.6\text{‰}$), *Epeorus* (1.1‰), *Leuctra* ($0.34 \pm 0.17\text{‰}$) and *Zapada* ($1.73 \pm 0.4\text{‰}$). The $\delta^{13}\text{C}$ fractionation value calculated in this experiment was $0.23 \pm 0.66\text{‰}$ for *Leuctra* and $-2.01 \pm 1.01\text{‰}$ for *Zapada* (Table 3-2). Scrapers had considerably more negative values than the food source presented to them during the experiment (biofilm on tiles), meaning that bulk biofilm did not adequately represent the food source (algae presumably) scrapers were assimilating. Therefore, fractionation values for $\delta^{13}\text{C}$ nor $\delta^{15}\text{N}$ could not be calculated for *Glossosoma* and *Epeorus*. With respect to $\delta^{15}\text{N}$, the leaves, biofilm and *Glossosoma* were enriched in ^{15}N by $0.02 \pm 0.12\text{‰}$, $0.26 \pm 0.52\text{‰}$ and $0.12 \pm 0.28\text{‰}$ during the experiment, respectively, whereas *Epeorus*, *Leuctra* and *Zapada* depleted by 0.07‰ , $0.38 \pm 0.18\text{‰}$ and $0.10 \pm 0.18\text{‰}$, respectively. The $\delta^{15}\text{N}$ fractionation over their food source was $3.88 \pm 0.20\text{‰}$ for *Leuctra* and $1.93 \pm 0.15\text{‰}$ for *Zapada*. Again, fractionation values for scrapers could not be calculated because tile biofilm was not representative of what scrapers were assimilating, i.e., scrapers had $\delta^{13}\text{C}$ values considerably more negative than biofilms.

3.3.4. *Mixing models*

3.3.4.1. 2-isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) mixing models for 2014 and 2015

The dietary contributions of algae (ΦA), CPOM (ΦC) and FPOM (ΦF) calculated from MixSIAR were correlated between different taxa within a functional feeding group, especially in 2015 (correlation coefficients ranged from 0.27 to 0.91 in 2014, and from 0.69 to 0.97 in 2015; see Appendix II Table A16); therefore, only one taxon per FFG will be presented herein (the taxon that was most represented across streams): *Baetis* (scraper/collector-gatherer),

Parapsyche (collector-filterer), *Diura* (predator), *Ephemerella* (collector-gatherer) and *Leuctra* (shredder).

Algae contributed to 50.0 and 55.6% of *Baetis* diet on average across streams in 2014 and 2015, respectively, but median ΦA was as low as 25% and as high as 75% across streams (Figure 3-3). CPOM contributed least to the *Baetis* diet, with median ΦC ranging from 0 to ~33% across streams. The contribution of FPOM (biofilm) to the diet of this genus was between that of algae and CPOM in most streams, but median ΦF reached values as high as 68.4% in the streams with lower ΦA values.

Algae was also the major food source of the collector-gatherer *Ephemerella*, contributing 48.4 and 51.1% of the diet on average across streams in 2014 and 2015, respectively; but, as with *Baetis*, ΦA also ranged between 25 and 75% across streams (Figure 3-3). Up to half of the diet came from CPOM or FPOM in some streams, whereas the contribution was lower than 10% in others.

In contrast, shredders from the genus *Leuctra* seemed to rely heavily on FPOM (72% of the diet on average in both years), with at least 50% of the diet coming from this source in every stream and in both years, and this value being as high as 90% in some streams. Algae and CPOM did not contribute significantly to their diet, with values lower than 25% in all but one stream and as low as 4.7% in BB01 in 2014 for both ΦA and ΦC .

Regarding the filterer-gatherer *Parapsyche*, FPOM was also the main food source in both years (69.3 and 62.2% of the diet on average), with the contribution being greater than 50% in every stream (except MC2 in 2014), and as high as 90% in some streams (Figure 3-3). ΦA and ΦC were lower than 25% in most streams, and as low as 8% and 3% in some streams, respectively.

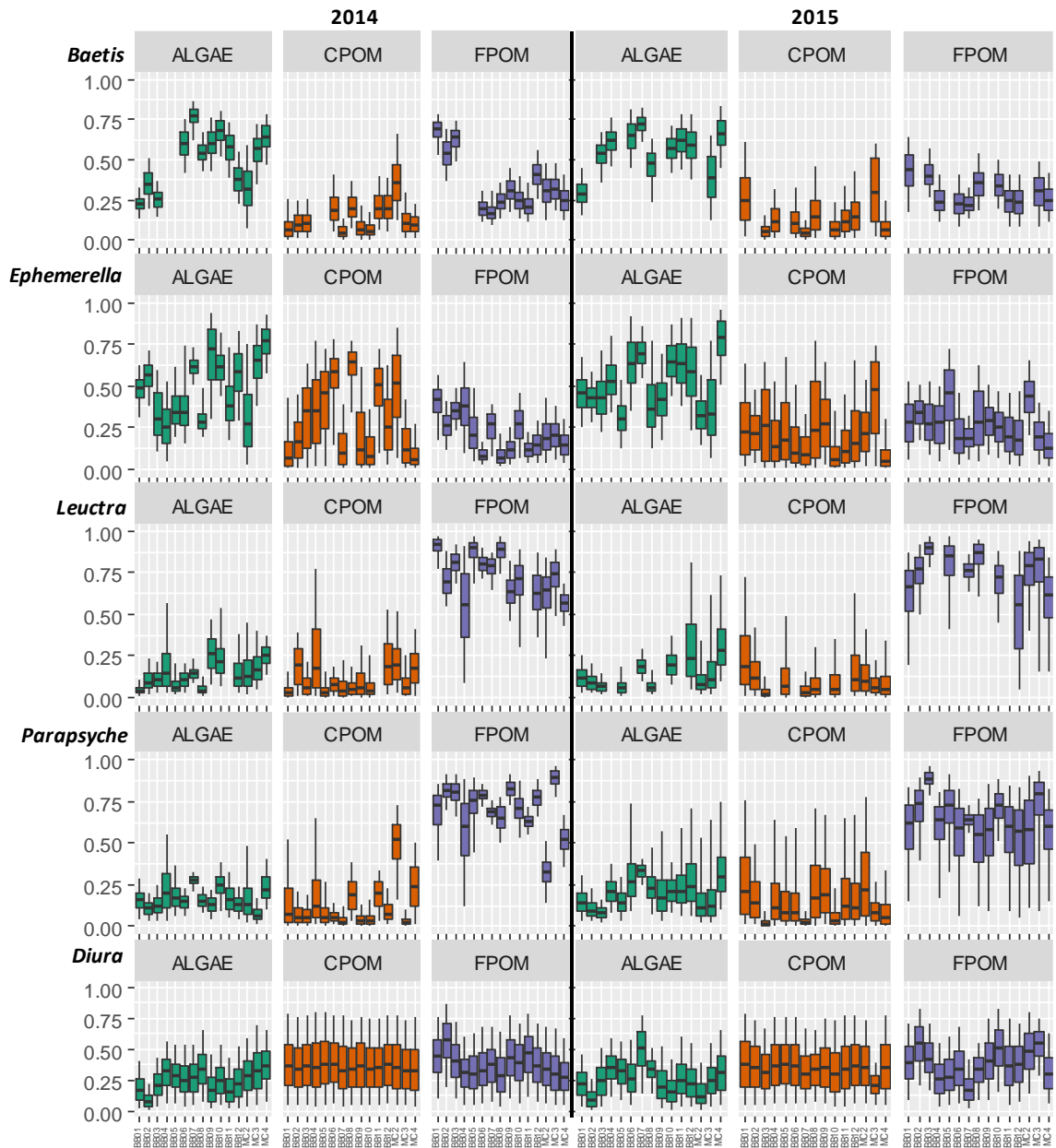


Figure 3-3: Boxplots showing the dietary contributions of algae (Y axis represents proportions between 0-1), CPOM and FPOM to the diets of *Baetis* (scraper/collector-gatherer), *Ephemerella* (collector-gatherer), *Leuctra* (shredder), *Parapsyche* (filterer) and *Diura* (predator) in 12 harvested (Black Brook, BB) and 3 reference (Mount Carleton, MC) streams (New Brunswick, Canada) in 2014 and 2015. Dietary contributions were calculated based on a Bayesian 2-isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) mixing models with MixSIAR. (The upper and lower hinges of each box correspond to the upper and lower quartiles of the probability distributions calculated with MixSIAR, and the line in between to the median; the whiskers represent 90% credibility limits or 5th and 95th percentiles of the probability distributions).

The predator *Diura* seemed to rely on all three food sources (i.e., on prey that fed on all three food sources) (Figure 3-3). The contribution of FPOM and CPOM to this taxon was similar, with an average of 35-38% of each in both years. Among site variability was low, especially in the case of CPOM. Algae contributed the least to *Diura* biomass, about 25% of their diet on average across streams.

The correlation between 2014 and 2015 median dietary contributions was highest for ΦA overall (ranging from $r = 0.41$ for *Ephemerella* to 0.73 for *Leuctra*), followed by ΦF (ranging from $r = 0.20$ for *Ephemerella* to 0.77 for *Baetis*), and ΦC showed the lowest interannual congruence across streams (ranging from $r = -0.04$ for *Ephemerella* to $r = 0.63$ for *Diura*) (Table 3-3). Furthermore, there were no significant differences between 2014 and 2015 in ΦA , ΦC or ΦF values (for all taxa combined [the year*taxon interactions were not significant] or within each taxon) (see Table 3-3 for ANOVA results).

Results from Mount Carleton reference streams tended to fall within the Black Brook range with respect to the contributions of algae, CPOM and FPOM to BMI diets. In fact, in some cases the MC range was as wide as the BB range, meaning that the range in diets observed across the harvested streams was also observed within reference streams (i.e., without anthropogenic disturbance). The reference stream MC4 tended to have higher algal contribution values than the other two reference streams and most BB streams, whereas MC2 tended to have among the highest ΦC values across all BB and MC streams.

Table 3-3: Results of mixed model ANOVA testing for differences between 2014 and 2015 contribution of food sources (algae, CPOM and FPOM) to the diets of 5 benthic macroinvertebrate genera collected in 12 Black Brook and 3 Mount Carleton streams in 2015 (New Brunswick, Canada). Column 2015-2014 describes the effect size or differences between 2015 and 2014 contributions. Column *r* shows the Pearson correlation coefficient between 2014 and 2015 contributions. Row “overall” indicates that all taxa were pooled together in the model and taxon was treated as a fixed factor; no significant interaction were observed between year and taxon.

	Algae				CPOM				FPOM			
	2015-2014	<i>F</i>	<i>p</i>	<i>r</i>	2015-2014	<i>F</i>	<i>p</i>	<i>r</i>	2015-2014	<i>F</i>	<i>p</i>	<i>r</i>
Overall *	0.02	0.55	0.46	0.84	-0.03	1.41	0.24	0.53	-0.009	0.06	0.81	0.87
<i>Baetis</i> **	0.04	0.80	0.38	0.63	-0.01	0.10	0.75	0.06	-0.04	1.15	0.31	0.77
<i>Ephemera</i> **	0.02	0.29	0.60	0.41	-0.11	3.10	0.09	-0.04	0.05	2.30	0.15	0.20
<i>Leuctra</i> **	0.00	0.16	0.69	0.73	-0.02	0.92	0.35	0.22	0.01	0.10	0.76	0.55
<i>Parapsyche</i> **	0.03	3.99	0.06	0.70	0.00	0.06	0.80	0.47	-0.04	1.72	0.21	0.47
<i>Diura</i> **	0.01	0.22	0.64	0.53	0.00	3.10	0.10	0.63	0.01	0.13	0.73	0.41

Note: * Contribution of algae/CPOM/FPOM ~ Year * Taxon + (1|Stream) model tested.

** Contribution of algae/CPOM/FPOM ~ Year + (1|Stream) model tested.

3.3.4.2. 2-isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) vs. 3-isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^2\text{H}$) mixing models for 2015

Algal contributions (i.e., median ΦA) for all genera combined in 2015 were significantly greater when including $\delta^2\text{H}$ in the mixing models (in addition to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, *CNH* herein) than when not (*CN*) by 9.2% on average (ANOVA, $F_{1,110} = 29.5$, $p < 0.001$), but because the interaction between mixing model method and taxon was significant (ANOVA, $F_{1,118} = , p < 0.001$), the CN vs. CHN comparison was conducted for each taxon individually. Algal contribution was greater for CNH than CN in the case of *Baetis*, *Parapsyche*, *Leuctra* and *Diura*, as shown by the significant differences in Table 3-4 and by the data from most streams falling under the 1:1 line in Appendix II Figure A10, but this increase was greater for some taxa (e.g., filterer *Parapsyche* by 16.6% and predator *Diura* by 12.1 %) than for others (shredder *Leuctra* 5.1%). In the case of the filterer *Parapsyche* and predator *Diura*, the greater the autochthonous contributions, the greater the mismatch between CN and CNH (as indicated by the slope coefficient being < 1). In the case of *Parapsyche*, one stream (BB12) had a high leverage effect on the regression slope and, after excluding this stream, the slope increased from 0.23 to 0.43

and the correlation between the methods increased from $r = 0.55$ to 0.66 . In the case of *Diura*, BB03 also had a high leverage and, when excluding this stream, the slope increased from 0.68 to 0.85 . Although autochthonous contribution values tended to be lower for CN than for CNH results, median dietary contributions obtained from these two mixing models tended to correlate quite strongly across streams, especially for *Baetis*, *Leuctra* and *Diura* ($r = 0.84$, 0.89 and 0.80 , respectively), whereas correlation values for collectors were lower ($r = 0.65$ for *Ephemerella* and 0.55 for *Parapsyche*) (Table 3-4).

Table 3-4: Results of mixed model ANOVA testing for differences between 2-isotope (CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and 3-isotope (CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) mixing models to calculate the median contribution of food sources (algae, CPOM and FPOM) to the diets of 5 benthic macroinvertebrate genera collected in 12 Black Brook and 3 Mount Carleton streams in 2015 (New Brunswick, Canada). Column CNH-CN describes the effect size or differences between contributions calculated with CNH and CN mixing models. Row "overall" indicates that all taxa were pooled together in the model; if the interaction between method and taxon was significant, the results for that model have been shaded. In bold are significant values at $\alpha = 0.05$. Column r shows the Pearson correlation coefficient between CNH and CN.

	Algae				CPOM				FPOM			
	CNH - CN	F	p	r	CNH - CN	F	p	r	CNH - CN	F	p	r
OVERALL *	0.092	29.5	<0.001	0.81	0.02	0.7	0.42	0.76	-0.062	24.3	<0.001	0.87
<i>Baetis</i> **	0.092	18.4	0.002	0.84	-0.021	1.2	0.29	0.64	-0.062	19.3	<0.001	0.80
<i>Ephemerella</i> **	-0.022	0.5	0.48	0.65	0.035	1.8	0.20	0.64	0.011	0.4	0.56	0.69
<i>Leuctra</i> **	0.051	23.1	<0.001	0.89	0.039	4.0	0.07	0.97	-0.079	9.1	0.012	0.74
<i>Parapsyche</i> **	0.166	18.1	<0.001	0.55	0.02	0.8	0.38	0.84	-0.165	25.0	<0.001	0.68
<i>Diura</i> **	0.121	39.6	<0.001	0.80	-0.023	0.6	0.44	0.40	-0.083	10.4	0.006	0.49

Note: * Contribution of algae/CPOM/FPOM ~ Method * Taxon + (1|Stream) model tested.

** Contribution of algae/CPOM/FPOM ~ Method + (1|Stream) model tested

Median ΦC values across all taxa did not differ significantly between CNH and CN mixing models (ANOVA, $F_{1,112} = 0.7$, $p = 0.42$), and they correlated strongly for *Leuctra* ($r = 0.97$) and *Parapsyche* ($r = 0.84$), and less strongly for *Baetis*, *Ephemerella* and *Diura* ($r = 0.64$, 0.64 and 0.40 , respectively) (Table 3-4). Median ΦF contributions were significantly lower when including $\delta^2\text{H}$ in the mixing models by an average of 6.2% (ANOVA, $F_{1,113} = 24.3$, $p < 0.001$), but because the interaction between type of mixing model and taxon was significant, the CNH vs.

CN comparison could only be assessed within each taxon separately. *Ephemerella* was again the only taxon with non-significant differences between CN and CNH dietary contributions, whereas *Parapsyche* showed the highest difference between methods (ΦF 0.16 lower with CNH than with CN) and (Table 3-4). Correlations in ΦF between the two mixing models were strongest for *Baetis* ($r = 0.80$) and weakest for *Diura* ($r = 0.49$). The low correlations for ΦC or ΦF between the CN and CNH results in the case of *Diura* were mainly driven by one stream (BB02); correlations became stronger ($r = 0.72$ for ΦF and 0.59 for ΦC) when excluding this stream, in which $\delta^{13}C$ indicated a stronger reliance on FPOM, whereas δ^2H indicated a stronger reliance on CPOM.

3.3.5. Relationships between dietary contributions and catchment and reach variables

The diet of the scraper *Baetis* reflected several factors directly or indirectly related to forest management (relationships between forest management and these variables are shown in Chapter 2). The exploitation of autochthonous energy sources by this genus was negatively correlated with road density, % riparian coniferous composition (only in 2015), fine inorganic sediments, WC_PC1, DOM aromaticity and humification, and % runs, and positively with dominance of mixed/deciduous forests (both at the catchment and riparian level), elevation, % riffles, % organic sediments and FI (microbial origin of DOC, only measured in 2015) in both years (see Appendix II Table A18). In 2014, *Baetis* ΦA was also positively correlated with the algal biomass measured on tile biofilms. The median *Baetis* ΦF and ΦC were also correlated with similar variables to the ones described for ΦA , but the direction of the correlations was reversed. In addition, their reliance on CPOM was positively correlated with % effective VSA, and negatively with the dominance of mature, deciduous forests in the catchment. ΦF was positively and ΦC negatively correlated with stream depth and % pool. Harvesting variables did

not show strong correlations ($r = 0.5-0.6$); but these correlations provided some indication that ΦA decreased and ΦF increased with recent harvesting (<5 and <10 years), and that ΦA increased with harvesting accumulated over a longer period of time (<20-30 years). Most correlations between *Baetis* diet and EVs tended to be stronger for those calculated using CN than CNH, especially in the case of ΦA and ΦF .

In both years, the contribution of algae to the diet of *Ephemerella* increased and that of CPOM decreased as stream algal biomass (measured on tiles) increased, and ΦA was also positively related to canopy openness in 2015 (see Appendix II Table A19). The relationship between *Ephemerella* ΦA and algal biomass in 2015, however, was significant only for CNH data. Median *Ephemerella* ΦF was positively related to harvesting in both years, and in 2014, also to roads, % riparian coniferous, fine inorganic sediments, % runs, WC_PC1, DOM aromaticity and biofilm biomass.

The reliance of the shredder *Leuctra* on algae or CPOM was negatively correlated with recent harvest (harvesting over the past 5 and 10 years), but positively correlated with harvesting accumulated over a longer period of time (harvesting over the past 20 and 30 years), whereas the reliance on FPOM followed the opposite trend (increased after recent harvesting and decreased after longer harvesting periods) (see Appendix II Table A20). The use by *Leuctra* of autochthonous resources was also positively correlated with % mixed riparian forest composition. In 2015, ΦC was also positively and ΦF negatively correlated with roads, % effective VSA, young coniferous plantations, fine inorganic sediments, WC_PC1 and PC2, and DOM aromaticity, which were shown to be related to high forest management intensity in Chapter 2. In contrast, ΦC decreased and ΦF increased as % pools and stream depth increased in 2015. Correlations were very different between 2014 and 2015 for *Leuctra*, but comparable

between CNH and CN for ΦA and ΦC in 2015 (most correlations tended to be stronger with CNH for ΦF).

In 2014, the algal contribution to the collector-filterer *Parapsyche* was positively correlated with algal biomass and canopy openness (see Appendix II Table A21). In 2015, it was positively correlated with % riffle and cobbles, and the organic proportion of sediments and biofilms, and negatively with fine sediments (detected with CN but not with CNH). Median ΦF was positively and ΦC was negatively correlated with mature, deciduous forests in both years. In 2014, ΦF increased and ΦC decreased with recent harvest. In 2015, ΦF increased and ΦC decreased with stream depth, and ΦC was positively correlated with fine inorganic sediments and DOM aromaticity and humification.

In 2014, ΦA in the predator *Diura* was positively correlated with algal biomass and % organic sediments, and negatively with large woody debris, whereas ΦF followed the opposite trend (see Appendix II Table A22). In 2014, ΦC for this taxon was negatively correlated with algal biomass. Again, *Diura* ΦC tended to be negatively and ΦF positively correlated with stream depth and % pools. In 2014, % effective VSA was negatively correlated with median *Diura* ΦA , and positively with ΦF .

Among all the correlated EVs in 2014, a subset was selected for redundancy analyses based on relative strengths of association and their frequency of significant correlations (algal biomass, biofilm biomass, WC_PC1, SUVA, fine inorganic sediments (FIS) and % organic sediments), which produced a statistically significant model (*adj. R*² = 0.60, *p* = 0.001). In 2014, the first axis RDA1 (*R*² = 0.36, *p* = 0.002) was characterized by a strong positive loading for inorganic sediments, water chemistry PC1 (related to conductivity, Ca, DIC, DOC...), SUVA and biofilm, and a negative loading for % organic sediments (Figure 3-4). ΦF for four out of five taxa scored positively on RDA1, whereas their ΦC scored negatively; the exception was the shredder

Leuctra, which scored around 0 for both ΦC and ΦF . The second axis ($R^2 = 0.29$, $p = 0.002$) was strongly and positively related to algal biomass, and negatively and less strongly to inorganic sediments and WC_PC1. ΦA for four out of five taxa scored positively on RDA2, with the predator *Diura* scoring around 0. ΦC for all five taxa and ΦF for three taxa (*Baetis*, *Ephemerella* and *Leuctra*) scored negatively on RDA2. *Baetis* and *Ephemerella* were the taxa that scored the most strongly on the RDA axes, with ΦA for *Baetis* being negatively and ΦF positively related to FIS/WC_PC1, and ΦC for *Ephemerella* being negatively related to algae and biofilm biomass.

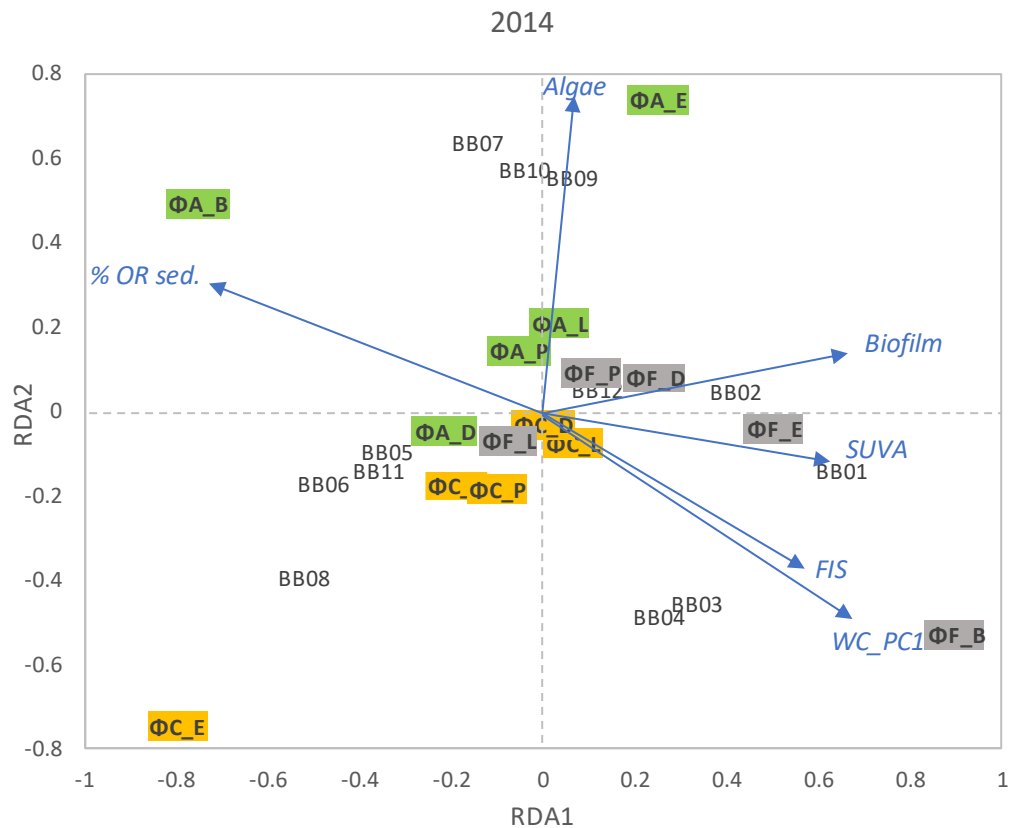


Figure 3-4: Results from redundancy analyses (RDA) on the relationships between relative contributions of algae (ΦA , green), CPOM (ΦC , yellow) and FPOM (ΦF , gray) to the diet of 5 benthic macroinvertebrate taxa (*Baetis*, B; *Ephemerella*, E; *Leuctra*, L; *Parapsyche*, P; *Diura*, D) in 12 Black Brook streams (New Brunswick, Canada) in 2014. Dietary contributions have been scaled with factor 2 for graphical purposes. Explanatory variables are shown by blue vectors (FIS: Fine Inorganic Sediments; WC_PC1: water chemistry PC1 (mainly related to cation and carbon concentrations); % OR sed.: % organic sediments).

The subset of EVs selected for redundancy analyses in 2015 (algal biomass, biofilm biomass, WC_PC1, DOM_PC1, fine inorganic sediments (FIS) and stream depth) also produced a statistically significant model (*adj. R*² = 0.57, *p* = 0.001). In 2015, RDA1 (*R*² = 0.39, *p* = 0.003) was characterized by a strong positive loading for inorganic sediments, WC_PC1, and a strong negative loading for tile algal biomass and DOM_PC1 (which is negatively related to DOM aromaticity and humification) (Figure 3-5). ΦA for all five taxa scored negatively on RDA1, meaning that the assimilation of autochthonous resources was negatively related to fine inorganic sediments and WC_PC1 and positively related to algal biomass and DOM_PC1. ΦC and ΦF followed the opposite trend to ΦA for all five taxa. RDA2 (*R*² = 0.20, *p* = 0.01) had a strong positive loading for depth and DOM_PC1, and a negative loading for biofilm biomass and fine inorganic sediments. ΦC for all five taxa scored negatively on RDA2; in contrast, ΦF for *Parapsyche*, *Ephemerella* and *Leuctra* scored positively, as well as ΦA for *Baetis* and *Diura*, on RDA2.

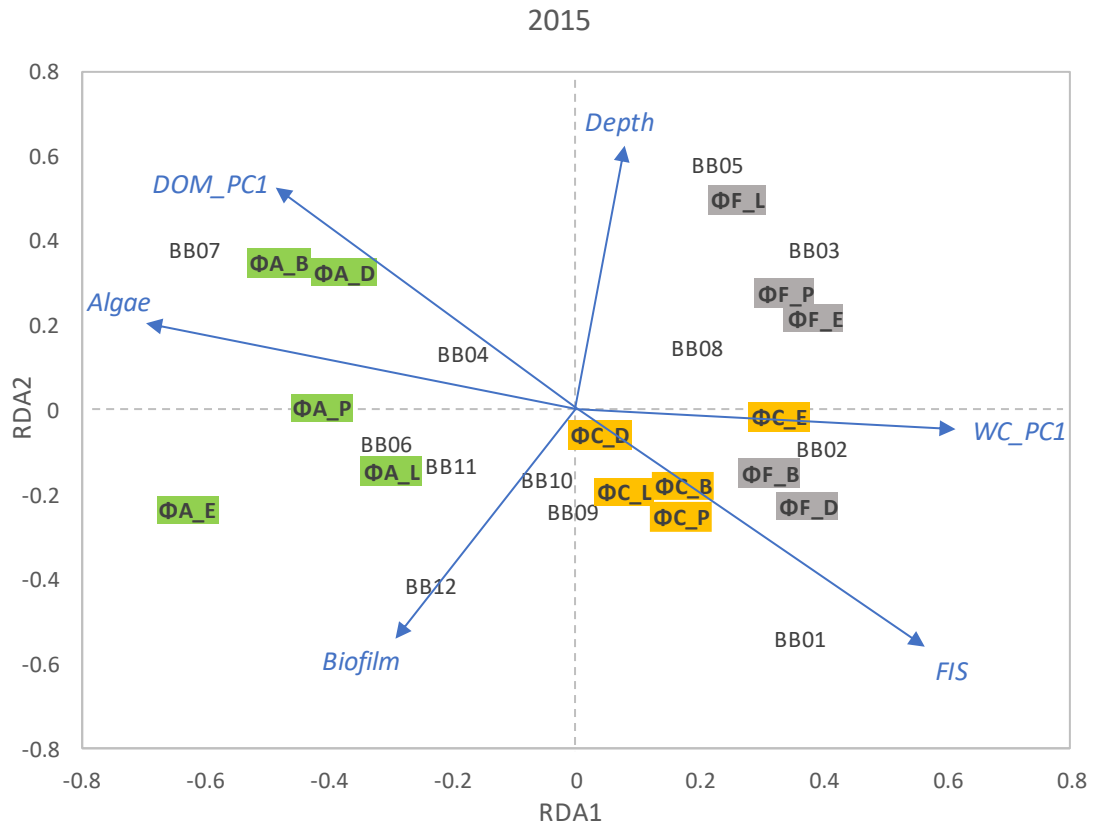


Figure 3-5: Results from redundancy analyses (RDA) on the relationships between relative contributions of algae (Φ A, green), CPOM (Φ C, yellow) and FPOM (Φ F, gray) to the diet of 5 benthic macroinvertebrate taxa (*Baetis*, B; *Ephemerella*, E; *Leuctra*, L; *Parapsyche*, P; *Diura*, D) in 12 Black Brook streams (New Brunswick, Canada) in 2015. Dietary contributions have been scaled with factor 2 for graphical purposes. Explanatory variables are shown by blue vectors (FIS: Fine Inorganic Sediments; WC_PC1: water chemistry PC1 (mainly related to cation and carbon concentrations); DOM_PC1: dissolved organic matter quality PC1).

3.4. Discussion

3.4.1. Algal contribution to BMI diets in headwater streams

My results showed that algae contribute considerably to the diets of BMIs in shaded headwater streams in northern New Brunswick (Canada). This adds evidence to the recent shift in our understanding that mainly allochthonous food sources fuel forested headwater streams due to their quantitative dominance (River Continuum Concept, Vanote et al. 1980), and emphasizes the considerable importance of aquatic primary producers to consumers in these

ecosystems (e.g., Mayer and Likens 1987; Finlay 2001; Hayden et al. 2016; Rosi-Marshall et al. 2016). This shift in perspective stems from the need to consider both resource quantity (main basis for the River Continuum Concept) and quality, the latter of which would explain why autochthonous production may contribute more to animal tissue than expected based on its small standing biomass relative to detritus in shaded headwater streams (Marcarelli et al. 2011; Rosi-Marshall et al. 2016).

