

**AN EXPERIMENTAL TEST OF FACTORS LIMITING LEAF LITTER MASS LOSS  
AND INVERTEBRATE ASSEMBLAGES IN RIPARIAN ZONES OF FORESTED  
HEADWATER STREAMS**

by

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## Abstract

Riparian zones support a broad diversity of organisms and ecosystem functions, like decomposition, which are integral to both terrestrial and aquatic ecosystems. Riparian zones are globally threatened, and management agencies are increasingly focused on protecting the ecological functions and diversity of these systems. Identifying factors limiting decomposition and invertebrate diversity in riparian zones can improve our understanding of how these ecosystems operate. In this thesis, I identified mechanisms contributing to the diversity of terrestrial invertebrates in riparian zones: flooding and drying cycles, nutrient and water availability, microclimate gradients, vegetation and microhabitat diversity, and unique food resources. I experimentally determined whether water, nutrients, and distance from stream limit (1) early-stage mass loss of leaf litter from red alder (*Alnus rubra*) and western red cedar (*Thuja plicata*) trees, and (2) terrestrial invertebrate abundance and diversity in headwater riparian zones in southwestern British Columbia. My experiments revealed that moisture is a limiting factor to red alder leaf litter mass loss during the summer dry period: watered litter lost 4% more mass than un-watered litter in four red alder litterbag trials. Nutrient availability may be limiting to western red cedar mass loss at my sites: leaf litter with nutrient additions lost 5% more mass than litter without nutrients in one of three western red cedar trials, suggesting that nutrients may be limiting to western red cedar mass loss at my sites. The terrestrial invertebrate community appeared sensitive to nutrient additions: pitfall trap abundance and order richness were lower at stations with nutrients. Trap abundance, taxonomic richness, and community composition also differed based on month of capture. I also documented differences in microclimate variables with distance from stream. Temperature and moisture conditions within 1 m of the stream differed

from conditions farther away during the summer dry period between July and August, but only temperature differed in winter between December and January. This small difference in microclimate with distance from stream did not appear to influence invertebrate abundance and diversity, or mass loss of either litter species. These results contribute to our understanding of which factors limit decomposition and diversity in headwater riparian zones.

## Lay Summary

Riparian zones are threatened globally, and there is an increasing need to determine what factors influence the ecological functions they perform and the diversity of the wildlife communities they support. I experimentally tested whether water, nutrients, and distance from stream limit (1) the decomposition of leaf litter from two riparian tree species, and (2) the abundance and diversity of invertebrate communities in forests surrounding small mountainous streams.

Decomposition of red alder (*Alnus rubra*) and western red cedar (*Thuja plicata*) leaf litter was dependent on water and nutrient availability, respectively. Invertebrate abundance and diversity was primarily limited by nutrient availability and month of capture. I also assessed microclimate with distance from stream, and determined that air temperature and moisture within 1 m of the stream differed from conditions further inland during summer and winter months. This work advances our understanding of factors influencing decomposition and invertebrate diversity in riparian zones.

## Preface

All of the work presented henceforth was conducted in the Stream and Riparian Research Laboratory at the University of British Columbia. All projects and associated methods were approved by my advisor, Dr. John S. Richardson, in the Faculty of Forestry, and committee, Dr. Cindy E. Prescott and Dr. Peter M. Kiffney.

A version of Chapter 2 has been published [Ramey TL, Richardson JS. 2017. Terrestrial invertebrates in the riparian zone: mechanisms underlying their unique diversity. BioScience 67: 808–819]. I was the lead investigator, responsible for all major areas of concept formation, data collection and analysis, and manuscript composition. J.S. Richardson was the supervisory author on this project and was involved throughout the project in concept formation, analysis, and manuscript edits.

A version of Chapter 3 has been published [Ramey TL, Richardson JS. 2018. Experimental test of water, nutrients, and microclimate on leaf litter mass loss in headwater riparian forests. Ecosphere 9: e02478]. I was the lead investigator, responsible for all major areas of concept formation, data collection and analysis, and manuscript composition. I conducted the field work, processed samples, and ran the statistical analysis. J. S. Richardson was the supervisory author on this project and was involved throughout the project in concept formation, data analysis, and manuscript edits.

I was the lead investigator for the projects located in Chapters 4 and 5, responsible for all major areas of concept formation, data collection and analysis, and manuscript composition. I conducted the field work, processed samples, and ran the statistical analysis. J. S. Richardson was the supervisory author on this project and was involved throughout the project in concept formation, data analysis, and manuscript edits. Versions of each chapter will also be submitted for publication in the future.

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## List of Abbreviations and Symbols

*	Denotes an interaction between factors
°C	Degrees Celsius
AFDM	Ash-free dry mass
AIC	Akaike's Information Criteria
ANOVA	Analysis of variance
AUC	Area under the curve
C	Carbon
CaH <sub>4</sub> P <sub>2</sub> O <sub>8</sub>	Triple superphosphate
CCA	Canonical correlation analysis
cm	Centimetre
D	Distance from bankfull edge of stream
dbh	Diameter at breast height
g	Gram
ha	Hectares
kPa	Kilopascal
L	Litre
m	Metre
m.a.s.l.	Metres above sea level
mm	Millimetre
N	Nitrogen
<i>n</i>	Number of samples or individuals

NH <sub>4</sub> NO <sub>3</sub>	Ammonium nitrate
P	Phosphorus
RH	Relative humidity
RI	Relative importance
RL	Relative likelihood
VPD	Vapour pressure deficit
$w_i$	Akaike weight

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*“...From so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.” – Charles Darwin, On the Origin of Species*

*“Ask the animals, and they will teach you, or the birds in the sky, and they will tell you; or speak to the earth, and it will teach you, or let the fish in the sea inform you...In His hand is the life of every creature and the breath of all mankind.” – Job 12: 7-8, 10*

# **Chapter 1: Introduction**

## **1.1 Ecosystem functions and biodiversity**

In ecosystems across the planet, complex interactions occur between biotic communities and the abiotic environment. At the ecosystem level, biogeochemical processes transform carbon into energy to build complex molecules and nutrients that are transferred between organisms, resulting in processes such as decomposition and nutrient cycling (Tansley 1935, Schowalter 2016). These processes, or ecosystem functions, occur in every ecosystem on the planet, from lush tropical jungles to deceptively sparse tundra, and can connect ecosystems through subsidies when organisms or materials move between them, such as between aquatic and terrestrial habitat (Nakano and Murakami 2001, Baxter et al. 2005, Richardson and Sato 2015, Bogan et al. 2017). Ecosystem functions refer to physical and biological processes, and when these functions and their products contribute to the social or economic welfare of humans, they are called ecosystem services (categorized as cultural, provisioning, regulating, and supporting services; Munns et al. 2016, Costanza et al. 2017). Ecosystem functions are often dependent on biodiversity, which refers to the variety of life on Earth; this encompasses everything from genes to ecosystems (Hooper et al. 2005). This connection between ecosystem functions and biodiversity is a topic that has been the focus of much debate over the last few decades (Schulze and Mooney 1993, Loreau et al. 2001, Loreau et al. 2002, Hooper et al. 2005, Lecerf and Richardson 2010a). At its premise, the Biodiversity-Ecosystem Function (BEF or BDEF) body of theory generally predicts that losses in biodiversity will reduce the rates and resilience of processes that occur at the ecosystem level (Srivastava and Vellend 2005). And indeed, research has shown positive links between biodiversity and ecosystem functioning at landscape scales such as grassland

ecosystems (e.g., Tillman and Downing 1994, Tillman et al. 1996) and at local scales such as microcosms (e.g., Hawksworth 1991, Van der Heijden et al. 1998). Positive links have also been found at organizational levels ranging from metaecosystems and metacommunities (e.g., Staddon et al. 2010, Vennail et al. 2010), to communities (e.g., Petchey and Gaston 2002, Grayston and Prescott 2005, Cardinale et al. 2006), to individual organisms (e.g., Symstad et al. 1998) and genes (e.g., Crutsinger et al. 2006). These studies have reached important conclusions: (1) losses in biodiversity can diminish both the rate at which ecosystem functions are performed and their ability to recover after a disturbance, (2) short-term experiments may miss long-term consequences of biodiversity loss on ecosystem functions, and (3) communities with greater functional diversity and niche complementarity can be more effective in performing ecosystem functions (Cardinale et al. 2012).

Biodiversity is a significant feature that sustains ecosystem functions (Cardinale et al. 2012), and understanding which mechanisms support diversity and maintain ecosystem functions has become fundamental to effective conservation management for ecosystems facing anthropogenic threats. This is especially true in the face of climate change which is predicted to increase the frequency of disturbances including floods, droughts, and fires, while potentially reducing the ability of some species to survive such changes (Bengtsson et al. 2000). The protection and restoration of heterogeneous ecosystems that are composed of various microhabitats and have complex resource distribution can in theory support higher species diversity (Shmida and Wilson 1985) and may include suitable habitat for species vulnerable to climate change (Hof et al. 2011). Conserving diversity at the community level can also protect multiple trophic or functional groups and thus encourage the resilience of ecosystem functions

due to spatial, temporal or resource partitioning within the community (Chesson 2000, Hof et al. 2011).

## 1.2 Riparian zones

Riparian habitat is the transitional zone between aquatic and terrestrial ecosystems that extends laterally into areas adjacent to freshwater bodies (e.g., rivers and lakes), into the soil and groundwater below, and vertically into the canopy (Gregory et al. 1991). These areas show direct interaction between the aquatic and terrestrial communities, as many riparian zones are susceptible to overbank flooding and water tables are close to the soil surface (Gregory et al. 1991, Naiman and Décamps 1997). Riparian zones are usually delineated by the bankfull edge of the waterbody, and the extent of terrestrial vegetation influenced by overbank flooding and elevated water tables relative to the soil surface (Naiman and Décamps 1997). Along streams, riparian zones provide a source of large wood and particulate organic matter to stream ecosystems, and canopies reduce temperatures of surface water, soil, and groundwater below (Sweeney et al. 2004). Riparian zones also trap sediment and filter nutrients originating from hillslopes, and vegetation increases stream bank stability (Naiman and Décamps 1997). Because of their transitional nature, riparian zones are integral to ecosystem functions in aquatic and terrestrial habitat such as decomposition, nutrient cycling, and propagule dispersal (Capon et al. 2013). Factors influencing decomposition in riparian zones are discussed in Chapter 3, Section 3.2.

Riparian zones can support a disproportionately large number and broad range of species relative to their area when compared to other habitats (Naiman et al. 1993, Patten 1998). Cyclical flooding and drying regimes can create differences in vegetation structure and composition, soil

nutrients, primary productivity, litterfall, and microclimate across riparian habitat (e.g., Groffman et al. 1992, Minore and Weatherly 1994, Brosowske et al. 1997, Naiman and Décamps 1997, Pabst and Spies 1998, Clinton et al. 2010, Weibel 2011). These differences create a complex mosaic of microhabitats that support a variety of wildlife (Naiman et al. 1993, Tockner and Stanford 2002, Sabo et al. 2005a). As sources of fresh water and natural corridors along river networks, riparian zones also offer pathways for migrating species (Oakley et al. 1985, Raedeke 1989, Skagen et al. 1998). They support species that can exist elsewhere but experience higher productivity within riparian zones (“riparian associates”), and also harbor specialized species that require access or close proximity to fresh water at some point in their life cycle (“riparian obligates”; Richardson et al. 2005).

Many studies have been conducted to determine how the taxonomic richness of riparian zones compares to habitat further inland from the waterbody. Knopf (1985) saw greater species richness of breeding birds in riparian sites along the Platte River in northern Colorado, USA, compared to habitat 100 m away from the edge of the riparian zone. Similarly, Doyle (1990) determined that small mammal abundance and species richness was greater in riparian forests than in habitat further inland on the western slope of the Cascade Range in central Oregon, USA. Unique communities of terrestrial invertebrates and amphibians associated with cool, moist stream banks have been documented within 1 to 2 m of the stream along headwaters in Oregon, USA (Sheridan and Olson 2003, Rykken et al. 2007b). By supporting unique species, riparian zones increase regional species richness, also known as gamma diversity (Sabo et al. 2005a). In a meta-analysis that included both plant and animal studies, Sabo et al. (2005a) showed that the average spatial turnover in cumulative species richness was greater in riparian zones than in habitat further inland. Gamma diversity is composed of two components: alpha diversity which

is diversity within a single site (called site species richness), and beta diversity which refers to the differences in community composition between sites (often referred to as species turnover; Whittaker 1960, Anderson et al. 2011). Although individual riparian areas may not have higher species richness than upslope habitat, this high spatial turnover makes them distinctive and thus increases the regional diversity of the landscape (Sabo et al. 2005a). In either case, riparian zones are an essential part of the broader landscape, supporting and connecting terrestrial and aquatic communities.

Riparian zones are threatened across much of the world due to anthropogenic activities such as river regulation, forest harvesting and fragmentation, agricultural development, and climate change (Nilsson and Berg 2000, Tockner and Stanford 2002, Poff et al. 2011, González et al. 2017, Stella and Bendix 2019). Complex interactions between these multiple stressors are causing declines in the biodiversity and functioning of riparian systems and adjacent freshwater systems (Dudgeon et al. 2006, Stella and Bendix 2019, Sullivan et al. 2019a). The protection of riparian habitat became an important aspect of freshwater conservation in the 1970s, but its focus was primarily on creating riparian buffer zones to maintain stream water quality, limit sedimentation, protect fish species, and reduce nutrient loading to streams (especially in agricultural areas; Welcomme 1979, Lowrance et al. 1984, Pusey and Arthington 2003, Blinn and Kilgore 2004). Riparian buffers are a specified width of intact riparian forest extending perpendicularly from the stream edge from which forest harvesting, vegetation removal, or other forms of land use are reduced or excluded (Naiman and Décamps 1997, Kiffney et al. 2003). Over the past few decades, management of riparian zones has shifted to protecting the range of ecological functions that occur within the riparian zone itself, and preserving or restoring habitat quality for numerous riparian species such as birds, small mammals, and invertebrates (Nilsson

1992, Naiman and Décamps 1997, Cockle and Richardson 2003, Richardson and Danehy 2007, Capon et al. 2013, Kuglerová et al. 2014). There is also an increasing awareness of the important role that riparian zones play in supporting key ecosystem services to human populations, such as water filtration and flood control (e.g., González et al. 2017). Many studies have described ecosystem functions such as decomposition in riparian zones, but there is a need to identify the relative importance of different factors (such as water and nutrient availability, habitat heterogeneity, sediment type, and the presence of microclimate gradients in riparian zones) that limit the rate at which these functions occur or the diversity of riparian communities (e.g., Wallace and Hutchens 2002, Rykken et al. 2007b, Tagwireyi and Sullivan 2015). Identifying and testing how specific factors influence the functioning and diversity of riparian systems can help understand how these ecosystems function, and ultimately improve the efficacy of riparian management strategies.

### **1.3 Decomposition**

Decomposition refers to the loss of plant litter mass due to leaching, fragmentation and consumption by detritivores, and activity by bacteria and fungi (Berg and McClaugherty 2014). The end result of decomposition can be either the mineralization of organic nutrients into compounds including CO<sub>2</sub> and nitrate, or the immobilization of organic compounds in decomposer tissues or humus (Haynes 1986). Decomposition is an important ecosystem function because it produces sizeable amounts of greenhouse gases, regulates nutrient cycles, controls humus formation (long-term carbon storage), and forms the basis of detritivore food webs which process greater amounts of fixed carbon per year than herbivore food webs globally (Swift et al. 1979, Berg and McClaugherty 2014).

As forests cover almost 33% of the Earth's terrestrial surface, they are a primary component of terrestrial decomposition processes with over 50% of their annual production entering detrital systems (Gosz et al. 1978, Gough et al. 2008). Litter components can include fine roots, fruit or cones, and woody material such as branches and bark (Berg and McClaugherty 2014), but leaves often constitute the majority (Bray and Gorham 1964). Within a forest, leaf litter provides habitat for ground-dwelling animals and can directly impact the growth and composition of plant and microbial communities (Molofsky and Augspurger 1992, Koivula et al. 1999). In riparian forests, fallen leaves offer food resources for both terrestrial and aquatic consumers (e.g., Richardson 1992, Cárcamo et al. 2000, Sabo et al. 2008, Suzuki et al. 2013, Richardson and Sato 2015), creating an energetic link between ecosystems.

Primary factors controlling rates of decomposition in leaf litter include environmental variables as well as physical and chemical properties of the leaf itself, such as nutrient levels, leaf toughness, and structural complexity (e.g., Prescott 2010, Berg and McClaugherty 2014). Leaves usually go through three stages of decay (early, late and final) during decomposition, which can overlap in time as decomposition is a continuous process (Berg and Matzner 1997, Berg and McClaugherty 2014). In early-stage decomposition, concentrations of water-soluble compounds such as monosaccharides and non-lignified carbohydrates in leaf litter decrease with leaching and microbial colonization (Aerts 1997, Prescott 2010, Berg and McClaugherty 2014). This phase often occurs rapidly and is generally regulated by environmental variables, including temperature and moisture availability, and litter concentrations of N and P relative to lignin (Aerts 1997, Prescott 2010, Berg and McClaugherty 2014). Detritivorous invertebrates such as enchytraeid worms, oribatid mites, isopods, and millipedes fragment and consume leaf litter; this activity also influences microbial activity by producing fecal pellets with higher bacterial to

fungal ratios, and exposing softer interior tissues of leaves to fungal colonization (e.g., Seastedt 1984, Hassall et al. 1987, Ponge 1991, Chapin et al. 2002). Early-stage decomposition of leaf litter in terrestrial habitats is generally slower than in aquatic environments as water promotes leaching and microbial colonization, and flowing water can cause physical abrasion and fragmentation (Brinson 1977, Witkamp and Frank 1969, Suberkropp et al. 1976, Driebe and Whitam 2000, Hutchens and Wallace 2002, Nakajima et al. 2006). Studies on early-stage decomposition of leaf litter generally examine mass loss after the first three to 12 months (e.g., Dyer et al. 1990, Hobbie et al. 2012, Pérez-Suárez 2012, Djukic et al. 2018).

Late-stage decomposition generally occurs more slowly than early-stage decay because the ratio of labile compounds to lignin and cellulose decreases (Prescott 2010, Berg and McClaugherty 2014). A matrix of lignin, cellulose, and hemicellulose form the rigid structure of leaf cell walls, and extracellular ligninolytic enzymes produced by fungi and bacteria are required to degrade lignin (Janusz 2017). As a result, late-stage decomposition is often regulated by the rate of decay for lignin (Prescott 2010, Berg and McClaugherty 2014). Concentrations of inorganic N in the environment can also influence rates of late-stage decomposition in leaf litter with greater concentrations of lignin (> 20% lignin; Knorr et al. 2005), as N enrichment can suppress ligninolytic enzyme production by microbes and alter microbial community composition (Carriero et al. 2000, Frey et al. 2004). Studies documenting terrestrial late-stage decay of leaf litter generally examine mass loss after at least 12 to 18 months (Berg and Ekbohm 1993, Prescott 1995, Moore et al. 1999, Trofymow et al. 2002, Hobbie et al. 2012). In the final stage of decomposition, the loss of lignin slows and the rate of decay for leaf litter approaches zero (Berg and Matzner 1997, Berg and McClaugherty 2014). Litter in this final stage can

develop into stable humus, a process that can last for years or even decades (Prescott 2010, Berg and McClaugherty 2014).