The reliance of BMIs on algae, however, was taxon and FFG dependent, but the trends within each taxon remained relatively constant across the two sampling years. The greatest contribution of algae to a BMI's diet was observed in scrapers (*Glossosoma* and Heptageniidae) and gatherers (*Baetis* and *Ephemerella*), and they seemed to be selectively ingesting or assimilating the algal portion of biofilms since they had considerably more negative $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values than those of the biofilms on which they were feeding in both 2014 and 2015 (Mayer and Likens 1987; McNeely et al. 2007; Chessman et al. 2009). The shredder *Leuctra*, on the other hand, derived up to only 25% of their biomass from autochthonous sources, which agrees with observations that even BMIs classified as obligate and facultative shredders assimilated energy from algae in shaded streams (Li and Dudgeon 2008; Lau et al. 2009; Hayden et al. 2016). Among allochthonous contributions, FPOM contributed considerably more than CPOM to *Leuctra*'s diet, opposite to what would have been expected. Since FPOM and bulk biofilm had similar isotope ratios in most of the streams in my study, it is possible that *Leuctra* was feeding selectively on the biofilm on leaves rather than ingesting the leaves themselves. My results agree with observations from Dangles (2002), who re-classified *Leuctra* as generalist collectors/scrapers after finding that, on average, 50% of their gut content was comprised of FPOM, 21.3% of CPOM, 14.9% of diatoms and 12.3% of filamentous algae.

Finally, predators from the streams in BB and MC seemed to feed on primary consumers whose energy was derived from both aquatic and terrestrial resources, but more so from the latter. It has been suggested that predators could select their prey based on their quality, in which prey dependent on autochthonous resources are preferred over those which use autochthonous resources less due to a higher content of highly unsaturated fatty acids (HUFAs) (Lau et al. 2014). In my study, however, stonefly predators seemed to indiscriminately feed on more or less autochthonous primary consumers. This could be explained, partly, by the abundance of *Glossosoma* - algae feeders - in these streams; predators tend to avoid them due to their protective stone-cases (Parker 1994), and these grazers could thus be diverting algal biomass away from predators (McNeely et al. 2007).

3.4.2. *Effects of forest management on the contribution of food sources to BMI diets*

The contribution of autochthonous resources to BMIs decreased as forest management intensity (namely recent harvesting and road density) increased, whereas the contribution of FPOM increased, especially in *Baetis* collector-gatherers/scrapers, heptageniid scrapers and *Leuctra* shredders. The decreased autochthonous contribution to BMI diets contrasts with several studies that reported an increase (based on $\delta^{13}\text{C}$ values) after logging (Rounick et al. 1982b; England and Rosemond 2004; Göthe et al. 2009). This was attributed to increased primary production due to reductions in stream canopy cover (there were no riparian buffers in these studies) and to decreased inputs of terrestrial detritus. In Black Brook, however, all streams retained ~30 m wide riparian buffer zones, thus stream canopy cover was not affected. I also observed a positive relationship between the use of autochthonous resources and algal biomass, which was mainly related to canopy openness (Chapter 2), but the increased fine inorganic sediments, and changes in aromaticity and humification of DOM and water chemistry

PC1 (related to cation and carbon concentrations) from harvesting negatively affected the reliance of BMIs on algae herein. As described in Chapter 2, increased concentrations of DOC resulting from higher forest management intensity favoured the growth of biofilms, despite the less labile nature of this DOC and the increase in entrained sediments. However, this increase in biofilm biomass was probably driven by heterotrophic organisms (fungi and bacteria) and detritus, since algal biomass was not related to forest management (see Chapter 2). Hence, it seems that BMIs in streams with higher forest management intensity tended to ingest and assimilate more terrestrial material, either directly via sediments entrained in biofilms or indirectly via microbes recycling terrestrial DOC. Therefore, not only did forest harvesting promote higher rates of terrestrial water-borne material transport to streams (Chapter 2; Kreuzweiser et al. 2008), but this terrestrial material was also incorporated into stream food webs, resulting in reduced rates of autochthonous resource use. Finally, based on the positive correlations between % effective VSA (stream-side areas with strong hydrological connectivity) in the catchment and CPOM or FPOM contribution to BMI diets reported in this chapter, it appears that VSAs facilitated a higher delivery of terrestrial OM to receiving waters, resulting in increased allochthony. This agrees with findings in Chapter 4, which showed an increase in FPOM on the streambed (based on visual surveys) and a decrease in algal biomass and % scrapers at VSA sites compared to non-VSA sites.

The contribution of algae to the diets of BMI decreased after recent harvesting (<5 and <10 years), but tended to increase when the harvesting had occurred over longer periods of time (<20 and <30 years). Ishikawa et al. (2016) also observed lower contributions of periphyton to stream food webs after clearcutting based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values (which they attributed to sediment and debris flows that followed the clearcutting), but the contribution increased during forest regrowth, peaked in 23-years old forests, and then

decreased in more mature forests. Hence, it could be hypothesized that once vegetation in the harvested catchment starts to return and the delivery of water-borne materials (namely sediments) decreases, stream food webs appear to recover to pre-disturbance levels of algal contribution, reducing their reliance on terrestrial resources.

Considering the higher nutritional quality of algae, especially in terms of PUFA content (Guo et al. 2016a), reduced intake of this resource could result in slower growth and development of consumers, as well as less efficient energy transfer to upper trophic levels (Müller-Navarra et al. 2000; Goedkoop et al. 2007; Gladyshev et al. 2011), leading to a potential decrease in fish production (Vizcaíno-Ochoa et al. 2010). In fact, in this study I observed that greater autochthonous resource use was associated with: a) greater BMI taxonomic richness and abundance (both in leaf pack BMIs – Chapter 2, and in electroshocked BMIs – not shown in the thesis), b) larger bodies of predator *Diura* and collector-gatherer *Ephemerella*, and c) higher predator and collector-gatherer densities, and lower shredder densities (both in leaf pack BMIs – Chapter 2, and in electroshocked BMIs – not shown in the thesis). Establishing cause-effect based on those correlations is not possible, but it could be hypothesized that higher quality algal diets supported more BMI individuals and genera, as well as larger individuals and higher predator density. However, effects of forest harvesting on algal contributions to BMIs were mainly observed in primary consumers and not in predators. This indicates that the effects of forest harvesting on food resource availability were transmitted to the consumers directly feeding on them (namely *Baetis* collector-gatherers, Heptageniidae scrapers and *Leuctra* shredders), but that the effects were dissipated in the next trophic level. In fact, the reliance of predators on algae (through the consumption of algae-eating prey) was more related to algal biomass and canopy openness than forest management.

It is possible that decreased algal contributions to BMI diets not only influenced BMI community structure, but also contributed to lower rates of leaf decomposition, an important ecosystem function (described in Chapter 2). Brett et al. (2009) observed that the use of CPOM by lake zooplankton was greater when offered a mixed diet (algae and terrestrial CPOM) compared to a purely CPOM-based diet, suggesting that algae consumption enhanced the use of low-quality terrestrial resources (Taipale et al. 2014). Similarly, Guo et al. (2016b) found that when nutrients were added, leaf decomposition increased due to the presence of more high-quality algae, which increased the PUFA content of the biofilm on the leaf litter and enhanced consumption of this resource by shredders. Danger et al. (2013) also observed an increase in microbial leaf decomposition when algae were added to decomposer mixtures (bacteria and fungi), and attributed this increase to the labile C exudates produced by algae. Therefore, the positive correlation between the reliance on algae and leaf decomposition observed in my study may provide field-based evidence in support of the above-mentioned lab studies. In fact, leaf decomposition in my study was negatively correlated with C:N ratios in tile biofilms and in *Leuctra* (data not presented), suggesting that leaf decomposition was boosted when biofilm quality improved (assuming that the stoichiometry of tile biofilms was comparable to the stoichiometry of leaf biofilms).

Finally, within allochthonous sources I observed a tendency towards a higher contribution of FPOM over CPOM as % recent harvesting and sediment loading increased, as well as stream depth and % pool increased. This suggests that the increased delivery of FPOM due to soil and forest floor organic matter disturbances by forest harvesting may lead to an increased incorporation of FPOM by stream consumers. And, because this FPOM tends to get deposited in deeper areas (e.g., pools), deeper streams tended to have BMIs with a greater contribution of FPOM over CPOM.

Although forest management intensity seemed to alter the resource use by stream food webs, the observed values fell within the natural variability observed in the reference streams in this study. Reference streams showed a wide range of algal contributions to BMI diets, with MC4 tending to have among the highest and MC2 among the lowest values across all 15 streams. Probably, the variability observed in reference streams stemmed from natural disturbances such as beaver dams (MC2) or riparian gap openings caused by tree fall (MC3 and MC4) (personal observations).

3.4.3. Effects of forest composition on the algal contribution to BMI diets

In addition to forestry intensity, riparian and catchment forest condition was also related to the contribution of food sources to BMI diets. Generally, the contribution of algae increased with the dominance of deciduous and mixed forests and with increased canopy height, whereas the dominance of coniferous forests tended to favour allochthony among BMIs. A potential explanation for this trend is that the dissolved carbon derived from coniferous forests could be favouring the heterotrophic organisms in biofilms over the primary producers. Under low light and nutrient availability and high allochthonous C supply, detritivores (bacteria and fungi) tend to competitively exclude primary producers (Daufresne and Loreau 2001; Mindl et al. 2005; Danger et al. 2007). Considering that % coniferous forest was positively correlated with inorganic and organic C in water ($r = 0.83$ and 0.56 , respectively) and negatively with P ($r = -0.66$), it seems plausible that these conditions would favour heterotrophic organisms thereby excluding autotrophic organisms in conifer-dominated streams. Furthermore, the DOM in streams with conifer-dominated catchments tended to be more humic and aromatic (see Chapter 2), which would contribute to nutrient limitation because nutrients bind strongly to this DOM and are less available to primary producers (Hessen 1998; Wetzel 2001; Findlay and

Sinsabaugh 2003). In contrast, the binding of P by humic substances in lakes can also increase its bioavailability by keeping it in the water column for longer and releasing it via photoreduction (Koenings and Hooper 1976). However, this mechanism is unlikely to control the bioavailability of nutrients in streams (unlike lakes, these are shaded systems with flowing shallow water); therefore, the most plausible explanation in my streams is that an increased concentration of humic DOM reduced the bioavailability of nutrients to algae.

Alternatively or complementarily, conifer-dominated riparian forests could be influencing the absorption of solar radiation differently despite a similar shading or obstruction of the sky compared to deciduous/mixed riparian forests (Macdonald et al. 2003; Moore et al. 2005). Hence, the lower PAR reaching streams could mean that light was a stronger limiting factor for primary production in conifer-dominated streams, which would translate into lower assimilation of algae by BMIs (Lesutiene et al. 2014). However, even though the algal contribution to BMI diets increased with mixed/deciduous forest cover, I did not detect a relationship between algal biomass and forest composition in Chapter 2. Since scrapers, especially *Glossosoma*, have been shown to be very efficient at lowering algal biomass in headwater streams (McNeely et al. 2007) and, since scrapers in combination with collector-gatherers (which showed a high degree of reliance on algae) were well-represented at my sites (~37% of the BMIs in leaf packs – Chapter 2, and in electroshocking samples – data not presented), algal biomass could be more controlled by top-down (grazing) than bottom up (light) mechanisms, hence the inability to detect the relationship between it and forest composition.

3.4.4. Methodological limitations and contributions

3.4.4.1. Biofilms

The main challenge in this study, as well as in most studies that use natural ratios of stable isotopes to track the energy transfer from food sources to consumers in streams (Brett et al. 2017), was to reliably determine the isotopic ratio of the autotrophic fraction of the bulk food source sampled, i.e., biofilm. In most of my streams, biofilm overlapped in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with terrestrial sources (mainly with FPOM). The most likely explanation is that the biofilms contained considerable amounts of terrestrially derived organic matter, as well as heterotrophic microbes feeding on terrestrial C, whereas algae comprised a minor component in terms of biomass (Jardine et al. 2009; Brett et al. 2017). However, due to the faster active cycling of algae (Dodds et al. 2014) and its higher nutritional quality (Guo et al. 2016a), algae can disproportionately contribute to consumers' diets (McCutchan and Lewis 2002); hence, it is very important to obtain good isotopic characterization of the autotrophic end-member to accurately estimate the reliance of food webs on aquatic production.

To address this issue and improve source separation, I first incorporated a third marker ($\delta^2\text{H}$), since the addition of H isotopes to stream food web studies has been shown to increase the resolution of dietary sources (Doucett et al. 2007; Jardine et al. 2009; Finlay et al. 2010). However, because algal $\delta^2\text{H}$ was also diluted by the $\delta^2\text{H}$ of the terrestrial components in biofilms, the source overlap remained. Another potential solution is to use isotopic values of herbivores as proxies for isotopic values of algae (Vander Zanden and Rasmussen 1999; Finlay 2001). This approach was implemented in my study by using *Glossosoma* scrapers (which are known to selectively feed on the algal portion of biofilms; Oemke 1984; McNeely et al. 2006b; Katano and Doi 2014) to reflect algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. *Glossosoma*, which was common in all

streams, had consistently more negative $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values than the biofilms on which it fed (4.1-16.6 and 33-89‰, respectively) and terrestrial food sources (3.9-12.1 and 40-96‰, respectively) and the most negative values of all BMI taxa. The main limitation of using this approach was that I needed to assume 100% herbivory by *Glossosoma*, as well as a constant degree of herbivory across streams. False assumptions would lead to an overestimation of autochthonous contributions. However, algal $\delta^2\text{H}$ was also estimated independently of *Glossosoma* by assuming a 170‰ depletion in ^2H compared to water during algal photosynthesis (Yakir and DeNiro 1990; Solomon et al. 2011; Hondula et al. 2014). The cage experiment showed that *Glossosoma* $\delta^2\text{H}$ was very similar to algal $\delta^2\text{H}$, suggesting that *Glossosoma* herbivory was close to 100% and that this assumption is appropriate. In fact, values for algal contributions tended to be higher when including $\delta^2\text{H}$ in mixing models than when only using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, meaning that the potential autochthony overestimations resulting from using *Glossosoma* to estimate algal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were of little concern. Despite the uncertainty in the absolute autochthony values, the relative changes were useful for assessing how forest management may affect the algal contribution to BMI diets. Future studies might consider separating algae from the detritus in biofilms via density fractionation in colloidal silica (Hamilton et al. 2005), although McNeely et al. (2007) were unsuccessful when they applied this approach.

3.4.4.2. 2- vs. 3-isotope mixing models

Algal contribution estimates tended to be 9.2% higher on average when including $\delta^2\text{H}$ in mixing models (CNH; except for *Ephemerella*) than when only using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (CN), whereas FPOM contributions tended to be higher with the CN than the CNH results. This difference was visible in $\delta^{13}\text{C}$ - $\delta^2\text{H}$ biplots, where consumers tended to be closer to the

allochthonous food sources on the $\delta^{13}\text{C}$ axis than on the $\delta^2\text{H}$ axis. Syväranta et al. (2016) also documented lower allochthony estimates in a lake with CNH than with CN modeling, especially for fish and zooplankton (and less so for BMIs). They hypothesized that this difference could stem from the considerably lower $\delta^2\text{H}$ values of lipids (Sessions et al. 1999) which, unless removed, would lead to underestimations of allochthony (due to algae having lower $\delta^2\text{H}$ values). In my study, lipid content could partly explain the higher algal contribution estimates obtained with CNH; in fact, the greater differences and lowest congruence between CNH and CN estimates were observed in *Parapsyche* (algal contributions to this genus were 16.6% higher on average), the only taxon with a significant negative relationship between C:N ratios (indicating lipid content) and $\delta^2\text{H}$. For the other taxa, there was no significant trend between C:N ratios and $\delta^2\text{H}$. Therefore, lipid extraction is recommended to obtain more accurate dietary contribution estimates, especially in the case of *Parapsyche*.

Although autochthonous contributions were higher for CNH than for CN results, the relative changes in autochthonous resource use across streams were quite similar when using either CN or CNH in the models. Correlations between autochthonous resource use and explanatory variables tended to be similar with both CN and CNH, although in some cases correlations were stronger with CN (e.g., *Baetis* and *Parapsyche* diets) and in other cases with CNH (e.g., ΦF for *Leuctra*, relationships between C/N stoichiometry and autochthonous contributions – data not shown). Therefore, even though using $\delta^2\text{H}$ alone may highlight trends in the use of autochthonous resources across streams (Doucett et al. 2007; Wilkinson et al. 2013a), combining both $\delta^{13}\text{C}$ and $\delta^2\text{H}$ may improve the robustness of the results, especially considering the fundamental uncertainties that still remain regarding the interpretation of $\delta^2\text{H}$ values in the context of food webs (Vander Zanden et al. 2016).

3.4.4.3. Fractionation and dietary water

The dietary water estimates from the cage experiment (0.17-0.27) fell within the range reported in the literature (Solomon et al. 2009; Wang et al. 2009; Wilkinson et al. 2015), and the uncertainty around the mean value used in this study (0.20 ± 0.1) was accounted for with Bayesian mixing models. Regarding the value used to estimate algal $\delta^2\text{H}$ based on water $\delta^2\text{H}$, this experiment added more evidence in favour of using -170‰ (Yakir and DeNiro 1990; Solomon et al. 2011; Hondula et al. 2014): the difference between water $\delta^2\text{H}$ and *Glossosoma* scrapers $\delta^2\text{H}$ was $-172.3 \pm 5.5\text{‰}$ when averaging across cages; and because this genus is known to be an algal feeder, and because $\delta^2\text{H}$ fractionation is believed to be 0 (Solomon et al. 2009), I can assume that the difference between water and scrapers is a good proxy of the difference between water and algae. Therefore, this could be a good approach to overcome the limitation of not separating algae and detritus in biofilms.

Fractionation values differed substantially between two shredder taxa: *Leuctra* had values that fell closer to the mean fractionation values reported by Post (2002) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($0.23 \pm 0.66\text{‰}$ and $3.88 \pm 0.20\text{‰}$, respectively), whereas *Zapada* had values that are less frequently reported, but that still fell within the range of reported values ($-2.01 \pm 1.01\text{‰}$ and $1.93 \pm 0.15\text{‰}$, respectively). A potential limitation of the cage experiment is that I did not assess whether organisms reached equilibrium with their food sources. Ideally, I would have regularly sampled the organisms to monitor isotopic changes over time and to ensure that consumers had enough time to reach equilibrium with food sources, but I was unable to do this due to logistic constraints in the field. However, based on BMI tissue turnover rates reported by other studies (e.g., Jardine et al. (2008) reported half-life times of 1.5 days for C and 7.8 days for N), 15 days was likely enough time for their tissues to reach equilibrium with their diet.

The taxon-specific fractionation values measured in this study address the call for more feeding studies (Phillips et al. 2014). Recently, a growing number of studies have documented greater variability in fractionation values, which is not accounted for if using the fixed values that were previously assumed (e.g., Yokoyama et al. 2005; Carvalho et al. 2015), and this variability has been shown to be one of the biggest sources of uncertainty in mixing models (Caut et al. 2008; Bond and Diamond 2011). Therefore, the importance of situation-specific feeding studies that will produce more reliable fractionation estimates is considerable as supported by my study.

3.4.5. Conclusions

Aquatic primary production contributed substantially to the biomass of BMIs in these headwater streams, especially in the case of scrapers and collector-gatherers. However, the algal contribution to food webs decreased as forest management intensity and conifer dominance increased. This trend was probably due to an increase in the delivery of organic and inorganic terrestrial materials (dissolved and in suspension) promoted by higher forest harvesting and road density, which resulted in more allochthonous biofilms. Considering the higher nutritional quality of algae, a decrease in its assimilation may result in a slower growth and development of consumers, with potential implications for higher trophic levels. Nevertheless, the range in algal contribution values observed across the harvested sites in Black Brook was comparable to the range observed across the reference sites in Mount Carleton. Finally, even though my findings clearly showed that algae contributed to all the BMI taxa to some extent, the exact contribution may have been overestimated due to methodological limitations when characterizing the isotopic signature of algae in biofilms.

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4. Do forest streamside wet areas influence in-stream habitats and communities?

4.1. Introduction

Riparian zones along streams are important discharge areas where groundwater is transferred from subsurface flowpaths to surface flowpaths, making these areas important for biogeochemical activity (Creed et al. 2011). However, because groundwater does not flow uniformly across riparian zones due to heterogenous local topography, riparian areas differ in hydrological and biogeochemical importance (Buttle 2002; Grabs et al. 2012). These riparian discharge areas, sometimes referred to as groundwater discharge areas (Jansson et al. 2007; Kuglerová et al. 2014b), reach contributing areas (LeCraw and Mackereth 2010) and variable source areas (Creed and Beall 2009; Mengistu et al. 2014), are areas of strong hydrological connectivity, where topography leads water to flow into and accumulate before delivery to receiving waters. Variable source area (VSA) refers to the fact that these riverside areas vary in size and configuration over time based on precipitation. Studies have shown that areas of groundwater discharge in riparian zones often contain “hotspots” of vegetation, with both greater species diversity and vegetation cover (Jansson et al. 2007; Kuglerová et al. 2014b), and this has been attributed to higher N availability and lower drought stress (Jansson et al. 2007; Creed and Beall 2009). This heterogeneity has led to considering these hydrologically-connected riparian areas as biogeochemical “hotspots” that may warrant special considerations (beyond the retention of conventional riparian buffers) in forest management operations to protect the ecological functions that hydrologically-connected riparian forests provide to streams.

The retention of riparian forest along streams is one of the most widely used best management practices to mitigate the effects of forestry on streams (Schilling 2009). Forest

harvesting can result in impacted water quality (e.g., more sediments and nutrients) (Croke and Hairsine 2006; Kreutzweiser et al. 2008b; Richardson and Béraud 2014; Webster et al. 2015), increased water temperature and thermal diel fluctuations (Moore et al. 2005), and decreased input of organic matter and woody debris to streams (Bilby and Ward 1991; England and Rosemond 2004; Santiago et al. 2011; Burton et al. 2016). But riparian buffer zones (retention of strips of riparian forest along streams) can mitigate to a large extent these impacts (Broadmeadow and Nisbet 2004; Cristan et al. 2016), and this has led to the widespread adoption of fixed-width riparian buffer zones, with 30-m wide riparian buffers being the most common configuration (Lee et al. 2004). However, these fixed-width buffers do not take into consideration the above-mentioned riparian heterogeneity. The riparian discharge areas can be wider than conventional riparian buffer zones, and thus be affected by harvesting, in which case buffer zones could locally fail their protection goals (Kuglerová et al. 2014a). Or under the emulation of natural disturbance paradigm, in which some harvesting of riparian buffers is proposed to mimic natural disturbances such as forest fires and insect outbreaks (Kreutzweiser et al. 2012; Sibley et al. 2012), harvesting within riparian buffer zones could lead to the disturbance of these VSAs. This is especially true in cases in which these streamside groundwater input areas are not distinct or visibly wet (similar to the cryptic wetlands described by Creed et al. 2003), and therefore harvesting operations could occur within them (as harvesters would not be aware of these less obvious wet areas). Stream reaches that have very high hydrological connectivity to adjacent riparian areas may have a high risk for riparian disturbances by harvesting to cause perturbation of stream ecosystems, but the high degree of soil moisture may preclude or reduce tree growth making them less likely to be harvested. On the other hand, areas of low connectivity may be subject to frequent soil drying and therefore be less optimal for tree growth, as well as show a lower risk for stream perturbation after

riparian disturbance due to low connectivity (Laudon et al. 2016). But, areas with intermediate to high connectivity (the cryptic wet areas) tend to be optimal for tree growth, and may show high sensitivity to physical disturbance due to being connected to receiving waters (Laudon et al. 2016); therefore, we could hypothesize that these are the areas at greatest risk from logging. Thus, the need to explicitly incorporate identification and protection of VSAs into forest management practices to protect water quality is being increasingly recognized (Creed et al. 2008; Kuglerová et al. 2014a; Laudon et al. 2016).

The biological implications of VSAs for the receiving stream ecosystems, however, are poorly understood. Water chemistry has been shown to differ in areas where groundwater is discharged into streams, delivering more organic carbon (Grabs et al. 2012; Ledesma et al. 2015) as well as water with higher pH, Na, Si, Ca (Zimmer et al. 2013). But few studies have actually assessed whether differences in water chemistry at VSAs translate into biological changes in the receiving waters. It is known that groundwater affects biological community structure and function (Boulton and Hancock 2006); for example, there are taxa specific to habitats such as hyporheic zones and springs, and lateral groundwater seeps are important refugia for cold-water fish species (Dugdale et al. 2013). But little is known about biological responses to VSAs, where the degree of hydrological connection varies over time and where the groundwater may be in contact with the organic soil before entering the streams and then diluted with stream water. In the same way that VSAs are riparian biogeochemical and vegetation diversity hotspots, it could be hypothesized that the stream reaches receiving water and materials from VSAs are of great ecological significance due to the input of nutrients and high-quality DOC from the riparian forest. This coupling to the surrounding land would be especially relevant during drier periods, since these stream sites would remain connected to the surrounding land while most stream reaches become decoupled due to low water tables.

Therefore, VSA stream reaches could be providing metabolic hotspots and biological refugia during periods of water stress. Hunt et al. (2006) found that a high groundwater discharge site in a stream had higher BMI abundance, richness and periphyton respiration than a weak groundwater discharge site or a groundwater recharge site. However, in this study there was no replication, and the streamside groundwater discharge areas were streamside wetlands which would not be harvested. LeCraw and Mackereth (2010) also documented differences in the BMI community between sites differing in hydrological connectivity with the surrounding land, with gatherers dominating at sites with large VSAs and filterers at sites with small VSAs. They concluded that further studies addressing the effects of local topography on land-water linkages and aquatic communities were necessary.

Considering the management implications of this issue (i.e., modification of riparian buffer guidelines) and the scarcity of studies investigating the effects of VSAs on stream ecosystems, the need for more studies is clear. To date, most studies have focused on one or a few components of these VSA-stream systems, such as vegetation composition or soil/water chemistry of the VSA, and water chemistry or temperature in receiving waters; but very few have addressed the structure and function of receiving stream ecosystems. To better assess the influence of VSAs, I employed a holistic approach consisting of detailed assessments of vegetation and soil conditions (another research team is leading the work studying soil condition) of streamside riparian landscapes, as well as of the condition of different components (abiotic, functional and structural) of stream ecosystems. And, because these components may operate and respond at different temporal and spatial scales to hydrological and biogeochemical queues, looking at them simultaneously is important. I used high-resolution LiDAR improved digital elevation models (DEMs) to predict water flow and accumulation points (Laudon et al. 2016). Multiple algorithms have been developed over the

past years to calculate hydrological pathways based on DEMs, such as the topographic wetness index (TWI, Beven and Kirkby 1979), topographic position index (Weiss 2001) and cartographic depth-to-water (Murphy et al. 2011). In this study, I used the TWI to detect effective VSAs (i.e., streamside areas with high TWI, VSA herein) and “dry” sites or sites that are hydrologically less connected to the surrounding land (i.e., streamside areas with low TWI).

The objective of this study was to compare riparian and stream conditions between sites differing in hydrological connectivity with the surrounding land (i.e., between VSA and dry sites). Riparian and stream conditions were assessed by following a multi-indicator approach; specifically, for this chapter I compared the terrestrial vegetation between riparian VSAs and dry sites, as well as the stream morphology, water chemistry, DOM quality, algal and biofilm biomass, leaf decomposition and BMI community at the stream reaches immediately downstream of the VSAs and dry sites. I hypothesized that VSAs would have higher riparian understory vegetation density and richness than dry sites, and that VSAs would deliver colder water with higher cation, nutrient and DOC concentrations. I expected that this would result in higher biofilm and algal biomass at VSA sites, which would, in turn, result in higher BMI richness and abundance.

4.2. Methods

4.2.1. Site selection and characterization

The study was conducted in 2015 in the Black Brook District described in section 2.2.1 of chapter 2; sites in the Mount Carleton Provincial Park had to be excluded due to lack of high-resolution LiDAR data (required for site selection as explained below). Out of the 12 streams used for Chapters 2 and 3, seven streams were selected for this study (BB01-BB04, BB06, BB07

and BB09); the streams ranged in forest composition (from deciduous- to coniferous-dominated) and forest management intensity (18-100% of the catchment harvested in the last 10 years; 21-89 m of road per ha, Table 4-1). Two sampling sites were selected within each stream: a VSA (hereafter referred to as V site) and a dry (D site, i.e., site of lower hydrological connectivity with the surrounding land). V and D site selection was conducted in two stages: 1) preselection based on maps depicting the wetness of each catchment cell, and 2) ground-truthing of the preselected sites (site selection criteria are provided in detail below).

Table 4-1: Coordinates, catchment size, harvesting intensity, number of stream crossings, road density, % coniferous (CON) and % deciduous (DEC) for each stream selected for this study (catchment characterization methods are provided in detail below). Watershed delineation for these catchments was conducted for sampling reaches used in Chapter 2.

Stream	Latitude	Longitude	Area (ha)	% harvested (last 10 years)	Stream crossings (per stream km)	Road density (road m per ha)	CON	DEC
BB01	47°27'24.7"N	67°48'56.3"W	100	40.9	1.63	89	92	0
BB02	47°27'53"N	67°49'11.9"W	147	87.6	0.40	45	81	19
BB03	47°29'36.3"N	67°47'41.4"W	205	50.8	0.64	28	8	88
BB04	47°28'23.9"N	67°49'07.5"W	97	100.9	1.74	68	63	34
BB06	47°34'52"N	67°49'10.1"W	144	34.2	0.36	39	66	26
BB07	47°34'34.9"N	67°51'55.6"W	115	47.3	0.00	32	14	63
BB09	47°30'37.5"N	67°56'31.3"W	66	18.1	0.00	21	17	68

Two types of maps were generated for each of the original 12 streams to assess where in the catchment water was most likely to flow and accumulate: VSA maps using Whitebox GAT (Lindsay, 2016; version 3.3) and reach contributing area (RCA) maps using ArcGIS (ESRI; version 10.4.1), both based on a 5-m LiDAR derived digital elevation model (DEM). VSA maps (Figure 4-1) were created following Mengistu et al. (2014); briefly, depressions were filled on a hydrologically conditioned DEM, and contributing areas were calculated by applying the D8 algorithm (a contributing area of 0.25 ha was used as a channelization threshold). Then, the topographic wetness index (TWI), i.e., an indicator of topographically driven soil wetness, was

calculated following the equation $TWI = \ln(\alpha/\tan \beta)$, where α is the upslope contributing area of a given grid cell based on a flow accumulation map calculated using the D-infinity algorithm, and β is the slope of that grid cell. To allow comparisons among catchments, TWI maps were normalized by subtracting average catchment TWI values from TWI for each grid cell. VSAs were estimated by starting at the stream and recursively moving to lower TWI values until there is a breakpoint where values start increasing again. Finally, VSA maps were colour-coded based on normalized TWI values, with lowest values shown in red (indicating the driest areas) and highest values in blue/green (indicating the effective VSA, i.e., wettest areas) (Figure 4-1). RCA maps were generated by calculating the number of grid cells flowing into each grid cell of the drainage network, based on a flow accumulation map calculated using the D8 algorithm. RCAs were delineated once a threshold value of 600 cells (1.5 ha) was exceeded.