There is evidence to suggest that decomposition occurs faster in riparian zones than in habitat further inland, with differences attributed to higher moisture and nutrient availability in riparian forests (Merritt and Lawson 1980, Peterson and Rolfe 1982, Shure et al. 1986, Hutchens and Wallace 2002). Patterns of decomposition in riparian zones and potential limiting factors based on these previous studies are discussed in Chapter 3, Section 3.2. Experimentally manipulating water and nutrients in riparian zones, and examining mass loss with distance from stream edge, can help determine the extent to which these variables limit mass loss of leaf litter in riparian zones. Riparian zones are often home to a diverse plant community (Gregory et al. 1991, Naiman et al. 1993, Little et al. 2013), thus the mass loss of litter species can respond to environmental manipulations differently due to physical and chemical variability between litter species (e.g., Keenan 1993). Given the importance of riparian zones to both terrestrial and aquatic ecosystem functions, and their threatened status due to anthropogenic activity and climate change, such investigations can provide information that will improve our understanding of decomposition processes in these unique ecosystems.

## 1.4 Terrestrial invertebrates

Invertebrates are the most abundant group of animals on the planet, representing 80% of the 1.6 million known eukaryotic species (Brusca and Brusca 2002, Prather et al. 2013). They perform essential functions that also provide ecosystem services for humans (Prather et al. 2013). Earthworms, termites and ants act as ecosystem engineers: their movement below ground mixes and aerates soil (Lavelle 1996). They also create casts and tunnels which provide structural

stability to soils (Jouquet et al. 2006). Butterflies and moths, bees, and many species of fly directly influence primary production through pollination (Vanbergen 2013), while invertebrates such as slugs, ants, and dung beetles disperse seeds (Giladi 2006, Nichols et al. 2008, Turke et al. 2010, Prather et al. 2013). Microarthropods, such as mites and springtails, as well as millipedes and earthworms fragment and consume leaf litter (Seastedt 1984, Cárcamo et al. 2000). This activity enhances the release of elements such as N from litter into the soil and can influence microbial species composition and respiration rates (Seastedt 1984, Cárcamo et al. 2000). Invertebrate predators such as spiders and ants influence the abundance and distribution of prey species, in some cases leading to changes in rates of herbivory and primary production (Schmitz et al. 2000). Though invertebrates comprise a large proportion of the Earth's diversity and have sizeable influences on ecosystem functions, they have received less attention and protection by conservation programs than vertebrates (Donaldson et al. 2016). A recent study investigated the number of conservation publications focusing on species listed as critically endangered, endangered, or vulnerable by the International Union for Conservation of Nature Red List, reporting that vertebrates were the focus of 12.3 and 5.3 times more papers published per species in terrestrial and freshwater habitats, respectively (Donaldson et al. 2016). This statistic reveals there is a need for management bodies to consider invertebrate communities when planning conservation or restoration efforts in threatened ecosystems.

Most research to date on terrestrial invertebrates, both ground and canopy-dwelling taxa, in riparian zones can generally be divided into three categories: (1) analyses of their importance as cross-ecosystems subsidies linking terrestrial and aquatic food webs, (2) descriptions of natural patterns in community composition and distribution, and (3) evaluations of terrestrial invertebrates as indicators of ecological disturbance, succession, and habitat quality. Terrestrial

invertebrates serve as both subsidies for aquatic predators when they fall from the canopy into streams, and as predators themselves when feeding on emergent or stranded aquatic prey (e.g., Paetzold et al. 2005, Richardson and Sato 2015). This flow of energy can greatly influence both terrestrial and aquatic ecosystems. For example, Wipfli (1997) found 50% of the biomass sampled in salmonid stomachs from creeks in southeastern Alaska, USA, was comprised of terrestrial invertebrates, and Kawaguchi and Nakano (2001) found the same pattern in salmonids from headwaters in northern Japan. Inhibiting terrestrial inputs to first-order streams using transparent covers reduced cutthroat trout (*Oncorhynchus clarki*) and brown trout (*Salmo trutta*) growth, respectively (Zhang and Richardson 2011; Erös et al. 2012). The input of terrestrial invertebrates can be more significant in first- and second-order streams compared to larger streams (Lotrich 1973), likely due to the greater canopy cover and fewer autochthonous resources associated with smaller streams (Richardson et al. 2005). On land, terrestrial invertebrates often prey on aquatic insects emerging from the stream and their distribution can be influenced by the availability of such aquatic resources. Marczak and Richardson (2007) revealed that riparian web-building spider distributions were controlled by fluxes in the availability of emergent aquatic insects in two first-order streams in western British Columbia, Canada. Isotope analyses revealed aquatic invertebrates made up 68% of ground-dwelling and almost 100% of web-building spider diets when spiders were sampled along the banks of Sycamore Creek close to Phoenix, Arizona, USA (Sanzone et al. 2003). Thus, terrestrial invertebrates play a unique role connecting aquatic and terrestrial ecosystems in riparian zones.

Terrestrial invertebrate assemblages in riparian zones are often composed of species with diverse habitat preferences and those adapted to recurrent natural disturbance (Sabo et al. 2005a). Many riparian communities experience high rates of spatial turnover and are therefore an

important aspect of regional diversity (Sabo et al. 2005a). Environmental variables such as substrate type (Manderbach and Hering 2001, Famenau et al. 2002), habitat heterogeneity (Sadler et al. 2004, Chan et al. 2007, Lambeets et al. 2009), air temperature (Famenau et al. 2002, Rykken et al. 2007b, Lambeets et al. 2009, Henshall et al. 2011, Rykken et al. 2011), moisture availability and proximity to water (Ballinger et al. 2005, Baker et al. 2006, Baker et al. 2007, Bates et al. 2007, Henshall et al. 2011) have been correlated with diversity, evenness and composition measures of riparian invertebrate communities. Most research has described riparian communities surrounding large, higher-order rivers (e.g., Sadler et al. 2004, Lambeets et al. 2009, Henshall et al. 2011) with extensive and well-defined floodplains, high vegetation diversity and structural complexity, and periodic flooding (Naiman et al. 2000; see Chapter 2, Section 2.4 for more detail). A more limited number of studies have examined terrestrial riparian invertebrate communities near lower-order headwater streams. Rykken et al. (2007b) examined invertebrate communities surrounding five first- and second-order streams in western Oregon between August 2000 and May 2002, and noted a unique community within 1 m of the stream edge that was correlated with cool, moist conditions close to the stream during summer months. Horn and Ulyshen (2009) sampled terrestrial invertebrates in the floodplain riparian forest near a small stream (3-4 m wide) in northeast Georgia, USA, and found 54% of species were restricted to exposed sand and gravel bars. Foster and Ziegelmum (2013) examined terrestrial mollusk communities along three first-order streams in southwest Washington, USA, and found a diverse community whose composition varied with soil moisture and total understory vegetation cover. Many of these studies suggest that environmental parameters may be influencing the distribution and diversity of terrestrial riparian invertebrates, but did not experimentally test which mechanisms are actually limiting this diversity. Identifying which variables directly influence the

distribution and diversity of invertebrates in the riparian zone using an experimental approach, and synthesizing what is known about mechanisms that contribute to this diversity, remains to be addressed (see Chapters 2 and 5).

Due to their varied and specific habitat preferences and diverse communities, terrestrial invertebrates are useful indicators of anthropogenic activities such as river regulation and forest harvesting (Taylor and Doran 2001, Andersen and Majer 2004, DeBano 2006, Smith DiCarlo and DeBano 2018, Sullivan et al. 2018). Because riparian communities are adjacent to freshwater bodies, they often experience effects from anthropogenic activities on rivers. River regulation can lead to lower water levels and cause channelization, which reduces the frequency and duration of overbank flooding; this can cause subsequent losses of habitat heterogeneity, and changes to both successional dynamics of riparian plant communities, and nutrient cycling in the riparian zone (Power et al. 1996, Nilsson and Berggren 2000, Nilsson and Svedmark 2002, Cowell and Stoudt 2002, Kennedy and Turner 2011). These changes also affect riparian invertebrate communities. For example, the taxonomic richness and density of terrestrial invertebrate communities were lower in channelized reaches of the Rio Grande, New Mexico, USA, compared to non-channelized reaches (Kennedy and Turner 2011). Channelized reaches showed 50% lower densities of emergent aquatic insects than non-channelized reaches, and thus a lower taxonomic richness and abundance of species that prey on emergent aquatic insects such as wolf spiders (Lycosidae) and toad bugs (Gelastocoridae; Kennedy and Turner 2011). The removal of riparian vegetation often occurs with channelization, and this loss of habitat can result in the lower abundance and diversity of web-weaving spiders which use vegetation for structure on which to build their webs (Laeser et al. 2005). Another threat to riparian ecosystems is forest harvesting, which can cause changes to the community composition and distribution of

riparian invertebrates between clearcuts and mature, unharvested forests due to changes in air and soil temperatures and RH (Rykken et al. 2007b, Rykken et al. 2011). These studies show that terrestrial invertebrates are useful indicators of environmental changes due to anthropogenic activity.

Terrestrial invertebrates can also serve as indicators of habitat quality and the effectiveness of restoration or management actions. Steward et al. (2018) recently analyzed terrestrial invertebrate communities in dry river beds in Queensland, Australia where riverine habitat and riparian zones are under threat from trampling by livestock and feral mammals. Grazing and trampling by livestock and feral mammals can reduce vegetation cover, increase erosion and sedimentation, and reduce interstitial spaces in dry riverbed gravel where invertebrates like spiders and ants seek cover (Steward et al. 2018). Steward et al. (2018) discovered that terrestrial invertebrate abundance and taxon richness were negatively correlated with the intensity of disturbance by grazing and trampling, and concluded that invertebrates were suitable indicators of dry riverbed health. In pastoral and agricultural landscapes, riparian buffers can provide protection for aquatic ecosystems from such stressors as erosion as well as a natural corridor for animals navigating the heavily managed landscape (Naiman et al. 1993). Though buffers provide habitat for riparian species in these disturbed landscapes, the quality of this habitat compared to natural, undisturbed riparian zones may not be similar. Stockan et al. (2014) discovered the community composition of carabid beetles was dissimilar between 41 unbuffered, grassy buffered, and forested riparian sites near agricultural developments within two river catchments in northeast Scotland. This difference was attributed to lower habitat heterogeneity in unbuffered riparian zones and those planted with tall grasses compared to

forested sites, and the authors concluded that in this instance, vegetated buffers failed to conserve riparian carabid assemblages (Stockan et al. 2014).

Other studies have shown buffers can provide high quality habitat for riparian invertebrates. Rykken et al. (2007b) examined ground-dwelling riparian arthropods in western Oregon, USA, and found that 30-m riparian buffers lying between the stream edge and clearcut slopes supported arthropod communities that were similar to mature riparian forests. This was because these riparian buffers exhibited similar microclimate gradients in air temperature and moisture to mature forest sites (Rykken et al. 2007b). Williams (1993) monitored terrestrial arthropods in riparian woodlands along restored sections of the San Luis Rey River in southern California, USA. To mitigate the effects of urban development, channel incision, and invasive species, degraded habitat along the river were replanted with vegetation that resembled the structure and composition of non-degraded riparian habitat (Williams 1993). Three years after the restoration, Williams (1993) determined that although total arthropod abundance was lower in restored sections, community composition by arthropod order was similar between restored and non-degraded reference areas and abundances of each order were expected to increase as the site matured. These examples illustrate how invertebrates can be used to determine whether restoration activities are effective at the community level. Managers should therefore take terrestrial invertebrates into account when developing conservation or restoration strategies in riparian zones and evaluating their effectiveness.

## **1.5 Thesis objectives and organization**

### **1.5.1 Aim and objectives**

The aim of my thesis was to determine experimentally how moisture and nutrient availability, as well as distance from stream edge, limit rates of leaf litter decomposition, and contribute to abundance and diversity patterns of terrestrial invertebrates in riparian zones near headwater streams. I chose to conduct my research in the coastal Pacific Northwest (PNW) of North America because studies of riparian areas in this region have recorded microclimate gradients in temperature and moisture extending from the stream edge into riparian forests (Brosofske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a). There is also evidence of soil N and P limitation in coastal forests of western hemlock, western red cedar, and Douglas-fir in this region (Tarrant 1951, Feller 1977, Feller and Kimmins 1984, Prescott et al. 1993a). Red alder (*Alnus rubra*) and western red cedar leaf litter (*Thuja plicata*) were my two focal species because they are commonly found in riparian areas in this region (Radwan and Harrington 1986, Richardson 1992, Keenan et al. 1993, Hibbs and Bower 2001, Edmonds and Tuttle 2010, Jackrel and Wooton 2014). They also represent typical deciduous and coniferous trees in the forest community, allowing for a comparison of litter species with different physical and chemical characteristics. The following are the five main objectives of my thesis:

**Objective 1:** Identify and review the mechanisms specific to riparian areas that are possible contributors to the diversity of riparian terrestrial invertebrates communities.

**Objective 2:** Experimentally determine whether water, nutrients, or distance from stream (alone or in combination) limit early-stage mass loss of red alder leaf litter in riparian

forests surrounding headwater streams in the mesic coastal climate of southwestern British Columbia.

**Objective 3:** Document small-scale changes in air temperature, RH, and vapour pressure deficit (VPD) at five distances between 1 and 40 m from the stream edge, and determine if patterns differ between summer (July and August) and winter (December to January) periods.

**Objective 4:** Experimentally determine whether water, nutrients, or distance from stream (alone or in combination) limit early-stage mass loss of western red cedar leaf litter in riparian forests surrounding headwater streams.

**Objective 5:** Experimentally determine whether terrestrial invertebrate abundance, taxonomic richness, and community composition is limited by water, nutrients, distance from stream, or month of capture (alone or in combination) near headwater streams.

## 1.5.2 Thesis Structure

The structure of this thesis follows a scholarly article-based format which is the standard format used by students at the University of British Columbia. This format is composed of an introductory chapter outlining primary themes of the thesis, followed by several chapters written as individual articles that can be edited and submitted for scholarly publication, and finally a concluding chapter that discusses the main findings, limitations, and contributions of the thesis as a whole. All chapters share common themes, and together address the main aim and objectives of the thesis. Each chapter also includes a synopsis, which functions like an abstract for published articles. The structure of my thesis and hypotheses for each chapter (denoted by H1 through H12) are listed below. Objectives and hypotheses are numbered and restated within each

chapter. Potential mechanisms such as increased microbial respiration or leaching due to water additions are listed before each set of hypotheses, however they are not stated within the hypotheses because these mechanisms were not tested in my experiments.

**Chapter 1.** This chapter provides background information on themes central to my research which link ecosystem function and invertebrate diversity with environmental gradients in riparian zones.

**Chapter 2.** I reviewed and synthesized published research on terrestrial invertebrates in riparian zones along streams and rivers. This review discusses five mechanisms influencing invertebrate diversity and illustrates how these mechanisms change with distance from the stream (a lateral gradient) and position within a catchment (a longitudinal gradient). Although many studies have examined riparian invertebrate taxa, this chapter synthesizes information on multiple mechanisms influencing invertebrate communities in riparian areas. As such, it resolves a gap I identified in the riparian literature in Section 1.4, and accomplishes Objective 1 of my thesis. This review also serves as a detailed description of environmental heterogeneity in riparian zones (including gradients in water and nutrient availability, microclimate, soil moisture, microhabitat and vegetation diversity). This information is referred to in Chapters 3, 4, and 5 to help explain differences in decomposition and invertebrate abundance and diversity based on moisture, nutrient availability, and distance from stream in riparian zones.

**Chapter 3.** This chapter is the first of three field studies, and is composed of two main parts. First, I analyzed the effect of water and nutrient additions and distance from stream

on red alder leaf litter mass loss using four litterbag trials that varied in duration from three months to one year between August 2012 and January 2014. Moisture and nutrient availability are known to limit decomposition rates of leaf litter (Prescott 2010, Berg and McClaugherty 2014); if these factors are limiting to decomposition of red alder at my site, then additions of water and nutrients could result in increases in mass loss. Additionally, gradients in moisture and nutrient availability with distance from stream have been documented in riparian zones (Brosofske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a) and have been linked to differences between decomposition of leaf litter near the stream compared to further inland (Merritt and Lawson 1980, Peterson and Rolfe 1982, Shure et al. 1986, Hutchens and Wallace 2002). Seasonal differences in temperature and precipitation may also influence mass loss (e.g., Zhang et al. 2008, Kang et al. 2009). This analysis accomplishes the Objective 2 of my thesis. Based on these mechanisms, I hypothesized the following:

**H1:** Red alder leaf litter watered during the summer dry period would lose more mass than un-watered leaf litter.

**H2:** Red alder leaf litter with nutrient additions would lose more mass than leaf litter without nutrient additions.

**H3:** Red alder leaf litter placed closer to the stream would lose more mass than leaf litter placed further away.

**H4:** Red alder leaf litter trials with a greater number of degree-days and higher average daily precipitation would lose more mass than leaf litter trials with fewer degree-days and daily precipitation (H4).

Second, I documented changes in air temperature, RH, VPD at 1, 5, 10, 20 and 40 m from the stream at my headwater sites using data loggers during the dry summer months of July to August 2013. Previous studies in Oregon (Danehy and Kirpes 2000, Rykken et al. 2007a) and Washington (Brosofske et al. 1997) have documented higher RH and lower air temperatures closer to the stream edge than further upland during summer months due to the cooling influence of the stream. I also examined microclimate variables with distance from stream during winter months between December 2012 and January 2013 to determine whether patterns differ between summer and winter seasons; to my knowledge, winter evaluations of microclimate in this region have not been done. Though microclimate is only one variable that has been documented to change with distance from stream (others include canopy cover, vegetation composition, flooding frequency, and substrate type and size; Day and Monk 1974, Johnson and Lowe 1985, Pabst and Spies 1998, Nierenberg and Hibbs 2000, Benda et al. 2004), this analysis could help to qualitatively explain potential changes in mass loss of red alder litter (or western red cedar litter in Chapter 4) that occur with distance from stream. This analysis accomplishes Objective 3 of my thesis. Based on these mechanisms, I hypothesized the following:

**H5:** A gradual decrease in RH and an increase in air temperature and VPD would occur with increasing distance from stream during the summer (July and August). No difference in variables would occur with distance from stream in

winter months when air temperature is near 0°C and precipitation is at a peak (December and January).

**Chapter 4.** In this second field study, I examined the effect of water and nutrients additions and distance from stream on early-stage mass loss of coniferous western red cedar leaf litter. Red cedar varies from alder in its chemical and structural characteristics: cedar litter has lower concentrations of N and P, higher concentrations of lignin, and lower concentrations of water-soluble compounds that can be lost through leaching (Harmon et al. 1990, Prescott et al. 2000, Keenan et al. 1996, Richardson et al. 2004). In addition, different leaf species can support different microbial and invertebrate communities (e.g., Blair et al. 1990, Bray et al. 2012). Patterns of mass loss in western red cedar leaf litter could therefore respond differently to experimental additions of water and nutrient and distance from stream than red alder leaf litter. Using a design similar to the red alder analysis, I ran three litter decomposition trials between January 2013 and January 2014. This analysis accomplishes Objective 4 of my thesis. Based on these mechanisms and those listed above for red alder, I hypothesized the following:

**H6:** Western red cedar leaf litter watered during the summer dry period would lose more mass than un-watered litter.

**H7:** Western red cedar leaf litter with nutrient additions would lose more mass than leaf litter without added nutrients.

**H8:** Western red cedar leaf litter placed closer to the stream would lose more mass than leaf litter placed further away.

**H9:** Western red cedar leaf litter trials in the field for a greater number of degree-days would lose more mass than leaf litter trials in the field for fewer degree-days. (This hypothesis does not include precipitation because only two trials were used to evaluate it, and the correlation between precipitation and degree-days was 1. This meant only one variable could be used in the analysis.)

**Chapter 5:** In my final field study, I assessed how the abundance and taxonomic richness of terrestrial invertebrates varied with nutrient and water additions and distance from stream using three collections of pitfall traps made between June and August 2013. Many terrestrial invertebrates are sensitive to small changes in factors such as air temperature, soil moisture, and vegetation or leaf litter composition (e.g., Thiele 1977, Bohac 1999, Ellis et al. 2001, Herrera and Dudley 2003, Rainio and Niemelä 2003, Yanahan and Taylor 2014). Air and soil moisture can limit the distribution, abundance, and composition of terrestrial invertebrates in riparian habitat (e.g. Wenninger and Fagan 2000, Rykken et al. 2007b, Rykken et al. 2011). High soil moisture and nutrient availability can increase primary production and microbial biomass (Baldrian et al. 2010, Brockett et al. 2012), and increase food resources for herbivorous and detritivorous taxa (Zimmer and Topp 1999, Berch et al. 2009, Wang et al. 2015). Therefore, adding water and nutrients to soils may produce changes in the abundance and diversity of riparian invertebrate communities. Distance from stream has also been associated with differences in the abundance (DeVito and Formanowicz 2003, Kato et al. 2004, Hagar et al. 2011) and community composition (DeVito et al. 2004, Bates et al. 2007, Rykken et al. 2007b) of terrestrial

invertebrates. This field study achieves Objective 5 of my thesis. I hypothesized the following:

**H10:** Traps at watered stations would show greater invertebrate abundance and taxonomic richness than traps at un-watered stations.

**H11:** Traps at stations with nutrient additions would show greater invertebrate abundance and taxonomic richness than traps at stations without nutrients.

**H12:** Traps closer to the stream edge would show greater invertebrate abundance and taxonomic richness than those further from the stream.

**H13:** Invertebrate abundance and community composition in traps would vary with the month of capture.

**Chapter 6:** This chapter serves as the conclusion of my thesis. I first summarized the main results of my thesis, and then reviewed the ecological implications and limitations of my work. Finally, I discussed key questions for future research based on my findings.

## **Chapter 2: Terrestrial invertebrates in the riparian zone: mechanisms underlying their unique diversity**

### **2.1 Introduction**

Invertebrates play significant roles in ecosystems around the world, such as soil aerators, pollinators, processors of organic matter, and members of food webs transferring energy across trophic levels and ecosystem boundaries (Prather et al. 2013, Richardson and Sato 2015). Many studies have analyzed the diversity and distribution patterns of invertebrates in riparian areas. However, most have either taken a taxa-specific approach, such as investigating patterns in beetle diversity and distribution (e.g., Sadler et al. 2004), or described a potential mechanism that controls diversity, such as flooding (e.g., Robinson et al. 2002). Others have examined community responses to anthropogenic activities, such as forest harvesting (e.g., Rykken et al. 2007a) or river regulation (e.g., Paetzold et al. 2008). Distinct riparian invertebrate communities have been documented (Rykken et al. 2007b, Soykan et al. 2012); however, my extensive literature search indicated that a synthesis about multiple mechanisms that contribute to the diversity of these invertebrate communities has not been completed.

In this chapter, I bring together these multiple lines of research to synthesize ideas on five mechanisms supporting obligate riparian terrestrial invertebrates in riparian zones (Table 2.1): disturbance by flooding and drying events, elevated water and nutrient availability, strong microclimate gradients, heightened microhabitat diversity and primary production, and unique food resources. I then consider how these mechanisms change along lateral and longitudinal environmental gradients within a catchment (Fig. 2.1). By identifying gaps in our current knowledge on how these mechanisms work to maintain diversity, this work contributes to our

understanding of invertebrate diversity in riparian zones. This chapter addresses Objective 1 of my thesis. Suggestions for future research based on my review are provided in Chapter 6, Section 6.5.

## 2.2 Disturbance by flooding and drying events

Here, disturbance refers to discrete events that disrupt the structure of populations or communities and alter the physical environment and availability of resources (Pickett and White 1985). Because of the intimate connection riparian zones have with aquatic ecosystems, many riparian communities experience disturbance through periods of flooding and drying (Steward et al. 2017). Although these wet and dry periods are part of their natural flow regime (Poff et al. 1997), they act as disturbances to the community by filtering species that can adapt to or survive variable moisture conditions (Poff 1997). Adaptations to flooding may confer a competitive advantage to certain species in wet patches or during wet periods that may not persist under drier conditions. As a result, riparian environments may be subject to temporal and spatial fluctuations in species composition and can exhibit higher beta diversity than upland areas (Sabo et al. 2005a, Corti and Datry 2016; Table 2.1).

In riparian zones that flood regularly, many organisms exhibit escape behaviours to survive. One example is some species within the genus *Bembidion* (Carabidae), beetles that live on gravel bars along rivers. These beetles prey on terrestrial insects, including emergent aquatic insects, and scavenge dead aquatic insects, thereby redistributing energy from aquatic to terrestrial habitat (Paetzold et al. 2005). They often have small bodies (2-8 mm) that allow them to hide in air-filled interstitial spaces beneath gravel, and fully developed wings fly away that help them to quickly escape floodwaters; consequently, *Bembidion* are one of the first to

recolonize recently flooded habitat (Januschke et al. 2011). Other escape behaviours include vertical migration onto tree trunks and into canopies, as has been seen in polyxenid millipedes (Battirola et al. 2009), as well as ballooning by the linyphiid spiders *Porrhomma pygmaeum* and *Erigone atra* (Linyphiidae), which use silk threads to catch the wind for transport to nearby trees (Adis and Junk 2002). Other invertebrates such as centipedes can use floating wood to escape inundation when seasonal floodwaters rise (Braccia and Batzer 2001). These examples illustrate how invertebrates survive a disturbance common to many riparian areas. They also illustrate escape behaviours in multiple trophic groups, which aids in the establishment of invertebrate communities that can perform multiple ecosystem functions when floodwaters recede.

Numerous species possess physiological characteristics that allow them to tolerate disturbance by inundation (Bogan et al. 2017). Many grasshopper, springtail, mite, and lithobiomorph centipede species can survive flooding as eggs (Adis and Junk 2002). Other species survive for periods underwater by bringing an oxygen store with them. For example, adults of the beetle *Carabus granulatus* (Carabidae) can survive underwater for up to 17 days by trapping air in a subelytral cavity (Kolesnikov et al. 2012). The beetle uses this air bubble to exchange oxygen and carbon dioxide with the surrounding water, creating a physical gill (also called plastron respiration; Larson et al. 2000, Adis and Junk 2002, Flynn and Bush 2008). Found in blackwater river floodplains of Central Amazonia, immature individuals of the millipede *Myrmecodesmus adisi* (Pyrgodesmidae) also use a physical gill by trapping air within a secretion that they form over their body (called a cerotegument; Adis and Junk 2002). When conditions in sediment or soil become anoxic, such as in flooded burrows where water is stagnant, species such as the larvae of the tiger beetle *Cincindela togata* (Carabidae) can switch to anaerobic metabolic pathways to survive (Hoback et al. 1998). All of these physiological

adaptations enable individuals of a species to survive periods of inundation in flood-prone riparian habitats. However, it is important to note that the duration and frequency of disturbance by flooding may limit the functional diversity of invertebrate communities as only species with certain traits like wings and small bodies will be able to survive frequently flooded habitats (Rothenbücher and Schaefer 2006, Lambeets et al. 2008, Gerish et al. 2012). As a result, the positive effect flooding may have on species richness could carry functional tradeoffs in frequently disturbed environments (Gerish et al. 2012).

Though many species have developed behavioural or physiological mechanisms to survive flooding, others have developed reproductive strategies. Age at maturity can influence reproductive success in flood-prone areas. Klok et al. (2004) examined multiple field studies on the earthworm *Lumbricus rubellus* (Lumbricidae) inhabiting floodplains in Germany, and determined that earthworms at frequently inundated sites reached maturity earlier and at a lower body weight than those at non-flooded sites. This difference ensures the earthworms survival to reproduction before flooding occurs (Klok et al. 2004). Timing of reproduction can also be crucial in frequently disturbed riparian habitats. The multivoltine wolf spider *Venatrix lapidosa* lives in floodplains in southeastern Australia and produces two overlapping cohorts per year that mature in spring and autumn, allowing individuals in different life stages to be abundant throughout the year (Framenau and Elgar 2005). Adults that matured in autumn exhibited higher survival rates during the winter months and were larger than those maturing in spring; however, females maturing in spring were more likely to produce egg-sacs and had larger offspring with higher winter survival rates than offspring of autumn-maturing females (Framenau and Elgar 2005). This overlapping cohort therefore increased the probability that the species as a whole will persist through major floods and extreme winter temperatures (Framenau and Elgar 2005).

Because these spiders are an abundant and active predator, this adaptation provides an important and continuing trophic link between their insect prey and predators of this spider. These flooding-adapted life history traits will confer a context-dependent trade-off to certain species; they are advantageous during wet periods but may not promote fitness during dry periods. In this way, riparian environments may be subject to temporal fluctuations in species composition, which promotes temporal beta diversity in the ecosystem.

The natural flow regime includes disturbance by flooding as well as periodic drying of rivers, and this creates spatial and temporal heterogeneity in the riparian landscape. Periodic drying is a characteristic of temporary rivers, which can be classified further as intermittent or ephemeral (Uys and O'Keeffe 1997, Datry et al. 2017). In intermittent rivers, surface flow disappears for a portion of the year leaving a network of exposed riverbed and small pools connected to subsurface flows; ephemeral rivers are dry for most of the year, with surface flows occurring for short periods after precipitation events (Feminella 1996, Uys and O'Keefe 1997). Dry riverbeds of these temporary streams represent novel habitat for terrestrial invertebrates (Wishart 2000, Steward et al. 2011, Corti and Datry 2012, McCluney and Sabo 2012, Steward et al. 2018). Temporary pools can provide a water source for terrestrial invertebrates as well as food resources such as stranded fish and aquatic invertebrates (Steward 2012). Terrestrial invertebrate assemblages of dry riverbeds can be distinct from those in adjacent riparian habitat (Steward et al. 2011) or subsets of riparian communities (Corti and Datry 2016). Dry riverbeds support numerous types of invertebrates (Wishart 2000, Corti et al. 2012, Bogan et al. 2017), such as ants (Formicidae) and springtails, both of which are important components of the soil community because they regulate and maintain soil structure, porosity, and nutrient availability (e.g., Steward et al. 2011). Terrestrial invertebrates living in dry riverbeds can experience large

diel fluctuations in temperature, with low moisture and little to no vegetation cover for refuge from desiccation or predators; these challenges can create greater spatial turnover rates and higher beta diversity in the community (e.g., Steward et al. 2011, Corti and Datry 2016). For example, Corti and Datry (2014) determined that drying did not diminish the taxonomic richness and abundance of riparian arthropod communities at four naturally intermittent sites on the Albarine River in eastern France, but did temporarily alter community composition. Drying can also occur through anthropogenic activities such as groundwater pumping and river diversions. These events alter the natural flow regime of rivers and negatively affect the riparian community. Municipal pumping of ground water has intensified the effects of drought on the San Pedro River in southern Arizona, leading to increasing periods of drying and resulting in lower overall abundance, diversity, and richness of riparian invertebrate communities when compared with flowing sites (McCluney and Sabo 2012). Nonetheless, sustainable management of riparian ecosystems should include some variation in environmental flows over time to preserve the natural flow regime of rivers and their associated environmental and biological diversity (Poff et al. 1997).

### **2.3 Elevated water and nutrient availability**

Generally, riparian zones offer easy and dependable access to fresh water. For obligate riparian species such as the tiger beetle *Oxycheila polita* (Cicindelidae), access to water is essential for both finding prey, such as aquatic invertebrates, and escaping predation itself by jumping into the stream and floating downriver (Cummins 1992). Riparian invertebrate communities can show higher rates of spatial turnover in species richness and therefore dissimilarity between perennial (with surface flow year-round), intermittent, and ephemeral

streams because of differences in the presence of surface water and the availability of groundwater (Moody and Sabo 2016). Riparian soil moisture is generally greatest closer to the stream edge than further upland (Lite et al. 2005), and this increase in moisture provides suitable habitat for species that are attracted to moist habitats or need high moisture levels to survive. For example, the rare beetle *Carabus variolosus* (Carabidae) found in Europe is associated with brooks, springs, and swampy floodplains; Matern et al. (2007) determined the occurrence of *C. variolosus* is associated with high soil moisture (> 60%) and short distances to the stream edge (< 1.5 m), suggesting the availability of water limits the distribution of this riparian species. A source of water may still be retained during dry periods in intermittent rivers, usually as shallow pools (Uys and O'Keeffe 1997, Costigan et al. 2017). If pools are not available, riparian trees such as cottonwoods (*Populus* spp.) and willows (*Salix* spp.) can offer moist green leaves as a source of water to herbivores such as crickets (Sabo et al. 2008); this water is then transferred through the food web to their predators, such as wolf spiders (McCluney and Sabo 2009). Thus, the steady availability of water from surface flow, groundwater, and phreatophytes can strongly influence riparian invertebrate communities (Table 2.1).

Riparian soils are also rich in nutrients, primarily because of regular flooding and closer access to groundwater. Flooding can lead to alluvial deposition of N and P bound to silt and clay into riparian soils (Weibel 2011). Flooding and drying also can encourage faster decomposition of organic litter and the release of nutrients (e.g., Langhans and Tockner 2006, Datry et al. 2018). This occurs because rewetting can cause leaching as well as the recolonization by or stimulation of microbes; microbial communities can shift from an inactive to an active state when water becomes available (Kuehn et al. 2004, Datry et al. 2018). However, this effect depends on the frequency and duration of dry periods due to the potential destruction of thin cell walls in

mycelia and spores of aquatic hyphomycetes (Bärlocher 2009, Bruder et al. 2011). Datry et al. (2011) determined that leaf litter decomposition rates decreased when the length and frequency of dry periods increased using litterbag experiments in the Albarine River, France. The distance from surface soils to the water table is lower in riparian habitat compared with that in upslope habitat, resulting in more frequent anaerobic soil conditions in which N-fixing soil bacteria can occur (Groffman et al. 1992). Certain pioneer plant species, such as red alder, are common near the water's edge and are capable of fixing N into the soil (Binkley et al. 1994). Temperate forests near the edge of salmon-bearing streams show greater tree growth and leaf production due to N from decaying salmon carcasses in the riparian zone (Quinn et al. 2018). These nutrient gradients can lead to greater primary productivity and foliar nutrient concentrations in plants closer to the stream than further inland (Shure and Gottschalk 1985, Clinton et al. 2010; see Chapter 2, Section 2.5 for more detail). Changes in primary productivity have a strong influence on invertebrates in streams: greater primary productivity and larger amounts of detritus has been positively correlated with the diversity and productivity of invertebrate consumers and their predators (Wallace et al. 1997, Wallace et al. 1999, Death and Zimmermann 2005), and nutrient enrichment increased the abundance and biomass of detritivores and their predators (Cross et al. 2006). Currently, whether terrestrial invertebrate productivity and diversity respond to gradients in primary productivity and nutrient availability in patterns similar to aquatic invertebrates remains to be seen.

## 2.4 Microclimate gradients

Riparian habitat is often characterized by gradients in soil moisture, RH, light availability, and air and soil temperatures that extend between 5 to 40 m from the water's edge

into upslope habitat, depending on local climate and topography (e.g., Brosofske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a). In vegetated riparian habitat in temperate forests, air temperature tends to be less variable because it is often cooler in the summer and warmer in the winter when compared with adjacent upslope habitat, and RH tends to be greater near the stream because of the presence of surface water (Brosofske et al. 1997; see Chapter 3, Sections 3.2 and 3.5 for further detail on the extent of documented microclimate gradients). As a result, riparian invertebrate communities within 1 m of the stream can differ from the communities further inland (Rykken et al. 2007b) because humid microclimates support invertebrates that are sensitive to desiccation, as well as hydrophilic and mesophilic taxa (Henshall et al. 2011, Allen 2016). For example, the endangered ground beetle *C. variolosus* and adults of some hydrophilic *Bembidion* spp. are restricted to bare patches of moist soil along stream banks (Henshall et al. 2011). In another study, higher wolf spider abundance and diversity at three riparian sites near Granite Reef Dam, in Phoenix, Arizona (an arid desert environment), were correlated with higher relative soil moisture and lower soil and air temperatures, as opposed to biotic factors such as prey abundance (Wenninger and Fagan 2000). Riparian zones with groundwater close to the soil surface can also support tree assemblages that increase soil moisture and shade while reducing variation in diel temperature fluctuations; this can indirectly influence arthropod productivity by offering a humid environment along with physical structure and a source of water (Allen 2016). Riparian zones can also act as refuges from desiccation during dry seasons and in dry climates. For instance, in the Namib Desert in southern Africa, the millipede *Cnemodesmus riparius* (Paradoxosomatidae) can only survive the dry season by migrating from the riparian zone into the moist sediment beneath dry riverbeds following flooding events (Shelley and Crawford 1996). This millipede is an essential part of this ecosystem through its role as a fungivore and

detrivore; its movement through the soil and feeding activity aids in the decomposition of organic matter by fracturing dead leaves and wood and producing faeces that promote microbial colonization (Shelley and Crawford 1996). These examples illustrate how distinct microclimates in riparian zones support productive, diverse, and often specialized invertebrate communities when compared with upslope habitat (Table 2.1).

The riparian zone provides ideal habitats for species that require specific microhabitats for reproduction. Although several studies have shown this is important for amphibians and reptiles (Semlitsch and Bodie 2003), research on riparian invertebrate reproductive behaviour is limited. High moisture is required for the Western viceroy butterfly (*Limenitis archippus obsolete*, Nymphalidae) as elevated humidity is essential for the growth and development of eggs and larvae, as well as for adults performing mating behaviours (Nelson 2003). This butterfly species is dependent on the Goodding's willow (*Salix gooddingii*) during its larval stage; it provides pollination services to this willow and other riparian tree species as an adult (Nelson 2003). Riparian zones are also a type of edge habitat; they exist at the intersection between aquatic and terrestrial habitat, resulting in abrupt changes in environmental conditions and the composition of the biotic community (Murcia 1995). Many riparian forests receive increased solar radiation in the canopy or on gravel bars of larger rivers where canopy closure is minimal (Gregory et al. 1991). This can be due to various deciduous plant species that allow greater penetration of light when leaves fall, resulting in greater herbaceous understory cover (Gregory et al. 1991, Pabst and Spies 1998). Species such as the beetle *Bembidion petrosum* (Carabidae), which has both humidity and light requirements, take advantage of conditions in the riparian zone: it exhibits photopositive behaviour and shifts its distribution seasonally, occupying sites

closer to the stream during the summer, when temperature and light levels are higher and greater moisture is required to complete mating activities (Andersen 2006).

Because of the high temporal and spatial variation in microclimate surrounding riparian areas, these ecosystems provide increased niche space for many invertebrate species. Moisture gradients provide habitat for diverse and varied invertebrate assemblages and can provide refuge from desiccation to many specialist and generalist species during dry and hot periods. In addition, light availability is higher near the banks of rivers and streams, producing further variation in microhabitats, increasing available niche space, and decreasing the potential for competitive exclusion.