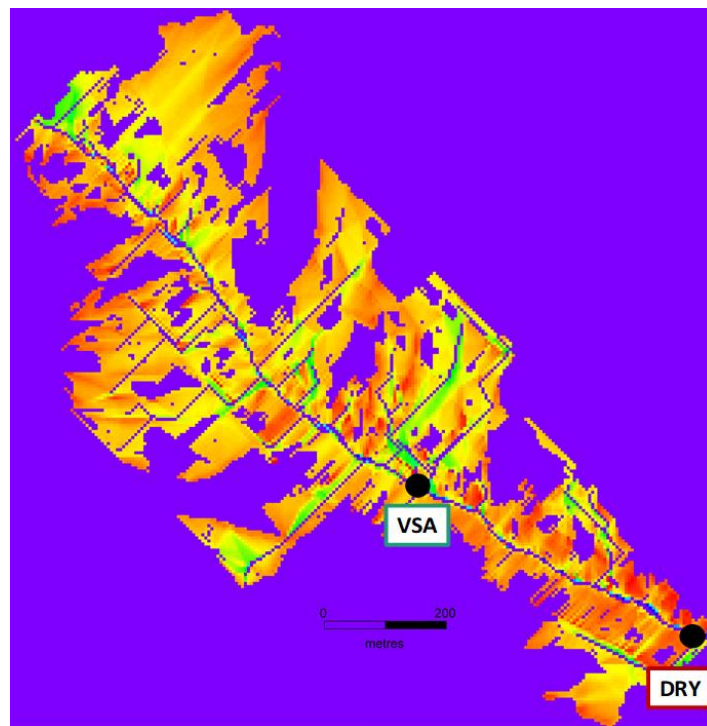


Figure 4-1: Variable source area (VSA) map generated with Whitebox for one of the study catchments (BB09) showing the two selected sites (VSA and dry). Colours indicate topographic wetness index, with red<orange<yellow<green<blue. Purple lines indicate channels based on a 0.25 ha channelization threshold.

The output maps for all 12 catchments were analyzed, and the catchments with the greatest potential for this study were preselected. To be preselected, the catchments needed to: 1) have stream reaches surrounded by distinct areas with high TWI (represented by blue/green in the VSA maps, and referred to as VSA or V sites herein; these are the areas with the highest wetness or effective VSAs) and low TWI (represented by red/orange in the VSA maps, and referred to as dry or D sites herein) (Figure 4-1), 2) have at least 200 m separation between a VSA and a dry site to minimize the influence of the VSA reach, and 3) VSA and RCA maps had to agree that the selected sites were more (V) or less (D) hydrologically connected with the surrounding land. Then, the preselected reaches were visited in June 2015 to ground-truth the GIS predictions to assess their accessibility, to ensure that those reaches sustained a perennial flow, and to confirm V sites by their topography and/or degree of soil wetness. Often, the most distinct VSA reaches were in the headwaters, but these areas were not selected due to the risk of drying up in summer. As a result, 14 sites (7 each of V and D) in seven streams were selected (Figure 4-2). The VSA site was upstream of the dry site in five streams (BB01, BB02, BB04, BB06, BB09) and downstream in two streams (BB03 and BB07). Three of the sites (BB01-D, BB02-D and BB09-D) coincided with the stream reaches sampled for chapters 2 and 3, meaning that the same samples were used for all three chapters in those three cases (e.g., BB01 from chapters 2 and 3 is BB01-D in chapter 4). In one of the catchments (BB07), the VSA map did not clearly predict a VSA site on a specific stream reach, but on-site observations led us to suspect it was a reach with strong hydrological connectivity (the topography along the reach and wetter soils), and the RCA map supported this observation. Therefore, this catchment was included in the analysis. Note that the hydrological connectivity between the riparian forest and the stream was estimated based on topography (i.e., based on where the water is most likely to flow according to elevation maps) and by assuming that water

in these catchment flows from highest to lowest elevations; direct measurements of groundwater inputs were not conducted.

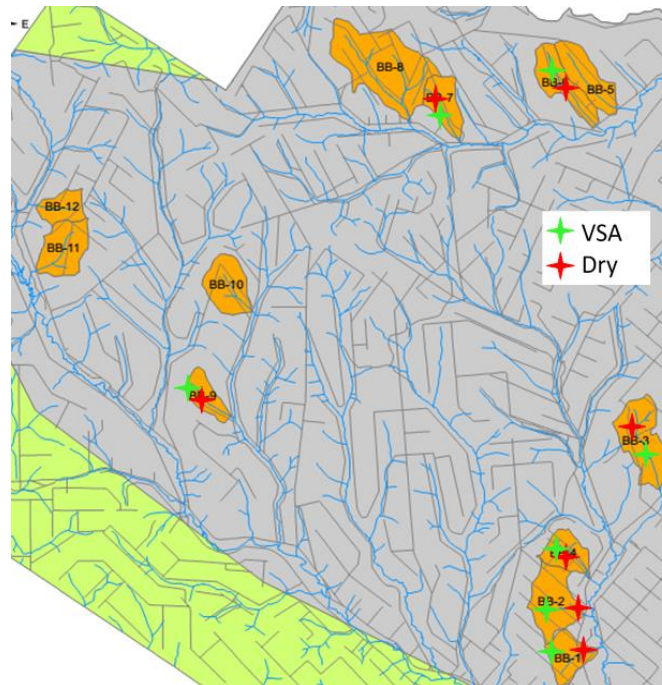


Figure 4-2: Map showing the seven VSA sites (variable source area, green star) and seven dry sites (red star) selected for this chapter from the 12 catchments selected for the study (in orange) in Black Brook Forestry District (in green). Roads (gray lines) and streams (blue lines) are also presented.

Sampling occurred within 40-m stream reaches at each site; at V sites, we attempted to select the reach downstream of the apparent entry point of the water from the VSA based on site topography. Two of the selected V reaches (BB04-V and BB06-V) dried over the summer, as 2015 was a relatively dry summer (136 mm between August and September); therefore, these sites had to be adjusted (i.e., moved ~100 m downstream within the same stream) during the sampling season to downstream locations with continuous flow.

The riparian forest and stream morphology of the sampling reaches were characterized following the same procedure described in Chapter 2 sections 2.2.3.4 and 2.2.3.5, but for this chapter the surveys were conducted along 60-m reaches (including the 40-m sampling reach

plus the next 20 metres upstream of the sampling reach). Briefly, riparian forest composition and structure were characterized by surveying the woody understory vegetation (<5 cm DBH) along 60-m transects parallel to the stream (one m from the stream edge on both sides of the stream); the species and height class of woody vegetation within 50-cm radius plots at 2-m intervals along the transect were recorded. The overstory composition and structure were recorded by identifying and measuring the DBH of every tree (> 5 cm DBH) within a belt transect 3 m wide starting from the stream edge and 60 m long. The relative abundance of each woody plant species was calculated and a non-metric multidimensional scaling (nMDS) analysis conducted (two dimensions were chosen prior to statistical analysis). Canopy cover was measured by taking pictures of the canopy from the stream every 10 m within the 60-m sampling reach with a Canon EOS 50D camera with a 185° SuperFisheye (5.6mm F/5.6) lens and a self-leveling mount on a tripod (Régent Instruments Inc. Ville de Quebec, QC). The pictures were processed using WinSCANOPY 2009a for Canopy Analysis (Régent Instruments Inc.). Stream morphology was characterized by visually surveying 10 m long sections and then averaging for the entire 60-m reach for flow structure (% riffle/ run/ pool), substrate composition (% bedrock/ boulder/ cobble/ gravel/ sand/ silt/ clay), width and averaged depth at each 10-m interval cross-section, and number of large woody debris (LWD > 10 cm diameter) structures.

4.2.2. Vegetation structure and composition

Vegetation structure and composition at VSA and dry sites were characterized with surveys. Note that this forest survey is different from the one described in the previous section; the methods described in section 4.2.1. were intended to characterize the riparian forest immediately influencing the sampling stream reaches (3 m wide bands along the stream). The

survey described in the current section was aimed at characterizing the vegetation at VSA and dry sites; therefore, circular plots, 23-m in diameter, were selected in the middle of each site. Because the sampling stream reaches were selected downstream of riparian VSA and dry sites, these two riparian forest characterizations did not overlap spatially. Within the circular plots, four 23-m long transects were run following north-south, east-west, northeast-southwest and northwest-southeast directions. Woody vegetation <7 cm DBH within a 30-cm diameter circle was recorded every 50 cm in each transect (i.e., 46 points per transect). The species as well as the height class (200-250 cm/ 150-200 cm/ 100-150 cm/ 50-100/ 0-50 cm) at which the species was present was recorded within each circle. Relative abundance expressed as percent occurrence for each species was computed by dividing the number of points at which a given species was present by the total number of points available (4 transects, 185 points in total). Understory density in specific height bins was calculated by counting the times a woody plant was recorded within a given height class (referred to as “hits”), and the vertical distribution was calculated by dividing the number of hits within a given height class by the total number of hits within the plot. Then the percent ground cover and category (moss/ fern/ non-woody seed plants) of the herbaceous vegetation was visually estimated within each circle. Finally, all trees >7 cm DBH within the 23-m diameter plot were identified and DBH measured, and from this data richness (number of tree species within the plot), density (number of trees within the plot) and basal area (sum of the basal area of all trees at BH) were calculated.

4.2.3. Measurement of indicators of stream condition

4.2.3.1. Water chemistry and DOM quality

Water grab samples were collected at the downstream end of each sampling reach in August, September and October of 2015, and water temperature, dissolved oxygen and

conductivity were recorded simultaneously with a handheld meter (YSI Model 85). Water samples were kept refrigerated until analysis. Water quality parameters were analyzed at the Great Lakes Forestry Centre (Sault Ste. Marie, ON, Canada) following standard methods (Hazlett et al. 2008), and included pH, conductivity, alkalinity, water cations and anions (Ca, K, Mg, Na, SO₄, Cl, SiO₂), nutrients (NO₂+NO₃, NH₄, total N, dissolved organic C – DOC, dissolved inorganic C – DIC, reactive P, total P) and metals (Al, Fe, Mn, Zn, Cd, Cu, Ni, Pb). Dissolved organic matter (DOM) was characterized at Laurentian University (Sudbury, ON, Canada) using Cary Eclipse and Cary 60 UV-Vis spectrophotometers; three-dimensional fluorescence scans were run at 5 nm excitation steps from 250 to 450 nm, and emissions were read at 2 nm steps from 300 to 600 nm. The generated excitation-emission matrices were then corrected and adjusted, and variables describing optical properties of DOM (e.g., humification index, fluorescence index, specific UV absorbance at 254 nm or SUVA) were calculated. PCA was conducted with the mean value (averaged across three months) of water chemistry (WC) variables and DOM characterization variables, and the first and second principal components (hereafter WC_PC1 and WC_PC2, and DOM_PC1 and DOM_PC2) were used to represent the collective water chemistry variables and DOM characteristics in subsequent statistical analyses (see section 4.3.2. for PCA results).

4.2.3.2. Leaf decomposition

Six coarse-mesh leaf packs were deployed within each reach and incubated for 33-35 days from mid-September to mid-October. Coarse-mesh packs (5 mm x 10 mm mesh size) contained 4.0 ± 0.1 g of speckled alder leaves (*Alnus incana* ((L.) Moench)) that were collected just before abscission in the 2014 fall in Saint John (New Brunswick, Canada), air-dried, pre-leached and oven-dried. Leaf packs were tied to bricks and the bricks placed on the stream

bottom, but in some streams leaf packs had to be tied to a rebar driven into the substrate as water levels were too low to use bricks. Upon retrieval, leaf pack contents were emptied into 400-ml plastic containers filled with stream water and then preserved in 37% formaldehyde (ca. 10% of the volume).

Once in the lab, invertebrates were removed and stored in ethanol for other studies not shown here, and the residual leaf material was washed with distilled water, dried in the oven at 60 °C for 48 h, cooled in a desiccator and weighed. Dried leaves were ashed in a muffle furnace at 500 °C for 2 h, cooled in a desiccator, and ash mass was weighed to calculate ash-free dry mass (AFDM) by subtracting ash mass from dry mass. Percent AFDM lost was calculated by subtracting the t_1 AFDM (i.e., AFDM calculated at the end of the incubation period) to the t_0 AFDM (which was calculated to be 95.2% of the starting dry mass during a preliminary study). Finally, % lost AFDM per day was calculated by dividing % lost AFDM by the number of incubation days. Ash mass (the inorganic fraction) was used as an indicator of the degree of very fine sediment entrainment in biofilms on leaf material.

4.2.3.3. Biofilm and algal biomass on tiles

To estimate the biomass of periphyton or algal communities and total biofilm (algae, bacteria, fungi) on rock surfaces in streams, rows of 10 unglazed clay tiles (4.7 x 4.7 cm) were incubated in three different riffles (one row per riffle) within the 40-m reach for 24-25 days in mid-July. The 10 tiles were glued to a duct tape band, and the band was secured to the streambed using rebar. Upon retrieval, tiles were scraped with scalpels and the slurry washed with stream water into Whirl-pak® bags. The slurry from five tiles was pooled to measure total biofilm biomass, and the slurry from the other five tiles was pooled to quantify chlorophyll a

content (periphyton or algal biomass). Samples were kept in the dark and on ice in the field, and frozen at the end of each day.

Once in the lab, samples were thawed and filtered through pre-combusted GF/C Whatman filters. Filters for chlorophyll a analysis were frozen, and filters for total biofilm biomass were oven-dried for 48 h at 60 °C, left to cool in a desiccator and weighed. Dried filters were ashed in a muffle furnace at 500 °C for 2 h, left to cool in a desiccator, and ash mass was weighed to calculate ash-free dry mass (AFDM) by subtracting ash mass from dry mass. Ash mass (the inorganic fraction) was used as an indicator of the degree of very fine sediment entrainment in biofilms of rock surfaces. Chlorophyll a was extracted by submerging the filters in 90 % ethanol in an 80 °C water bath for 7 minutes. After cooling, chlorophyll a concentration of the extract was measured using a Turner Designs Trilogy fluorometer. Autotrophic index was calculated by dividing chlorophyll a concentration (algal biomass) by total biofilm biomass.

4.2.3.4. Benthic macroinvertebrate community

BMIs were collected by electroshocking (250-350 V DC, 30 Hz and 4 ms pulse width) within a 25 cm wide and 100 cm long rectangular sample area for one minute (three intervals of 20 s separated by 10 s breaks). Drifting invertebrates were collected with a 363 µm mesh size drift net placed on the downstream edge of the rectangle. The net was rinsed with stream water and the content emptied into a white sorting tray. After shocking, five rocks within the rectangle were inspected and the BMI picked. The number of rocks was normalized at each site based on the size of the rocks (e.g., five average size cobbles, three big cobbles and 10 gravel stones). This procedure was followed at 3 riffles per stream at the start, middle and end of each 40-m reach, and treated as three subsamples. All the invertebrates were live-sorted into the lowest possible taxonomic level in the field and frozen until further analysis. BB01 was

eliminated from the comparison of V and D BMI communities, because BB01-V did not have enough flowing water to conduct electroshocking. These samples are considered semi-quantitative, because the same area was sampled for the same duration in every stream.

Once in the lab, BMIs were identified to genus (with exceptions being *Chironomidae* and *Simuliidae*, which were identified to family), body length measured (in millimeters) and classified according to their functional feeding group (FFG) using Merritt et al. (2008). These data were used to calculate abundance, richness, Margalef's richness, Shannon-Wiener Diversity Index (H), abundance of each FFG, and size of taxa (body length measured in millimetres) represented across all sites.

4.2.4. *Statistical analysis*

Woody understory vegetation and BMI community dissimilarity across sites were visualized in 2 dimensions in separate non-metric multidimensional scaling (NMDS) graphs. To test whether differences in community structure between V and D sites were statistically significant, permutational multivariate analysis of variance (PERMANOVA) was conducted. PERMANOVA returns p values after conducting permutations (999 for this study) with pseudo-F ratios (Anderson and ter Braak 2003). The underlying Bray-Curtis similarity matrices for NMDS graphs and PERMANOVA were calculated from abundance-based matrices in the case of both vegetation and BMIs. The contribution of each taxon to the dissimilarity between V and D sites was assessed by calculating the similarity percentage (SIMPER).

Linear mixed models of ANOVA were used to analyse the influence of the degree of wetness (i.e., V or D) on univariate vegetation and stream variables. The degree of wetness was treated as a fixed effect predictor variable and stream as a random effect predictor variable; in the case of variables with site replication, site was nested within stream. In the case of water

chemistry and DOM quality variables, differences between V and D were analysed for each month separately as well as for all three sampling months grouped together (in the latter models sampling month was treated as a fixed factor and the interaction between degree of wetness and sampling month was tested). Linear mixed models were run using the *lme4* package (Bates et al. 2017) and the significance of the differences between V and D were tested using the *lmerTest* package, with the degrees of freedom calculated based on Satterthwaite's approximation (Kuznetsova et al. 2016). Alpha was set to 0.1 to increase the power of the analysis due to low replication ($n = 7$). All statistical analyses were performed in R 3.0.1 (R Core Team 2013).

4.3. Results

4.3.1. Vegetation structure and composition

There was a wide range of vegetation density and vertical distribution (measures of structure) across sites, as well as differences between the VSA and the dry sites which differed significantly in both understory and overstory layers. The site with the greatest woody understory vegetation density (<7 cm DBH) had almost 10 times the number of hits than the site with the lowest density (86 hits at BB04-D vs. 776 hits at BB01-V). The first layer (0-0.5 m) tended to be the densest, with the proportion of total hits within this layer ranging between 25% (BB04-D) and 81% (BB07-V), whereas the fifth layer (2-2.5 m) had the lowest density, with between 1% (BB09-V) and 16% (BB02-D) of total hits (see Appendix III Figure A11). Overstory tree density (>7 cm DBH) ranged between 30 (BB09-V) and 126 trees per plot (BB06-D), and the sum of the basal area of these trees ranged between 0.19 (BB01-V) and 3.40 m² (BB02-V). The understory woody vegetation was denser at V sites (ANOVA, $F_{1,6} = 11.9$, $p = 0.01$), with this

difference being driven mainly by the 0-0.5 m layer (ANOVA, $F_{1,6} = 17.4$, $p = 0.006$) (Table 4-2).

Density in the other four layers did not differ significantly between V and D sites; however,

when excluding BB07 (stream selected based on site observations rather than on VSA map

predictions), density was significantly greater between 0.5-1 and 1-1.5 m at V compared to D

sites. The vertical distribution of vegetation was also significantly different between V and D,

with V sites having a greater proportion of hits in the 0-0.5 m layer (ANOVA, $F_{1,6} = 6.8$, $p = 0.04$)

and a lower proportion in the 1.5-2 m and >2 m layers (ANOVA, $F_{1,6} = 9.6$ and 9.8 , $p = 0.02$) (see

Appendix III Figure A11). V sites also tended to have a greater herbaceous cover compared to D

sites (46.7% vs. 35.2%), especially of moss (28.5% vs. 16.4%) and horsetails (*Equisetum*, 1.2% vs.

0%), but the differences were not statistically significant (ANOVA, $F_{1,6} = 2.7$, $p = 0.15$). D sites

had more trees than V sites (ANOVA, $F_{1,6} = 10.7$, $p = 0.02$), but there were no statistical

differences in basal area between V and D sites (ANOVA, $F_{1,6} < 0.001$, $p = 0.98$), since trees

tended to be larger at V than D sites.

Table 4-2: Results of mixed model ANOVA testing for differences between VSA (variable source area, V) and dry (D) stream-side sites on woody understory and overstory vegetation composition and structure at 7 Black Brook streams (New Brunswick, Canada). Column V-D describes the effect size or differences between V and D (positive values mean V>D and negative values V<D). In bold are significant values at $\alpha = 0.1$.

		Composition			Structure					
	Layer	Richness			Density (# hits)			Vertical distribution (% hits)		
		V-D	F	p	V-D	F	p	V-D	F	p
Understory (<7 cm DBH)	> 2m	-0.57	0.46	0.52	-2.57	0.06	0.81	-5.3	9.8	0.02
	1.5-2m	0.14	0.058	0.82	-3.3	0.04	0.85	-9.1	9.6	0.02
	1-1.5m	1.14	1.41	0.28	19.7	1.6	0.25	-1.7	0.7	0.42
	0.5-1m	1.43	1.35	0.29	34.14	2.01	0.21	-0.31	0.01	0.92
	0-0.5m	-0.14	0.017	0.90	111.9	17.4	0.006	16.4	6.8	0.04
	Total	0.57	0.36	0.57	119.4	11.9	0.01	-	-	-
Overstory (>7 cm DBH)	Richness			Density (# trees)			Basal area (m ²)			
	V-D	F	p	V-D	F	p	V-D	F	p	
	-0.86	0.94	0.37	-39.9	10.7	0.02	0.008	<0.001	0.98	

Note: Vegetation parameter ~ VSA/dry + (1|Stream) model tested.

Regarding forest composition at these sites, richness of woody understory vegetation ranged between 8 (BB04-D) and 20 (BB03-D) species and tree richness between 3 (BB01-D) and 10 (BB03-D) species, but these variables did not differ between V and D sites for any layer (Table 4-2). For four streams, richness of woody understory vegetation was greater at V than D sites, whereas in the other three streams, richness was greater at D than V sites (see Appendix III Figure A12). However, as shown in the NMDS ordination, understory vegetation differed significantly between wetness types (PERMANOVA, $F_{1,13} = 1.93$, $p = 0.045$) (Figure 4-3). Species such as cedar, willow, alder, current and red-osier dogwood were significantly more common at V than D sites.

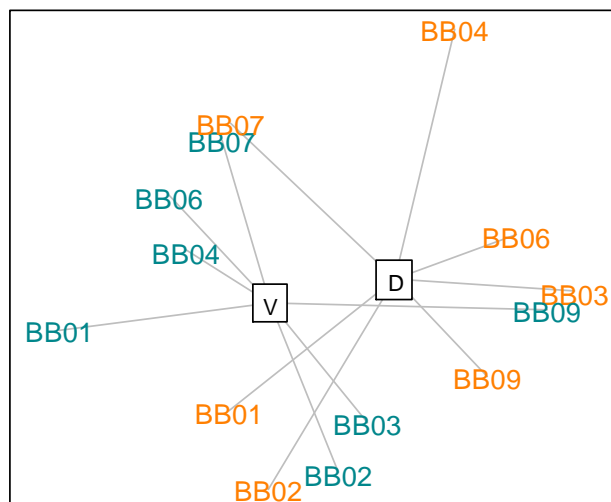


Figure 4-3: NMDS of understory woody vegetation (DBH<7 cm) based on abundance community data at variable source area (blue, V) and dry (orange, D) sites in 7 Black Brook catchments (New Brunswick, Canada) (stress value = 0.16). Boxes represent group (V or D) centroids.

4.3.2. *Streamside vegetation and physicochemical stream habitat characteristics*

Riparian forest composition and structure (alongside sampling stream reaches) and stream morphology differed across streams, but only some characteristics differed between V and D sites. Riparian forest density ranged between 75 (BB04-D) and 369 hits/transect (BB01-

V), with most of the hits concentrating on the first layer (between 25 and 79% of the hits), and richness ranged between 12 (BB07 V and D) and 18 (BB09-D) species. However, riparian forest structure (see Appendix III Table A23) and composition (Figure A10) did not differ significantly between V and D sites (PERMANOVA, $F_{1,13} = 0.75$, $p = 0.68$), only among streams (PERMANOVA, $F_{6,13} = 2.1$, $p = 0.005$). Regarding stream morphology, riffles occupied between 6 (BB01-V) and 95% of the stream reach (BB06-D), with V reaches having 28% less riffles and 24% more runs than D reaches on average (ANOVA, $F_{1,6} = 26.6$ and 14.2 , $p = 0.002$ and 0.009 , respectively). The streambed substrate composition ranged between 1 (BB09-V) and 74.6% (BB01-V) silt, with V sites having 18% more silt and 13% less cobble than D sites (ANOVA, $F_{1,6} = 5.2$ and 3.6 , $p = 0.06$ and 0.08 , respectively) (Table 4-3). Width (1.04-2.77 m), depth (4.60-14.55 cm), % pool (0-34%), gravel/sand cover and canopy openness (10.5-37.0%) did not differ significantly between V and D sites. However, when looking at the position of the sites within the stream rather than their hydrological connectivity, stream width and canopy openness differed significantly between upstream and downstream sites, with upstream sites being narrower but having a more open canopy (ANOVA, $F_{1,6} = 4.0$ and 16.7 , $p = 0.09$ and 0.006 , respectively); all the other stream morphology variables did not differ significantly between upstream and downstream sites (Table 4-3).

Even though V sites tended to have a greater proportion of silt than D sites, this did not translate into a greater proportion of fine inorganic sediments entrained in leaf packs (values ranged between 0.11 and 0.59 g across all sites; ANOVA, $F_{1,6} = 2.2$, $p = 0.19$) and tile biofilms (values ranged between 0.006 and 0.40 g m⁻²; ANOVA, $F_{1,6} = 1.0$, $p = 0.33$) (see Appendix III Figure A14). But, when considering the position of the V and D sites within the stream, downstream sites showed greater fine inorganic sediment entrainment in leaf packs than upstream sites (ANOVA, $F_{1,76} = 17.08$, $p < 0.001$), suggesting that downstream sites (notably

BB01, BB02, BB03 and BB04) collected more inorganic sediments derived from the catchment (Appendix III Figure A14).

Table 4-3: Results of mixed model ANOVA testing for differences between VSA (variable source area, V) and dry (D) sites, and upstream (US) and downstream (DS) sites on stream morphology at 7 Black Brook streams (New Brunswick, Canada). Column V-D and US-DS describe the effect size or differences between V and D (positive values mean V>D and negative values V<D) and US and DS, respectively. In bold are significant values at $\alpha = 0.1$.

Stream morphology	*V-D	F (V-D)	P (V-D)	**US-DS	F (US-DS)	P (US-DS)
Width (m)	0.06	0.16	0.70	-0.25	4.0	0.09
Depth (cm)	0.14	0.12	0.73	-0.08	0.04	0.84
Riffle (%)	-28.5	26.62	0.002	-10.5	0.75	0.42
Run (%)	24.3	14.25	0.009	7.4	0.42	0.54
Pool (%)	4.9	1.14	0.33	3.7	0.6	0.46
Boulder (%)	-0.22	0.02	0.89	0.06	0.002	0.97
Cobble (%)	-13.1	3.6	0.08	-8.1	1.16	0.30
Gravel (%)	-2.9	0.13	0.73	0.12	~0	0.99
Sand (%)	-1.05	0.13	0.73	-3.5	1.9	0.21
Silt (%)	18.0	5.2	0.06	12.3	1.6	0.25
Large woody debris (#)	-0.12	0.04	0.84	-0.69	1.67	0.24
Canopy openness (%)	4.1	1.16	0.30	9.0	16.7	0.006

Note: *Steam morphology parameter ~ VSA/dry + (1|Stream) model tested.

** Steam morphology parameter ~ Upstream/downstream + (1|Stream) model tested.

Most water chemistry parameters differed more across streams than between V and D sites, as inferred from the close ordination of V and D sites from the same stream on the PCA plot (Figure 4-4); however, some variables differed significantly between V and D sites. The first water chemistry PC captured 51.8% of the variability and was strongly and negatively related to conductivity, Ca, DIC, alkalinity and pH, and positively to SiO₂ and TP (Figure 4-4). The second PC captured 24.6% of the variability and was positively correlated with Fe, Al, Cl and DOC. V sites had significantly lower DOC (AVOVA, $F_{1,30} = 7.10$, $p = 0.01$) and Al concentrations than D sites (AVOVA, $F_{1,30} = 3.55$, $p = 0.07$) when considering all three months together, as well as lower Fe concentrations in October (AVOVA, $F_{1,6} = 4.3$, $p = 0.08$) (the interaction between VSA/dry and sampling month was significant in the case of Fe, AVOVA, $F_{1,30} = 4.30$, $p = 0.03$) (see Appendix III Table A24). Ca and Mg tended to be higher at V than D sites in September

(AVOVA, $F_{1,6} = 3.58$ and 4.03 , $p = 0.10$ and 0.09 , respectively). V sites had 4.4% less oxygen saturation than D sites (AVOVA, $F_{1,20} = 8.79$, $p = 0.008$), and these differences were more pronounced in September than in August (Appendix III Table A24). Stream water temperatures ranged between 8.1 (BB06-V) and 14.6 °C (BB01-D), were warmer in September than in August and tended to be 0.73 °C colder at V than D sites in September on average (AVOVA, $F_{1,6} = 3.23$, $p = 0.12$). Overall, physical and chemical water properties tended to be more dissimilar between V and D in October and September than in August (Appendix III Table A24).

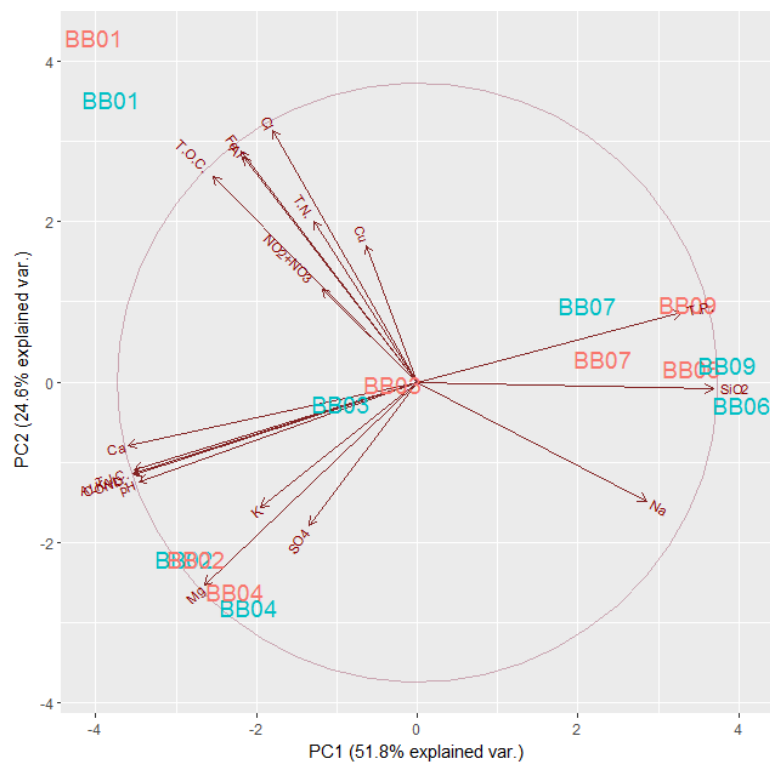


Figure 4-4: Principal component analysis with water chemistry parameters (indicated by red arrows) at variable source area (blue) and dry (red) sites in 7 Black Brook streams (New Brunswick, Canada) averaged for August, September and October 2015.