## **2.5 Heightened microhabitat diversity, primary production, and vegetation diversity**

Regular flooding creates spatial variation in habitat characteristics such as sediment type and size, large-wood distribution, and leaf-litter depth (Naiman and Décamps 1997, Hering et al. 2004). These characteristics contribute to the development of microhabitats that encourage the establishment of a diverse invertebrate community (Sadler et al. 2004, Bates et al. 2007, Tagwireyi and Sullivan 2016a; Table 2.1). Greater spatial heterogeneity is often associated with an increase in invertebrate biodiversity, because a range of microhabitat patches can vary in size, age, vegetation, microclimate, and food availability; this, in turn, increases species turnover between patches (beta diversity) and results in greater regional diversity (Datry et al. 2014). Restoration studies have provided examples of how microhabitat availability influences invertebrate communities. In a study conducted in exposed gravel bars in central Germany, Jähnig et al. (2009) found higher carabid beetle species richness in restored floodplains with a

greater diversity of microhabitats compared with that in degraded rivers. Sadler et al. (2004) found that larger exposed bars with a greater diversity of microhabitats supported greater beetle species richness, many of which were rare or exposed riverine sediment specialists. High variation in microhabitat diversity, usually created by fluctuations in the water table that redistribute sediment and large wood (Naiman and Décamps 1997), therefore helps support a number of riparian invertebrate species.

Spatial variation in soil characteristics and water availability also influences vegetation diversity and primary production. Many rivers show multiple fluvial landforms that vary in elevation above the stream and therefore have differing frequencies and durations of inundation (Hupp and Osterkamp 1985). As a result, more flood-tolerant plant species and earlier successional communities can be found closer to water, with more established communities and less tolerant species farther from the stream (Hupp and Osterkamp 1985, Naiman and Décamps 1997). Thus, the interaction between landform and flooding disturbance creates a riparian zone that is often composed of structurally complex, heterogeneous plant communities (Naiman et al. 1993, Little et al. 2013). The plant communities can house an array of invertebrate species: for example, greater density and complexity of plant communities in early successional wetlands were correlated with higher species richness in carabid beetles in eastern Germany (Brose 2003). Vegetation structure, such as stem density, canopy height, and percentage of soil cover of leaf litter and herbs, has also explained much of the variation in species composition and distribution of riparian carabid beetles (Antvogel and Bonn 2001), spiders (Greenstone 1984, Tagwireyi and Sullivan 2016b), and ants (Tagwireyi and Sullivan 2016a). High spatial diversity of plants in riparian zones creates abundant microhabitats, potentially reducing competitive exclusion in invertebrate communities.

Riparian zones can also exhibit a high diversity of deciduous trees and shrubs due disturbance by flooding and varying light levels (Gregory et al. 1991). Compared with coniferous species, deciduous species such as red alder have been shown to support greater numbers of invertebrates living in canopies (Allan et al. 2003). Greater mean terrestrial invertebrate taxonomic richness and biomass were also seen in deciduous leaf and wood litter, respectively, when compared with that found in coniferous litter (LeSage et al. 2005). This is likely the result of deciduous trees producing leaves and litter with lower C:N ratios, less overall lignin, and lower leaf toughness than coniferous trees, providing higher-quality and more palatable resources for herbivorous and detritivorous invertebrate species (Ober and Hayes 2008). A higher-quality resource base can potentially support greater numbers of invertebrates, possibly reducing competitive exclusion and allowing a broader range of invertebrate species to inhabit the riparian zone.

Many plant species are riparian obligates (or specialists), and others show greater productivity when growing in riparian habitat compared with upslope habitat. Riparian plant assemblages can differ from those species in adjacent upslope habitat, especially in arid environments such as the southwestern USA (Naiman et al. 1993, Sabo et al. 2005a), and therefore provide unique opportunities for invertebrate specialization. For example, the Valley elderberry longhorn beetle (*Democerus californicus dimorphus*, Cerambycidae) depends solely on riparian plants for survival and cannot be found outside riparian ecosystems (Collinge et al. 2001); they have formed mutualistic relationships with their riparian hosts (the blue elderberry, *Sambucus mexicana*, and the red elderberry, *Sambucus racemosa*) by providing pollination services. Hydrophytic plants that flourish near water bodies such as cattails (*Typha* spp.) and bulrushes (*Scirpus* spp.), and flood-resistant plants such as willows can tolerate inundation or

recolonize shortly after disturbance (Cowardin et al. 1979, Amlin and Rood 2002), providing stable habitat and resources to invertebrate species.

Primary productivity can be higher and its subsequent effects on invertebrate communities can be more significant in riparian habitat compared with those in upland areas. For example, forested wetlands produce higher amounts of leaf litter than non-wetland habitat, possibly because of increased nutrients and water from river floods (Shure and Gottschalk 1985). Leaf litter is an important food resource for many detritivorous invertebrate species (e.g., Cárcamo et al. 2012, Sabo et al. 2008, Suzuki et al. 2013) and can also provide shelter for predatory invertebrates such as spiders (Sabo et al. 2005b). There is also evidence that plant communities are more productive where there are higher lateral groundwater inflows (Kuglerová et al. 2014). Preferential flow pathways of groundwater carry nitrate, base cations, and other substances that can support greater primary productivity, even compared with areas within riparian habitat with less groundwater (Kuglerová et al. 2014). Heightened productivity and taxonomic richness of benthic invertebrates have been linked to wetlands receiving groundwater discharge (Hunt et al. 2006), so it is possible that groundwater input may contribute to a more productive riparian food web by attracting greater densities of riparian predators with more benthic and terrestrial prey.

## 2.6 Unique food resources

Water bodies contribute unique food sources to riparian habitat in the form of cross-ecosystem resource subsidies, such as adult aquatic insects that are emerging from or flying near the stream (e.g., Henschel et al. 2001, Richardson and Sato 2015; Table 2.1). Emergent aquatic insects such as caddisflies, mayflies, and stoneflies represent one of the largest resource

subsidies for terrestrial predators, and some specialize on capturing this resource. For instance, predatory larvae of the New Zealand glowworm *Arachnocampa luminosa* (Keroplatidae) consume emergent aquatic insects by attracting them with a bioluminescent lure and trapping them on sticky silk threads (Meyer-Rochow 2007). Beetles and spiders also consume large numbers of emergent aquatic insects (e.g., Paetzold et al. 2005, Leigh et al. 2013). In fact, Collier et al. (2002) found that free-living spiders near streams obtained 55% of their body carbon from aquatic invertebrates and emergent adults, whereas web-building spiders obtained 61%. There are also terrestrial predators that actively search for prey within the water body. For example, fishing spiders of the genus *Dolomedes* (Pisauridae) will hunt aquatic invertebrates and small fish by monitoring the tension of the water's surface and striking when prey comes near (Nyffeler and Pusey 2014). Likewise, the beetle *Carabus clathratus* (Carabidae), commonly found near bogs and peatlands, dives into the water to prey on small crustaceans, snails, and even tadpoles (McFerran et al. 1995). Subsidies also occur via organic matter that has washed ashore during overbank flooding or peak flows. Bodies of stranded aquatic invertebrates provide food for scavenging invertebrates, altering their spatial and temporal distribution (Hering and Plachter 1997). Salmon carcasses that are washed or carried into riparian forests by large mammals provide food for the scavenging burying beetle *Nicrophorus investigator* and the rove beetle *Anthobium fimetarium* (Hocking et al. 2009, Quinn et al. 2009). Algae that has washed ashore can subsidize terrestrial detritivores such as grasshoppers (Bastow et al. 2002). These subsidies can provide food resources on more barren, exposed habitat patches such as gravel bars (Hering and Plachter 1997, Paetzold et al. 2005). These examples highlight the unique resources streams provide for invertebrate predators and scavengers living in the riparian zone.

Increased availability of prey species may also attract predaceous invertebrates through reproductive benefits. Unique and spatially-restricted food resources, such as emergent aquatic insects, are generally at peak abundance in spring and early summer in temperate forests (Nakano and Murakami 2001). Occupying riparian habitat during this time can therefore benefit terrestrial invertebrate predators by offering a large energy source for the production and maturation of eggs (Henshall et al. 2011). This idea has been suggested by Henshall et al. (2011), who noted that during June when more food is required for egg maturation and overwintering preparation, some *Bembidion* spp. tended to be more numerous in wet plots with food additions on exposed riverine sediments than in plots receiving only water. Such a combination of increased moisture and food availability during spring and summer seasons may provide suitable habitat for reproductively active terrestrial invertebrates. In special cases, seasonal differences in the productivity of aquatic and terrestrial invertebrates can result in cross-ecosystem resource subsidies that appear complementary. In the Horonai Stream in the Tomakomai Experimental Forest near Hokkaido, Japan, the emergence of adult aquatic insects peaks in spring and provides a subsidy to terrestrial predators when terrestrial production is low (Nakano and Murakami 2001). In summer, this emergence declines rapidly and terrestrial invertebrate inputs to streams begin to rise and peak in late summer or autumn (Nakano and Murakami 2001, Baxter et al. 2005). This terrestrial input is an allochthonous resource to aquatic predators during a period when in-stream production of benthic invertebrates is low (Baxter et al. 2005). Thus, terrestrial invertebrates serve as both predator in riparian habitat and prey in the stream, connecting energy flows between aquatic and terrestrial ecosystems.

## **2.7 The influence of lateral and longitudinal gradients on riparian invertebrate diversity**

The key mechanisms in riparian zones outlined above (Table 2.1) can shape invertebrate communities, but the strength of their influence is dependent on (1) distance from the stream edge (a lateral gradient at the reach scale; Fig. 2.1a) and (2) position in the stream network (a longitudinal gradient at the catchment scale; Fig. 2.1b).

Rivers are complex networks, and measurable and visible differences occur between riparian zones along small streams (first- to third-order) and large rivers (fourth-order and above; Frissell et al. 1986, Allan and Castillo 2007; Fig. 2.2). Characteristics such as altitude, substrate type and size, vegetation cover and diversity, flooding frequency, and the availability of resource subsidies are influenced by differences in hydrological and geomorphological patterns, landscape position, and between river sections that vary in stream order (Benda et al. 2004). Forested headwater streams often show a higher degree of canopy cover and larger sediment instream and on river banks than downstream reaches due to lower discharge and accumulations of large wood that trap coarser gravel and boulders (e.g., Gomi et al. 2002, Famenau et al. 2002). As a result, invertebrate communities can differ between headwater riparian zones and those further downstream. In the Victorian Alps of southeastern Australia, Famenau et al. (2002) examined arthropod communities on gravel bars in upland and lowland streams. They found wolf spider abundance was higher at upstream sites compared with those downstream, and that species composition was dependent on altitude and gravel size (Famenau et al. 2002). For example, the small nocturnal wolf spider *Venatrix arenaris* only occurred in sandy floodplains of lower elevation downstream reaches where it could burrow into sediment to avoid desiccation during the day, whereas the larger-bodied nocturnal *V. lapidosa* which does not burrow was found only

in higher elevation upstream reaches with larger gravel under which it could seek refuge (Framenau et al. 2002). Manderbach and Hering (2001) found a similar difference in groups of *Bembidion* species between upstream and downstream reaches at 185 riparian sites throughout central Europe, noting elevation and sediment size as the main factors driving *Bembidion* community patterns. These studies show that riparian communities respond to longitudinal gradients in substrate size and altitude within a catchment.

Larger rivers create unique challenges for invertebrate communities due to the presence of gravel bars with little vegetation (Fig. 2.2a, 2.2b). Exposed sediment maintained by regular flooding events occurs along many large rivers, and is a patchy but vital resource for specialized invertebrates such as the grasshopper *Chorthippus pullus* (Acrididae). These species are poor dispersers that cannot easily travel through riparian forests or cross large streams, and populations existing on gravel bars face isolation or local extinction when water levels rise (Maag et al. 2013). Individuals take refuge on larger, higher gravel bars that remain dry during annual floods and move between populations when stream sections dry out or as lower gravel bars become exposed when floods recede (Maag et al. 2013). This habitat can also offer unique opportunities to species that have adapted to extreme disturbance, such as some *Bembidion* spp. which are gravel bar specialists that can both avoid inundation and quickly recolonize gravel bars (Hering et al. 2004). Following extreme events such as large overbank flows, they can use this adaptation to rapidly increase in density because predators and competitors that lack such adaptations are largely reduced (Hering et al. 2004). Gravel bars along banks of larger rivers thus provide habitat for many species that may not persist along smaller streams.

Flooding disturbance and inundation duration also occur in a lateral gradient perpendicular to the waterbody edge. Generally, inundation duration decreases farther from the

stream edge, producing a gradually decreasing soil moisture profile (Johnson and Lowe 1985). Hering (1998) examined carabid beetle communities in a floodplain along the River Elbe, in Germany, and found that flood duration and groundwater depth were primary factors explaining species occurrence patterns along the lateral gradient. Similarly, Gallardo et al. (2009) discovered the composition and functional group richness (based on biological traits including feeding behaviour, locomotion, and life-span) of invertebrate communities changed in a lateral direction extending from the Ebro River into the floodplain, in association with gradients in flood duration and frequency. The extent of riparian microclimate gradients varies depending on topography, position in the catchment, and climate (Richardson et al. 2005). Small streams can have lateral gradients that are spatially limited because of steep hillsides that constrain the extent of stream-mediated microclimates (Richardson et al. 2005). Riparian habitat around small streams often has a more closed canopy (Fig. 2.2c, 2.2d) relative to the riparian habitat of larger streams (Fig. 2.2a, 2.2b), and the stream has a greater influence on the forest microclimate (Moore et al. 2005). In mesic forests, the extent of the gradient around small streams (1 to 5 m wide) can range from 5 m to 60 m from the stream edge (Brosofske et al. 1997, Rykken et al. 2007a); this gradient may be shorter in more arid climates, reaching only 5–10 m from the stream (e.g., Danehy and Kirpes 2000). The extent of the stream's influence on the riparian zone varies by stream size, climate, flood frequency, vegetation characteristics, and other underlying environmental gradients, but there has been little study of these potentially interacting patterns.

Cross-ecosystem resource subsidies such as emergent aquatic insects represent a significant resource for riparian predators (e.g., Richardson and Sato 2015, Tagwireyi and Sullivan 2016b), and the influence of this resource varies along both longitudinal and lateral riparian gradients. The availability of emergent aquatic prey exists as a gradient extending from

the stream as the majority of emergent aquatic insects do not move far into the riparian zone (Henschel et al. 2001, Briers et al. 2005), likely because of a combination of obstructive riparian vegetation and a weak dispersal ability of many emergent aquatic species (e.g., O'Callaghan et al. 2013). At the stream edge, emergent aquatic insects occur in large numbers in some seasons and can constitute 40% to 80% of riparian spider diets (Briers et al. 2005, Gergs et al. 2014). Briers et al. (2005) found that at a distance of 20 m from the stream edge, this proportion dropped to < 1%. A similar pattern has been observed in the diet of the predacious beetle *Bembidion atrocaeruleum* near headwater stream sites along the River Severn in Wales (O'Callaghan et al. 2013). At the stream edge, 60% of the beetle's diet was composed of aquatic prey; this changed to only 30% farther from the stream where perennial vegetation was established and inundation occurred less frequently (O'Callaghan et al. 2013). The density and dispersal of riparian predators can also be related to the lateral gradient in the presence of emergent aquatic insects. For example, in New Zealand, riparian spider biomass and web density increased with increasing proximity to the stream edge, and stream insect biomass was positively associated with both variables (Burdon and Harding 2008). Therefore, lateral gradients in aquatic subsidies can shape the abundance and distribution of riparian invertebrate populations, which can consequently influence the ecosystem functions they provide (Henschel et al. 2001).

The lateral availability and influence of emergent aquatic insects on riparian communities also change longitudinally along the course of the stream network. Power and Rainey (2000) suggested that along small, shaded headwaters, the lateral migration of emergent aquatic insects is limited by lower temperatures and in some cases steep, constrained hill slopes, whereas further down the network, channels widen and experience greater levels of wind and solar radiation. These changes can influence emergent aquatic insect movement: wind can carry them away from

the channel and further into the riparian zone, or insects may move inland away from the hotter, sunnier channel to avoid desiccation (Power and Rainey 2000). Kato et al. (2004) suggested this pattern may be responsible for the difference seen between their study on a small (2 to 5 m wide) headwater stream in Japan, which showed little evidence of aquatic carbon in web-building spiders (Linyphiidae) 150 m from the stream edge, and that of Power and Rainey (2000), who noted that at least half of the carbon in linyphiid spider diets was aquatic derived at similar distances along the larger, more open fifth-order South Fork Eel River in California, USA. In addition, King (2014) found the number of emergent aquatic insects entering the first 1 m of the riparian zone adjacent to the stream (or emergence flux) increased with stream order (first- to seventh-order), as did ground beetle and arboreal spider densities.

Gradients in key mechanisms such as flooding disturbance, microclimate gradients, and cross-ecosystem resource subsidies influence the composition, distribution, and abundance of invertebrate communities in riparian zones. These gradients extend laterally from the stream edge into upslope habitat and down the river network as small streams flow into larger and larger rivers. These gradients offer unique opportunities both for observational studies into how stream size and position in a network influence the composition and spatial turnover of invertebrate communities and for empirical research that can shed light on the strength and extent to which these gradients control regional invertebrate diversity.

## 2.8 Conclusion

Riparian invertebrates are important members of both terrestrial and aquatic food webs. They represent a large and distinct segment of biological diversity in these zones (e.g., Steward et al. 2011, Moody and Sabo 2016), and as riparian zones are under increasing threats from

anthropogenic activities and climate change (Nilsson and Berg 2000, Tockner and Stanford 2002, Poff et al. 2011, González et al. 2017), so too is the diversity of riparian invertebrate communities. Key mechanisms including recurrent disturbances, high nutrient and moisture content, biophysical and vegetative diversity, and the presence of unique microclimates and aquatic resource subsidies contribute to the diversity of riparian invertebrates. Conserving invertebrates by protecting the dynamic nature of riparian zones can be complex. These are not static mechanisms that work in isolation but rather dynamic factors that often strongly interact. For example, flooding can create changes in sediment and moisture gradients while dispersing plant propagules. Flooding thus combines elements of disturbance, vegetation diversity, and microclimate that all interact to alter invertebrate abundance and diversity. Therefore, research on terrestrial invertebrates in riparian zones should address multiple mechanisms to help us understand how each contributes to the organization and diversity of this distinct community. Special emphasis should be placed on experimental work that tests the relative importance of these mechanisms and their interactions (see Chapter 6, Section 6.4 for suggestions on future research).

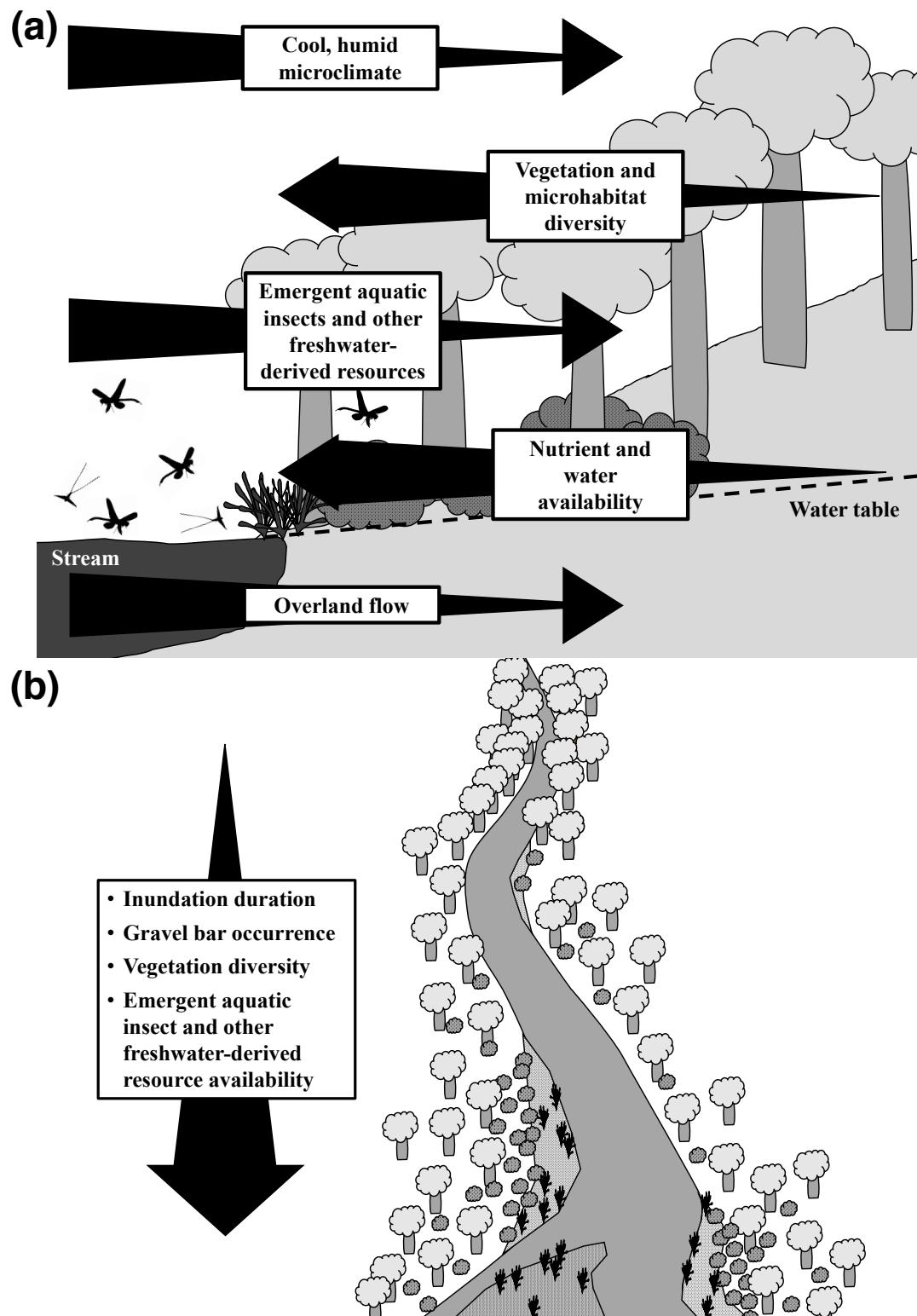
Here, I have synthesized the role multiple mechanisms play in maintaining terrestrial invertebrate communities in the riparian zone. Riparian invertebrates represent unique and sometimes endangered species, perform various functions that support ecosystem processes, and are important members of food webs in both terrestrial and aquatic ecosystems. Understanding how their diversity is created and maintained—and how we can potentially protect or restore the key mechanisms in riparian habitat that contribute to this diversity—is essential for successful riparian conservation and management.

**Table 2.1** Five key mechanisms in the riparian zone that may contribute to the diversity of associate and obligate riparian terrestrial invertebrate communities. References include examples of how these mechanisms influence invertebrate behaviors, physical characteristics, and resource bases.

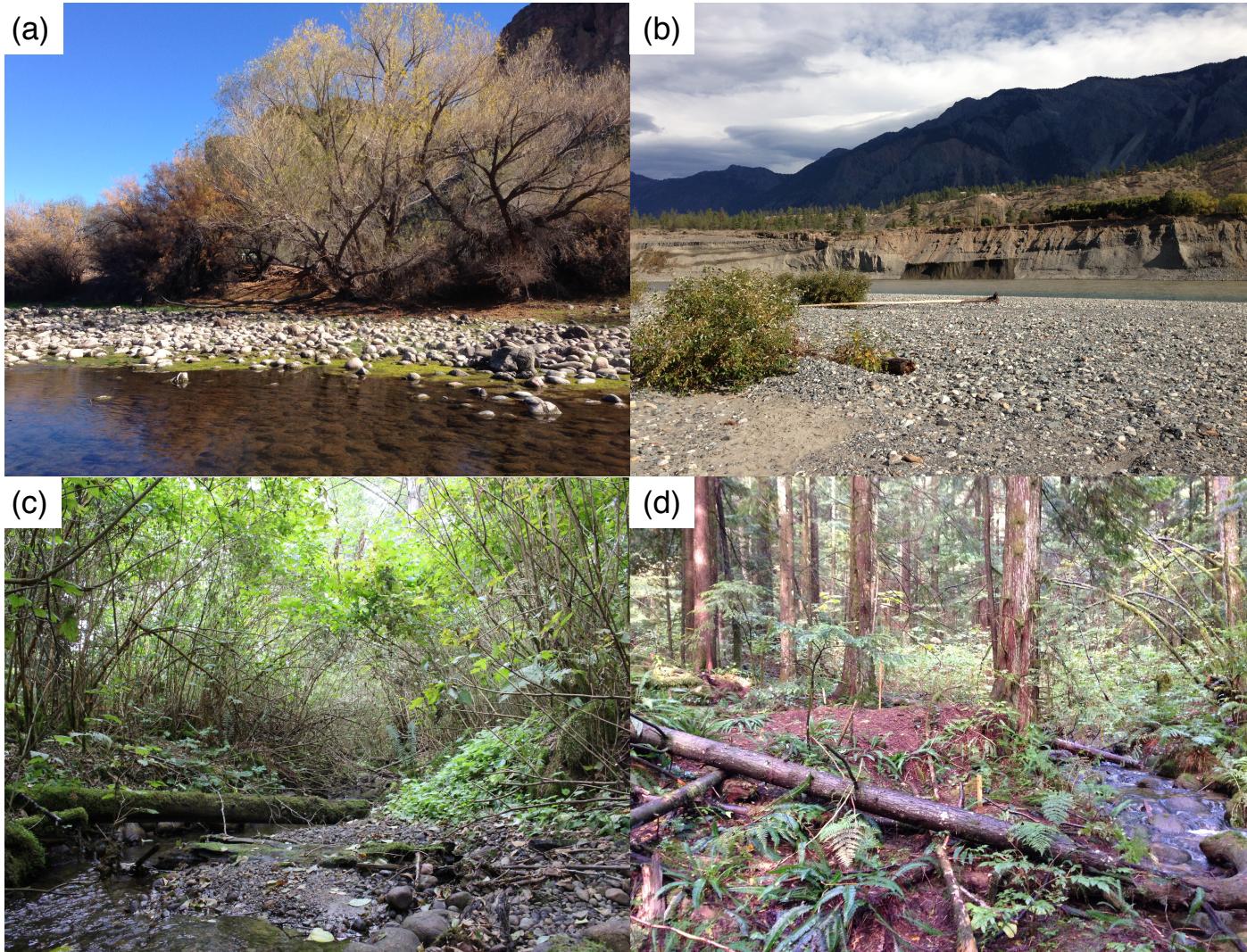
Mechanism	Reason	Effect on invertebrates	References
Disturbance by flooding and drought	Long periods of inundation (onset can occur rapidly)	Filtering and evolution of species with flooding-resistant life stages or escape behaviours	Cummins 1992, Adis and Junk 2002
	Reduces vegetation cover and exposes bare sediment	Adaptation to gravel bars and bare sediments	Hering et al. 2004, Sadler et al. 2004, Bates et al. 2005, Horn and Ulyshen 2009, Henshall et al. 2011
	Cyclical flooding with intermediate dry periods	Natural variation in community composition and extent of terrestrial habitat available for colonization	Hering 1998, Gallardo et al. 2009, Steward et al. 2011, Corti and Datry 2016
Enhanced water and nutrient availability	Alluvial deposition by flooding, low depth to water table	Increased availability of nutrients and water to invertebrate species, as well as primary producers	Wenninger and Fagan 2000, Sabo et al. 2008
	Nitrogen-fixing pioneer plants, deciduous trees and shrubs with low C:N ratios	Higher quality and quantity of food resources for herbivorous and detritivorous invertebrates	Allan et al. 2003, LeSage et al. 2005, Ober and Hayes 2008
Microclimate gradients	Moist, humid conditions created by the stream	Habitat for species that prefer moist soils or are prone to desiccation	Wenninger and Fagan 2000, Rykken et al. 2007b, Rykken et al. 2011, Allen 2016

Mechanism	Reason	Effect on invertebrates	References
Elevated microhabitat diversity and primary production	Natural edge habitat	Moist soil and water-rich food resources during dry periods when surface flow slows or stops	Shelley and Crawford 1996, Allen 2016
	Riparian-specialist plants	Potential for more light and complex microclimates	Nelson 2003, Andersen 2006
	Heterogeneous mosaic of bare soil and vegetation that varies in age class and composition	Opportunity for invertebrate specialization on riparian plants	Collinge et al. 2001
Unique food resources	Greater primary productivity <sup>a</sup>	Multiple niches associated with various microhabitats, and high species turnover between habitat patches that leads to greater beta and regional diversity	Sadler et al. 2004, Sabo et al. 2005a, Jähnig et al. 2009, Datry et al. 2014
	Cross-ecosystem resources subsidies such as emergent aquatic insects or stranded invertebrates	Larger pool of resources for invertebrate consumers, and consequently invertebrate predators	Wallace et al. 1997, Wallace et al. 1999, Death and Zimmermann 2005
	Increased food availability	Specialist terrestrial predators on aquatic prey Alternative resources for predators	Nyffeler and Pusey 2004, Meyer-Rochow 2007
		Able to support a larger number of individuals	Henschel et al. 2001, Nakano and Murakami 2001, Baxter et al. 2005, Richardson and Sato 2011

<sup>a</sup>These sources are for aquatic ecosystems, but potentially show mechanisms that may increase productivity of terrestrial communities.



**Figure 2.1** Conceptual diagrams of lateral (a) and longitudinal (b) gradients of five key riparian mechanisms that may support obligate riparian terrestrial invertebrates. Each arrow indicates where the magnitude of the influence is greatest (widest) and in which direction.



**Figure 2.2** Photographs of riparian habitat along large rivers (fourth-order and above; (a) Salt River, near Phoenix, Arizona, USA and (b) Fraser River, near Lillooet, British Columbia, Canada) and small streams (first- to third-order; (c) Spanish Banks Creek, in Vancouver, British Columbia, Canada, and (d) Mike Creek, in University of British Columbia's Malcolm Knapp Research Forest, Maple Ridge, British Columbia, Canada). (Photographs by T. L. Ramey)

## **Chapter 3: An experimental test of water, nutrients, and microclimate of early-stage mass loss of alder leaf litter in headwater riparian forests**

### **3.1 Synopsis**

The first objective of this chapter was to determine whether water, nutrients, or distance from stream (alone or in combination) limit early-stage mass loss of red alder leaf litter in riparian zones near headwater streams. I hypothesized that mass loss of red alder leaf litter would be greater with water and nutrient additions compared to litter without these additions, and greater closer to the stream than further away. I also examined seasonal variability in red alder mass loss, and hypothesized that litter exposed to higher levels of precipitation would lose more mass than those exposed to less precipitation. I ran three litterbag trials filled with red alder leaf litter at four headwater riparian sites between August 2012 and January 2014, which varied in duration between three months and one year. Litterbags were placed at five distances from the stream, and were either controls or treated with one of the following: water addition, nutrient addition, or addition of both water and nutrients. Water additions increased mass loss by 4% on average compared to un-watered litter. This result suggests moisture is a limiting factor to red alder leaf litter decomposition, even in mesic regions like coastal southwestern British Columbia. There were no clear effects of nutrients or distance from stream on red alder mass loss.

The second objective of this chapter was to document small-scale changes in air temperature, RH, and VPD at five distances between 1 and 40 m from the stream edge, and determine if patterns differ between summer (July and August 2013) and winter (December 2012 to January 2013) periods. I placed data loggers at the same four riparian sites at each distance from the stream to record average daily values for ambient air temperature and RH, and then

calculated VPD using these microclimate data. I determined that RH was on average 2.6% higher, air temperature 0.25°C lower, and VPD 0.14 kPa lower at 1 m from the stream compared to distances further inland during the summer period. This pattern changed during winter: air temperature was 0.1°C higher at 1 m compared to distances further inland, but there were no differences in RH and VPD. This analysis shows that the effect of the stream on riparian microclimate at my sites is more spatially-limited compared to previous studies in the Pacific Northwest, and that temperatures at 1 m from the stream are slightly higher in winter months than distances further inland.

## 3.2 Introduction

As ecotones between aquatic and terrestrial habitat Gregory et al. 1991, Naiman and Décamps 1997), riparian zones offer a unique opportunity for evaluating the influence of environmental variables on ecosystem functions such as decomposition. Moisture and nutrient availability are limiting factors in early-stage mass loss of leaf litter (Prescott 2010, Berg and McClaugherty 2014; see Chapter 1, Section 1.3). Riparian zones are generally characterized by high availability of moisture and nutrients (Johnson and Lowe 1985, Groffman et al. 2002, Lite et al. 2005, Weibel 2011), and there is evidence to suggest decomposition rates occur faster in riparian zones than in habitat further from the stream edge (Merritt and Lawson 1980, Peterson and Rolfe 1982, Shure et al. 1986, Malanson 1993). In this chapter, I examine the role of water, nutrients, and distance from stream in limiting rates of leaf litter mass loss in riparian zones.

Moisture is a primary factor contributing to leaf litter decomposition (Prescott 2010, Berg and McClaugherty 2014). Water influences mass loss by promoting leaching of water-soluble compounds (Aerts 1997, Prescott 2010, Berg and McClaugherty 2014). The amount of mass lost

through leaching is related to the readily leachable fraction of litter; litter species with higher concentrations of water-soluble compounds such as monosaccharides and non-lignified carbohydrates have higher readily leachable fractions and lose more mass via leaching (Harmon et al. 1990, Berg and McClaugherty 2014, Zukswert and Prescott 2017). Water can also influence microbial populations that are part of the decomposer community. Moist soils generally have higher microbial biomass (Baldrian et al. 2010, Brockett et al. 2012), and cyclical rewetting and drying of litter due to flooding can lead to increases in microbial activity following on litter following rewetting (Polunin 1984). Colonization of leaf litter by microbes increases its palatability to detritivores due to its high nutrient content, leading to increased rates of consumption and further mass loss (Seastedt 1984, Xiong and Nilsson 1997). The role of water in decomposition has been shown in watering experiments. For example, Riutta et al. (2012) showed faster decomposition of litterbags in watered plots than un-watered plots in an ash forest near Oxfordshire, UK, which was attributed to increases in leaching and microbial activity. Schimel et al. (1999) saw a similar result for watered paper birch (*Betula papyrifera*) leaf litter in birch forests near Fairbanks, Alaska, USA. Yahdjian et al. (2006) examined mass loss of the grass species *Stipa speciose* under precipitation-exclusion shelters that varied the amount of precipitation to which litter was exposed. They found greater mass loss of litter exposed to higher amounts of precipitation, again attributed to increases in leaching and microbial activity.

The presence of the water body, overbank flooding, and higher water tables relative to the soil surface can cause higher RH and soil moisture as well as less variable air temperatures in riparian zones compared to non-riparian habitats (Brosofske et al. 1997, Danehy and Kirpes 2000, Burt et al. 2002, Moore et al. 2005, Rykken et al. 2007a; see Chapter 2, Sections 2.4 and 2.5). In riparian zones with floodplains, water can lead to higher rates of mass loss due to

leaching, abrasion as water flows over the leaf, and aquatic invertebrate consumption (Peterson and Rolfe 1982, Shure et al. 1986, Gessner et al. 1999, Hutchens and Wallace 2002). However, if flooding leads to sedimentation, litter can be buried and decomposition rates can decline as conditions become anoxic (Chauvet 1988). Along smaller rivers that show little to no flooding, decomposition of leaf litter can be limited by moisture in the litter layer or soils (Hutchens and Wallace 2002). Coastal forests in the PNW exhibit lower precipitation between June and September, and soil moisture shows subsequent declines even in headwater riparian areas (Chin 2007). Decomposition in riparian zones that do not flood could be limited by moisture during this period, and manipulating moisture availability with water additions provides an opportunity to test whether increasing moisture increases mass loss of riparian leaf litter.

Exogenous nutrient availability is a second factor that can influence decomposition rates of leaf litter (Berg and McClaugherty 2014, Prescott 2010). Nutrients such as P and N can promote the growth and activity of microbes (Berg and Matzner 1997), and much like moisture, this microbial growth can lead to greater processing of leaves by microbes and consumption by detritivores (Seastedt 1984, Xiong and Nilsson 1997). The close proximity of groundwater to riparian surface soils, the increased frequency of N-fixing pioneer species like red alder, and the alluvial deposition of N and P from flooding contribute to high nutrient content in riparian soils compared to habitat further inland (e.g., Groffman et al. 1992, Binkley et al. 1994, Wiebel 2011; see Chapter 2, Sections 2.2 and 2.5 for more detail). This elevated nutrient status has led to greater primary productivity and foliar nutrient concentrations in riparian plants (Shure and Gottschalk 1985, Clinton et al. 2010; see Chapter 2, Section 2.5 for more detail), but it may also contribute to differences in decomposition between riparian zones and habitat further inland (Merritt and Lawson 1980, Peterson and Rolfe 1982, Shure et al. 1986). Hefting et al. (2005)

examined decomposition rates of tree leaf litter (species included black alder *Alnus glutinosa*, black poplar *Populus nigra*, and white willow *Salix alba*) in forested riparian buffers across six European sites, revealing a positive correlation between % mass loss and soil nitrate concentrations.

In tropical and temperate non-riparian forests, applications of exogenous nutrients has had positive (Hunt et al. 1988, Dale et al. 2015), negative (Hobbie 2008) and neutral (Prescott 1995, Magill and Aber 1998, Hobbie and Vitousek 2000, Knorr et al. 2005) effects on leaf litter mass loss. The effect is often dependent on the initial chemistry of the litter and whether decomposition is early- or late-stage (e.g., Fog 1988, Hobbie et al. 2008). Generally, nitrogen additions can increase decomposition in litter with high initial N concentrations and more labile compounds during early-stage decay (Berg et al. 1982), but may slow mass loss of litter with higher lignin:N ratios during late-stage decay due to suppression of ligninolytic enzymes produced by microbes or decreases in the abundance and activity of white rot fungi (Carreiro et al. 2000; see Chapter 4, Section 4.2 for a review on nutrients and high-lignin leaf litter). Few studies have examined the role of nutrients in decomposition of riparian litter (see Hefting et al. 2005, Matkins 2009). Whether N and P additions can stimulate decomposition in riparian forests and how decomposition varies with distance from stream remains unclear. Primary production in coastal western hemlock-western red cedar forests in southwestern British Columbia is limited by soil N and P (Tarrant 1951, Feller 1977, Feller and Kimmins 1984, Prescott et al. 1993a), and may also be limiting to decomposition. Experimental manipulations of nutrient additions to leaf litter in riparian zones near headwater streams can help to determine whether N and P are limiting to decomposition in these systems.