Variables describing the optical properties of DOM also showed differences across streams and between V and D sites. The first DOM quality principal component captured 74% of the variability, and it was strongly related to variables describing the humification and aromaticity of DOM (e.g., HIX and SUVA) (see Appendix III Figure A15). This PC1 did not differ

significantly between V and D sites, and neither did the individual components of that PC1 (see Appendix III Table A25). However, in October the aromaticity of DOM was significantly lower at V than D sites (ANOVA, $F_{1,6} = 4.71$ and 5.15 , $p = 0.07$ and 0.06 for SUVA and SAC340, respectively). The second PC, which captured 18% of the variability, differed between V and D sites (ANOVA, $F_{1,6} = 4.71$, $p = 0.07$). PC2 was positively related to the fluorescence index (FI, which indicates the source of DOM (microbial (high FI~1.8) or terrestrial (low FI~1.2)), with V sites tending to have higher FI values than D sites on average, although the differences were not significant (ANOVA, $F_{1,27} = 1.75$, $p = 0.20$) (Figure 4-5). PC2 was also negatively related to the freshness index (β/α , which indicates the contribution of recently produced DOM), with V sites having lower β/α values than D sites on average (ANOVA, $F_{1,30} = 2.87$, $p = 0.10$). Therefore, DOM at VSA sites tended to be of greater microbial origin, but was less fresh than that of D sites. However, these differences were driven mainly by BB04, BB06, BB07 and BB09, with these streams having a more terrestrial and fresh DOM at the D sites, and more microbial and less fresh DOM at the V sites (Figure 4-5). BB01-BB03 had mainly terrestrially derived DOM at both the V and D sites, as well as similar freshness values. In addition, V sites in BB04, BB06, BB07 and BB09 had greater variance than their D counterparts and than the BB01-03 streams, meaning that temporal differences were greater at these VSA sites. Finally, differences in DOM optical characteristics between V and D averaged across all streams were stronger in October than in September or August (see Appendix III Table A25).

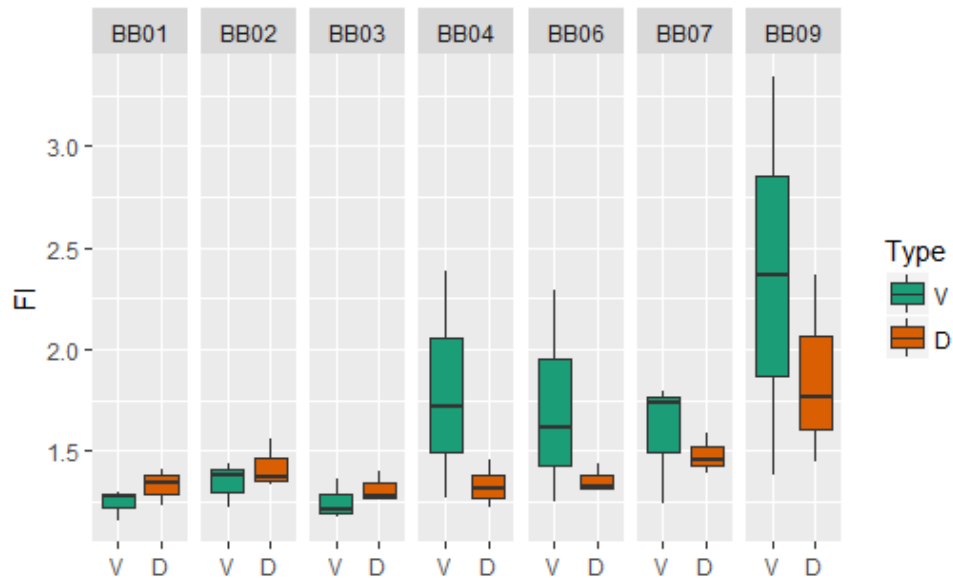


Figure 4-5: Fluorescence index of dissolved organic matter in water samples at variable source area (V) and dry (D) sites in 7 Black Brook streams (New Brunswick, Canada). Water samples were collected on three occasions (August, September and October) in 2015. (The upper and lower hinges of each box correspond to the upper and lower quartiles, and the line in between to the median; the whiskers correspond to values higher or lower than the third and first quartiles).

4.3.3. Biotic in-stream indicators

Biofilm and algal biomass, and leaf decomposition varied widely across streams, but differences between V and D sites were more subtle. There was a wide range in total biofilm biomass across sites (0.24-5.10 g m⁻²), with V sites having 0.81 g m⁻² more on average than dry sites; but this difference was non-significant and mainly driven by BB03 and BB07 (ANOVA, $F_{1,34} = 1.7, p = 0.17$) (Figure 4-6a). Algal biomass (which also showed a wide range between 0.60 and 12.1 mg m⁻²), however, was greater on average at D sites than V sites by 1.97 mg m⁻² (ANOVA, $F_{1,6} = 3.97, p = 0.09$) (Figure 4-6b). Total leaf decomposition ranged from 0.56 to 1.10% lost AFDM per day, and did not differ significantly between V and D sites, with some streams having faster decomposition at V sites and others at D sites (ANOVA, $F_{1,6} = 0.21, p = 0.66$) (Figure 4-6c). None of these variables differed significantly between downstream and upstream sites

(ANOVA, $F_{1,6} = 1.14$ and 1.07 , $p = 0.33$ and 0.34 for biofilm and algal biomass, respectively; $F_{1,6} = 0.16$, $p = 0.70$ for leaf decomposition).

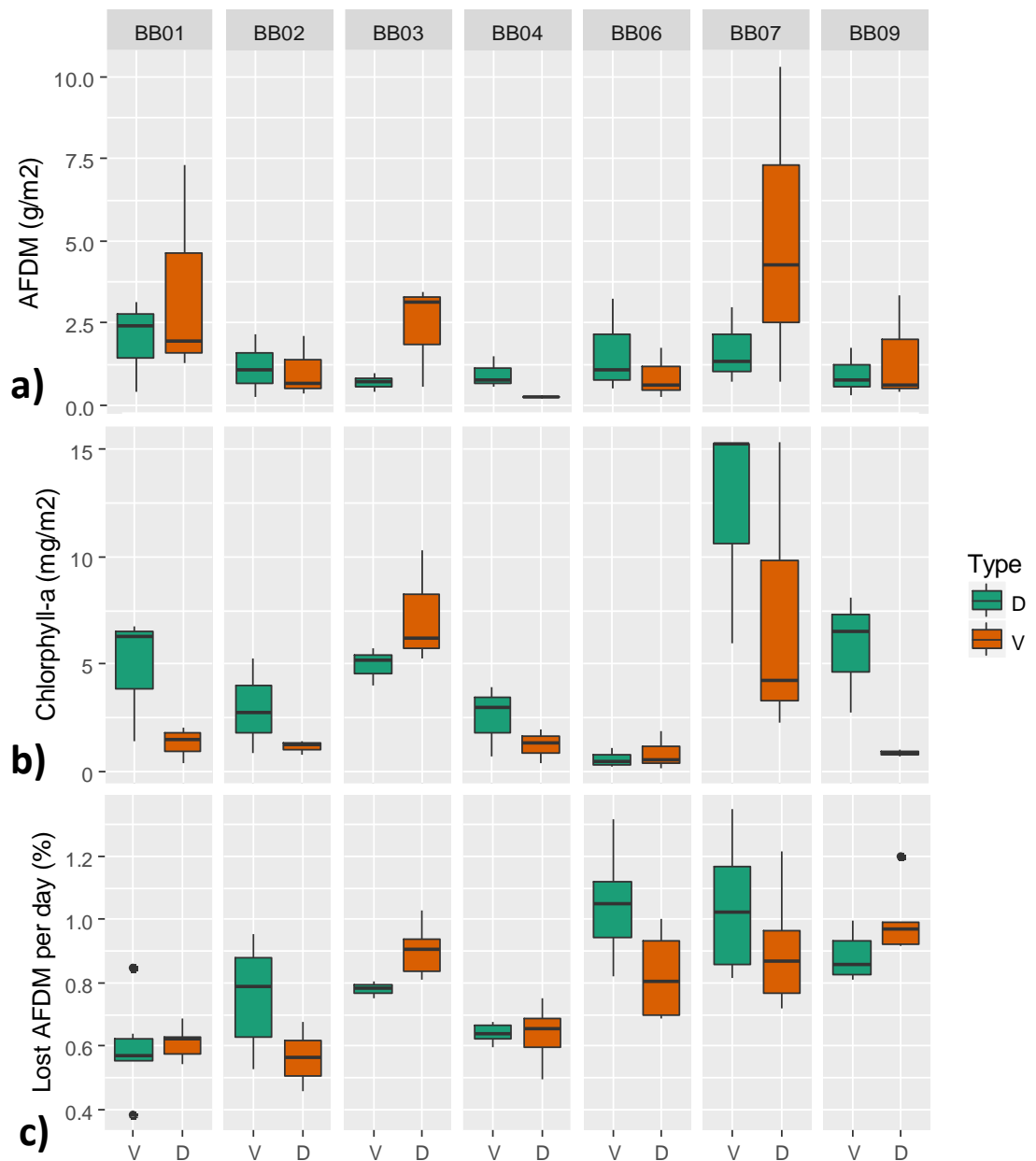


Figure 4-6: Box plot showing a) the total biofilm biomass (ash free dry mass) and b) the algal biomass (chlorophyll-a content) in samples scraped from tiles ($n = 3$), and c) the percent organic mass (ash free dry mass) lost per incubation day in leaf pack samples ($n = 6$), at variable source area (V) and dry (D) sites in 7 Black Brook streams (New Brunswick, Canada) in 2015 (see Figure 4-5 for box plot description).

Finally, metrics describing the BMI community also differed across streams, but only a few metrics differed significantly between V and D sites. Metrics describing the abundance (ranged between 216 and 2772 individuals per shocked m² across streams), richness (12-21 taxa) or diversity (1.53-2.13 Shannon's index) of BMI communities did not differ significantly between V and D sites (see Appendix III Table A26). Likewise, the centroids and spread in the NMDS ordinations of BMI communities were not significantly different for V and D sites (PERMANOVA, $F_{1,11} = 1.35$, $p = 0.28$), but they were significantly different among streams (PERMANOVA, $F_{5,11} = 4.62$, $p = 0.001$); V and D sites from the same stream ordinated closely together, except for BB04 where community composition seemed very different between the V and D sites (Figure 4-7). SIMPER did not identify any taxon as being differently represented at V and D sites. Regarding functional feeding groups (FFGs), the proportion of each FFG ranged widely across sites; for example, shredders ranged from being the most abundant FFG (~70%) to the least abundant FFG (0.8%), collector-gatherers ranged between 10.6 and 70.1%, filterers between 1.9 and 29.2%, scrapers between 0.6 and 19.3% and predators between 4.7 and 40.3%. V sites had higher absolute abundance of collector-gatherers – by 62 individuals on average – across all streams and lower abundance of scrapers – by 3.4 individuals on average – (ANOVA, $F_{1,5} = 4.65$ and 4.35 , $p = 0.08$ and 0.09 , respectively), as well as 17% more collector-gatherers and 9% less predators (ANOVA, $F_{1,5} = 6.9$ and 5.8 , $p = 0.047$ and 0.06 , respectively) (see Appendix III Figure A16, Table A26). The individuals from the genus of collector-gatherers *Ephemerella* were significantly smaller at V than D sites by 0.55 mm (ANOVA, $F_{1,5} = 22.8$, $p = 0.005$); the predator genus *Rhyacophila* was also smaller at V sites (ANOVA, $F_{1,10} = 3.74$, $p = 0.08$). The size of the remaining five genera did not differ significantly between V and D sites (see Appendix III Table A26). All these variables describing the BMI community did not differ significantly between upstream and downstream sites, except for *Glossosoma* (scraper) and

Rhyacophila (predator) being significantly larger at downstream sites (see Appendix III Table A26).

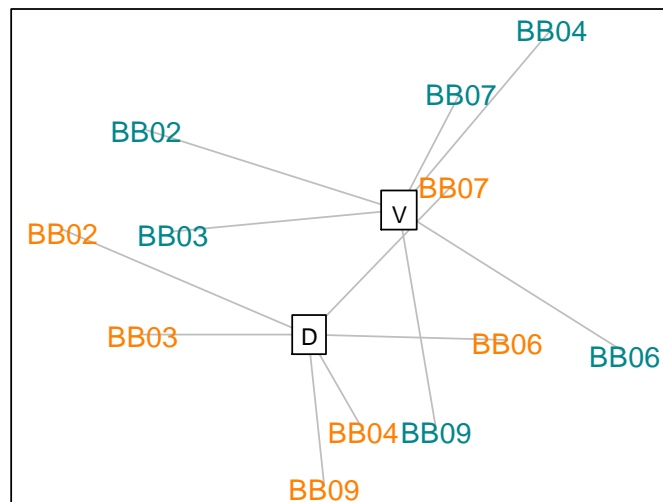


Figure 4-7: NMDS of benthic macroinvertebrates based on abundance data at variable source area (blue, V) and dry (orange, D) sites in 6 Black Brook catchments (New Brunswick, Canada) (stress value = 0.15). Boxes represent group (V or D) centroids.

4.4. Discussion

4.4.1. Riparian vegetation

Our study supports the notion of hydrological connectivity near streams resulting in distinct streamside plant communities (Jansson et al. 2007; Kuglerová et al. 2014b). The greatest differences in this study were observed in vegetation structure, with V sites having a greater woody understory (especially within the 0-0.5 m height layer) density and herbaceous vegetation ground cover, and lower density of trees. Lower tree density could be a result of suboptimal tree growth conditions in these areas (Laudon et al. 2016). However, there were no significant differences in basal area, so the fewer trees that grew at V sites were no smaller in size. This could be due to these areas not having been harvested (e.g., soils too wet, trees growing at VSAs not being of commercial interest – e.g., cedar). Contrary to findings by Jansson

et al. (2007) and Kuglerová et al. (2014b), I did not detect significant differences in vegetation richness, probably because, unlike the above-mentioned studies, I only measured richness of woody vegetation. However, a composition shift was clear with both woody and herbaceous species that thrive in wetter habitats being more represented (e.g., cedar, willow, horsetails, mosses...).

4.4.2. *In-stream indicators*

Even though VSA sites had a distinct riparian vegetation, I found that only a few stream ecosystem components tended to or clearly differed between VSA and dry sites. These differences were more pronounced with physicochemical habitat attributes (stream morphology, water and DOM quality) than with biotic characteristics, meaning that even though habitats differed abiotically, they generally were not reflected by strong differences in biotic communities or their function.

Regarding stream morphology, VSA stream reaches tended to be less turbulent (fewer riffles and more runs), which resulted in higher accumulation of silt and benthic FPOM, coinciding with the findings by LeCraw and Mackereth (2010). This was probably the result of the topography at these sites affecting the stream morphology: VSAs by definition are streamside areas with a high topographic wetness index, i.e., they have high contributing areas (water from a large area converges at these sites) and gentle slopes, resulting in water flowing to and accumulating in these streamside areas. Therefore, VSAs tended to be flatter than dry sites, with corresponding stream reaches having lower gradients and therefore higher tendency to deposit water-borne particles. The substrate classified as silt was composed mainly of FPOM rather than inorganic sediments, based on personal observations. These personal observations are supported by the fact that the amount of inorganic sediments entrained in leaves and

biofilms did not differ between VSA and dry sites. Therefore, the local topography associated with VSAs influenced stream channel gradients and reduced the ability of these reaches to transport particles, resulting in accumulation of FPOM on streambeds at V sites.

Contrary to what I hypothesized and to what has been previously observed (Creed et al. 2003; Grabs et al. 2012; Ledesma et al. 2015), the stream water at V sites had significantly less DOC than at D sites. A possible explanation is that the groundwater flowing to these VSAs could be discharged into streams from deeper mineral soil layers, which would result in no or less contact with the organic soil layer and, therefore, a lower chance to collect DOC (Boyer et al. 1995). This hypothesis is supported by the fact that in September the water at V sites was higher in cations (Ca and Mg) and colder (which coincides with the sampling time with lowest stream water levels, and thus, greatest groundwater influence on stream water characteristics – see next section for more details on temporal variability). However, based on personal observations of VSAs having obvious wet or saturated soils during periods of high water tables, it seems unlikely that the groundwater entered streams directly without being in contact with the organic soil at VSAs for at least some time. An alternative and more likely explanation for the reduced DOC at VSAs could be that when the groundwater surfaces and accumulates, longer residence times (due to flatter topography and denser vegetation slowing water down) in the VSAs could increase the rate of mineralization of organic carbon by microorganisms (Battin et al. 2008). Therefore, greater proportions of organic carbon would be microbially-processed at V than D sites before entering streams due to favorable microbial conditions in the VSAs. The optical properties of DOM indicated that DOM at VSA stream sites was more microbial than terrestrial in origin in October, and therefore of lower aromaticity. This observation supports my suggestion that shallow groundwater at VSAs enhances microbial processing of organic matter, resulting in greater microbially-processed and more labile DOM

being delivered to receiving waters compared to D sites. This would also explain why DOM was less fresh at these V sites, reinforcing the hypothesis of longer residence times of water and DOM at these wet riparian sites. Previous studies have shown that forest soils with a tendency to be wet during certain times of the year have higher rates of microbial processing and this is likely true of streamside wet areas with direct hydrologic connection to stream reaches. For example, Webster et al. (2008) observed that respiration in critical transition zones (which they defined as “transiently saturated areas in isolated depressions or adjacent to wetlands, streams and lakes”, and therefore would include VSAs) was significantly larger than in adjacent wetlands or hillslopes, and they attributed this to optimal temperature and moisture conditions as well as the large pool of high quality organic matter that accumulates in these areas. Mengistu et al. (2014) measured a negative relationship between the proportion of effective VSAs in the catchment and DOC export, and they suggested that as % effective VSA increased, the transport of water through mineral-rich soils would be greater, which would result in greater DOM adsorption (Findlay and Sinsabaugh 2003). Stream microorganisms at VSA stream reaches could also be depleting the DOC pool due to enhanced activity, reinforced by the lower oxygen saturation measured at V sites, but the biotic endpoints I measured do not support this. Therefore, it can be speculated that a combination of biological (enhanced DOC mineralization) and physical (DOC adsorption in mineral soils) factors could be contributing to the reduced DOC concentrations observed at stream sites draining V sites, but measurements of microbial activity at VSAs and of groundwater DOC concentrations are required to test this hypothesis.

The stream morphology characteristics described at V sites could explain the lower algal biomass recorded at these sites. The significantly higher accumulation of FPOM on the streambed means that there is less optimal substrate for the growth of biofilm, and that biofilms could be covered in FPOM and therefore receive less sunlight for photosynthesis. The

lower iron concentrations at V sites could also be limiting algal growth (Morel et al. 1991). It could be argued that because V sites were more upstream than D sites (5 out of 7 streams), V sites would have a closer canopy, limiting sunlight penetration. However, canopy openness tended to be greater at V sites than D sites, refuting this explanation. The larger quantities of benthic FPOM and lower algal production would explain the higher abundance of collector-gathers and lower abundance of scrapers observed at V sites, which agrees with findings by LeCraw and Mackereth (2010). This indicates that stream morphology, influenced by local topography at VSA sites, had a stronger influence on the algal and BMI communities than VSA inputs. Finally, the lower algal biomass at V sites could also partly explain why individuals from the genera *Ephemerella* and *Rhyacophila* were smaller at these sites, since the higher nutritional quality of algae (especially in terms of essential fatty acid content; Guo et al. 2016) has been shown to support higher growth rates of macroinvertebrates than less nutritious allochthonous food sources (Müller-Navarra et al. 2000; Goedkoop et al. 2007; Gladyshev et al. 2011). The smaller body sizes could also be a result of the colder (0.73°C on average) water temperatures measured at V sites, since growth rates and life cycles of BMIs are linked to temperature (Ward 1992). Overall, I found little evidence that biological communities differed between V and D sites within a stream.

4.4.3. *Underscoring the V in VSA: temporal variability*

I found considerable temporal variability in water and DOM chemistry measurements, which resulted in differences between V and D varying over time. This is not surprising considering that the extent and wetness of VSAs vary over time depending on the height of water tables (Creed and Beall 2009; Mengistu et al. 2014). When water tables rise after rain events, groundwater intersects with surface soils that have accumulated materials during the

dry period, resulting in the mobilization and transport of these materials to receiving waters (Creed et al. 1996; Boyer et al. 1995; Kalbitz et al. 2000). The differences in water and DOM chemistry between V and D stream sites were lowest in August, which coincided with the sampling time in which water levels in streams were the highest, right after the rising limb of the hydrograph following a summer rain storm, mainly in BB04, BB06, BB07 and BB09 (i.e., streams with strongest differences in DOM over time) (see Appendix III Figure A17). This probably means that streams were being influenced mainly by runoff from rainwater quite uniformly along the stream, diluting the effects of VSAs on stream water chemistry. And because stream discharge was higher in August, the solutes delivered by VSAs were diluted and mixed into a larger water volume in streams. However, when water levels were lower, streams were being fed proportionally more by groundwater delivered through VSAs, and therefore the differences in water chemistry between V and D sites were more pronounced. This is supported by the fact that differences in Ca, Mg and conductivity were greatest in September, when flows were the lowest (see Appendix III Figure A17). Therefore, this suggests that the importance of VSAs to stream metabolism may be especially critical during periods of lower flows and drier conditions, i.e., when VSA stream reaches, unlike non-VSA reaches, remain hydrologically connected with the surrounding land.

However, differences in DOM quality were greatest in October. VSA sites had a greater microbial origin in October than in September and August, but a similar shift was negligible in dry sites. In August, when a summer storm caused higher stream levels from rainfall runoff, microbial-origin DOM from VSAs may have been swamped by runoff bearing mainly terrestrial-origin DOM. Additionally, lower accumulation of organic matter from leaf fall and senescent vegetation on riparian soils during August may have led to lower microbial processing of organic matter at VSAs in comparison to rates after leaf fall. In September, lower water tables

and drier soils could have reduced microbial processing of organic matter in VSA soils and lessened the export of microbial-origin DOM from riparian soils to streams, since nutrient export to streams is closely linked to water delivery (Boyer et al. 1995; Ledesma et al. 2015). In October, however, stream water levels rose (based on hydrographs, see Appendix III Figure A17), indicating that more water was being accumulated at VSAs and delivered to streams. Under increased soil moisture conditions, optimal conditions may have enhanced the microbial processing of organic matter accumulated during senescence and leaf fall, leading to October increases in microbial-origin DOM at VSA sites compared to D sites (Kalbitz et al. 2000).

4.4.4. Forest management and VSAs

My results give some evidence that forest management can affect VSA inputs to streams and their influence on stream ecosystems. For some of the variables there seemed to be two types of responses, which could be linked to the harvesting intensity of the catchment. Among the 7 study catchments, BB01, BB02, BB03 and BB04 had higher forest management intensity than BB06, BB07 and BB09 (see Table 4-1 and Chapter 2), as indicated by the higher fine inorganic sediment entrainment (Appendix III Figure A14). BB04 seemed to receive most of the sediment loading between the upstream V and downstream D sites, suggesting that the V site was less affected by forest management than the D site. BB04, BB06, BB07 and BB09 had greater temporal variation in DOM quality at V sites, shifting from more terrestrial in August to more microbial in October, whereas BB01, BB02 and BB03 had predominantly terrestrial origin during all three sampling times. BMI abundance and leaf decomposition also tended to be higher at V sites than D sites in the less intensively managed catchments, although there were a couple of exceptions. Therefore, I hypothesize that the faster and greater delivery of water-borne materials observed in catchments with high forest management intensity (Chapter 2)

could mask the differences between V and D in stream habitat regardless of their hydrological connectivity with the catchment, which may in turn lead to a reduction in spatial habitat diversity. Although my study was not designed to capture the interactive effects of forestry on the influence of VSAs on stream ecosystems, the evidence and mechanisms I present indicate potential interactive effects, and these should be explored through further study.

4.4.5. Conclusions and management implications

Others have previously suggested that streamside areas of high hydrological connectivity such as the VSAs in this study should receive increased protective measures during forest harvesting because they likely have a disproportionately higher influence on adjacent streams than streamside areas of low connectivity (Buttle 2002; Creed et al. 2008; Kuglerová et al. 2014a; Laudon et al. 2016). However, although some in-stream habitat features differed between V and D, I found little evidence that inputs from streamside VSAs had significant effects on stream communities and their ecological function. There was considerable natural heterogeneity among catchments and sites, and this undoubtedly reduced the power to detect differences between V and D influences across only 7 catchments. I did find evidence that the VSAs supported a more dense and distinct understory vegetation community which may be important for contributing to overall plant biodiversity (Jansson et al. 2007; Kuglerová et al. 2014b), and therefore critical habitat for animals such as forest birds (MacArthur and MacArthur 1961; Godinho et al. 2009). In this regard, although their direct influence on in-stream habitats and communities were equivocal, streamside VSAs may provide other important services such as the support of terrestrial biodiversity (as indicated by the denser understory vegetation at my V sites) and biogeochemical hotspots that may contribute to

overall catchment and stream productivity (as indicated by the distinct DOM quality and quantity at my V sites).

The paired V and D sites comparisons in my study may have been overwhelmed by catchment-level or larger reach-level influences on stream condition (such as forest harvesting and roads), making the site to site comparison within streams less effective at detecting influences of VSAs. At these broader scales, streamside VSAs may be important contributors to whole-stream conditions, such that streams in catchments with higher VSA densities may differ from streams in catchments with lower VSA densities (Creed and Beall 2009; LeCraw and Mackereth 2010; Mengistu et al. 2014) (see Chapter 5). Furthermore, these VSAs were not disturbed, with all of them falling almost entirely within riparian buffer zones. It could very well be that once these hotspots are disturbed (e.g., harvested), the receiving waters are disproportionately affected due to their higher hydrological connectivity and consequent vulnerability to disturbance. Further study is required to quantify the ecological significance of these streamside cryptic wet areas, as well as the implications of disturbing these areas, but it is likely that they represent a landscape feature that should receive special attention in the design and application of riparian buffers for forest harvesting.

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5. General discussion

Headwater streams can be considered the capillaries of the landscape: their integrity is vital to that of the downstream river ecosystems and to the delivery of aquatic ecosystem services such as clean drinking water, fish production and flood protection; in turn, headwater stream integrity is intimately connected to the surrounding land, so disturbance to the land has implications for receiving waters. Forest harvesting has been shown to affect stream ecosystems by, for example, altering water quality and quantity, which results in changes to stream organisms and functions. Although the main effects of forest harvesting on streams have been well documented over the past few decades, most studies have 1) focused on short-term, post-harvest effects, 2) used relatively few indicators, with a focus on abiotic ones, and 3) only considered fixed-width buffers, without considering the heterogeneity in hydrological connectivity between streams and riparian forests. However, the influence of forest management on streams is the result of the cumulative effects of several factors (e.g., multiple harvesting times, different techniques, and compounded by roads and other operations...), which are expected to intensify in the near future. And, because different components of stream ecosystems respond to harvesting disturbance in a unique way and over different spatial and temporal scales, more holistic studies that go beyond the assessment of one or a few (especially abiotic) indicators are necessary. In particular, there is a scarcity of studies exploring the effects of forest management on stream food webs, even though they can be sensitive to catchment disturbance and changes to food web dynamics are extremely relevant ecologically. My PhD thesis attempted to address these knowledge gaps by: 1) investigating the effects of varying intensities of forest management on different components of stream ecosystems (represented by a suite of indicators of stream ecosystem integrity) in a holistic two-year study – Chapter 2; 2) studying the effects of intensive forest management on

headwater stream food web dynamics – Chapter 3; and 3) comparing stream ecosystem condition (assessed by measuring a suite of abiotic and biotic indicators) between stream reaches with different degrees of hydrological connectivity to the surrounding land – Chapter 4. This two-year study was conducted in the Black Brook (BB) forestry district (New Brunswick, Canada), which is one of the most intensively managed forests in Canada, yet it was third-party certified as sustainably managed under the Sustainable Forestry Initiative (Etheridge et al. 2005). Therefore, working in BB allowed me to assess how intensive forestry under best management practices (e.g., 30-m wide riparian buffer zones along streams) may affect stream ecosystems. To estimate how these effects compared to the range of natural variability observed in undisturbed systems, I also studied three reference streams in Mount Carleton Provincial Park (MC).

5.1. Effects of forest management intensity

Most indicators measured in my thesis seemed to detect the gradient in forest management intensity (FMI), with abiotic indicators showing the strongest relationships (Chapter 2). More fine sediments were delivered to streams in catchments with higher road density and more stream crossings, and the inorganic proportion also increased. Aqueous cation (especially Ca) and carbon (especially DIC) concentrations were also higher in streams with higher road density and recent harvest, and dissolved organic matter (DOM) aromaticity and humification (indicating a more refractory composition of DOM) increased as road density increased. Stream water temperature was positively correlated with recent clearcut and road density, but riparian condition seemed to have a stronger influence on temperature than forest management. Therefore, it seems that increased harvesting-related ground disturbance led to more water-borne materials being transported from the catchment to the streams, with this

transport being facilitated by a denser road network and heavier traffic in the most intensively managed catchments (Figure 5-1). Similar abiotic responses to forest harvesting have been reported before (e.g., Moore et al. 2005; Croke and Hairsine 2006; Kreutzweiser et al. 2008; Webster et al. 2015), but my study shows that even when applying best management practices (e.g., leaving riparian buffer zones, employing efforts in low-impact stream crossings), physical and chemical stream characteristics still reflected the increases in forest management intensity.