Previous riparian studies have documented higher levels of moisture and nutrient availability close to the stream edge within the riparian zone (Johnston et al. 1984, Brosowske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a, Clinton et al. 2010, Ostojić et al. 2013). Distance from stream is also associated with changes in air temperature, canopy cover, vegetation diversity, primary production, and litterfall (Day and Monk 1974, Pabst and Spies 1998, Minore and Weatherly 1994, Brosowske et al. 1997, Naiman and Décamps 1997, Clinton et al. 2010, Weibel 2011). These variables can all influence moisture and nutrient availability in riparian zones. As mentioned above, these variables have been attributed to differences in decomposition between streamside forests and those further inland (Merritt and Lawson 1980, Peterson and Rolfe 1982, Shure et al. 1986, Malanson 1993). Yet, most of these studies were conducted along larger rivers in riparian habitat that flood; exceptions include Hutchens and Wallace (2002) who cited faster mass loss closer to the stream edge due to increases in moisture, and Clinton et al. (2010) who found the opposite pattern. The reason for greater mass loss further from the stream in Clinton et al. (2010) is unclear, as soil moisture and nutrient concentrations were higher near the stream edge. Further examination of the effect of distance from stream in headwater riparian zones would be useful for understanding decomposition processes in these ecosystems, especially as lateral microclimate gradients in temperature and moisture have been documented along small streams (Brosowske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a).

My objective for this chapter was to determine whether water and nutrient availability, and distance from stream limit, decomposition rates of red alder leaf litter in riparian forests along headwater streams in southwestern British Columbia. Red alder is a common tree species in this region (Binkley et al. 1994, Hibbs and Bower 2001, Edmonds and Tuttle 2012), and has

been studied in previous decomposition studies (Harmon et al. 1990), including two in riparian zones (Matkins 2009, Edmonds and Tuttle 2010). I hypothesized that red alder leaf litter watered during the summer dry period would lose more mass than un-watered leaf litter (H1), and that leaf litter with nutrient additions would lose more mass than those without added nutrients (H2). I also hypothesized that red alder leaf litter located closer to the stream edge would lose more mass than litter placed further inland (H3). As part of this analysis, I examined whether microclimate gradients occurred with distance from stream; I expected lower values of RH and higher values for air temperature to occur with increasing distance from stream, as previously documented in Washington and Oregon (H5; Brosfske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a).

To contrast seasonal differences in mass loss rates, I ran four trials that differed in both the duration that litter was in the field and the season in which decomposition began. In coniferous forests of the coastal PNW, winter months are characterized by cool temperatures and high levels of precipitation, whereas summers are warmer and drier (Waring and Franklin 1979, Feller and Kimmins 1979). As stated above, moisture is primary factor limiting leaf litter decomposition (e.g., Prescott 2010), but temperature can also influence decomposition. Increasing temperatures can lead to increased rates of microbial and detritivore activity (Witkamp 1966, Block et al. 1990, Lloyd and Taylor 1994, Uchida et al. 2005). In temperate regions, temperature is generally more limiting to decomposition than moisture (Prescott 2010). Differences across climatic regions in mean annual precipitation and temperature, and mean actual evapotranspiration (which is related to moisture and temperature) are positively correlated with first-year mass loss in leaf litter studies across the globe (Dyer et al. 1990, Aerts 1997, Zhang et al. 2008, Kang et al. 2009). I hypothesized that red alder leaf litter trials with a greater

number of degree-days and higher average daily precipitation would lose more mass than leaf litter trials with fewer degree-days and daily precipitation (H4). I also expected mass loss would increase with a greater number of degree-days, but total precipitation and degree-days were likely related and including both in models could confound results (this is explored in Section 3.3.2). These leaf litter trials and microclimate analysis achieve Objectives 2 and 3 of my thesis.

### **3.3 Materials and methods**

#### **3.3.1 Study sites and design**

Trials were conducted between August 2012 and January 2014 in riparian forests adjacent to four first- and second-order, perennial headwater streams (East, GH, Griffith, and Mike creeks) within the University of British Columbia's Malcolm Knapp Research Forest (Standard UTM: NAD83/10N/531070.1E/5456925.4N; Fig. 3.1). A detailed map of sites in relation to the entire stream network with elevation lines is available in Appendix C, Fig. C.1. This temperate coniferous rainforest is 5157 ha and is located approximately 60 km east of Vancouver, British Columbia, in the Coast Mountain Range. It is in the Coastal Western Hemlock biogeoclimatic zone (Cfb climate subtype under the Köppen-Geiger climate classification; Peel et al. 2007), which is characterized by wet, mild winters and warm, dry summers. Daily average temperatures peak between June and August, and reach their lowest between December and January. Approximately 70% of annual precipitation occurs between October and March (Feller and Kimmins 1979), peaking between February and March; precipitation rates are at their lowest in July and August. Daily temperature and precipitation records for the study period were accessed through the Government of Canada, under the station name Haney UBC RF Admin ([http://climate.weather.gc.ca/historical\\_data/search\\_historic\\_data\\_](http://climate.weather.gc.ca/historical_data/search_historic_data_)

e.html). These data were useful for tracking general weather patterns in the area but were taken at a lower elevation within the forest (147 m.a.s.l.) than my data loggers (195 to 380 m.a.s.l); as a result of higher elevations and closed canopies at my sites, values for seven-day average daily temperature were about 2°C lower than those recorded at the Haney station.

Stream discharge during the summer months (June to August) is low, but increases in September (Feller & Kimmins 1979, Perkins 2000). The probability of overbank flooding was highest during October and March when discharge peaked for East and Griffith Creeks based on data collected by Leach (2014) between September 2012 and May 2013. Evidence of overbank flooding at my sites only occurred within 1 m of the stream at GH Creek along two transects during one alder trial. Flooding was evident from vegetation disturbance and sediment on leaf litterbags; these alder litterbags were removed from the study.

The forest soils are composed of a layer of coarse-textured humo-ferric podzols over compacted glacial till or acid igneous bedrock (Feller 1977, Feller and Kimmins 1979). I did not analyze soil composition at my sites, but Feller (1977) described soils close to stream channels in this forest as generally > 1 m deep and variable in texture. Soils further from the stream were shallower (50 to 150 cm) and coarser in texture (sandy loam to loamy sand; Feller 1977). Soils are permeable, with average hydraulic conductivities reported between  $10^{-4}$  to  $10^{-3} \text{ ms}^{-1}$  for soils and  $10^{-7}$  to  $10^{-6} \text{ ms}^{-1}$  for underlying till (Utting 1979, Cheng 1988, Leach and Moore 2017). This permeability means the vast majority of precipitation reaching the ground infiltrates the soil and flows downslope between the soil and till or bedrock (Leach and Moore 2017). Subsurface flow dominates runoff into streams during precipitation events, with little generated by saturation excess overland flow (Leach and Moore 2017). Soil moisture is generally lowest (< 18% volumetric water content) between mid-June and mid-August when precipitation declines

(ranging between 20 to 27% for the rest of the year), and is higher in soils nearer streams than further inland where hillslopes rise (Feller 1977, Chin 2007).

Forest sites are dominated by two coniferous tree species: western hemlock (*Tsuga heterophylla*) and western red cedar. Douglas-fir (*Pseudotsuga menziesii*) also occurs, but is not a dominant species at my sites. Dominant understory species include western swordfern (*Polystichum munitum*), salmonberry (*Rubus spectabilis*), and huckleberry (*Vaccinium ovatum*). Step moss (*Hylocomium splendens*) also occurred in the understory, especially at GH and East Creeks. Vine maple (*Acer circinatum*) and skunk cabbage (*Lysichiton americanus*) occurred in the understory along the banks at East Creek. Skunk cabbage and devil's club (*Oplopanax horridus*) occurred in the understory along the banks of GH Creek. Red alder is present in the research forest along my four streams, but not along the reaches within my sites. Large wood is plentiful in the streams and throughout the understory at each site (Fig. 3.2).

All sites used in this study were 80 year-old second-growth reference sites which were logged > 100 years previously, and then burnt in a wildfire in 1931 (see Kiffney et al. 2003 for more detail). Stands are dense with 550-650 trees per ha; trees have an average diameter at breast height (dbh) of 40 cm and an average stand height of 45 m (Kiffney et al. 2003). Two creeks had a portion of their length logged in 1998 as part of a riparian management experiment: East Creek was clear-cut 600 m upstream of my site, and GH Creek has both a 30-m riparian buffer 180 m upstream and 10-m riparian buffer 180 m downstream of my site (Kiffney et al. 2003, Kiffney and Richardson 2010). Riparian buffers represent a specified width of intact riparian forest extending perpendicularly from the stream edge from which forest harvesting is excluded; its function is to protect the stream from potential negative consequences of harvesting such as an increase in stream temperature or high levels of sedimentation (Naiman and Décamps 1997,

Kiffney et al. 2003). Ranges for elevation, catchment area, average stream wetted width, stream gradient, and stream order for each site are provided in Table 3.1. All streams were constrained, with narrow bankfull widths and valley floors, and showed little to no floodplain development. Photographs and 3D models of my plots in the riparian zone for each stream are provided in Fig. 3.2. Photographs of each stream are provided in Fig. 3.3. A 40 m by 40 m plot was established along one bank of the stream and was composed of nine transects 5 m apart that extended perpendicularly 40 m into the forest from the bankfull edge of the stream. Distances of 1, 5, 10, 20 and 40 m from the stream edge were marked along each transect for litterbag placement, with the 1-m<sup>2</sup> area surrounding the marker defined as a station (Fig. 3.4). Average elevations above stream for each distance across sites and within each site based on a mean of the nine transects are provided in Appendix A, Tables A.1 and A.2.

To record ambient air temperature and RH conditions at each site, I placed a set of five Onset HOBO® Pro v2 data loggers at each site (along one control transect at each distance, for a total of 20 loggers). This data logger model has an accuracy of  $\pm 0.21^{\circ}\text{C}$  when ambient temperatures are 0 to  $50^{\circ}\text{C}$ . The loggers recorded data every 15 minutes between August 2012 and January 2013, as well as from June 2013 through January 2014. Loggers were primarily used to track changes in air temperature and RH over these distances during winter (December to January) and summer (July to August) periods, but were also used to supplement general weather data from the Haney UBC RF field station. The gap in logger data between January and June 2013 occurred because the logger equipment was not available for use.

I used a fully crossed experimental design, manipulating the addition of water and/or nutrients to litterbags along a gradient of five distances to determine whether these three factors limit litter mass loss and if they interact. To construct litterbags, I used air-dried red alder leaves

collected from the UBC Farm in Vancouver, BC during the previous autumn (August to October 2011). The UBC Farm (est. 2000) is located on the University of British Columbia's southern campus. We collected leaves from beneath an 80 m<sup>2</sup> patch of about 15 young red alder trees (~15–20 cm dbh) on the farm property which is surrounded by coastal forest that includes western red cedar, Douglas-fir, and bigleaf maple (*Acer macrophyllum*; Masselink 2001). We collected leaves here as we could easily monitor litterfall and make frequent collections, thus reducing the rate of initial decomposition after senescence. Leaves were weighed to 4 g ( $\pm 0.04$  g) and placed in 16 × 16 cm litterbags with a coarse mesh size of 9 mm which allowed in larger detritivorous invertebrates. Leaves were of comparable size across treatments and sites. I made a total of 720 litterbags, which consisted of 4 trials of 180 litterbags each (four streams × nine transects × five distances); the final  $n$  was lower for each trial due to the loss of litterbags in the field or damage during processing (see Appendix A for Tables A.3, A.4, and A.5 with litterbag totals by distance and treatment for each trial). Multiple trials were run to determine seasonal effects of precipitation (Fig. 3.5). The four trials ran from 17 August 2012 – 21 November 2012 (97 days;  $n = 163$ ), 17 August 2012 – 28 August 2013 (377 days;  $n = 163$ ), 23 January 2013 – 28 August 2013 (218 days;  $n = 166$ ), and 3 June 2013 – 29 January 2014 (241 days;  $n = 161$ ). At times, multiple trials were in the field simultaneously, so litterbags were kept within 1 m<sup>2</sup> of each station. Litterbags were placed on the flattest portion within each station to prevent movement down the hillslope; in areas where hillslopes were steep, litterbags were held in place by two small dowels (6.4 mm diameter) that were pushed through the mesh on the edges of the litterbag about 20 cm into the soil. Placement was made on open soil and not under western swordfern fronds or branches of huckleberry and salmonberry bushes; if step moss covered the station, litterbags were placed atop it.

At every site, transects were randomly assigned a treatment: control (3 transects), addition of nutrients (2), addition of water (2), and addition of both nutrients and water (2; Fig. 3.4). Nutrient additions consisted of one application of crystallized ammonium nitrate ( $\text{NH}_4\text{NO}_3$ ;  $5.7 \text{ g m}^{-2}$  or  $57 \text{ kg ha}^{-1}$ ;  $19.4 \text{ kg N ha}^{-1}$ ) and triple superphosphate ( $\text{CaH}_4\text{P}_2\text{O}_8$ ;  $1.9 \text{ g m}^{-2}$  or  $19 \text{ kg ha}^{-1}$ ;  $8.7 \text{ kg P ha}^{-1}$ ) distributed over the  $1 \text{ m}^2$  station at the beginning of each trial and another half way through, with the exception of the trial lasting only 3 months which received only one application (Fig. 3.5). Amounts of each compound were determined using a  $4:1 \text{ kg ha}^{-1}$  ratio for N:P recommended by Binkley (1986) for fertilization of managed western hemlock, western red cedar, and Douglas-fir stands in the Pacific Northwest. Ammonium nitrate and triple superphosphate were chosen because they are commonly used to fertilize managed cedar-hemlock forests (Miller and Tarrant 1983, Barclay and Brix 1984, Weetman et al. 1989, Binkley et al. 1999, Bennett et al. 2003). For water treatments, 3 L of stream water in a watering can were used to wet each  $1 \text{ m}^2$  station once a week for the duration of the dry summer period. This dry summer period was between 18 August and 30 September in 2012, as well as 1 June 2013 and 31 August 2013; watering was not done in September 2013 because a total of 187 mm fell that month, compared to only 15 mm in September 2012. Water additions were not made between October and May because over 70% of annual precipitation falls during this period (Feller and Kimmins 1979; see precipitation totals for each trial in Section 3.4.2). Watering was done in the early to mid-morning to reduce immediate evaporation. I used 3 L as this amount was sufficient to thoroughly wet the litterbags and soil at each station; this amount remained constant regardless of the number of litterbags present at each station. A watering can with a perforated nozzle was used to limit any physical abrasion of the litter or its microbial film by the flow of water. I also measured the elevation above stream for each station as this variable can influence microclimate

(Eskelson et al. 2013); it was correlated ( $r = 0.51$ ,  $t = 13.68$ ,  $p < 0.001$ ) with distance from stream, therefore I left elevation above stream out of my models.

Upon collection, I placed litterbags in 4-L Ziploc bags and preserved them by placing them in a -20°C freezer until processing. I then thawed and gently washed them to remove dirt and invertebrates; any red alder pieces broken in washing were collected and processed with the leaves, but potential faunal fecal matter was not identified and removed with washing. By not including fecal pellets, decomposition rates may have been overestimated; therefore, mass loss here refers to loss of litter mass that no longer exists in the form of leaf litter. I placed the washed litter in a drying oven at 60°C for 72 hours. To obtain initial ash-free dry mass (AFDM) values for red alder litter, I assembled five litterbags of 4 g of dry red alder litter that had not been in the field. I combusted this litter in a muffle furnace at 500°C for 1.5 hours and averaged the mass of the five litterbags, calling it the initial AFDM; this value was  $3.75 \pm 0.02$  g (6% ash). I then weighed litter from my trials, combusted it as above, and weighed the ash. I subtracted the AFDM of the decomposed leaves from the initial AFDM to calculate the mass loss of the litter. The decomposition rate constant  $k$  was calculated using the following formula for negative exponential decay (Bärlocher 2005, Karberg et al. 2008):

$$\frac{M_t}{M_0} = e^{-kt} \quad \text{or} \quad k = \frac{-\ln \frac{M_t}{M_0}}{t}$$

$M_t$  is the mass of litter remaining at time  $t$  and  $M_0$  is the initial mass of the litter. To allow for comparison with a wide range of published decomposition studies, I calculated  $k$  using both days and years. For example, in the August 2012 to November 2012 trial,  $k$  was calculated with  $t = 97$  days and  $t = 0.27$  years.

### 3.3.2 Statistical analysis

All statistical analyses were done in RStudio (Boston, Massachusetts, USA; Version 1.0.143) using the packages *stats* (V. 3.2.0), *lme4* (V. 1.1-7), *multcomp* (V. 1.4-6) and *MuMin* (V. 1.15.1). Using temperature and RH data from the HOBO® loggers, I calculated average daily values for air temperature and RH. I also used minimum and maximum daily temperature and RH values to calculate average VPD. VPD is the difference between the level of moisture actually in the air and how much the air could potentially hold when it is saturated, and is a function of both temperature and RH. The atmospheric demand for water is driven by rising VPD, and increases in VPD are associated with decreases in soil moisture (Duff et al. 1997, Sulman et al. 2016). Measuring VPD and RH together is useful for identifying times when moisture may be limited. VPD was calculated using saturation vapour pressure ( $e_s$ ) and actual vapour pressure ( $e_a$ ). Note the  $e_a$  calculation pairs  $e_s$  using min T with max RH, and  $e_s$  using max T with min RH (Yoder et al. 2005).

$$e_{s(\max T)} = 0.6108 \exp \left[ \frac{17.27 \times \max T}{\max T + 237.3} \right] \quad e_{s(\min T)} = 0.6108 \exp \left[ \frac{17.27 \times \min T}{\min T + 237.3} \right]$$

$$e_s = \frac{e_{s(\max T)} + e_{s(\min T)}}{2}$$

$$e_a = \frac{\left( e_{s(\min T)} \times \frac{RH_{max}}{100} \right) + \left( e_{s(\max T)} \times \frac{RH_{min}}{100} \right)}{2}$$

$$VPD = e_s - e_a$$

I used two methods to test my hypothesis that a gradual decrease in RH and an increase in air temperature and VPD would occur with increasing distance from stream during the summer (JH5). First, I integrated the area under the curve (AUC) for average daily T, RH, and VPD between July 1 and August 31, 2013 (62 days). This time period was used because temperatures are at a maximum and differences between distances are most likely to be captured. I then created generalized linear mixed-effects models (GLMMs) that used the AUC values as the response variable to eliminate the effect of a time series, with distance as a fixed effect and site as a random factor. ANOVAs were used to determine whether distance was a significant factor explaining differences in AUC patterns. I used post-hoc Tukey tests to determine whether differences in average daily T, RH and VPD between pairs of distances were significant; differences were tested for ten pairs as there were five distances. I used the *glht* function specifying multiple comparisons (mcp) with “linfct=mcp(distance = "Tukey")”. I also did a similar analysis for December 1, 2012 to January 22, 2013 (53 days) to test my hypothesis that no difference in these variables would occur with distance from stream during winter months (H5). Second, I calculated seven-day running averages for each microclimate parameter and determined the week when the highest maximum seven-day average air temperatures occurred (August 4-10, 2013). I then created generalized linear mixed-effects models with daily averages of T, RH and VPD as response variables, distance as a fixed effect, and site as a random factor. I made distance a factor in these models to determine how the distances varied in each parameter. I compared each model to a null model (without distance) using ANOVAs to determine whether distance was a significant factor affecting patterns in microclimate parameters. I did a similar analysis for the week of January 13-19, 2013 (the coldest portion of the year) to compare results

in winter with those in summer. Statistical significance was determined based on an alpha level of 0.05.