Biological communities seemed to respond to this increased delivery of materials from the catchment. Biofilm biomass responded positively, but this was mainly driven by heterotrophic organisms and/or fine particulate organic matter entrained in biofilms (Chapter 2). This resulted in food webs becoming more supported by allochthonous (terrestrial) rather than autochthonous (aquatic) carbon as FMI increased, since BMIs incorporated this increased input of terrestrial materials into the food webs (Chapter 3) (Figure 5-1). This contrasts with previous studies that reported an increase in autochthonous resource use after forest harvesting, which was attributed to increased light availability for primary production due to the removal of the riparian forest (Rounick et al. 1982a; England and Rosemond 2004; Göthe et al. 2009). In contrast, I now demonstrate that forest management can shift food webs towards increased allochthonous dependency when riparian buffers are maintained. The decline in the algal contribution to primary consumers observed in streams with high FMI was surprising considering that I did not detect any significant relationship between algal biomass or the autotrophic index of biofilms and catchment characteristics (algal biomass was positively correlated with canopy openness, suggesting that light was the main abiotic factor influencing algal growth in these streams, Chapter 2). The reason for this mismatch could stem from the fact that consumers can incorporate more algae than the standing stock that we can measure

at any point of time (McNeely et al. 2007; Guo et al. 2016a). Because algal biomass in shaded headwater streams tends to be low, yet of high nutritional quality (namely diatoms) and with fast turnover rates, consumers readily ingest the new algal growth (Rosemond et al. 1993), which can obscure our ability to measure the actual amount of algal biomass available to consumers. Therefore, in this study, food web structure was a more reliable indicator than algal biomass to detect the effects of forestry, since food webs offer a time integrated measure of algal growth and ingestion, whereas measuring the standing stock of algae only offers a snapshot in time. Based on indirect evidence from the food web indicators (Chapter 3), it can be hypothesized that the amount of algae available to consumers may have been negatively affected by intensive forest management (e.g., due to scouring/shading by sediments and/or due to a competitive exclusion by biofilm decomposers in streams with more aromatic/humic DOM), leading to lower algal contributions to the diet of some BMI taxa. Alternatively or complementarily, it could also be that the composition, rather than biomass, of photosynthetic communities changed. The composition of stream primary producers has been shown to respond to factors such as light, nutrients or grazing (Rosemond et al 2000, Davies et al. 2008, Guo et al 2006b), and because forestry can directly and indirectly influence these factors, it can lead to compositional changes in algal communities (Naymik et al. 2005; Danehy et al. 2007). Therefore, it could be hypothesized that the composition of primary producers shifted with FMI in this study; and because primary producers differ in their nutritional quality (e.g., diatoms are of higher nutritional quality than filamentous green algae or cyanobacteria – Brett and Müller-Navarra 1997; Danehy et al. 2007), compositional changes may have affected the assimilation of autochthonous resources by BMIs. Incorporating measurements of algal community composition into future work (I did not look at that in this study) may be helpful to shed some light on the mechanism explaining the decreased assimilation of autochthonous resources with

increased FMI observed in this study. But regardless of the mechanism, this decreased reliance on algae could result in lower polyunsaturated fatty acid (PUFA) content in BMIs, since algae (namely diatoms) are the main source of PUFAs for BMIs (Torres-Ruiz et al. 2007). In turn, this lower PUFA content in BMIs could be transferred into higher trophic levels and result in lower fish growth rates (Brett and Müller-Navarra 1997; Vizcaíno-Ochoa et al. 2010). However, my study did not measure FA composition and further studies to test this hypothesis in the context of forest management are needed.

The abiotic changes and the likely alteration in food source availability resulting from high FMI affected other aspects of ecosystem structure and function in addition to the algal contribution to BMI diets. For example, shredder densities increased, whereas grazer and collector-gatherer densities decreased (Chapter 2). Considering that grazers and collector-gatherers obtain a considerable amount of their diet from algae (Chapter 3), it makes sense that these were the functional feeding groups that responded most strongly to the presumably lower algal/diatom availability, whereas shredders, which commonly feed on terrestrial OM (Chapter 3, Merritt et al 2008), responded positively to increased terrestrial contributions (Figure 5-1). Regarding ecosystem functioning, FMI was negatively correlated with the critical function of leaf decomposition. The exact mechanism linking FMI and leaf decomposition is unclear, but it could be related to either the higher inorganic sediment entrainment in leaves making them less palatable for decomposers, or to the lower algal content in leaf biofilms reducing leaf consumption by BMIs (Guo et al. 2016b) and/or the activity of microbial decomposers (Danger et al. 2013) (Figure 5-1). While I detected a negative association between FMI and leaf decomposition, measurable invertebrate-mediated decomposition of leaf material did occur even at the most intensively managed sites.

There is a wide range of biotic responses to forest harvesting documented in the literature, with positive, negative and no changes reported for most of the above-mentioned indicators (Richardson and Béraud 2014). My study shows that these indicators were related not only to area harvested, but also to roads, forest structure and composition and stream morphology, which could explain the breadth of responses found in the literature, since they would depend on the particular design of the study (e.g., presence/absence of roads, coniferous/deciduous forest or type of harvesting). In addition, my study shows that assessing a gradient in forest management intensity rather than a discrete category (presence/absence of harvesting) or categories helps to better understand the directionality of the change in stream indicators. For example, I measured leaf decomposition rates in BB harvested streams that were higher, lower and similar to the ones measured in MC reference streams, and these differences between harvested and reference sites captured all three types of responses reported in the literature (Mckie and Malmqvist 2009; Kreutzweiser et al. 2008a; Lecerf and Richardson 2010). But because my study considered a gradient in FMI, I could determine that leaf decomposition responded positively to lower FMI and negatively to higher FMI in comparison to reference streams. Therefore, my study contributed to clarifying how these biotic indicators respond under different intensities of forest management.

As shown in Figure 5-1, these stream indicators were related not only to FMI, but also to other catchment and reach variables that were correlated with FMI, namely riparian and catchment forest composition. Discerning between causation and correlation in such a setting is not easy (see section 5.5 for a more detailed discussion on the limitations), therefore it is important to acknowledge and report this complexity. The lowest elevation catchments had the highest road density and recent harvest, which resulted in higher sediment deposition and entrainment. But these high FMI catchments also tended to be characterized by a certain forest

condition (lower canopy height and %mixed/deciduous, higher %coniferous) and stream morphology (less riffles and more runs), which may have facilitated the delivery and deposition of sediments in streams. Similarly, forest condition (namely riparian forest condition) may have also contributed to the differences in DOM quality observed across streams, with deciduous/mixed forests delivering less refractory (i.e., less humic and aromatic) DOM than conifer plantations. As explored in Chapter 3, this lower DOM quality but higher carbon quantity associated with coniferous forests, as well as the potentially lower light conditions under coniferous riparian forests may have affected food webs by favouring heterotrophic pathways over algal production. Thus, algal contribution to BMI diets was lower and biofilm biomass higher in streams with a greater proportion of coniferous trees in the catchment and in riparian forests. Additionally, based on the correlations between stream morphology and leaf decomposition and biofilm biomass reported in Chapter 2, streams with more riffles may have enhanced physical leaf litter breakdown, whereas streams with less riffles may have contributed to higher biofilm biomass (e.g., due to lower physical dislodging and/or due to facilitating the deposition/entrainment of fine particulate organic matter).

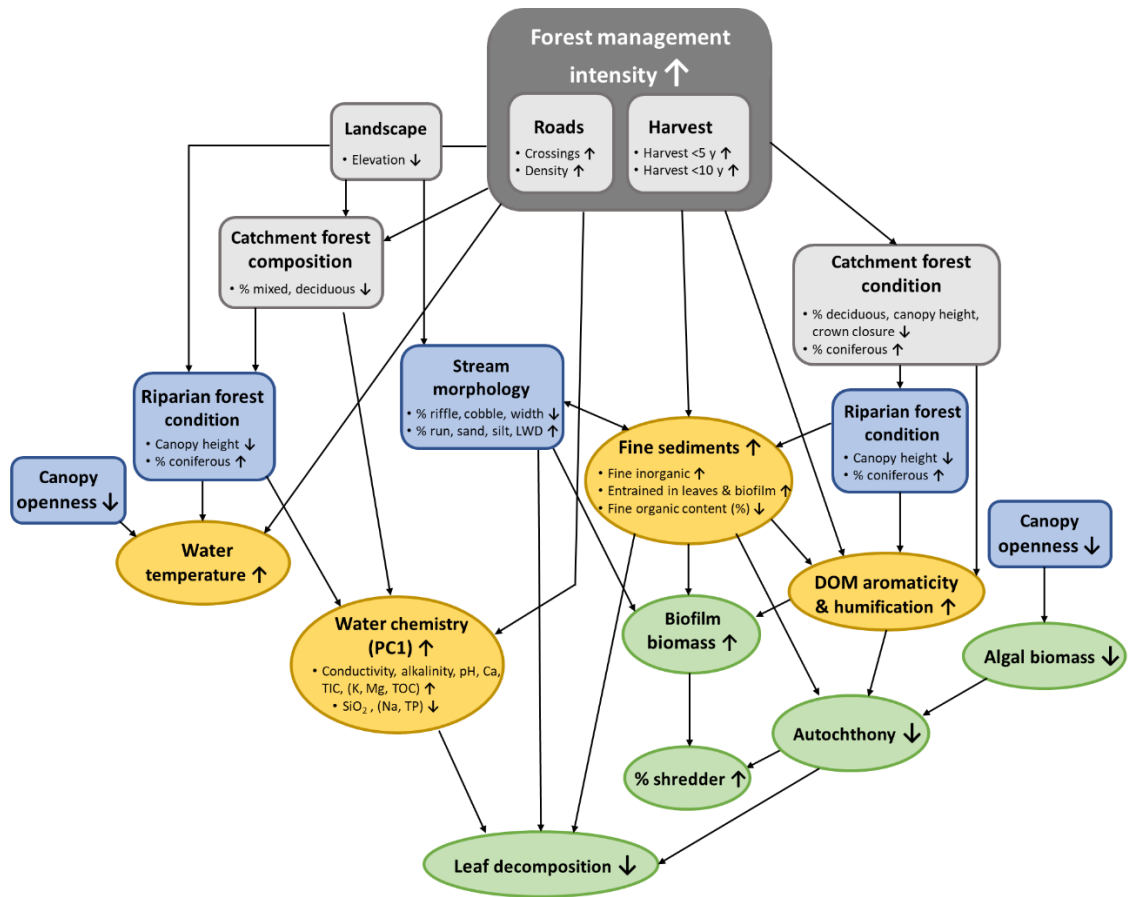


Figure 5-1: Diagram summarizing the relationships among catchment and reach explanatory variables (gray and blue boxes, respectively), and abiotic and biotic stream indicators (yellow and green circles, respectively). Arrows indicate the hypothesized relationships between the box/circles that the arrow links based on the results from Chapters 2 and 3, and the up/down arrows after variables indicate positive/negative relationships.

5.2. Land-water linkages

Because most abiotic and biotic changes observed in this study were linked to an increase in water-borne materials in high FMI catchments, understanding the movement of water from the catchment to the streams is important. The strong relationships between stream-indicators and roads indicate that the delivery of these materials was, partly, via roads. This is not surprising considering that water follows along the path of least resistance and that roads, and their associated roadside ditches, are typically engineered to convey water into local waterbodies (Croke and Hairsine 2006). Relationships tended to be stronger between

indicators and roads than between indicators and harvesting (as shown in Table 2-11 in Chapter 2), suggesting that the observed effects were more related with the delivery of materials (as well as the direct release of materials associated with road building and maintenance, since these are all gravel/dirt roads) rather than with the release of those materials when disturbing the soil during harvesting (Chapters 2 and 3). This has been reported in the literature before, but the opposite trend (i.e., effects being more related to harvesting than roads) too (e.g., Kreuzweiser et al. 2005; Croke and Hairsine 2006; Kara et al. 2014). My study also provides some evidence to suggest that the amount of road traffic may be an important determinant of in-streams effects (Reid and Dunne 1984; Luce and Black 1999). More specifically, BB01 was the BB stream with the most distinct abiotic and biotic characteristics (Chapters 2 and 3), and it was the only stream in this study downstream of a high traffic road (i.e., main road used daily by company trucks, as opposed to logging roads used only during harvesting operations) (personal observations and JDI staff personal communication). Therefore, road traffic and its influence on stream ecosystem integrity is a factor that should be incorporated in future work to better interpret the observed results (Alchokhachy et al. 2016).

I hypothesized that another pathway to deliver materials released during soil disturbance would be via variable source areas (VSAs), since these are areas of strong hydrological connectivity, where topography leads the water to flow into, converge and accumulate in these flatter areas before being delivered to the receiving waters (Mengistu et al. 2014). I hypothesized that the increased flow of nutrients from these biogeochemical hotspots would result in higher stream productivity (e.g., higher algal biomass and BMI abundance); however, my results indicated that the increased inputs of terrestrial materials (e.g., sediments) from VSAs resulted in lower algal productivity and incorporation into food webs, thus the effects of

organic matter inputs likely overrode the potential effects of increased nutrient inputs. But the evidence supporting that statement was conflicting. Effective VSA density in the catchment (Chapter 2) was positively correlated with sediments, DOC, biofilm biomass (2014), % shredders, and contribution of terrestrial food sources to BMI diets (Chapter 3), and negatively with autotrophic index (2015), % collector-gatherers, and contribution of algae to BMI diets. Therefore, this evidence supports the idea of VSAs contributing the delivery of terrestrial water-borne materials to stream ecosystems. However, when comparing VSA and dry sites (Chapter 4), the evidence was less clear. On the one hand, I measured lower algal biomass and grazer density at VSA sites. In contrast and opposite to what I expected, DOC concentrations were lower at VSA stream sites than at dry sites, which contradicts the idea of higher delivery of terrestrial water-borne materials through VSAs. The most likely explanation for this phenomenon is that water seemed to accumulate at these wet streamside areas before entering streams, where DOC could be processed by microbes (as evidenced by more microbial and less fresh origin of DOM at VSA sites), resulting in DOC-depleted water entering streams. A food web study at these VSA and dry sites could be helpful to shed some light on this puzzle by testing whether stream food webs at VSA sites derived more carbon from terrestrial sources (as opposed to aquatic sources) than at dry sites.

It has been previously suggested that streamside areas of high hydrological connectivity, such as the VSAs in this study, should receive increased protection during forest harvesting because they likely have a disproportionately higher influence on adjacent streams than streamside areas with lower connectivity (Buttle 2002; Creed et al. 2008; Kuglerová et al. 2014a; Laudon et al. 2016). Even though I detected some differences between VSA and dry sites, I found little evidence that input points from streamside VSAs had significant effects on stream BMI communities and their ecological function. Possible reasons for this weak signal

could include low sample size (N = 7 paired sites), spatial and temporal limitations, and heterogeneity among catchments (e.g., forest management intensity) reducing the power to detect differences. Spatial limitations included the difficulty to accurately estimate the area where water from the VSA entered the stream; I tried to be conservative by selecting the sampling reach some metres downstream of the most likely area to make sure I was not missing it, but this distance may have been enough to dilute the effects of the VSA. However, if that were the case and effects are not detectable several metres downstream of the entry area, it indicates that the influence of VSAs on stream ecosystems is spatially limited. It is also possible that my dry sites were influenced by VSA inputs from further upstream and their effects carried downstream farther than expected. I attempted to ensure my V and D sites were at least 200 m apart, but there may have been inputs from more subtle VSAs closer to my D sites. This may have diminished instream differences between V and D sites because of overlapping influences. If these potential spatial issues are true, it means that the effects of VSAs on streams should be assessed at the stream level rather than the reach level, i.e., by comparing streams with high and low VSA influence rather than by comparing VSA and dry stream reaches. This is backed by the fact that the evidence about the influence of VSAs on stream ecosystems was clearer in Chapter 2 (in which relationships between % effective VSA and stream indicators were assessed) than in Chapter 4 (in which stream indicators were compared between VSA and dry stream reaches).

In terms of temporal limitations, because VSAs are temporally variable and closely linked to precipitation, the timing of sampling could have affected the detection of differences from the dry sites, with my water chemistry and DOM quality data (Chapter 4) supporting this claim. But again, if VSA effects are only temporary and do not translate into permanent ecosystem changes, the influence of VSAs on stream ecosystems seems to be less crucial, although

seasonal variability may be as important as permanent changes for several structural and functional stream ecosystem attributes. Future work should attempt to track the entry of the water from VSAs and the stream distance required for the effects to be diluted in the stream (e.g., by using dyes, piezometers, high-resolution thermal detectors, or measuring soil moisture content) to shed some light on the spatial and temporal extent of the inputs from VSAs. In addition, most VSAs in my study fell within riparian buffer zones and were, thus, undisturbed. It could be hypothesized that the influence of VSAs on stream ecosystems becomes especially obvious once these systems become disturbed, with VSAs being more sensitive to disturbance due to their higher land-stream connectivity. Therefore, future studies should look at the effects of disturbance from harvesting on VSAs when they venture out into harvested areas beyond riparian buffers, and their subsequent influences on stream ecosystems. Finally, my results (Chapter 4) show some evidence that forestry could be masking the differences between VSA and dry sites (e.g., by sediments overriding the spatial diversity created by VSA inputs). I did not study VSAs in my reference streams due to lack of high-resolution LiDAR data required for site selection, but repeating a similar study in undisturbed catchments is recommended. In summary, I believe that this thesis greatly contributes to the understanding of the ecological significance of VSAs, since, to my knowledge, it is the first study looking at multiple stream ecosystem components in relation to VSAs, but it also underscores the need for further studies looking at the relationship between VSA inputs and stream ecosystems, as well as the influence of forestry on this relationship.

5.3. Harvested (BB) vs. reference (MC)

Although, most indicators responded to the gradient in forest management intensity, there was little indication of impaired biological communities in these streams when compared

to data from the reference streams. The Mount Carleton reference streams differed the most from BB streams in terms of abiotic endpoints, namely in sediment deposition (less fine sediments and higher organic fraction in MC) and water chemistry (lower conductivity, Ca, Mg, DIC, SO₄, pH ... in MC). These differences probably stemmed from the absence of soil disturbance (harvesting) and roads in the unmanaged MC catchments as opposed to the managed BB ones. However, differences in water chemistry could also be attributed to the different geology underlying these areas: felsic volcanic rocks (characteristic from MC) are known to be rich in elements such as Si, Na and K, which would explain the higher levels of these elements in MC streams compared to BB streams; sedimentary rocks (characteristic from BB), on the other hand, tend to be richer in dolomites and calcium carbonates, which would explain the higher pH, Mg, Ca and C levels in BB streams (Feller 2005). However, biotically, most BB stream data tended to fall within the range of MC values, indicating that MC and most BB streams were comparable in terms of stream ecosystem structure and function. But, the most sediment-influenced BB streams (BB01-BB04) showed reduced rates of leaf decomposition and algal contribution to food webs in comparison to reference streams. In particular, BB01 tended to be most different from reference or lower intensity sites based on various metrics, likely reflecting the much higher road traffic at one of the stream crossings upstream of the sampling reach.

Among reference streams, MC2 tended to have the most extreme values for most of the indicators, with the most likely explanation being that the sampling reach was about 800 m downstream of a beaver dam. In MC2, I measured higher water temperatures, sediment deposition, water DOC/Fe/Mg, and DOM alkalinity/humification, and lower water SiO₂, decomposition rates, BMI richness and abundance, and algal contribution to food webs than in the other two reference streams. Therefore, MC2 shared many of the same characteristics as

the most intensively managed catchments in BB. Although this study was not designed to assess the effects of beaver dams on stream ecosystems, these results indicate that natural (beaver dam) and anthropogenic (forestry) disturbances shift stream ecosystems in similar directions and via similar mechanisms. This mechanism could be the release of terrestrial materials into the water, with this release facilitated by the inundation of soils in the case of beaver dams (Catalán et al. 2017) and by soil disturbance in the case of forestry. Finally, I showed that the range of values for some stream indicators in MC streams was as wide as the range of values in BB streams (e.g. reliance of some consumers on algae, water temperature), suggesting that, for those stream indicators, the variability resulting from anthropogenic disturbances fell within the range of natural variability.

5.4. Reliability of results

This study demonstrates the advantages of assessing a suite of indicators rather than focusing on a few, since different components of stream ecosystems responded to disturbance differently, over variable spatial/temporal scales, and often in unpredictable ways. For example, by looking only at sediment dynamics or leaf decomposition I would have concluded a negative effect of FMI; by studying biofilms I would have concluded that FMI boosted stream productivity; and by measuring algal biomass or abundance of leaf pack BMIs I would have concluded that FMI did not influence stream ecosystems. But, simultaneously assessing the response of different components of the ecosystems contributed to a more holistic understanding of the linkages between disturbance and effects.

There is some spatial and temporal evidence that adds robustness to the conclusions drawn from my study. Despite the differences detected within each stream between VSA and dry sites, I observed that differences tended to be greater across than within streams (Chapter

4). Therefore, it could be deduced that the FMI effects observed in the sampling reaches in Chapters 2 and 3 reflected the actual condition of the entire stream upstream of the sampling reach, and that the location of the sampling reach did not greatly bias the interpretation of the results. In terms of temporal robustness, overall the relationships between indicators and explanatory variables remained relatively constant between 2014 and 2015. Therefore, this suggests that the effects observed in Chapters 2 and 3 are not ephemeral or stochastic, but rather that they likely provide true indications to the condition of stream ecosystems. However, most of the harvesting-related effects were strongest for recent harvesting (<10 years), suggesting that stream ecosystems in BB seemed to recover from the impacts of older harvesting (>20 years). This agrees with many studies documenting that the effects of forest harvesting on stream ecosystems are typically temporary and that they tend to recover within some decades, with recovery time depending on the particular component of stream ecosystems studied (e.g., water chemistry may recover faster than leaf decomposition) (Jackson et al. 2007; Webster et al. 2015; Yeung et al. 2017).

5.5. Limitations of the study

One of the main challenges in this study, as in most ecological field studies, was to discern between causation and correlation. Explanatory variables (EVs) tended to be correlated with one another. For example, FMI was correlated with 1) catchment and riparian forest composition and structure – FMI was higher in catchments with more coniferous and lower canopy forests, 2) landscape variables – FMI was higher at lower elevation catchments, and 3) stream morphology – streams in lower FMI catchments tended to be wider and more turbulent. Leaf decomposition exemplifies this complexity, since it was related to all EV categories: it was negatively correlated with recent harvest and road density (FMI category),

fine sediments, and water chemistry PC1 (related to cation and carbon concentrations), and positively with elevation (landscape category), % mixed forest (catchment and riparian forest composition categories), and % riffle (stream morphology category). Based on my results and on the literature, all these variables could be influencing leaf decomposition, or only few could be influencing the process while the other relationships were simply a result of confounding variables. But by separating the independent effect of a given EV on a stream indicator from the joint effect in Chapter 2 (summarized in Table 2-11), I was able to disentangle those correlations and propose mechanisms that explained the observed results (summarized in Figure 5-1).

My method to characterize the influence of forest harvesting on streams, as well as the methods used by other studies, did not consider distance of the harvesting from the stream, even though the influence of harvesting on stream endpoints is expected to decrease as its distance from the stream increases. Time since harvesting was considered to some extent, but the method to quantify the temporal dimension did not capture the different influence of, for example, one-year old harvesting and five-year old harvesting (they were grouped into the same category). Therefore, the method to quantify forest harvesting should be optimized for future work by incorporating both spatial and temporal dimensions. To my knowledge, there is not such a method available in the literature yet, so the development of a metric that includes area harvested, time since harvesting and distance from the stream is strongly recommended.

The main challenge in my food web study, as well as in most studies that use natural ratios of stable isotopes to track the energy transfer from food sources to consumers in streams (Brett et al. 2017), was to reliably determine the isotopic ratio of the autotrophic fraction of the bulk food source sampled, i.e., biofilms. The isotopic ratio of biofilms was not representative of the food source being assimilated by some BMIs, since some taxa were

selectively feeding on the algal fraction of biofilms (Chapter 3). To calculate the algal isotopic values, assumptions had to be made, so the veracity of those assumptions may have affected the reliability of the diet estimates. In addition, because bulk biofilm overlapped in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with terrestrial food sources, I was not able to discern between the relative contributions of these sources to BMI.

5.6. Future directions

Fatty acids: My research showed that food web studies can be powerful for assessing the effects of forest management on freshwater systems. The resolution of this tool, however, depends on our ability to differentiate between terrestrial and aquatic food sources, which can be problematic in streams. Therefore, future studies should be directed at increasing the resolution by, for example, incorporating fatty acids as biomarkers and/or by trying to separate the autotrophic and heterotrophic fractions in biofilms (Hamilton et al. 2005), although, to date, the latter has not been overly successful. Different food sources (e.g., algae, bacteria and leaves) have characteristic fatty acid compositions, and these are transferred from primary producers to higher trophic levels without change, making them suitable diet tracers (Parrish et al. 2000; Torres-Ruiz et al. 2007; Taipale et al. 2009). In addition, measuring the fatty acid composition and content of BMIs is recommended to test whether the decreased autochthonous contribution to BMIs resulting from intensive forest management observed in Chapter 3 results in lower BMI condition and fish food quality. Measuring compositional changes in the algal community in relation to forestry will also be helpful to better interpret the decreased reliance on autochthonous resources.

Mercury: Mercury is a pollutant transported atmospherically and deposited in ecosystems, where it can be converted to the organic form methylmercury by some bacteria.

Methylmercury, in turn, is a neurotoxin with a strong tendency to bioaccumulate in aquatic organisms (Morel et al. 1998). Some recent studies have suggested that forest management enhances the export of this pollutant from catchment to stream, where it can accumulate in stream food webs (Bishop et al. 2009; Eklöf et al. 2016). Because mercury mobility and bioavailability have been shown to be linked to DOC quantity and quality (Ravichandran 2004), and because in this study both DOC quantity and quality changed with forest management intensity and hydrological connectivity (Chapters 2 and 4), it would be interesting to measure whether mercury dynamics in these catchments are also affected by forest harvesting intensity and VSAs and to assess whether mercury levels in BMIs and fish are of concern.

VSAs: As mentioned earlier, this study provided some answers regarding the uniqueness of VSAs and their importance for stream ecosystems (Chapter 4), but it also raised more questions: since VSAs are variable by nature, is their effect on streams also temporally variable? Does the influence of VSAs on streams escalate when these systems are disturbed? Was forest harvesting in BB masking some of the VSA contributions to streams that would occur under undisturbed conditions? Therefore, further studies addressing these questions are vital to advance our knowledge on VSAs and to potentially applying this knowledge towards redesigning riparian buffer zones.

Hydrology: One of the most important endpoints that this study did not include is hydrology, an endpoint that is known to change with forest harvesting (Moore and Wondzell 2005; Buttle et al. 2009) and that it can have strong implications for stream ecosystems (Poff et al. 1997). In my study, stream water levels were monitored continuously during the sampling season, but due to some methodological issues, discharge measurements could not be obtained, which are necessary to convert water level measures into discharge measures (i.e., to build rating curves); thus, this endpoint was not included in the modeling. But by looking at

changes in water level (not shown in the thesis), I could see that the most intensively managed catchments had higher and narrower peaks in levels after rain events. This means that more rain water tended to reach streams faster (probably via roads and reduced infiltration), whereas in streams with less harvesting/roads (and especially in reference streams) the lag time between the rain event and peak stream level was longer, and it took longer for high water levels to return to baseline, suggesting that water was infiltrating soils and being delivered to streams more slowly and over a longer period of time. This physical change in hydrology would also explain the higher levels of water-borne terrestrial materials (e.g., sediments, cations...) in the most intensively managed catchments (Chapter 2), since these would be more readily transported by the faster and larger volumes of runoff to streams after rain events. But to quantify this currently indirect evidence, continuous monitoring of stream flow in similar future studies is strongly recommended.

Harvest intensity quantification: The method used to quantify the influence of forest harvesting on stream ecosystems should be optimized by incorporating spatial (distance from the stream) and temporal (time since harvesting) dimensions into a metric reflecting the degree of harvesting within a catchment.

Other biomes: The results reported in my study are related to the specific climate, topography, geology and vegetation of my study sites; thus, the results could vary in locations differing in any of these factors. For example, in drier climates and/or flatter landscapes the observed effects could be dissipated/mitigated because the transport of water-borne materials from the catchment to the streams would be reduced, whereas the opposite trend could be observed in wetter climates and/or in landscapes with a higher relief. Therefore, similar studies to mine but in different biomes are necessary to build upon our understanding of how high intensity forest management may affect freshwater ecosystems globally. Nevertheless, my

results should be applicable to other temperate, mixed-wood forests with similar geology and topography, such as the southern reaches of the eastern Canadian boreal zone.

Downstream and cumulative effects: The main question that arises from this study is: how far downstream are the effects of ecological significance? Do the effects observed in some of these headwater streams accumulate as more low-order streams converge, or are they diluted by larger water volumes? Although the capacity of AESs is concentrated in headwater streams, most of these services are realized downstream where people live (e.g., fishing, drinking water, canoeing, flood protection ...); therefore, it is important to study how changes in headwater streams from forest harvesting are expressed in larger downstream rivers.

5.7. Management recommendations

My study showed that an increase in the delivery of water-borne materials (especially sediments, carbon quality and quantity) in the most intensively managed catchments of the BB district influenced biotic indicators of stream integrity, as evidenced by reduced rates of leaf decomposition and algal contributions to BMI diets. Relationships between indicators and explanatory variables tended to be stronger with roads than with harvesting. This suggests that harvesting-related soil disturbances are primarily the result of road construction, maintenance and stream crossings, and that ultimately it is the roads and their ditches that have the greatest influence by delivering those mobilized materials to streams. To target this delivery of materials via stream crossings, proper installation and maintenance of culverts, diversion swales, and other sediment abatement practices are crucial. For example, in the most sediment-influenced stream, I observed that the diversion swale on the road was too close to the stream and that the distance of the forest between the swale and the stream was not enough to filter the runoff. To target the over-land delivery of materials, wider riparian buffer zones around the

most hydrologically connected areas, VSAs, are recommended. The stream indicators were correlated with both road crossings and road density, suggesting that both over-land delivery and the delivery at stream crossings are important sources of sediments. However, studies identifying the main sediment sources to BB streams are recommended, so that the allocation of resources aimed at minimizing sediment delivery is optimized.

Although my study does not provide definite evidence for the need to further protect VSAs, theoretically and based on personal observations, their configuration makes them more susceptible to disturbance due to their being hydrologically connected to receiving waters, having softer soils and being biogeochemical and diverse and unique vegetation hotspots. For this reason, machinery entering these areas could have disproportionate effects on stream ecosystems, as well as on terrestrial plant and animal diversity. Further study is required to quantify the ecological significance of these streamside cryptic wet areas, as well as the implications of disturbing these areas, but it is likely that they represent a landscape feature that should receive special attention in the design and application of riparian buffers for forest harvesting. However, even though the BMPs in place at BB did not offer full protection from catchment disturbance, they were effective overall at maintaining healthy stream communities.

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Appendix I: Chapter 2

Table A1: Explanatory variables within each category considered for regression analyses in BB. In bold are variables available for both Black Brook and Mount Carleton that were used to compare correlation coefficients.

CATCHMENT			REACH	
Harvest	Landscape	Catchment forest condition	Riparian forest condition	Stream morphology
Partial <5 y	Road crossings	% coniferous	Total richness	Width
Partial <10 y	Road density	% deciduous	Understory richness	Depth
Partial <20 y	Elevation	% mixed	Overstory richness	% Riffle
Partial <30 y	Slope	VCI	Canopy openness	% Run
Clearcut <5 y	Catchment area	P90	% coniferous	% Pool
Clearcut <10 y	Stream length	CrC2	% deciduous	% Boulder
Clearcut <20 y	Stream density	CrC10	% mixed	% Cobble
Clearcut <30 y	% effVSA	S2	% P90 > 5m	% Gravel
Total <5 y		S10		% Sand
Total <10 y				% Silt
Total <20 y				Large woody debris
Total <30 y				

Table A2: Correlation matrix among 2014 forest harvest variables in 12 Black Brook (New Brunswick, Canada) catchments. In green are significant ($p < 0.05$) and positive Pearson's correlation coefficients, and in red are significant and negative correlation coefficients. (PH = partial harvest, CC = clearcut, TOT = total (PH+CC)).

	PH_10y	PH_20y	PH_30y	CC_5y	CC_10y	CC_20y	CC_30y	TOT_5y	TOT_10y	TOT_20y	TOT_30y
PH_5y	0.11	0.15	0.29	-0.17	-0.26	-0.31	0.16	0.75	-0.03	-0.12	0.42
PH_10y		0.88	0.88	-0.55	-0.48	-0.69	-0.54	-0.27	0.85	0.33	0.39
PH_20y			0.96	-0.66	-0.58	-0.47	-0.45	-0.31	0.66	0.64	0.54
PH_30y				-0.64	-0.56	-0.50	-0.35	-0.17	0.67	0.57	0.66
CC_5y					0.99	0.29	0.05	0.53	-0.04	-0.45	-0.57
CC_10y						0.30	0.02	0.44	0.05	-0.36	-0.52
CC_20y							0.70	-0.07	-0.61	0.37	0.10
CC_30y								0.17	-0.60	0.14	0.47
TOT_5y									-0.05	-0.41	-0.02
TOT_10y										0.16	0.13
TOT_20y											0.65

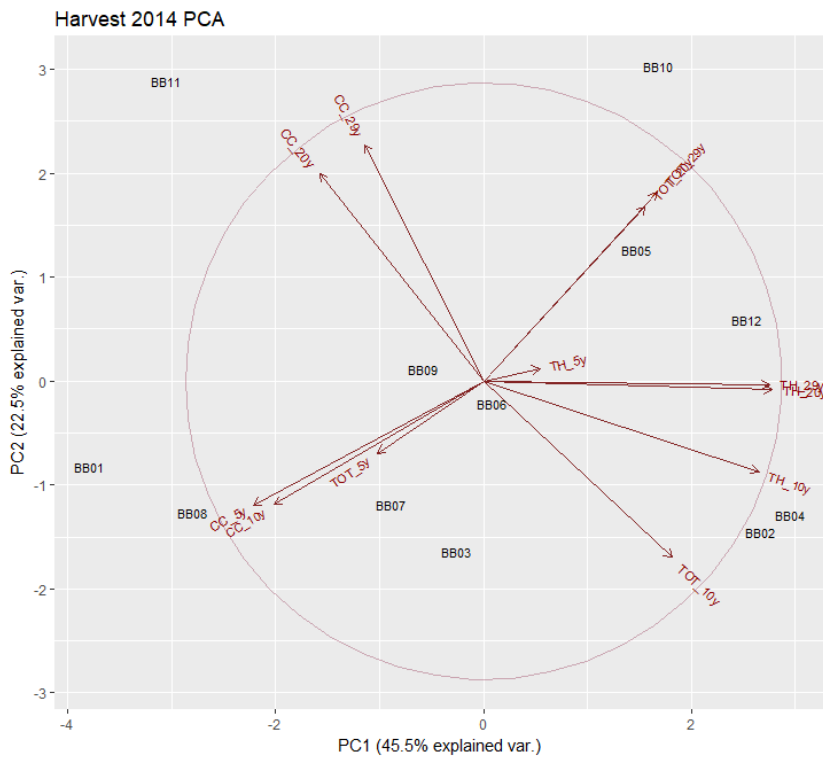


Figure A1: Principal component analysis with 2014 forest harvest variables (in red) for 12 Black Brook catchments (shown in black).

Table A3: Correlation matrix among 2015 forest harvest variables in 12 Black Brook (New Brunswick, Canada) catchments. In green are significant ($p < 0.05$) and positive Pearson's correlation coefficients, and in red are significant and negative correlation coefficients. (PH = partial harvest, CC = clearcut, TOT = total (PH+CC)).

PH_5y	PH_10y	PH_20y	PH_30y	CC_5y	CC_10y	CC_20y	CC_30y	TOT_5y	TOT_10y	TOT_20y	TOT_30y
PH_5y	0.57	0.45	0.56	-0.50	-0.49	-0.69	-0.38	0.59	0.28	-0.05	0.33
	PH_10y	0.92	0.93	-0.16	-0.16	-0.49	-0.46	0.45	0.86	0.55	0.61
		PH_20y	0.97	-0.17	-0.17	-0.31	-0.39	0.32	0.78	0.75	0.71
			PH_30y	-0.24	-0.20	-0.36	-0.34	0.37	0.77	0.69	0.77
				CC_5y	0.90	0.46	0.20	0.40	0.32	0.15	-0.15
					CC_10y	0.46	0.14	0.32	0.37	0.15	-0.14
						CC_20y	0.72	-0.30	-0.23	0.39	0.12
							CC_30y	-0.22	-0.36	0.13	0.33
								TOT_5y	0.59	0.09	0.21
									TOT_10y	0.60	0.50
										TOT_20y	0.77

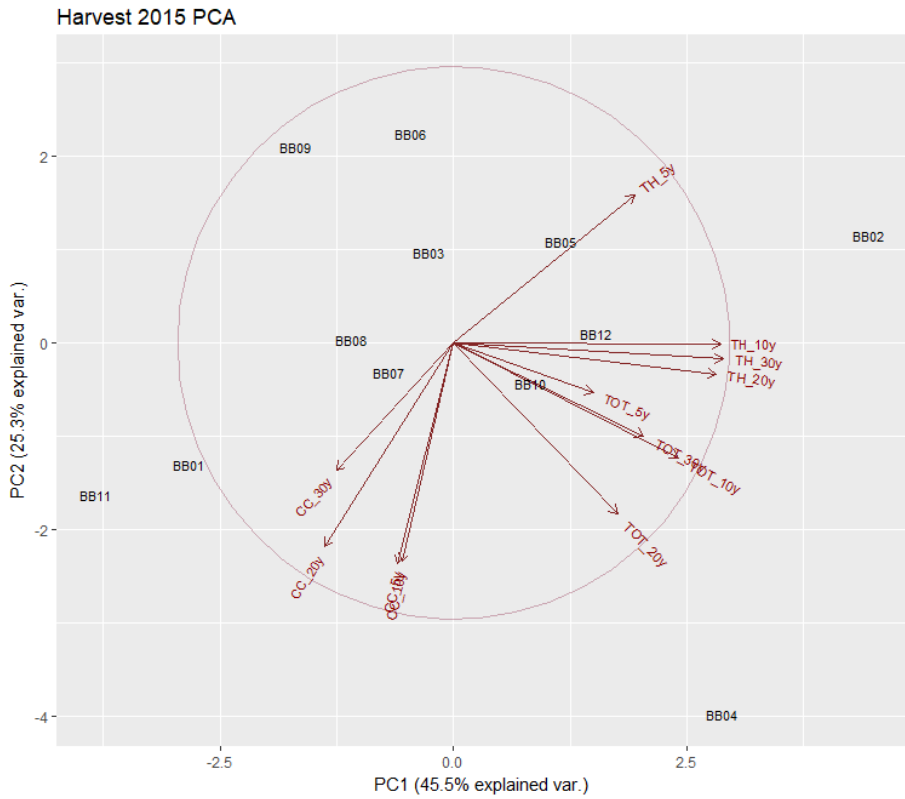


Figure A2: Principal component analysis with 2015 forest harvest variables (in red) for 12 Black Brook catchments (shown in black).

Table A4: Correlation matrix among forest condition (composition and structure) variables in 12 Black Brook (New Brunswick, Canada) catchments. In green are significant ($p < 0.05$) and positive Pearson's correlation coefficients, and in red are significant and negative correlation coefficients.

	% deciduous	% mixed	VCI	P90	CrC2	CrC10	S2	S10
% conifer	-0.89	-0.35	-0.45	-0.70	-0.18	-0.82	0.04	-0.90
% deciduous		0.05	0.64	0.82	0.43	0.82	-0.26	0.89
% mixed			-0.46	-0.19	-0.51	0.01	0.71	0.18
VCI				0.93	0.88	0.78	-0.88	0.62
P90					0.74	0.94	-0.68	0.85
CrC2						0.48	-0.90	0.37
CrC10							-0.46	0.93
S2								-0.26

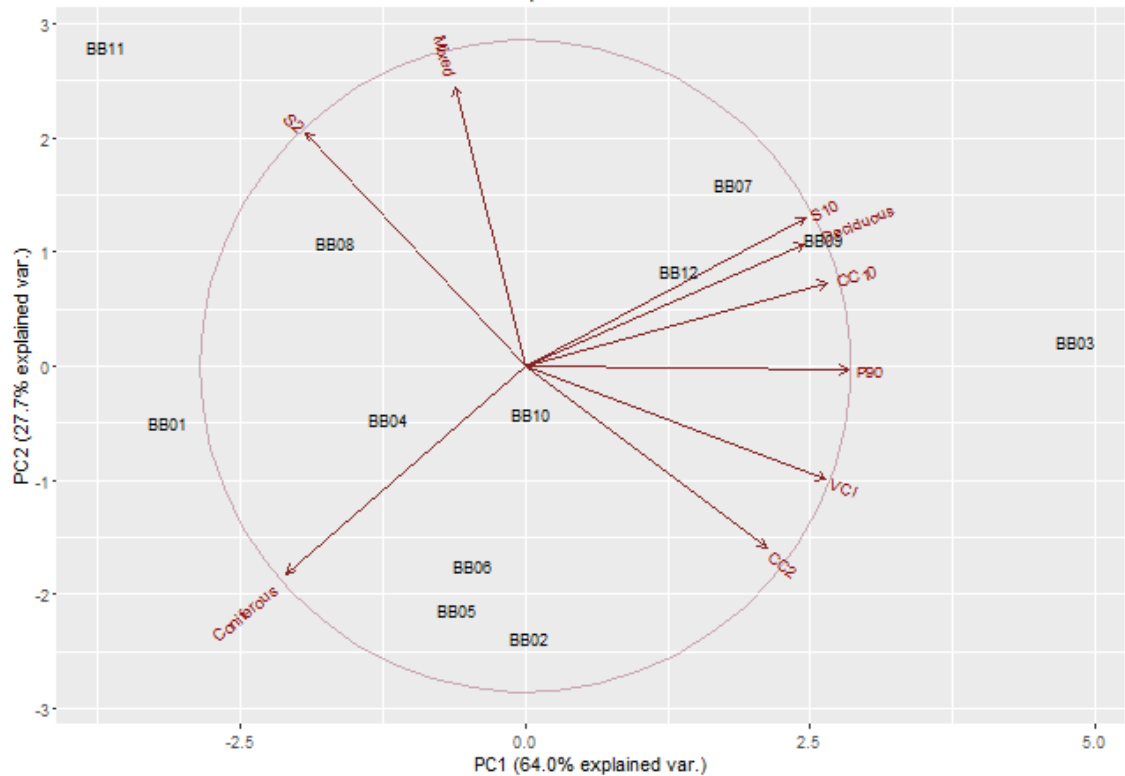


Figure A3: Principal component analysis with catchment forest composition and structure variables (in red) for 12 Black Brook streams (shown in black).

Table A5: Correlation matrix among stream morphology variables in 12 Black Brook (New Brunswick, Canada) streams. In green are significant ($p < 0.05$) and positive Pearson's correlation coefficients, and in red are significant and negative correlation coefficients. (LWD = large woody debris).

	Depth	% riffle	% run	% pool	% boulder	% cobble	% gravel	% sand	% silt	LWD
Width	0.09	0.45	-0.42	-0.06	0.08	0.25	0.49	-0.39	-0.69	-0.34
Depth		-0.18	0.10	0.26	0.13	-0.43	0.20	0.44	-0.12	0.07
% riffle			-0.92	-0.34	0.26	0.75	-0.01	-0.37	-0.73	-0.57
% run				-0.04	-0.27	-0.62	0.07	0.15	0.70	0.30
% pool					-0.06	-0.44	-0.08	0.57	0.17	0.69
% boulder						0.10	-0.63	0.13	-0.10	-0.20
% cobble							-0.16	-0.74	-0.40	-0.51
% gravel								-0.26	-0.51	-0.08
% sand									0.29	0.55
% silt										0.40

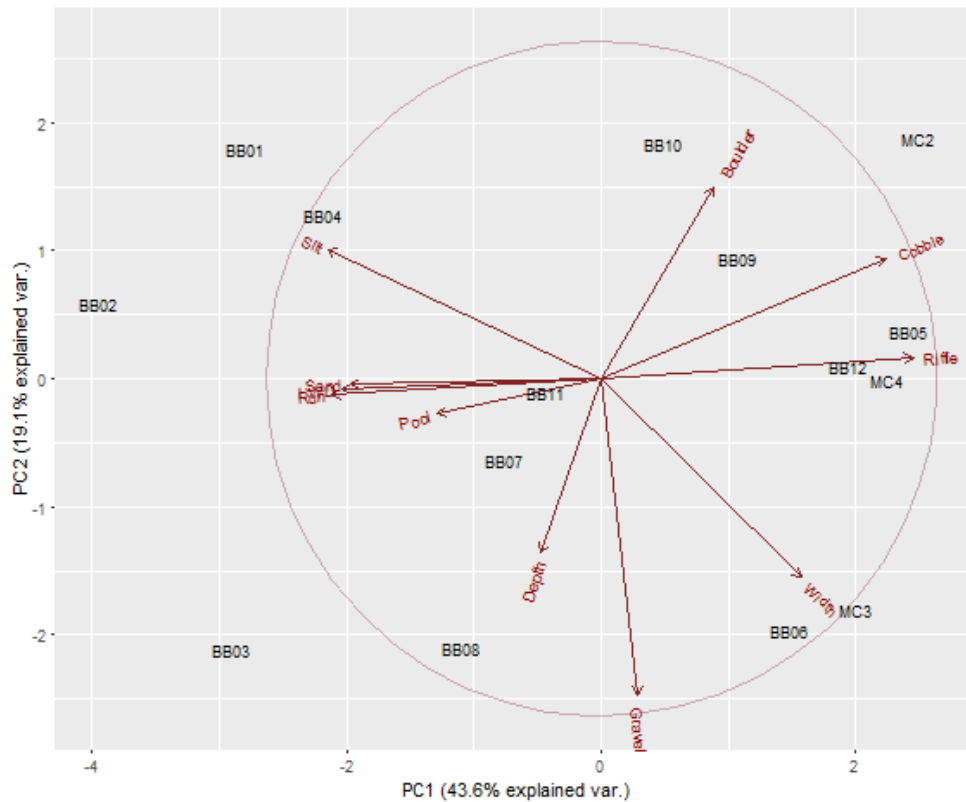


Figure A4: Principal component analysis with stream flow structure, substrate composition, width and depth variables (in red) for 12 Black Brook (BB_) and 3 Mount Carleton (MC_) streams (shown in black).

Table A6: Correlation matrix among landscape variables in 12 Black Brook (New Brunswick, Canada) catchments. In green are significant ($p < 0.05$) and positive Pearson's correlation coefficients, and in red are significant and negative correlation coefficients.

	Road density	Area	Stream length	% effVSA	Elevation	Slope
Crossings	0.78	0.01	-0.04	0.15	-0.53	-0.10
Road density		-0.07	-0.10	0.25	-0.74	-0.35
Area			0.99	-0.39	0.20	-0.39
Stream length				-0.44	0.24	-0.35
% effVSA					-0.48	0.23
Elevation						0.47

Landscape PCA

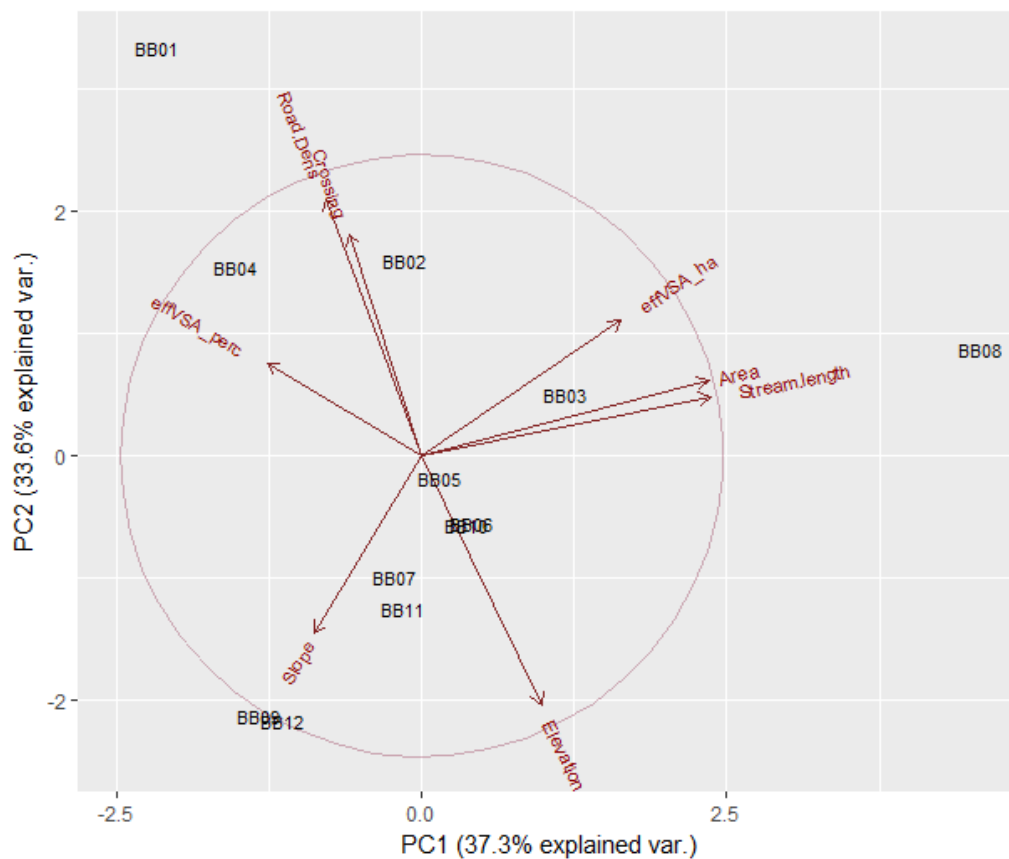


Figure A5: Principal component analysis with landscape variables (in red) for 12 Black Brook catchments (shown in black).

Table A7: Correlation matrix among riparian forest condition variables in 12 Black Brook (New Brunswick, Canada) streams. In green are significant ($p < 0.05$) and positive Pearson's correlation coefficients, and in red are significant and negative correlation coefficients. (US = understory vegetation, OS = overstory vegetation).

	% conifer	% deciduous	% mixed	Canopy	Richness	US richness	OS richness
P90 <5m	-0.48	0.30	0.32	-0.44	0.29	0.23	0.26
	% conifer	-0.52	-0.87	-0.16	-0.05	-0.18	0.06
		% deciduous	0.16	-0.20	-0.36	-0.39	-0.15
			% mixed	0.19	0.20	0.35	0.04
				Canopy	-0.30	-0.17	-0.49
					Richness	0.94	0.57
						US richness	0.36

Riparian forest PCA

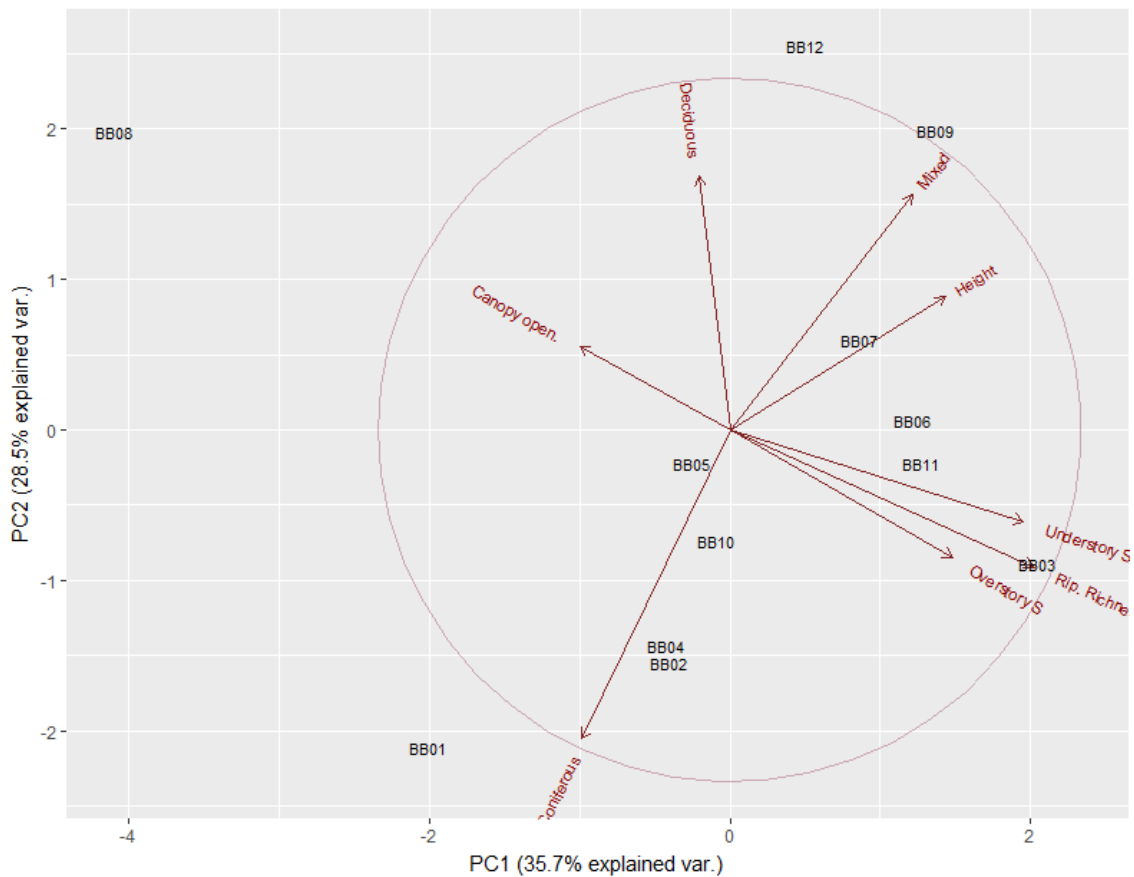


Figure A6: Principal component analysis with 2014 forest harvest variables (in red) for 12 Black Brook catchments (shown in black).

Table A8: Summary of the correlation matrix between explanatory variables (rows) and fine inorganic sediments (FIS, <0.25 mm), total inorganic sediments (TIS, all size classes), leaf inorganic mass (LIM) and biofilm inorganic mass (BIM) for 2014 and 2015 sampling seasons. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown. In bold are the explanatory variables that were present in all three response variables. ^ after correlation coefficient represents p value between 0.05 and 0.1; ^^ represents p value between 0.1 and 0.2; and no sign represents $p < 0.05$.

		2014			2015				
		FIS	LIM	BIM	FIS	LIM	BIM		
Catchment	Harvest	Partial <5 y			-0.70	Total <5 y	0.53 ^	0.52 ^	
						Clearcut <5 y	0.52 ^	0.83	
						Clearcut <10 y		0.70	
	Landscape	Road crossings	0.78	0.69	0.91	Road crossings	0.64	0.67	0.78
		Road density	0.65	0.86	0.74	Road density	0.77	0.86	0.91
		Elevation	-0.60	-0.89	-0.57 ^	Elevation	-0.77	-0.90	-0.70
		Slope		-0.55 ^					
	Forest	% mixed		-0.60 ^		% deciduous		-0.57	-0.54 ^
		% deciduous		-0.51 ^^					
		CC2			-0.67				
Reach	Riparian	% P90 >5 m		-0.59 ^		% P90 >5 m	-0.79	-0.68	-0.51 ^
		% coniferous	0.60 ^	0.84	0.63	% coniferous	0.58	0.77	0.69
		% deciduous	-0.50		-0.67	% deciduous			-0.66
		% mixed		-0.77		% mixed		-0.61	
	Stream	Width	-0.61	-0.66	-0.71	Width	-0.60	-0.66	-0.68
		% riffle	-0.76	-0.67		% riffle	-0.79	-0.71	-0.52 ^
		% run	0.73	0.69	0.56 ^	% run	0.79	0.70	0.56 ^
		% cobble	-0.82			% silt	0.79	0.81	0.92
		% sand	0.58						
		% silt	0.74	0.79	0.88				
	Water	WC_PC1	0.69	0.82	0.55 ^	WC_PC1	0.72	0.87	0.71
		SUVA		0.82	0.56 ^	SUVA	0.93	0.85	0.66
						DOM_PC1	-0.86	-0.71	

Table A9: Summary of the correlation matrix between explanatory variables (rows) and water chemistry PC1, PC2 and DOM optical properties PC1 for 2014 and 2015 sampling seasons. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown. In bold are the explanatory variables that were present in both sampling years.

		Water chemistry PC1		Water chemistry PC2		SUVA				
		2014	2015	2014	2015	2014	2015			
Catchment	Harvest	Clearcut <5 y		0.54 ^	Clearcut <5 y	0.77		Clearcut <5 y	0.66	
		Total <5 y		0.79	Clearcut <10 y	0.76		Clearcut <10 y	0.65	
		Total <10 y	0.68	0.64	Clearcut <20 y	0.51 ^				
					Partial <10 y	-0.71	-0.69			
					Partial <20 y	-0.64	-0.72			
					Partial <30 y	-0.66	-0.71			
	Landscape	Road crossings	0.61	0.65				Road cross.	0.57	0.56 ^
		Road density	0.74	0.79				Road density	0.77	0.77
		Elevation	-0.92	-0.94				Elevation	-0.69	-0.63
		Slope	-0.57 ^	-0.54 ^						
	Forest	% mixed	-0.63	-0.62				% deciduous	-0.54 ^	-0.57
	Riparian	% coniferous	0.86	0.86	Canopy openness	0.62	0.65	% P90 >5 m	-0.88	-0.91
% mixed		-0.79	-0.78	% P90 >5 m	-0.81	-0.77	% coniferous	0.56	0.53	
% coniferous		0.86	0.86							
Stream	Width	-0.77	-0.78	% run	0.62	0.55 ^	% riffle	-0.71	-0.75	
	% riffle	-0.66	-0.66	% sand	-0.56 ^	-0.63	% run	0.77	0.81	
	% run	0.56 ^	0.59				% silt	0.75	0.71	
	% silt	0.71	0.74							
	LWD	0.58	0.53 ^							
Sediments	< 250 µm IN	0.69	0.72	< 250 µm IN		0.52 ^	< 250 µm IN		0.93	
	< 250 µm IN+OR	0.58 ^	0.66				< 250 µm IN+OR		0.88	
	% OR < 250 µm	-0.53 ^	-0.76				% OR < 250 µm	-0.68	-0.78	

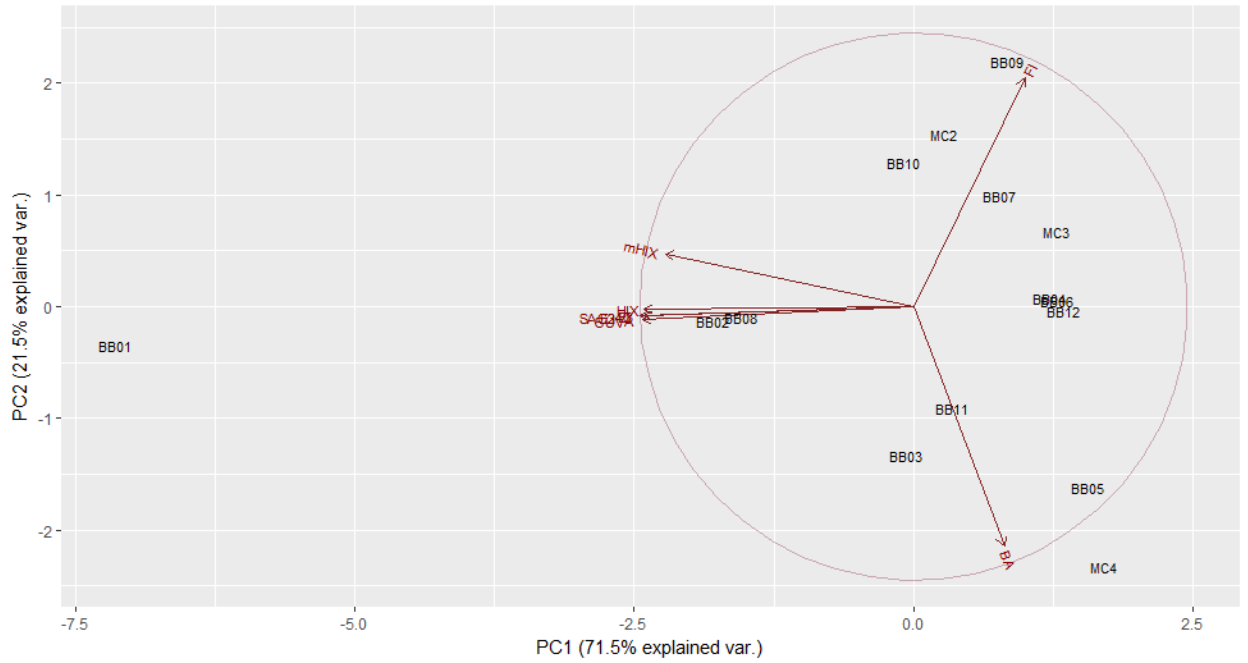


Figure A7: Principal component analysis with dissolved organic matter optical properties (in red) for 12 Black Brook (BB_) and 3 Mount Carleton (MC_) streams (shown in black).

Table A10: Summary of the correlation matrix between explanatory variables (rows) and averaged daily maximum August water temperatures for 2014 and 2015. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown. In bold are the explanatory variables that were present in both sampling years. ^ after correlation coefficient represents p value between 0.05 and 0.1; ^^ represents p value between 0.1 and 0.2; and no sign represents $p < 0.05$.

		Maximum August temperature		
		2014	2015	
Catchment	Harvest	Clearcut <5 y	0.80	
		Clearcut <10 y	0.79	0.58
		Total <30 y		-0.52 ^
	Landscape	Road crossing	0.53 ^	0.51 ^
		Road density	0.53 ^	0.58
Reach	Riparian	Canopy openness	0.57 ^	0.60
		% P90 >5 m	-0.73	-0.80
	Stream	% riffle	-0.80	-0.84
		% run	0.82	0.84
		% cobble	-0.59	-0.56 ^
		% silt	0.58	0.61
	Sediments	< 250 μm IN	0.67	0.75
		< 250 μm IN+OR	0.64	0.79
		% OR < 250 μm	-0.52 ^	-0.56 ^
	Water	WC_PC2	0.56 ^	0.65
		DOM_PC1	-	-0.86
		DOM - SUVA	0.63	0.82

Table A11: Summary of the correlation matrix between explanatory variables (rows) and percent leaf AFDM lost per degree-day for 2014 and 2015 sampling seasons. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown. In bold are the explanatory variables that were present in both sampling years. ^ after correlation coefficient represents *p* value between 0.05 and 0.1; ^^ represents *p* value between 0.1 and 0.2; and no sign represents *p*<0.05.