Generalized linear mixed-effects models examining litter mass loss were also created for each trial, as well as for an additional data frame including all trials together. Data were normally distributed, and not transformed for this analysis. In global models for each trial, mass loss (g AFDM) was a function of nutrient and water additions, distance from stream, and site as a random factor. The R code using the *lmer* function was as follows, with asterisks indicating interactions: mass loss ~ nutrients \* water \* distance + (1|site). I included interactions between all factors within the global model. I created a series of 16 models using all possible combinations of factors and their interactions for each trial (listed in Appendix B, List A). To determine the effect of time, temperature, and precipitation on mass loss, I combined datasets for every red alder leaf litter trial, and included two parameters as covariates: the number of degree-days litterbags were in the field and average daily precipitation for each trial. Degree-days were calculated by counting the number of degrees above 0°C, the temperature below which microbial and invertebrate activity slows or stops (e.g., Block et al. 1990, Uchida et al. 2005), for each day based on the daily average temperature and summing them over each trial period. Mass loss per degree-day for each trial was determined by taking the average mass loss for each treatment divided by the number of degree-days in that trial. Average daily precipitation ( $\text{mm d}^{-1}$ ) was calculated by taking the total amount of precipitation recorded within a trial and dividing it by the number of days in that trial). Degree-days and average daily precipitation were not correlated ( $r = 0.07$ ,  $p = 0.05$ ), so both parameters were used in mass loss models. A series of 40 models with every combination of factors was run for the dataset with all four trials. The models

included interactions between water, nutrients, and distance from stream (but not with degree-days or precipitation), and are listed in Appendix B, List B.

Differences in average mass loss as a result of treatment type varied with site. Because I had no specific hypotheses related to differences resulting from site, I included it as a random factor in all models to control for site-related variation (differences in mass loss by site for each treatment can be seen in Appendix C, Fig. C.3). I selected the best model using Akaike's Information Criterion (AIC). Model selection using AIC and AICc, a corrected AIC score that takes sample size into account (Burnham and Anderson 2002), yielded similar results; I therefore used AIC scores in my analyses. The best model was that with the lowest AIC value, highest Akaike weight ( $w_i$ ), and greatest relative likelihood (RL) within a set of models. The  $w_i$  value represents the probability that a model is the best given the data and other possible models, and normalizes the RL values for the model set (Burnham and Anderson 2002). Values of  $w_i$  and RL for the top model were compared to those of the second-best model for each trial in Section 3.4. These comparisons are helpful when  $w_i$  and RL values are similar between models, suggesting that both the best and second-best models fit the data equally well. Conditional R<sup>2</sup> values were also calculated using the *r.squaredGLMM* function in the *MuMIn* package; these values represent the variation explained by both fixed and random factors in each model (Nakagawa and Schielzeth 2013). I chose to include both AIC and R<sup>2</sup> values as AIC tests which model best fits the data (relative to the other models) and R<sup>2</sup> tells us how useful the model is in explaining the data (Nakagawa and Schielzeth 2013). I averaged candidate models with  $\Delta\text{AIC} \leq 2$  to create an averaged model to determine the relative importance (RI) of each factor for each trial. I used this threshold as  $\Delta\text{AIC}$  values  $< 2$  offer substantial empirical support for models (Burnham and Anderson 2002). The RI for a parameter is calculated by taking the sum of Akaike weights of

models that include that parameter divided by the sum of weights for all models in a trial. I also calculated means and standard errors from the raw data to show patterns of mass loss; this was done for each treatment regardless of site or distance, as well as treatments by site and distance from stream. I also ran an independent linear regression analysis using values for the average mass loss of red alder leaf litter for each treatment in each trial. Linear models were created for mass loss including (1) degree-days only, and (2) average daily precipitation only. ANOVAs were run to determine the significance of the independent relationship between each variable and mass loss. Average mass loss values for each treatment in each trial and their relationship with degree-days and average daily precipitation were then graphed.

## 3.4 Results

### 3.4.1 Weather patterns and riparian microclimate

During my study period from 18 August 2012 to 14 January 2014, the average daily temperatures for the Haney weather station were highest in August 2012 (17.4°C) and August 2013 (19.3°C); the highest daily maximum temperature was 32.5°C in August 2013 and 34.0°C in July 2013. The lowest average daily temperatures were in January 2013 (1.4°C) and December 2013 (1.5°C); the lowest daily minimum temperatures occurred in the same months at -1.1°C and -0.7°C, respectively (Fig. 3.6a). Monthly total precipitation was highest in December 2012 (299 mm) and November 2013 (229 mm; Fig. 3.6b, c), and the highest monthly total snowfall occurred in December 2012 (15 cm) and December 2013 (23 cm). Values of VPD calculated from logger data on air temperature and relative humidity were lowest between October and January during both 2012 and 2013 (at or near 0 kPa), and the highest values for VPD between August and October 2012 (around 0.4 kPa) and June and August 2013 (0.6 kPa). Trends in

weather data from the Haney weather station as well as from data loggers for average daily air temperature, RH, and VPD can be seen in Fig. 3.6. Details on weather conditions during each trial are listed in Section 3.4.2. Average daily temperatures for each month during my study period were similar to climate normals recorded at the Haney RF weather station at Malcolm Knapp Research Forest between 1981 to 2010 (Appendix C, Fig. C.2). Total precipitation was higher than climate normals between February and May 2013. Total precipitation in periods between July to August 2013 and October 2013 to January 2013 were lower than climate normals.

Average daily air temperature, RH, and VPD were significantly influenced by distance from the stream during July to August 2013. Average daily air temperatures were lower 1 m from the stream when compared to 10 m by  $0.3^{\circ}\text{C}$  ( $z = 4.047$ ,  $df = 13$ ,  $p < 0.001$ ) and 20 m by  $0.2^{\circ}\text{C}$  ( $z = 3.118$ ,  $p = 0.016$ ); differences between 1 m and 5 m or 40 m were not significant. Average daily RH was greater at 1 m than at other distances by 3% on average (5 m,  $z = -3.598$ ,  $p = 0.003$ ; 10 m,  $z = -4.951$ ,  $p < 0.001$ ; 20 m,  $z = -4.674$ ,  $p < 0.001$ ; 40 m,  $z = -3.064$ ,  $p = 0.018$ ). VPD was lower at 1 m than at 10 m by 0.14 kPa ( $z = 3.236$ ,  $p = 0.011$ ) and by 0.13 kPa at 20 m ( $z = 2.972$ ,  $p = 0.025$ ) from the stream; differences between 1 m and 5 m or 40 m were not significant. Differences between combinations of 5, 10, 20, and 40 m were not significant for any climate variables. Models including distance compared to null versions were different for seven-day moving averages of mean daily RH ( $\chi^2 = 14.75$ ,  $df = 4$ ,  $p = 0.005$ ) and VPD ( $\chi^2 = 9.92$ ,  $df = 4$ ,  $p = 0.042$ ) during the hottest week of my study, August 4-10, 2013. The model including distance for seven-day moving averages of mean daily air temperature was different from the null model ( $\chi^2 = 9.33$ ,  $df = 4$ ,  $p = 0.05$ ). This trend for lower air temperature and VPD, as well as higher RH 1 m from the bankfull edge can be seen in Fig. 3.7 which tracks microclimate data for

the hottest week in 2013. A similar analysis for December 2012 to January 2013 revealed average daily air temperatures were higher at 1 m when compared to 10 m and 40 m by 0.1°C ( $z = -2.998$ ,  $df = 16$ ,  $p < 0.023$ ;  $z = -3.094$ ,  $p = 0.017$ ); no differences in average daily RH and VPD between distances were found for this period. The week of January 13-19, 2013 showed no effect of distance on temperature ( $\chi^2 = 8.12$ ,  $df = 4$ ,  $p = 0.09$ ) or RH ( $\chi^2 = 2.73$ ,  $df = 4$ ,  $p = 0.60$ ); VPD was 0 at all distances during that period (Fig. 3.8).

### 3.4.2 Model results for each trial

#### *August 2012 – November 2012*

Litterbags in this trial were in the field for 1187.2 degree-days, with 97 of 97 days reaching an average daily temperature  $> 0^\circ\text{C}$ . Minimum and maximum average daily temperatures during this trial were 1.5°C (in November) and 23.5°C (in August), respectively. Average mass loss for litterbags without nutrient or water additions was  $1.23 \times 10^{-3}$  g AFDM per degree day. A total of 541 mm of rain fell during this trial, of which 523 mm (97%) fell between 1 October and 21 November 2012 (when water additions were not made to litterbags).

Three models were averaged for this trial (Table 3.2). Water and nutrients were significant predictors in these models, with the best model including only water and nutrient additions (Table 3.3). The  $w_i$  (0.258) and RL (1.000) of the best model was 1.5 times greater than that of the second-best model ( $w_i = 0.173$ , RL = 0.669). Models explained between 21 to 23% of variation in the data ( $R^2 = 0.210$  and 0.225, respectively). The averaged model included water and nutrients as significant factors affecting mass loss (Table 3.2). Average mass loss for litter without water or nutrient additions (control litterbags) was  $1.46 \pm 0.03$  g AFDM (39% of initial AFDM over 97 days,  $k = 0.0051 \text{ d}^{-1}$  or  $1.83 \text{ y}^{-1}$ ). Leaf litter with only water additions lost  $1.60 \pm$

0.05 g AFDM (43%), and litter with only nutrient additions lost  $1.53 \pm 0.03$  g AFDM (41%); litter with both water and nutrient additions lost  $1.70 \pm 0.04$  g AFDM (45%; Fig. 3.9a). All watered litter ( $1.65 \pm 0.03$  g AFDM) lost on average 4% more mass than all un-watered litter ( $1.49 \pm 0.02$  g AFDM;  $z = 3.459$ ,  $p < 0.001$ ; Table 3.3). All litter with nutrient additions ( $1.61 \pm 0.03$  g AFDM) lost on average 3% more mass than all litter without nutrient additions ( $1.51 \pm 0.03$  g AFDM;  $z = 2.105$ ,  $p = 0.035$ ; Table 3.3). Mass loss was similar across sites, with the exception of litter treated with both water and nutrients which showed high variation in mass loss between sites (Appendix C, Fig. C.3).

#### *August 2012 – August 2013*

Litterbags in this trial were in the field for 3959.5 degree-days, with 365 of 377 days reaching an average daily temperature  $> 0^\circ\text{C}$ . Minimum and maximum average daily temperatures during this trial were  $-3.0^\circ\text{C}$  (in January 2013) and  $25^\circ\text{C}$  (in July 2013), respectively. Average mass loss for litterbags without nutrient or water additions was  $6.34 \times 10^{-4}$  g AFDM per degree day. A total of 2239 mm of rain fell during this trial, of which 2085 mm (93%) fell between 1 October 2012 and 31 May 2013 (when water additions were not made to litterbags).

Three models were averaged for this trial (Table 3.2), and water was the only factor present in all three models, with the best model including just water and distance from stream with no interaction. The  $w_i$  (0.310) of the best model was 1.8 times greater than that of the second-best model (0.170), and its relative likelihood (1.000) was 2.2 times greater (0.549). Models explained between 13 to 14% of variation in the data ( $R^2 = 0.141$  and 0.126, respectively). The averaged model included water as the only significant factor affecting mass

loss (Table 3.2). Average mass loss for leaf litter without water or nutrient additions was  $2.51 \pm 0.05$  g AFDM (66% of initial AFDM over 377 days,  $k = 0.0029 \text{ d}^{-1}$  or  $1.05 \text{ y}^{-1}$ ). Leaf litter with only water additions lost  $2.69 \pm 0.09$  g AFDM (71%), and litter with only nutrients additions lost  $2.54 \pm 0.08$  g AFDM (68%); litter with both water and nutrient additions lost  $2.70 \pm 0.07$  g AFDM (72%; Fig. 3.9b). All watered litter ( $2.70 \pm 0.05$  g AFDM) lost on average 5% more mass than all un-watered litter ( $2.52 \pm 0.04$  g AFDM;  $z = 2.668$ ,  $p = 0.008$ ; Table 3.3). Mass loss was similar across sites for litter with and without both water and nutrient additions; litter with only water additions or only nutrient additions showed high variation between sites (Appendix C, Fig. C.3).

#### *January 2013 – August 2013*

Litterbags in this trial were in the field for 2611.7 degree-days, with 216 of 218 days reaching an average daily temperature  $> 0^\circ\text{C}$ . Minimum and maximum average daily temperatures during this trial were  $-3.0^\circ\text{C}$  (in January) and  $25.0^\circ\text{C}$  (in July), respectively. Average mass loss for litterbags without nutrient or water additions was  $6.78 \times 10^{-4}$  g AFDM per degree day. A total of 1426 mm of rain fell during this trial, of which 1112 mm (78%) fell between 1 January and 31 May 2013 (when water additions were not made to litterbags).

Three models were averaged for this trial (Table 3.2). Water was the only factor present in all models, with the best model including only water. The  $w_i$  (0.333) of the best model was 2.5 times greater than that of the second-best model (0.140), and its relative likelihood (1.000) was 2.4 times greater (0.420). Each model explained 13% of variation in the data ( $R^2 = 0.129$  and 0.130, respectively). The averaged model included water as the only significant factor affecting mass loss (Table 3.2). Average mass loss for leaf litter without water or nutrient additions was

$1.77 \pm 0.04$  g AFDM (47% of initial AFDM over 218 days,  $k = 0.0029 \text{ d}^{-1}$  or  $1.06 \text{ y}^{-1}$ ). Leaf litter with only water additions lost  $1.81 \pm 0.05$  g AFDM (48%), and litter with only nutrients additions lost  $1.74 \pm 0.03$  g AFDM (46%); litter with both water and nutrient additions lost  $1.87 \pm 0.05$  g AFDM (50%; Fig. 3.9c). All watered leaf litter ( $1.84 \pm 0.03$  g AFDM) lost on average 2% more mass than all un-watered litter ( $1.76 \pm 0.02$  g AFDM;  $z = 2.324$ ,  $p = 0.020$ ; Table 3.3). Variation in mass loss between sites was higher in litter with both water and nutrient additions compared to other treatments (Appendix C, Fig. C.3).

#### *June 2013 – January 2014*

Litterbags in this trial were in the field for 2734.7 degree-days, with 225 of 241 days reaching an average daily temperature  $> 0^\circ\text{C}$ . Minimum and maximum average daily temperatures during this trial were  $-5.5^\circ\text{C}$  (in December 2013) and  $25^\circ\text{C}$  (in July 2013), respectively. Average mass loss for litterbags without nutrient or water additions was  $5.23 \times 10^{-4}$  g AFDM per degree day. A total of 935 mm of rain fell during this trial, of which 768 mm (82%) fell between 1 September 2013 and 29 January 2014 (when water additions were not made to litterbags).

Five models were averaged for this trial (Table 3.2), and water was the only factor present in all models. The best model included an interaction between water and nutrients. The  $w_i$  (0.215) and RL (1.000) of the best model was 1.5 times greater than that of the second-best model ( $w_i = 0.141$ , RL = 0.655). Each model explained 18% of variation in the data ( $R^2 = 0.175$  and 0.183, respectively). The averaged model included water and an interaction between water and nutrients as significant factors affecting mass loss (Table 3.3). Average mass loss for leaf litter without water or nutrient additions was  $1.43 \pm 0.04$  g AFDM (38% of initial AFDM over

241 days,  $k = 0.0020 \text{ d}^{-1}$  or  $0.72 \text{ y}^{-1}$ ). Leaf litter with only water additions lost  $1.66 \pm 0.07 \text{ g AFDM}$  (44%), and litter with only nutrients additions lost  $1.61 \pm 0.08 \text{ g AFDM}$  (43%; Fig. 3.9d). All watered leaf litter ( $1.61 \pm 0.04 \text{ g}$ ) lost on average 3% more mass than all un-watered litter ( $1.51 \pm 0.04 \text{ g AFDM}$ ;  $z = 2.016$ ,  $p = 0.044$ ). The interaction between nutrient and water additions was negative ( $z = 2.421$ ,  $p = 0.016$ ; Table 3.3); leaf litter with both water and nutrient additions ( $1.57 \pm 0.04 \text{ g AFDM}$  or 42%) lost 1 to 2% less mass than litter with only water or only nutrient additions (Fig. 3.9d). Variation in mass loss between sites was high in litter with only water additions and only nutrient additions (Appendix C, Fig. C.3).

### 3.4.3 Averaged models and the effect of precipitation

Water was the only factor that was significant in every averaged model (Table 3.3) and best model for each trial (Table 3.2), leading to an increase in mass loss by 2 to 5%. The addition of nutrients was a significant factor in two of the four averaged models, resulting in both positive and negative effects on mass loss. Distance from stream was not significant in any of the averaged models but was included in two of the top models for each trial (Table 3.3). Average mass loss per degree day was highest in the August 2012 to November 2012 ( $1.23 \times 10^{-4} \text{ g AFDM}$ ); this rate was twice as fast as the rate for the other three trials (on average,  $6.12 \times 10^{-4} \text{ g AFDM}$  per degree day). Mass loss by treatment for every distance in each trial can be seen in Appendix C, Fig. C.4.

Five models were averaged for the dataset including all four trials (Table 3.2). Water, degree-days, and average precipitation per day significantly influenced mass loss, with the best model including just these three factors. The  $w_i$  (0.228) and RL (1.000) of the best model was 1.2 times greater than that of the second-best model ( $w_i = 0.197$ , RL = 0.866). Each model explained

54% of variation in the data ( $R^2 = 0.538$  and  $0.540$ , respectively). Water additions ( $z = 3.993$ ,  $p < 0.001$ ), degree-days ( $z = 23.055$ ,  $p < 0.001$ ), and average daily precipitation ( $z = 10.638$ ,  $p < 0.001$ ) were significant factors in the averaged model (Table 3.3). Watered red alder leaf litter ( $1.96 \pm 0.03$  g AFDM) lost 4% more mass than un-watered litter ( $1.81 \pm 0.03$  g AFDM). The number of degree-days red alder leaf litter was in the field for was positively related to average mass loss ( $R^2 = 0.66$ ,  $p < 0.001$ ; Fig. 3.10a). Though average daily precipitation was a significant factor in the averaged model, there was no significant independent relationship with mass loss of red alder leaf litter ( $R^2 = 0.17$ ,  $p = 0.107$ ; Fig. 3.10b). The proportion of variation in the data explained the best model including degree-days and average daily precipitation (0.538) was greater than the variation explained by the best models of individual trials (0.164 on average).

### 3.5 Discussion

In this chapter, I determined whether water and nutrient availability limited red alder mass loss rates in riparian forests along headwater streams. I also examined whether mass loss was influenced by distance from stream edge, and whether lateral gradients in T, RH, and VPD existed at my sites. Water played a significant role in the decomposition of red alder. Water additions increased mass loss by 2-5%, depending on the trial, with an average of 4% across trials. This result supports my hypothesis that red alder leaf litter watered during the summer dry period would lose more mass than un-watered litter (H1). This study tested and confirmed that moisture is a primary variable influencing mass loss rates in leaf litter (along with temperature, leaf nutrient content, and leaf structure; see Bunnell et al. 1977, Prescott 2010, Riutta et al. 2012), even at my mesic sites that receive around 2900 cm of rain annually (Kiffney and Richardson 2010).