		2014	2015	
Catchment	Harvest	Total <5 y	-0.50 ^^	-0.68
		Total <10 y		-0.53 ^
	Landscape	Elevation	0.81	0.80
		Road density	-0.57 ^	-0.65
		Road crossings		-0.62
		Slope	0.67	
	Forest	S2	0.51 ^^	
		% coniferous		0.62
		% deciduous		-0.62
		% mixed	0.50 ^^	0.52 ^^
Reach	Riparian	% coniferous	-0.70	-0.75
		% deciduous		0.51 ^^
		% mixed	0.75	0.62
	Stream	Width		0.55 ^
		% riffle	0.73	0.52 ^
		% run	-0.61	
		% cobble	0.83	
		% silt	-0.51 ^	-0.59
		Large woody debris		-0.58
	Sediments	< 250 μm IN	-0.82	-0.58
		< 250 μm IN+OR	-0.77	-0.51 ^
		% OR < 250 μm	0.51 ^^	0.66
	Water	Chemistry PC1	-0.82	-0.88
		DOM - SUVA	-0.50 ^^	

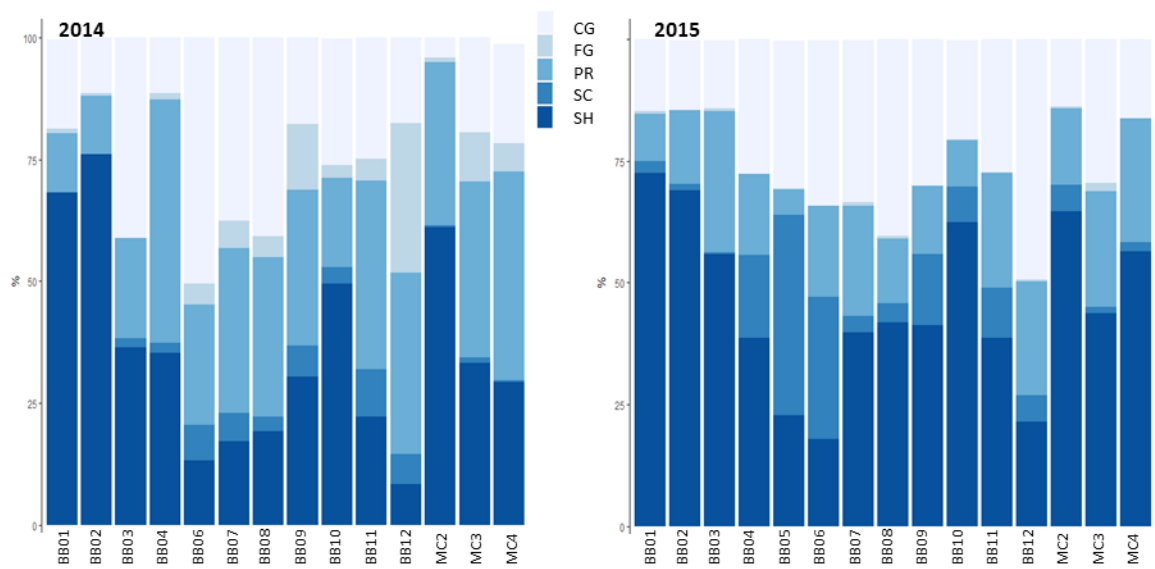


Figure A8: Proportion of benthic macroinvertebrates collected in leaf packs corresponding to each functional feeding group (CG = collector-gatherers; FG = filterer-collectors; PR = predators; SC = scrapers or grazers; SH = shredders) in 2014 and 2015 in 12 harvested Black Brook (BB_) and 3 reference Mount Carleton (MC_) streams (New Brunswick, Canada).

Table A12: Summary of the correlation matrix between explanatory variables (rows) and benthic macroinvertebrate abundance, richness and shredder proportion collected in leaf packs ($n = 6$) in 2014 and 2015. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown. In bold are the explanatory variables that were present in both sampling years. ^ after correlation coefficient represents p value between 0.05 and 0.1; ^^ represents p value between 0.1 and 0.2; and no sign represents $p < 0.05$.

			Abundance		Richness		% shredders	
			2014	2015	2014	2015	2014	2015
Catchment	Harvest	Partial <10 y			-0.63			
		Partial <20 y			-0.59^			
		Clearcut <5 y			0.53^			
		Clearcut <10 y				0.58		
		Total <5 y			0.52^^			
	Landscape	Area	0.95	0.58	0.59^	0.78		
		Stream length	0.97	0.59	0.59^	0.77		
		Road density					0.52^^	
		% effVSA				-0.54^	0.68	
		Elevation					-0.78	-0.59
	Forest	% coniferous					0.53^	
		% deciduous			-0.53^			
		% mixed					-0.54^	
		VCI			-0.50^^			
	Reach	Riparian	Canopy openness		0.72		0.61	
% P90 >5 m					-0.62		-0.53 ^	-0.63
% coniferous							0.79	0.57
% mixed							-0.65	
Richness						-0.66		
% P90 >5 m					-0.62		-0.53 ^	-0.63
Stream		Width						-0.52^
		Depth		0.58		0.62		
		% riffle						-0.78
		% run						0.65
		% cobble						-0.57^
		% silt						0.69
		LWD						0.57^
Sediments		LIM					0.77	0.70
		< 250 μ m IN					0.61	0.75
		< 250 μ m IN+OR						0.88
		% OR < 250 μ m					-0.63	-0.72
Water		Chemistry PC1					0.76	0.57^
		DOM - SUVA					0.68	0.66
Temperature		Max. August	0.60^		0.76	0.52^		0.67
Leaf		Decomposition					-0.64	
Biofilm	% organic						-0.67	
	Total biomass					0.65		
	Algal biomass		0.54^					

Table A13: Correlation between catchment and reach variables, and leaf pack benthic macroinvertebrate community non-metric multidimensional scaling (NMDS) ordinations for 12 harvested Black Brook streams (New Brunswick, Canada) in 2014 and 2015. Numbers correspond to squared correlation coefficients after fitting variables to NMDS ordination as linear vectors; only significant correlations ($p < 0.1$) are shown; numbers in bold correspond to correlations with $p < 0.05$. Variable names in bold mean that a variable was significantly correlated ($p < 0.05$) in both years.

			2014	2015
Catchment	Harvest	PC1		
		PC2	0.45	
	Landscape	Road density		0.39
		% effVSA		
	Forest	FC_PC1		0.47
		FC_PC2		
Reach	Riparian	Canopy openness		
		% riparian conifer	0.59	
	Stream	Morphology PC1	0.78	0.73
	Abiotic indicators	LIM	0.55	0.56
		WC PC1	0.70	0.60
		WC PC2	0.50	
		SUVA	0.57	0.58
MAT		0.74	0.60	

Table A14: Summary of the correlation matrix between explanatory variables (rows) and biofilm biomass and chlorophyll-a content for 2014 and 2015 sampling seasons. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown. In bold are the explanatory variables that were present in both sampling years.

		AFDM			Chlorophyll a		
			2014	2015		2014	2015
Catchment	Harvest	Clearcut <5 y	0.55 ^	0.54 ^			
		Clearcut <10 y	0.54 ^				
	Landscape	Road density	0.66	0.72			
		% effVSA	0.60				
		Elevation	-0.66				
	Forest	S10		-0.52 ^			
Reach	Riparian	Overstory richness		-0.56 ^	Canopy openness	0.55 ^	0.58
		% P90 >5 m	-0.69				
		% deciduous	-0.61	-0.55 ^			
	Stream	% Silt	0.85	0.63			
		% Run	0.62				
		% Riffle	-0.68				
	Sediment	Leaf inorganic mass	0.68	0.55 ^	< 250 µm O	0.54 ^	
		< 250 µm IN		0.53 ^			
		< 250 µm IN+OR		0.54 ^			
	Water	Chemistry PC1	0.51 ^				
		Chemistry PC2	0.64				
		DOM - SUVA	0.87	0.53 ^			

Table A15: Summary of AICc model selection for linear regression models with biotic stream indicators as response variables (leaf decomposition, BMI abundance and richness, % shredders BMIs, biofilm and algal biomass) and abiotic indicators as explanatory variables for 2014 and 2015 in 12 Black Brook streams (NB, Canada). The abiotic explanatory variables included in the four best regression models are presented, as well as their corresponding $\Delta AICc$, weight (%) and R^2 (R^2 for simple regression models and adjusted R^2 for multiple regression models). The symbol at the end of each variable indicates the sign of the coefficient for that variable within that regression model. In bold are the best models (lowest AICc value). (WC_PC1 = water chemistry PC1, LIM = leaf inorganic mass, MAT = maximum August temperature).

		Catchment	$\Delta AICc$	ω_i	R^2	
Leaf decomposition	2014	WC_PC1 (-)	0	40.5	0.70	
		WC_PC1 (-) & MAT (-)	1.24	21.7	0.74	
		LIM (-)	2.53	11.4	0.63	
		WC_PC1 (-) & LIM (-)	3.99	5.5	0.67	
	2015	WC_PC1 (-)	0	62.0	0.77	
		WC_PC1 (-) & MAT (-)	3.3	11.9	0.75	
		WC_PC1 (-) & SUVA (+)	4.25	7.4	0.73	
		WC_PC1 (-) & WC_PC2 (+)	4.38	6.9	0.73	
BMI abundance	2014	MAT (+) & SUVA (-)	0	49.8	0.64	
		MAT (+) & LIM (-)	1.75	20.7	0.58	
		MAT (+)	3.56	8.4	0.36	
		-	4.49	5.3	0	
	2015	LIM (-) & MAT (+)	0	32.2	0.45	
		-	1.17	17.9	0	
		SUVA (-) & MAT (+)	2.75	8.2	0.31	
		LIM (-)	3.18	6.6	0.13	
	BMI richness	2014	MAT (+)	0	46.0	0.57
			MAT (+) & WC_PC1 (-)	1.26	24.5	0.63
			MAT (+) & LIM (-)	2.92	10.7	0.56
			MAT (+) & SUVA (-)	4.13	5.8	0.51
2015		MAT (+)	0	21.8	0.27	
		-	0.17	20.0	0	
		MAT (+) & SUVA (-)	0.82	14.5	0.36	
		MAT (+) & LIM (-)	1.20	12.0	0.34	
% shredder BMIs	2014	SUVA (+) & WC_PC2 (-)	0	55.7	0.76	
		LIM (+)	3.01	12.4	0.6	
		WC_PC1 (+)	3.57	9.3	0.58	
		SUVA (+) & WC_PC2 (-) & MAT (+)	5.7	3.2	0.77	
	2015	LIM (+)	0	20.6	0.50	
		SUVA (+) & WC_PC2 (-)	0.79	13.9	0.64	
		MAT (+)	0.94	12.9	0.46	
		SUVA (+)	1.39	10.3	0.43	
Biofilm	2014	SUVA (+)	0	69.9	0.76	
		SUVA (+) & MAT (-)	4.25	8.4	0.77	
		SUVA (+) & WC_PC2 (-)	4.98	5.8	0.76	
		SUVA (+) & LIM (-)	5.00	5.7	0.76	
		LIM (+)	0	21.5	0.30	

Algal biomass	2015	SUVA (+)	0.31	18.3	0.28
		-	0.58	16.1	0
		WC_PC2 (+)	1.74	9.0	0.19
	2014	-	0	54.0	0
		WC_PC1 (-)	3.69	8.5	0.02
		SUVA (-)	3.82	8.0	0.004
		WC_PC2 (+)	3.92	7.6	0.004
	2015	-	0	48.3	0
		WC_PC2 (+)	3.48	8.5	0.01
		LIM (-)	3.49	8.4	0.01
		MAT (-)	3.56	8.2	0.009



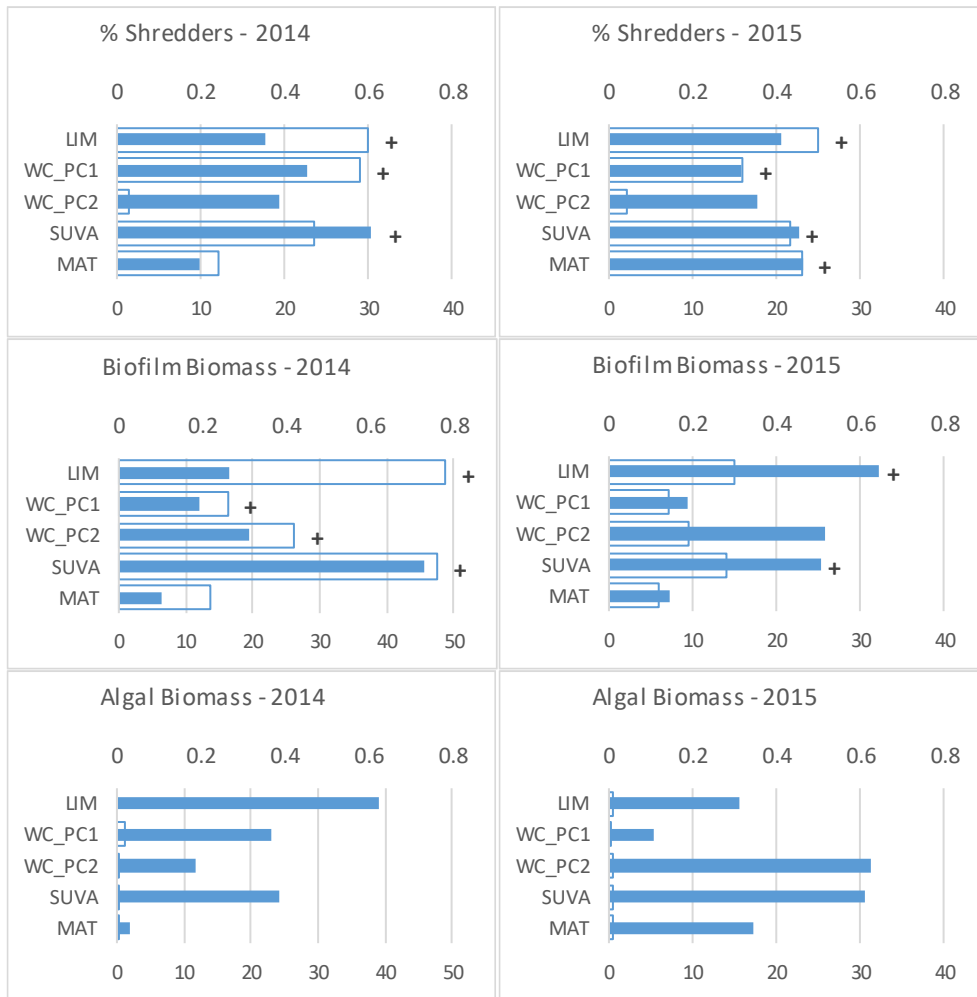


Figure A9: Distribution of the percentage of independent effect of each abiotic stream explanatory variable on the variability of biotic stream indicators (leaf decomposition, BMI abundance and richness, % shredders BMIs, biofilm and algal biomass) in 2014 and 2015 (dark bars, bottom X axis) in 12 Black Brook streams (NB, Canada). The wider white bars and the top X axis represent the R^2 of the simple linear regression between that explanatory variable and the response variable; the + or – signs correspond to the slope of significant univariate regression models at $\alpha = 0.1$. (WC_PC1 = water chemistry PC1, LIM = leaf inorganic mass, MAT = maximum August temperature).

Appendix II: Chapter 3

Table A16: Results of mixed model ANOVA testing for differences between predators with (w) and without (wo) guts in C and N isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), content (% C and % N) and C:N ratio. Samples were collected in 12 Black Brook and 3 Mount Carleton streams in 2014 (New Brunswick, Canada). Column w-wo describes the effect size or differences between predators with and without guts (positive values mean $w > wo$ and negative values $w < wo$). Column “overall” indicates that all taxa were pooled together and that taxon was treated as a fixed factor; if the interaction between gut removal and taxon was significant, the results for that model have been shaded. In bold are significant values at $\alpha = 0.05$.

	Overall *			<i>Rhyacophila</i> **			<i>Sweltsa</i> **			<i>Diura</i> **		
	w-wo	F	p	w-wo	F	p	w-wo	F	p	w-wo	F	p
$\delta^{13}\text{C}$	~0	~0	~1	-0.02	<0.001	0.98	-0.33	4.50	0.05	0.31	1.68	0.22
$\delta^{15}\text{N}$	-0.06	0.2	0.70	0.12	0.10	0.75	-0.13	0.55	0.47	-0.09	0.94	0.35
% C	-1.50	29.9	<0.001	-1.28	2.62	0.16	-2.88	26.8	<0.001	-1.50	8.1	0.01
% N	-0.78	14.0	<0.001	0.42	2.9	0.14	-1.12	40.2	<0.001	-0.79	30.9	<0.001
C:N	0.14	0.07	0.80	-0.28	7.9	0.03	0.18	6.8	0.02	0.14	5.3	0.04

Note: * $\delta^{13}\text{C}/\delta^{15}\text{N}/\%C/\%N/C:N \sim \text{Guts (yes/no)} * \text{Taxon} + (1|\text{Stream})$ model tested.

** $\delta^{13}\text{C}/\delta^{15}\text{N}/\%C/\%N/C:N \sim \text{Guts (yes/no)} + (1|\text{Stream})$ model tested.

Table A17: Summary of correlations between taxa from one same functional feeding group in dietary contributions of algae (Φ_A), CPOM (Φ_C) and FPOM (Φ_F) to each taxon. Food web sampling was conducted in September 2014 and 2015 in 12 Black Brook streams (New Brunswick, Canada), and dietary contributions were calculated with MixSIAR. In bold are significant Pearson correlation coefficients.

	2014			2015		
	Φ_A	Φ_C	Φ_F	Φ_A	Φ_C	Φ_F
Collector-filterers: <i>Parapsyche</i> vs. Philopotamidae	0.58	0.27	0.50	0.69	0.72	0.70
Predators: <i>Diura</i> vs. <i>Sweltsa</i>	0.74	0.60	0.76	0.95	0.69	0.91
Scrapers: <i>Baetis</i> vs. Heptageniidae	0.55	0.91	0.65	0.96	0.97	1.00

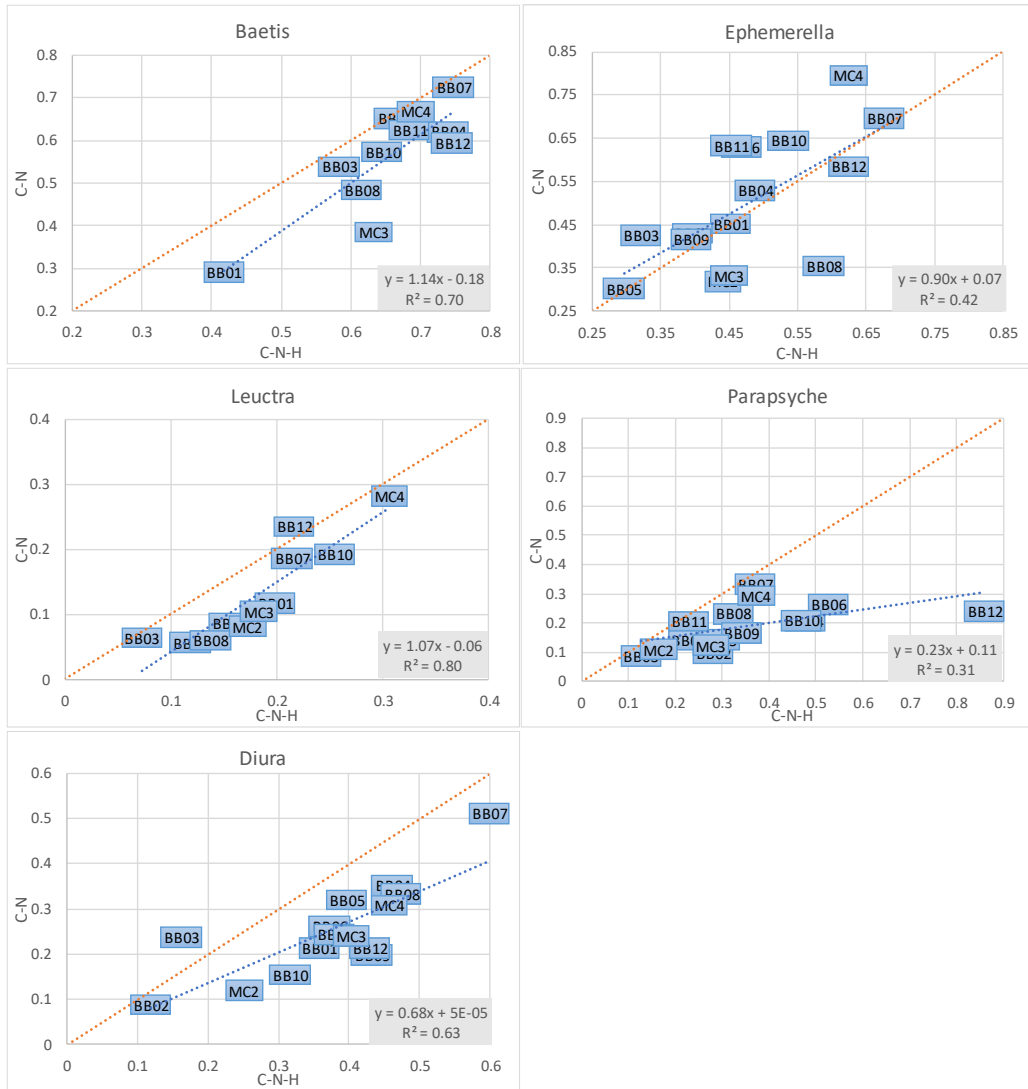


Figure A10: Relationships between the median algal contribution to the diets of 5 consumer taxa calculated based on 2-isotope (Y axis, CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and 3-isotope (X axis, CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) mixing models in 12 Black Brook (harvested, BB) and 3 Mount Carleton (reference, MC) streams in 2015, New Brunswick, Canada. In blue is the fitted linear regression line, and in red the 1:1.

Table A18: Summary of the correlation matrix between explanatory variables (rows) and the contribution of algae, CPOM and FPOM to the diet of *Baetis* in 12 Black Brook streams (New Brunswick, Canada). Dietary contributions were calculated with a Bayesian 2-isotope mixing model (CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in 2014 and 2015, and with a Bayesian 3-isotope mixing model (CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) in 2015. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown.

<i>Baetis</i>		ALGAE			CPOM			FPOM		
		2014	2015		2014	2015		2014	2015	
		CN	CNH		CN	CNH		CN	CNH	
Management	PH_5y								0.59	
	PH_30y						-0.55			
	TOT_5y								0.53	
	TOT_10y	-0.54						0.54		
	TOT_20y			0.53						
	Crossings	-0.53	-0.54			0.56		0.52		
Forest	Road density	-0.52	-0.68			0.77	0.63	0.57		
	% deciduous					-0.63	-0.60			
	% mixed	0.57						-0.63		
Landscape	P90					-0.68	-0.53			
	Elevation	0.64	0.58	0.60	0.55		-0.54	-0.80	-0.53	
Riparian	% effVSA			-0.51		0.57	0.69	0.51		
	% P90>5 m		0.87	0.72		-0.74	-0.78		-0.71	
	% conifer		-0.57	-0.58				0.57	0.54	
Stream	% mixed		0.56	0.60					-0.64	-0.72
	Width	0.74	0.51					-0.83		
	Depth					-0.72	-0.74		0.54	
	% riffle	0.57	0.72	0.52				-0.65	-0.80	
	% run	-0.58	-0.84	-0.62		0.55	0.55	0.61	0.84	
Sediments	LWD	-0.55	-0.51					0.62		
	Leaf IN	-0.54	-0.81	-0.72	-0.56	0.69	0.78	0.71	0.67	
	Fine IN	-0.50	-0.91	-0.69		0.79	0.82	0.64	0.74	
	Fine IN+OR		-0.88	-0.62		0.76	0.76		0.77	
Water	% OR	0.77	0.90	0.62		-0.73	-0.71	-0.80	-0.80	
	WC_PC1	-0.70	-0.61	-0.56				0.79	0.55	
DOM	WC_PC2		-0.72	-0.64					0.52	
	DOM_PC1	NA	0.87	0.72	NA	-0.72	-0.78	NA	-0.74	
	SUVA	-0.58	-0.91	-0.78		0.80	0.85	0.68	0.75	
	HIX	NA	-0.91	-0.76	NA	0.76	0.83	NA	0.76	
Biofilm	FI	NA	0.70	0.74	NA	-0.54	-0.64	NA	-0.62	
	Biomass				-0.52					
	Algae biomass	0.60			-0.69			0.56	-0.51	
Leaf decomposition		AI	0.58		-0.70					
							-0.52	-0.59		

Table A19: Summary of the correlation matrix between explanatory variables (rows) and the contribution of algae, CPOM and FPOM to the diet of *Ephemera* in 12 Black Brook streams (New Brunswick, Canada). Dietary contributions were calculated with a Bayesian 2-isotope mixing model (CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in 2014 and 2015, and with a Bayesian 3-isotope mixing model (CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) in 2015. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown.

<i>Ephemera</i>		ALGAE		CPOM		FPOM	
		2014	2015	2014	2015	2014	2015
		CN	CNH	CN	CNH	CN	CNH
Management	CC_30y				-0.56		
	PH_5y					0.58	
	TOT_30y						0.66
	TOT_10y					0.50	
	Crossings					0.59	
	Road density					0.63	
Forest	% coniferous						0.63
	% mixed						-0.54
Landscape	Area	-0.52		0.61			
	Elevation					-0.77	
Riparian	% open canopy		0.71				
	% coniferous					0.71	
Stream	% mixed					-0.56	
	Width					-0.71	
	% riffle					-0.55	
	% gravel			0.68			
	% silt					0.77	
	LWD				0.60		
Sediments	Biofilm IN					0.64	
	Leaf IN					0.80	
	Fine IN					0.66	
	Fine IN+OR					0.58	
Water	WC_PC1					0.73	
DOM	SUVA					0.57	
	BA						-0.53
Biofilm	Biomass					0.61	
	Algae biomass		0.58	-0.61			
	AI	0.59		-0.60			
Leaf decomposition							-0.58

Table A20: Summary of the correlation matrix between explanatory variables (rows) and the contribution of algae, CPOM and FPOM to the diet of *Leuctra* in 12 Black Brook streams (New Brunswick, Canada). Dietary contributions were calculated with a Bayesian 2-isotope mixing model (CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in 2014 and 2015, and with a Bayesian 3-isotope mixing model (CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) in 2015. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown.

<i>Leuctra</i>		ALGAE			CPOM			FPOM		
		2014	2015		2014	2015		2014	2015	
		CN	CNH		CN	CNH		CN	CNH	
Management	CC_5y	-0.56						0.68		
	CC_30y				-0.59			0.57		
	PH_5y				-0.56			0.52	0.53	
	PH_10y				0.81			-0.59		
	PH_30y				0.59			-0.60		
	TOT_5y		-0.62		-0.82			0.94	0.58	
	TOT_20y		0.61	0.64	0.74			-0.50		
	Crossings					0.60	0.69			-0.55
	Road density					0.86	0.88			-0.80
Forest	% deciduous	0.55				-0.64	-0.66			0.56
	P90	0.51				-0.71	-0.63			0.62
Landscape	% effVSA					0.74	0.58			-0.50
	Elevation					-0.61	-0.68			
Riparian	Area		-0.60					0.51	0.68	0.55
	% P90>5 m					-0.68	-0.64	-0.53		0.63
	% conifer		-0.54							
Stream	% mixed	0.57	0.70							
	Depth					-0.87	-0.85		0.72	0.83
	% boulder	0.56		0.52						
Sediments	% silt					0.64	0.63			-0.63
	Biofilm IN					0.74	0.76			-0.79
	Leaf IN					0.78	0.84			-0.70
	Fine IN					0.79	0.80			-0.68
	Fine IN+OR					0.73	0.74			-0.66
Water	% OR					-0.72	-0.74			0.59
	WC_PC1	-0.50	-0.55			0.61	0.64			
DOC	WC_PC2				-0.58	0.52	0.51	0.58		-0.53
	DOM_PC1					-0.73	-0.69			0.66
	SUVA					0.77	0.76			-0.67
	HIX					0.78	0.77			-0.68
	FI		0.74	0.50		-0.50				
Biofilm	BA		-0.54	-0.82						0.55
	Biomass					0.74	0.76		-0.60	-0.81
Leaf decomposition	AI	0.66								
			0.62	0.52		-0.58	-0.66			

Table A21: Summary of the correlation matrix between explanatory variables (rows) and the contribution of algae, CPOM and FPOM to the diet of *Parapsyche* in 12 Black Brook streams (New Brunswick, Canada). Dietary contributions were calculated with a Bayesian 2-isotope mixing model (CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in 2014 and 2015, and with a Bayesian 3-isotope mixing model (CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) in 2015. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown.

<i>Parapsyche</i>		ALGAE		CPOM		FPOM	
		2014	2015	2014	2015	2014	2015
		CN	CNH	CN	CNH	CN	CNH
Management	PH_5y			-0.64		0.52	
	Crossings					-0.54	
Forest	% deciduous				-0.60		
	% mixed						-0.54
	P90			-0.62		0.60	0.51
	S2			0.80		-0.71	-0.61
Landscape	% effVSA				0.75		
Riparian	% P90>5 m			-0.55	-0.72		
	% open canopy	0.56					
Stream	Depth			-0.65	-0.61	0.50	0.52
	% riffle	0.57	0.61				
	% run		-0.54				
	% cobble	0.70					
	LWD					0.55	
Sediments	Leaf IN				0.68		
	Fine IN	-0.50		0.59	0.81		
	Fine IN+OR	-0.59		0.62	0.83		
	% OR	0.54			-0.60		
Water	WC_PC2				0.54		
DOC	DOM_PC1			-0.58	-0.78		
	SUVA			0.57	0.77		
	HIX	-0.60		0.56	0.79		
Biofilm	Biomass					-0.55	-0.51
	Algae biomass	0.86					
	AI	0.67				-0.56	

Table A22: Summary of the correlation matrix between explanatory variables (rows) and the contribution of algae, CPOM and FPOM to the diet of *Diura* in 12 Black Brook streams (New Brunswick, Canada). Dietary contributions were calculated with a Bayesian 2-isotope mixing model (CN: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in 2014 and 2015, and with a Bayesian 3-isotope mixing model (CNH: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^2\text{H}$) in 2015. Only variables with correlation coefficients > 0.5 (in green) or < -0.5 (in red) are shown.

<i>Diura</i>		ALGAE		CPOM		FPOM		
		2014	2015	2014	2015	2014	2015	
		CN	CNH	CN	CNH	CN	CNH	
Management	CC_10y		0.52					
	PH_5y				-0.51		0.58	
	PH_30y				-0.57			
Forest	% mixed		0.53					
	S10				-0.59			
Landscape	% effVSA	-0.72				0.71		
Riparian	% open canopy		0.58	-0.62				
Stream	Depth			-0.50	-0.60			
	% pool			-0.51	-0.74	0.56	0.50	
	% sand			-0.53	-0.72		0.72	
	LWD	-0.75	-0.60			0.81	0.69	
Sediments	Fine OR			-0.71				
	Fine OR+IN			-0.51				
	% OR		0.58	0.57				
Water	WC_PC2				0.53		-0.54	
Biofilm	Biomass					0.56		
	Algae biomass		0.75	0.81	-0.67		-0.71	-0.51
	Autotrophic index		0.57	0.66	-0.54		-0.56	
	% OR	0.52					-0.53	-0.60
Food web length			-0.55	-0.59			0.68	0.51

Appendix III: Chapter 4

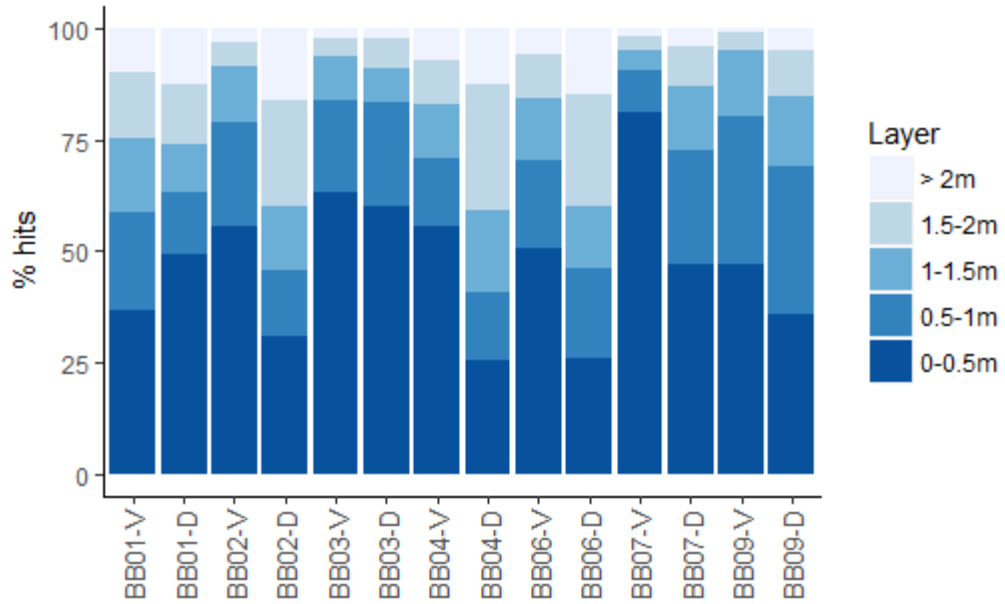


Figure A11: Proportion of vegetation “hits” recorded in each height class (i.e., vegetation density) at the understory vegetation plots at variable source area (V) and dry (D) sites in 7 Black Brook streams (New Brunswick, Canada).

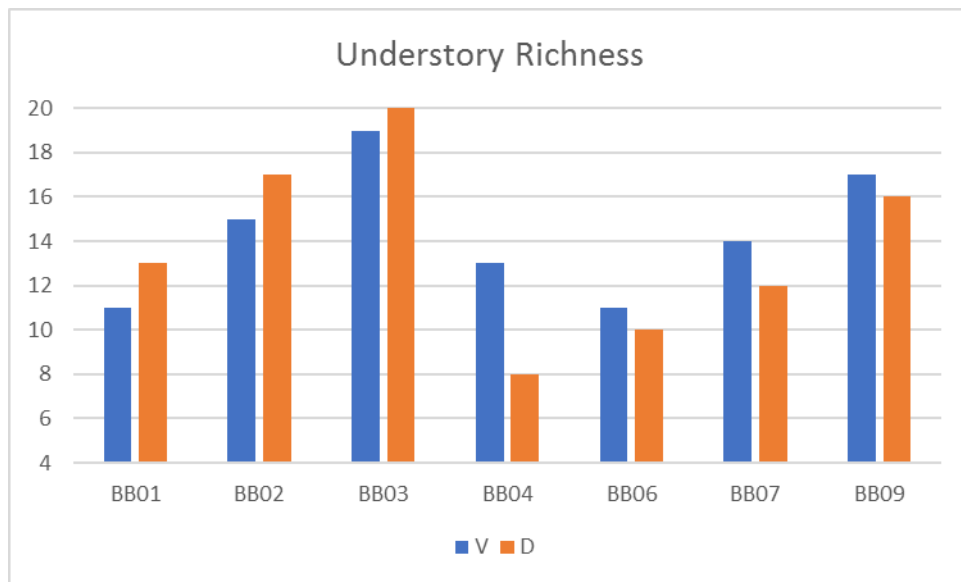


Figure A12: Woody understory vegetation (<7 cm DBH) richness (number of species) recorded at variable source area (V, in blue) and dry (D, in orange) sites in 7 Black Brook streams (New Brunswick, Canada).

Table A23: Results of mixed model ANOVA testing for differences between VSA (variable source area, V) and dry (D) stream-side sites on understory and overstory riparian vegetation composition and structure at 7 Black Brook streams (New Brunswick, Canada). Column V-D describes the effect size or differences between V and D (positive values mean V>D and negative values V<D). In bold are significant values at $\alpha = 0.1$.

	Layer	Composition			Structure					
		Richness			Density (# hits)			Vertical distribution (% hits)		
		V-D	F	p	V-D	F	p	V-D	F	p
Understory (<5 cm DBH)	> 2m				3.57	0.15	0.71	-0.42	0.04	0.85
	1.5-2m				7.14	0.57	0.46	2.1	0.73	0.43
	1-1.5m	-1.29	1.3	0.3	5.71	0.38	0.55	2.2	0.89	0.36
	0.5-1m				10	0.78	0.39	4	5.06	0.06
	0-0.5m				-3	0.1	0.76	-7.9	1.06	0.32
	Total	-0.54	0.4	0.54	12.3	0.51	0.5	-	-	-
	Overstory (>5 cm DBH)	Richness								
	V-D	F	p							
	-0.29	0.25	0.63							

Note: Vegetation parameter \sim VSA/dry + (1|Stream) model tested.

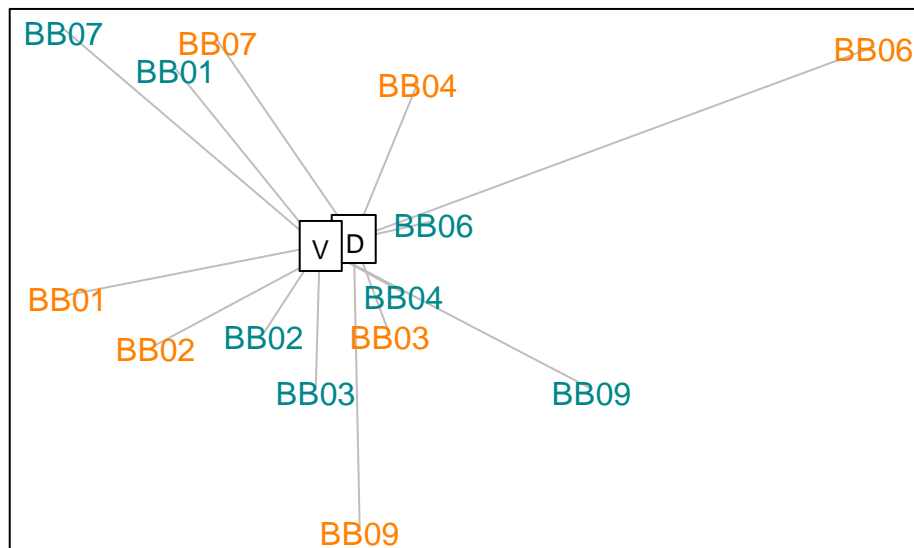


Figure A13: NMDS of riparian understory woody vegetation (DBH<5 cm) based on abundance community data at variable source area (blue, V) and dry (orange, D) sites in 7 Black Brook streams (New Brunswick, Canada) (stress value = 0.11). Boxes represent group (V or D) centroids.

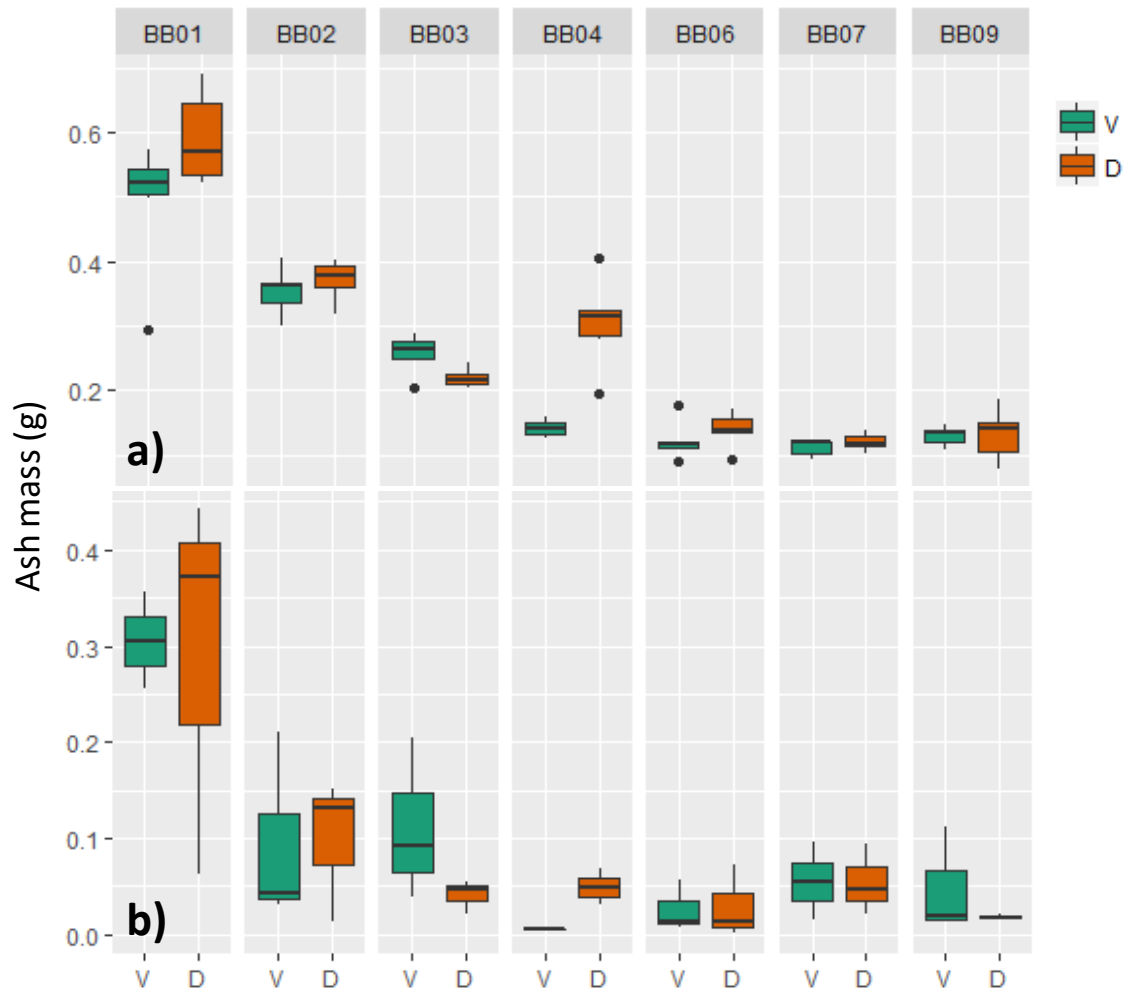


Figure A14: Inorganic mass in a) coarse-mesh leaf packs and b) biofilm tiles, at variable source area (V) and dry (D) sites in 7 Black Brook streams (New Brunswick, Canada). (The upper and lower hinges of each box correspond to the upper and lower quartiles, and the line in between to the median; the whiskers correspond to values higher or lower than the third and first quartiles; dots represent outliers or values that are higher or lower than 1.5 times the interquartile range).

Table A24: Results of mixed model ANOVA testing for differences between VSA (variable source area, V) and dry (D) stream-side sites on physical and chemical water parameters at 7 Black Brook streams (New Brunswick, Canada) and 3 sampling times (August, September and October). Column V-D describes the effect size or differences between V and D (positive values mean V>D and negative values V<D). In bold are significant values at $\alpha = 0.1$. Column “Aug+Sep+Oct” indicates that the three sampling times were pooled together and that sampling time was treated as a fixed factor; if the interaction between VSA/dry and sampling time was significant, the results for that model are shaded.

	Aug + Sep + Oct*			August**			September**			October**		
	V-D	F	p	V-D	F	p	V-D	F	p	V-D	F	p
Temperature	-0.4	0.57	0.46	-0.07	0.28	0.61	-0.73	3.23	0.12	-	-	-
% DO	-4.44	8.79	0.008	-1.66	2.23	0.18	-7.2	8.44	0.03	-	-	-
pH	-0.009	0.34	0.56	0.007	0.09	0.77	-0.008	0.08	0.79	-0.02	0.95	0.37
Conductivity	1.29	0.16	0.69	0.88	0.23	0.65	1.59	0.60	0.46	1.4	0.59	0.47
Alkalinity	0.006	0.03	0.87	0.008	0.18	0.68	-0.004	0.03	0.86	0.01	0.51	0.50
Ca	1.12	1.44	0.24	-0.5	0.79	0.41	2.5	3.58	0.10	1.39	2.72	0.15
K	0.008	0.18	0.67	-0.0008	0.02	0.89	0.04	2.29	0.18	-0.015	2.01	0.21
Mg	0.11	0.81	0.37	-0.015	0.05	0.82	0.32	4.03	0.09	0.03	0.07	0.80
Na	0.02	0.28	0.60	-0.001	0.04	0.84	0.09	2.8	0.14	-0.02	0.54	0.49
SO ₄	-0.03	0.45	0.50	-0.02	0.42	0.54	-0.057	2.04	0.20	-0.02	0.28	0.61
Cl	-0.003	0.07	0.80	0.002	0.06	0.80	-0.009	0.93	0.37	-0.001	0.017	0.90
SiO ₂	-0.01	0.02	0.89	-0.03	0.17	0.69	0	0	1.00	-0.001	0.0003	0.99
DOC	-0.15	7.10	0.01	-0.15	7.10	0.04	-0.11	3.54	0.10	-0.28	17.2	0.006
DIC	-0.5	0.47	0.49	0.28	0.94	0.37	0.29	1.25	0.31	-2.1	2.08	0.20
TP	<0.001	0.06	0.81	0.0002	0.22	0.66	-0.001	2.48	0.17	0.001	3.38	0.11
TN	-0.02	0.27	0.60	-0.08	0.66	0.45	0.006	0.05	0.83	0.01	0.16	0.70
Al	-0.002	3.8	0.06	-0.001	0.19	0.67	-0.002	0.96	0.36	-0.002	1.94	0.20
Fe	<0.001	0.26	0.61	0	0	1.00	0.006	2.14	0.19	-0.004	4.30	0.08
Cu	<0.001	0.17	0.68	-0.0006	1.60	0.23	0.0004	3.11	0.12	-0.0002	0.12	0.74

Note: * Water parameter ~ VSA/dry * Sampling month + (1|Stream) model tested.

** Water parameter ~ VSA/dry + (1|Stream) model tested.

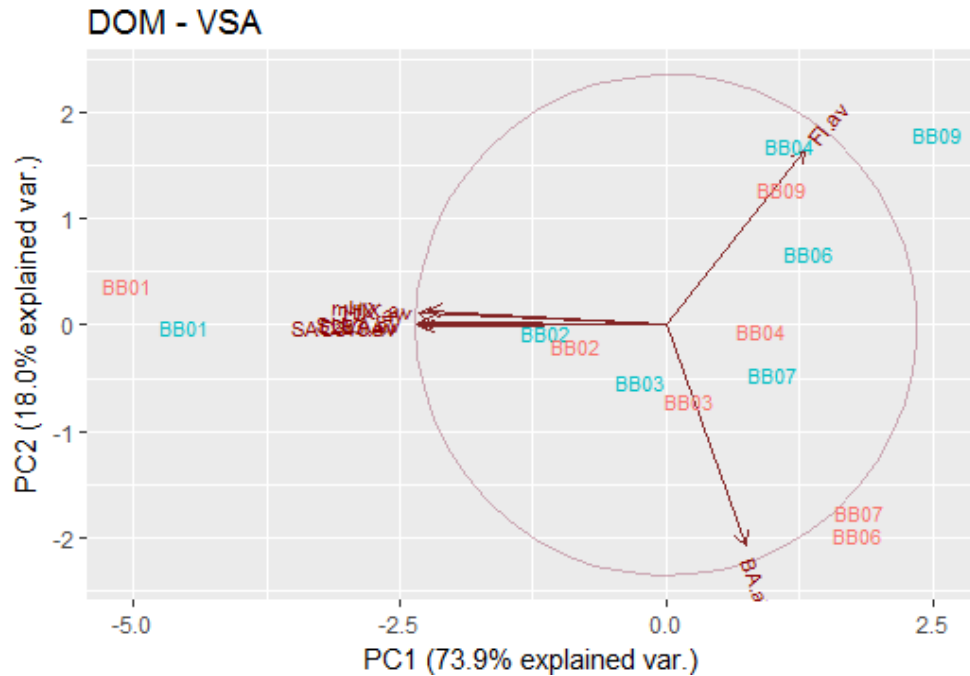


Figure A15: Principal component analysis with dissolved organic matter optical properties (indicated by red arrows) at variable source area (blue) and dry (red) sites in 7 Black Brook streams (New Brunswick, Canada) averaged for August, September and October 2015.

Table A25: Results of mixed model ANOVA testing for differences between VSA (variable source area, V) and dry (D) stream-side sites on DOM optical properties at 7 Black Brook streams (New Brunswick, Canada) and 3 sampling times (August, September and October). In bold are significant values at $\alpha = 0.1$. Column "Aug+Sep+Oct" indicates that the three sampling times were pooled together and that sampling time was treated as a fixed factor; no significant interaction were observed between VSA/dry and sampling time.

	Aug + Sep + Oct*			August**			September**			October**		
	V-D	F	p	V-D	F	p	V-D	F	p	V-D	F	p
BA	-0.05	2.87	0.10	-0.05	1.9	0.22	-0.03	0.21	0.66	-0.08	2.5	0.14
FI	0.14	1.75	0.20	0.007	0.01	0.94	-0.01	0.02	0.89	0.39	3.02	0.13
E2E3	-0.005	0.03	0.87	0.03	0.88	0.38	-0.0009	0.0003	0.98	-0.04	2.3	0.18
SAC340	-4.55	1.94	0.17	1.7	0.38	0.55	-0.97	0.06	0.80	-14.4	5.15	0.06
SUVA	-0.44	1.34	0.25	0.16	0.32	0.59	-0.29	0.002	0.96	-1.44	4.71	0.07
HIX	0.30	0.76	0.39	-0.15	0.08	0.78	-0.2	0.49	0.51	1.3	2.99	0.13
mHIX	0.01	0.51	0.48	0.007	0.09	0.77	0.004	0.029	0.87	0.02	0.39	0.55
PC1	-0.16	0.01	0.92	-	-	-	-	-	-	-	-	-
PC2	0.87	4.71	0.07	-	-	-	-	-	-	-	-	-

Note: * DOM quality parameter ~ VSA/dry * Sampling month + (1|Stream) model tested.

** DOM quality parameter ~ VSA/dry + (1|Stream) model tested.

Table A26: Results of mixed model ANOVA testing for differences between VSA (variable source area, V) and dry (D) stream-side sites on metrics describing benthic macroinvertebrate (BMI) community at 7 Black Brook streams (New Brunswick, Canada). Column V-D and US-DS describe the effect size or differences between V and D (positive values mean V>D and negative values V<D) and US and DS, respectively. In bold are significant values at $\alpha = 0.1$.

		V-D	F (V-D)	P (V-D)	US-DS	F (US-DS)	P (US-DS)
BMI community	Diversity	-0.14	1.58	0.22	-0.17	2.14	0.15
	Richness	0.44	0.35	0.56	-0.55	0.55	0.46
	Abundance	18.3	0.03	0.85	-0.5	~0	0.99
	Margalef's S	-0.02	0.01	0.91	-0.17	1.34	0.25
BMI functional feeding groups	Shredders (%)	-5.5	1.18	0.33	3.9	0.52	0.50
	Scrapers (%)	-4.2	2.00	0.22	-3.6	1.33	0.30
	Gatherers (%)	16.7	6.90	0.047	8.7	0.93	0.38
	Filterers (%)	1.88	0.18	0.68	-1.1	0.07	0.80
	Predators (%)	-8.9	5.77	0.06	-7.8	3.50	0.12
	Shredders (#)	-33	1.14	0.33	29.2	0.87	0.39
	Scrapers (#)	-3.4	4.35	0.09	-0.8	0.14	0.72
	Gatherers (#)	62	4.65	0.08	-4.1	0.01	0.92
	Filterers (#)	12.4	0.62	0.45	-8.9	0.31	0.59
	Predators (#)	-20.2	1.10	0.34	-15.8	0.62	0.46
BMI size	<i>Diura</i> (mm)	-0.25	1.50	0.27	-0.03	0.01	0.91
	<i>Ephemerella</i> (mm)	-0.55	22.8	0.005	-0.09	0.12	0.73
	<i>Sweltsa</i> (mm)	0.009	0.004	0.95	-0.07	0.20	0.67
	<i>Baetis</i> (mm)	0.03	0.03	0.85	0.08	0.26	0.62
	<i>Parapsyche</i> (mm)	0.94	0.57	0.48	0.67	0.28	0.62
	<i>Glossosoma</i> (mm)	-0.45	0.72	0.43	-1.08	12.33	0.02
	<i>Rhyacophila</i> (mm)	-2	3.74	0.08	-2.85	11.65	0.007

Note: * BMI endpoint ~ VSA/dry + (1|Stream) model tested.

** BMI endpoint ~ Upstream/downstream + (1|Stream) model tested.

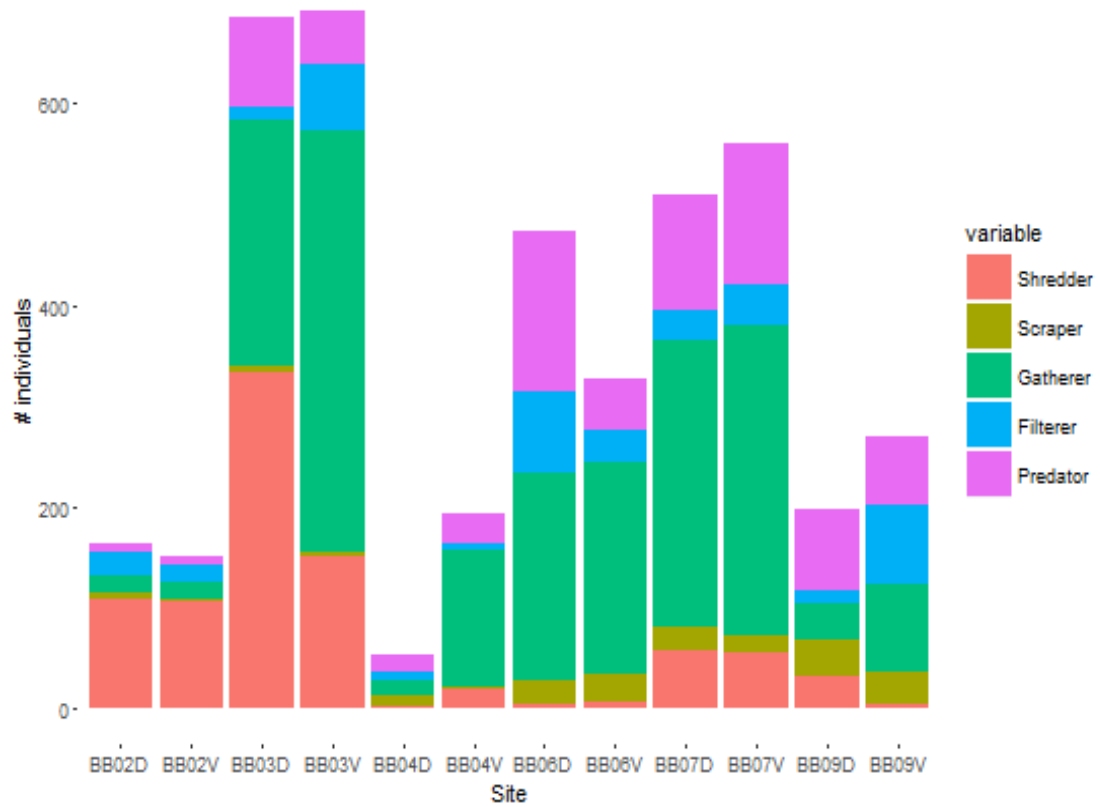


Figure A16: Number of benthic macroinvertebrates collected by electroshocking (n = 3) corresponding to each functional feeding group at variable source area (V) and dry (D) sites in 6 Black Brook streams (New Brunswick, Canada).

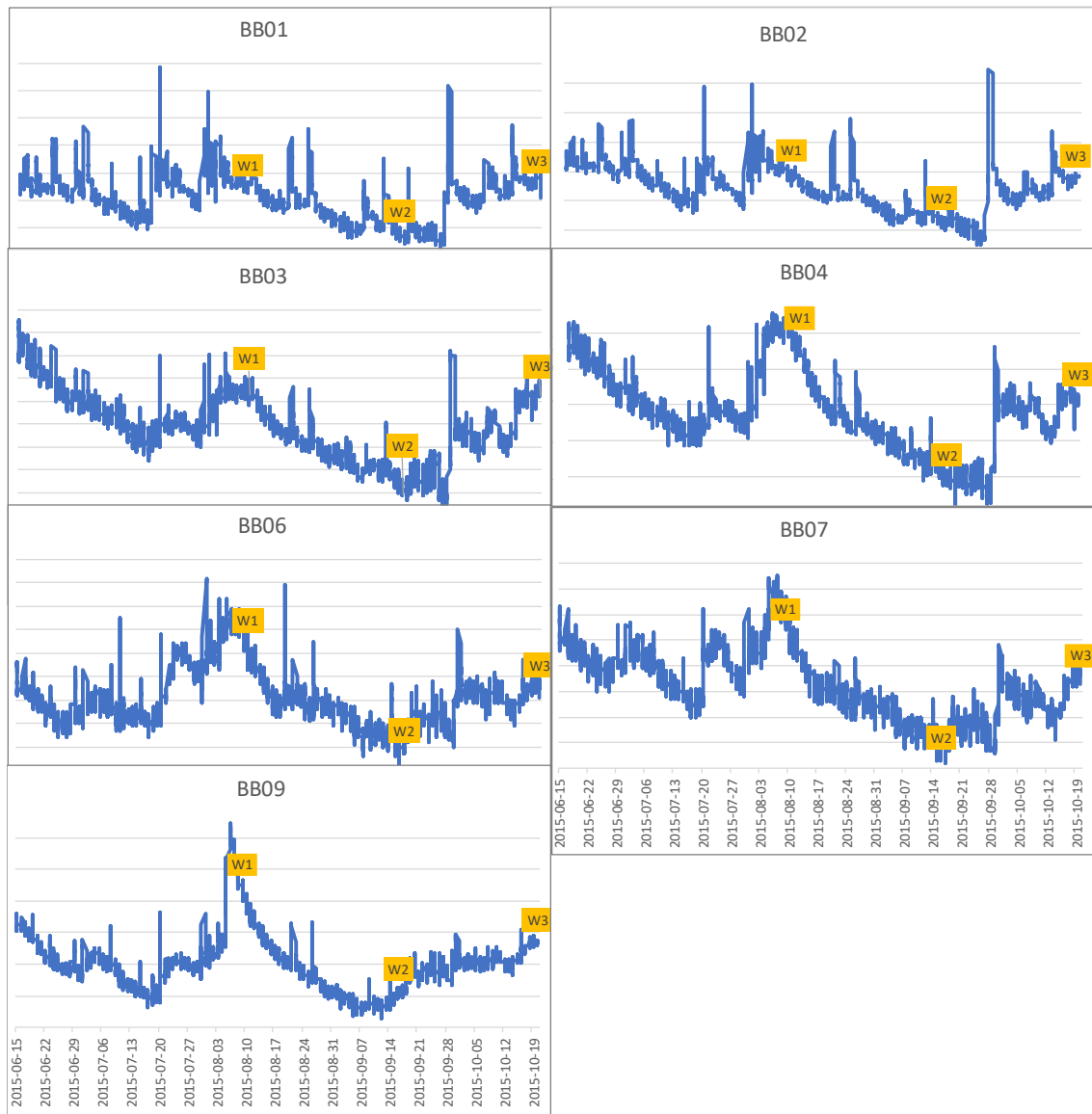


Figure A17: Water levels in 7 Black Brook (New Brunswick, Canada) streams from June 15th to October 20th. The three water sampling times are indicated by W1, W2 and W3.

Curriculum Vitae

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Master of Science, Kristianstad University (Sweden), 2012

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Conference Presentations:

Erdozain, M., Kidd, K., Kreutzweiser, D.P., and Sibley, P.K. Oral presentation. Food web structure and other aquatic indicators in streams with different forest conditions. New Brunswick Enhanced Inventory Project meeting. January 13, 2015. Fredericton, NB, Canada.

Erdozain, M., Kidd, K., Kreutzweiser, D.P., and Sibley, P.K. Oral presentation. Food web structure and other aquatic indicators in streams with different forest conditions. Forest Research Advisory Committee meeting with JD Irving. January 20, 2015. Fredericton, NB, Canada.

Erdozain, M., Kidd, K., Kreutzweiser, D.P., and Sibley, P.K. Poster presentation. Food web structure and other aquatic indicators in streams with different forest conditions. 3rd Annual Meeting for Canadian Network for Aquatic Ecosystem Services. April 28, 2015. Sault Ste Marie, ON, Canada.

Erdozain, M., Kidd, K., Kreutzweiser, D.P., and Sibley, P.K. Oral presentation. Food web structure and other aquatic indicators in streams with different forest conditions. Society for Freshwater Science Annual Meeting. May 18, 2015. Milwaukee, Wisconsin, United States.

Erdozain, M., Kidd, K., Kreutzweiser, D.P., and Sibley, P.K. Oral presentation. Food web structure and other aquatic indicators in streams with different forest conditions. Enhanced Forest Inventory National Working Group Meeting. January 19, 2016. Fredericton, NB, Canada.

Erdozain, M., Kidd, K., Kreutzweiser, D.P., and Sibley, P.K. Oral presentation. How do aquatic indicators of stream health change with forest condition? 4th Annual Meeting for Canadian Network for Aquatic Ecosystem Services. May 4, 2016. Guelph, ON, Canada.

Erdozain, M., Kidd, K., Kreutzweiser, D.P., and Sibley, P.K. Oral presentation. How do aquatic indicators of stream health change with forest condition? Society for Freshwater Science Annual Meeting. May 23, 2016. Sacramento, CA, United States.

Erdozain, M., Kidd, K., Kreutzweiser, D.P., and Sibley, P.K. Oral presentation. How do aquatic indicators of stream health change with forest condition? Seminar at the Norwegian Institute for Water Research (NIVA). September 23, 2016. Oslo, Norway.

Erdozain, M., Kidd, K., Kreuzweiser, D.P., and Sibley, P.K. Poster presentation. Linking stream ecosystem integrity to catchment and reach conditions in an intensively-managed forest landscape. 5th Annual Meeting for Canadian Network for Aquatic Ecosystem Services. April 27, 2017. Toronto, ON, Canada.

Erdozain, M., Kidd, K., Kreuzweiser, D.P., and Sibley, P.K. Oral presentation. How do aquatic indicators of stream health change with forest management intensity? Forest Research Advisory Committee meeting with JD Irving. May 30, 2017. Saint Leonard, NB, Canada.

Erdozain, M., Kidd, K., Kreuzweiser, D.P., and Sibley, P.K. Oral presentation. How do aquatic indicators of stream health change with forest management intensity? Society for Freshwater Science Annual Meeting. June 8, 2017. Raleigh, NC, United States.