Leaching, microbial colonization, and detritivore consumption may explain why water was such an important factor in my study. Water can promote mass loss by leaching that occurs rapidly in early-stage decomposition, and in red alder this process can be significant; Zukswert and Prescott (2017) saw a leaching mass loss of about 10% after 24 hours of submersion in distilled water for red alder leaves collected from the UBC Farm, the same location where I collected red alder leaves for my experiments. Water can also stimulate microbial growth and activity, which can periodically enhance mass loss when leaves are wetted through precipitation or flooding (Polunin 1984, Xiong and Nilsson 1997, Nielsen and Ball 2015, Datry et al. 2018), or in my case, weekly watering during the summer dry period. An increase in microbial respiration and biomass following weekly watering was seen by Schimel et al. (1999) in litterbags filled with paper birch (*Betula papyrifera*) leaves that were placed in a birch stand near Fairbanks, Alaska during the summer dry period between July and August. This microbial growth can lead to greater consumption and fragmentation by invertebrates such as millipedes (Cárcamo et al. 2000), and ultimately greater mass loss of the leaf litter. Water has played multiple roles in regulating leaf litter decomposition in previous studies, whether directly through leaching or indirectly via microbes and invertebrates, and its addition resulted in greater mass loss of red alder leaves at my riparian sites.

The addition of nutrients had mixed effects on leaf litter mass loss, neither fully rejecting nor supporting my hypothesis that red alder leaf litter with nutrient additions would lose more mass than litter without nutrient additions (H2). Nutrient additions were included in several of the top candidate models for each trial, and were a significant factor in two of four averaged models, but were not significant in the model including datasets for all trials. Unlike water additions which resulted in a higher mass loss in all trials, nutrient additions had both positive

and negative effects on litter mass loss. Decomposition of low-lignin litters with more labile components has been accelerated by N additions in other studies (Berg et al. 1982, Hobbie 2000, Knorr et al. 2005). Red alder leaves have a low initial lignin:N ratio (between 6 to 9; Edmonds 1980, Matkins 2009), but this high nitrogen content may have caused a mixed response to nutrient additions. Red alder leaves have high N due to its ability to fix N through its symbiotic relationship with the actinomycete *Frankia alni* (Binkley et al. 1994, Prescott et al. 2004), and N resorption during senescence is quite low (5%; Urgenson et al. 2009). Though N has been described as a limiting nutrient in my sites (Feller 1977, Feller and Kimmins 1984), the high N content of the red alder litter may have made the N additions ineffective. Similarly, Matkins (2009) did not find a difference in decomposition rates of red alder litterbags placed in fertilized and unfertilized Douglas-fir riparian forests near Eugene, OR, USA; however, these forests were only fertilized with ammonium nitrate and urea, with no P additions. As my sites were located in coastal western red cedar-western hemlock forests which exhibit low soil N and P (Tarrant 1951, Feller 1977, Feller and Kimmins 1984, Prescott et al. 1993a), I hypothesized that nutrients additions may encourage microbial colonization (Berg and Matzner 1997) resulting in greater mass loss in litterbags with added nutrients compared to controls if N and P were limiting at my sites. My mixed results may mean that neither N or P were limiting to decomposition at my site. However, the significant positive effect of nutrients on mass loss in the August 2012 to November 2012 trial does indicate nutrients were a limiting factor in this trial. This trial was the shortest at 97 days, and previous studies on red alder have noted rapid mass loss in the first four to six months followed by a large decline in the rate of decomposition (Prescott et al. 2004, Matkins 2009). In a comparison between red alder and more lignin-rich Douglas-fir litter, Prescott et al. (2004) saw no differences in mass remaining between the two species after six

months. It is possible that I was able to detect a positive effect of nutrient additions on initial mass loss rates in this three-month trial between August 2012 and November 2012, but not in the longer trials.

Mass loss did not vary with distance from the stream, rejecting my hypothesis that western red alder leaf litter placed closer to the stream would lose more mass than litter placed further inland (H3). Though it was included in some of the top candidate models for each trial, it was not a significant factor in any of the averaged models. This result is different than results reported in previous studies (Bell et al. 1978, Peterson and Rolfe 1982, Shure et al. 1986, Malanson 1993), where litterbags closer to the stream showed greater mass loss than litterbags placed further inland. Possible reasons for this difference include how far inland litterbags were placed compared to the streamside, and the prevalence of flooding at sites in previous studies. Peterson and Rolfe (1982) conducted their study on a fourth-order section of the Sangamon River in central Illinois, USA, comparing litterbags placed near the stream edge (floodplain site) with those placed 500 m inland (upland site). Bell et al. (1978) conducted their study at the same location, comparing litterbags placed in the upland site with those placed in a transitional zone between the floodplain and upland sites. Shure et al. (1986) compared litterbags placed on the bank of a third-order stream in South Carolina, USA, to those located 30, 60 and 90 m away in a floodplain forest, with overbank flooding diminishing within 45 m of the stream. These previous studies all took place on higher-order streams with floodplains where flooding can cause changes in water or nutrient availability and vegetation composition with distance from stream (Johnson et al. 1976, Lite et al. 2005; see Chapter 2, Section 2.9). My first- and second-order streams showed little to no differentiation between canopy cover and vegetation at the streamside and further inland; soil and nutrient gradients were not assessed at my sites. Litterbags in previous

studies along larger order streams were also placed at greater distances from the stream than the distances I compared in my analysis, and were subjected to overbank flooding during the experiment, which could have potentially led to mass loss from leaching and physical abrasion (Bell et al. 1978, Peterson and Rolfe 1982, Shure et al. 1986); litterbags in my analysis were not flooded. The lack of flooding, absences of differentiation in canopy cover and vegetation, and minimal floodplain development at my sites likely produced little change between streamside and inland habitat, with no subsequent effect of distance from stream on mass loss rates in my analysis.

My microclimate analysis revealed that mean daily air temperature, RH, and VPD were significantly influenced by distance from stream during July to August 2013, with loggers at 1 m recording higher values of RH and lower values of temperature and VPD than other distances. This result partially supports my hypothesis Differences did not occur beyond 1 m from the stream. These results are consistent with my hypothesis (H5), but also partially reject it as differences did not occur gradually with increasing distance from the stream. Distance from stream did not influence RH or VPD during winter months (December 2012 to January 2013); however, average daily air temperature was higher at 1 m from the stream than further inland. Results for RH and VPD in the winter analysis partially support my hypothesis, but the results for temperature also reject it as I expected that temperature also would not differ with distance from stream (H5). My recorded differences in temperature and RH are smaller and less extensive than those found by Brosofske et al. (1997) in western Washington and Rykken et al. (2007a) in western Oregon. Brosofske et al. (1997) recorded an average increase of 2°C in air temperature and an 8% increase in RH within 16 to 32 m of the stream during July through September in 1993, while Rykken et al. (2007a) reported an average increase of 3°C in air temperature and

decrease of 15% in RH within 10 m from the stream during May through September 2002. When compared to my data, these studies describe changes in microclimate variables that are larger in magnitude and extend further into the riparian zone. The absence of a gradient may help to explain the lack of an effect of distance from stream on red alder litterbag mass loss rates, though microclimate data were not included in the mass loss analysis and are only one component of potential environmental changes associated with distance from stream.

Differences in the magnitude and spatial extent of riparian microclimate gradients between studies could possibly be due to variation in precipitation between study locations. My sites in British Columbia receive on average 2900 mm precipitation annually (Kiffney and Richardson 2010), whereas the H. J. Andrews Experimental Forest studied in Rykken et al. 2007a) receives on average 800 mm less precipitation annually (Waichler and Wigmosta 2003, Brockett et al. 2012). The stream's influence on air temperature and RH in the riparian zone at my wetter sites may not have been as great as seen in drier sites. Gradients in temperature and RH extending 10 m and 5 m from the stream, respectively, were also seen by Danehy and Kirpes (2000) in the semi-arid climate of the eastern Cascades in Washington and Oregon where annual precipitation is < 500 mm. This gradient extended for a shorter distance into the riparian forest compared to Brosofske et al. (1997) and Rykken et al. (2007a), however this was likely due to steep hillsides that constrained water vapour and cool air created by the stream (Danehy and Kirpes 2000, Richardson et al. 2005). My sites were all generally constrained as each stream was narrow (between 1.5 to 2 m wide) and the elevation of the riparian zone began to rise above the stream within 10 m from the stream edge (Fig. 3.2, see Griffith Creek for an exception). Thus, the constrained nature of my streams and humid conditions likely contributed to the smaller and more spatially-restricted microclimate at my sites.

Temperature and precipitation were significant factors influencing mass loss of red alder leaf litter. Mass loss of red alder leaf litter was greater in trials where litter was in the field for a greater number of degree days, a result that supports my hypothesis (H4). Soil microbial respiration rates and feeding activity of soil invertebrates increase as temperatures rise (Lloyd and Taylor 1994, Chapin et al. 2002, Gongalsky et al. 2008), and warmer temperatures in spring and summer are known to stimulate microbial colonization and growth on leaves (Witkamp 1963, Langhans et al. 2008). Bell et al. (1978) observed greater mass loss of leaf litter in river floodplains of Illinois during spring and summer compared to winter when activity by microbes and detritivores is low. Langhans et al. (2008) also suggested that leaves in the floodplain of the Tagliamento River, Italy, begin to quickly decompose only after temperatures increase in the spring. Average daily precipitation was also a significant factor influencing red alder mass loss. Greater levels of precipitation directly affect decomposition rates by increasing mass loss through leaching and microbial activity (e.g., Trofymow et al. 2002, Joly et al. 2016). Precipitation exclusion experiments have shown slower mass of leaf litter attributed to reductions in leaching and microbial activity (e.g., Yahdjian et al. 2006). Regional to global-scale analyses have also documented greater mass loss for both deciduous and coniferous leaf litter species in regions with higher precipitation (Zhang et al. 2008, Kang et al. 2009), though indirect effects of precipitation on vegetation composition and litter quality across regions can confound this effect (Yahdjian et al. 2006). Portillo-Estrada et al. (2016) conducted a reciprocal leaf litter transplantation experiment to determine how changes in climate without changes in litter quality influence decomposition; they confirmed that mass loss of single litter species collected from a single location was greater in climates with higher annual precipitation. It is important to note that average daily precipitation did not have a significant independent effect on red alder mass

loss when it was analyzed with a regression. This measure of precipitation is extremely coarse, given that trials ranged in duration from 3 months to one year, and average daily precipitation varies between 0 to 30 mm throughout the year (Fig. 3.6b and c). This coarseness may explain the lack of an independent relationship between mass loss and precipitation. The disparity between model results for precipitation's significant influence on mass loss and the non-significant result of the independent regression neither fully supports nor rejects my hypothesis that litter with higher levels of precipitation would lose more mass than litter with lower levels of precipitation (H4).

I conclude from my study that moisture is a limiting factor for the mass loss of red alder during the drier summer season, even in mesic headwater riparian forests of southwestern coastal British Columbia. Though N and P are limiting to primary production in this region (Tarrant 1951, Feller 1977, Feller and Kimmins 1984, Prescott et al. 1993a), I did not find clear evidence that they are limiting to red alder leaf litter decomposition as nutrient additions had both positive and negative impacts on mass loss depending on the trial. I found no evidence that distance from stream was limiting to red alder leaf litter mass loss, and that gradual gradients in microclimate parameters did not exist between the stream edge and 40 m into the forest during summer months. The presence of the stream did produce a step-change in microclimate with higher RH and lower air temperature and VPD at 1 m from the stream edge compared to distances further inland. This spatially-limited difference in microclimate occurred during the summer months, but the difference in RH and VPD were lost during the winter likely due to high levels of precipitation. These results add to our understanding of which factors are limiting to red alder leaf litter decomposition in riparian zones, and the extent to which streams influence riparian microclimate. When compared to other analyses of headwater riparian microclimate in the

coastal PNW, including Brossofske et al. (1997) in Washington and Rykken et al. (2007a) in Oregon, these results reveals how riparian microclimates vary geographically. Potential implications of these results in light of climate change and forest harvesting, and suggestions for future experiments into the role of water and nutrients in limiting red alder leaf litter mass loss, are provided in Chapter 6, Section 6.4.

**Table 3.1** Physical characteristics of reference streams in Malcolm Knapp Research Forest in Maple ridge, British Columbia, Canada. Elevation values were obtained using Google Maps. Values with subscripts were retrieved from published data.

Stream	Stream order	Elevation (m.a.s.l.)	Catchment area (ha)	Wetted width (m)	Stream gradient (%)
East	2	195	44 <sup>a</sup>	2.0	8 <sup>a</sup>
GH	2	230	84 <sup>a</sup>	2.0	4 <sup>a</sup>
Griffith	1	380	11 <sup>b</sup>	1.5	5 <sup>c</sup>
Mike	1	294	30 <sup>a</sup>	1.5	8 <sup>a</sup>

<sup>a</sup> Kiffney and Richardson 2010

<sup>b</sup> Leach and Moore 2016

<sup>c</sup> Guenther et al. 2014

**Table 3.2** Comparison of top candidate models for each trial describing ash-free dry mass loss of red alder leaf litter as a function of water (W) and nutrient (N) additions, and distance from the bankfull edge (D). An analysis containing data from all four trials (“All trials”) also includes the number of degree-days (dd) and average precipitation per day (precip) for each trial. All models include site as a random factor. Interactions are indicated with an asterisk (\*). Results for each model include Akaike Information Criterion (AIC), change in AIC relative to the best model ( $\Delta$ AIC), Akaike weight ( $w_i$ ), relative likelihood (RL), and conditional  $R^2$ .

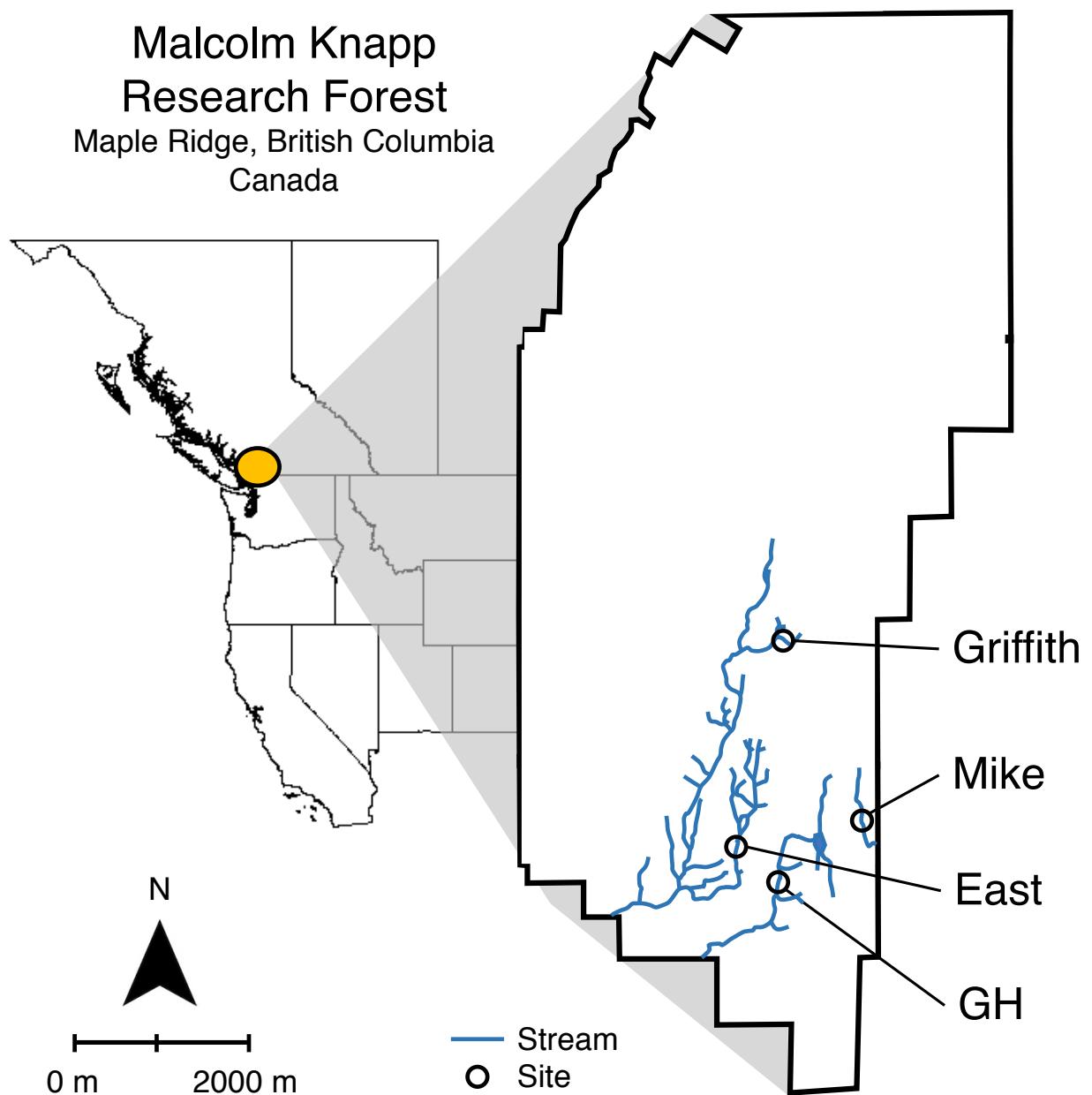
Trial	Model	df	AIC	$\Delta$ AIC	$w_i$	RL	$R^2$
Aug 12 – Nov 12	<b>W + N</b>	5	<b>-14.157</b>	<b>0.000</b>	<b>0.258</b>	<b>1.000</b>	<b>0.210</b>
	W*D + W+N+D	7	-13.352	0.804	0.173	0.669	0.225
	W + N + D	6	-12.832	1.325	0.133	0.516	0.214
Aug 12 – Aug 13	<b>W + D</b>	5	<b>198.571</b>	<b>0.000</b>	<b>0.310</b>	<b>1.000</b>	<b>0.141</b>
	W	4	199.772	1.201	0.170	0.549	0.126
	W + N + D	6	200.478	1.907	0.120	0.385	0.141
Jan 13 – Aug 13	<b>W</b>	4	<b>20.149</b>	<b>0.000</b>	<b>0.333</b>	<b>1.000</b>	<b>0.129</b>
	W + D	5	21.882	1.733	0.140	0.420	0.130
	W + N	5	21.997	1.848	0.132	0.397	0.130
Jun 13 – Jan 14	<b>W*N + W + N + D</b>	7	<b>140.260</b>	<b>0.000</b>	<b>0.215</b>	<b>1.000</b>	<b>0.175</b>
	W*N + N*D + W + N + D	8	141.107	0.846	0.141	0.655	0.183
	W	4	141.282	1.022	0.129	0.600	0.137
	W*N + W*D + W + N + D	8	142.150	1.889	0.084	0.389	0.176
	W + N	5	142.153	1.893	0.084	0.388	0.144
All trials	<b>W + dd + precip</b>	6	<b>593.943</b>	<b>0.000</b>	<b>0.228</b>	<b>1.000</b>	<b>0.538</b>
	W + N + dd + precip	7	594.231	0.288	0.197	0.866	0.540
	W + D + dd + precip	7	595.574	1.630	0.101	0.443	0.539
	W + N + D + dd + precip	8	595.807	1.864	0.090	0.394	0.540
	W*D + W + N + D + dd + precip	9	595.888	1.945	0.086	0.378	0.541

**Table 3.3** Average parameter estimates (mass loss g AFDM) with standard errors (SE) for the top models of each red alder trial. Significant parameters are in bold. Parameter terms are water additions (W), nutrient additions (N), distance from the bankfull edge (D), number of degree-days (dd), and average daily precipitation (precip). Abbreviations include standard error (SE), 95% confidence interval (CI), the relative importance (RI) of each parameter, and the number of models each parameter is in for each trial. Interactions are indicated with an asterisk (\*).

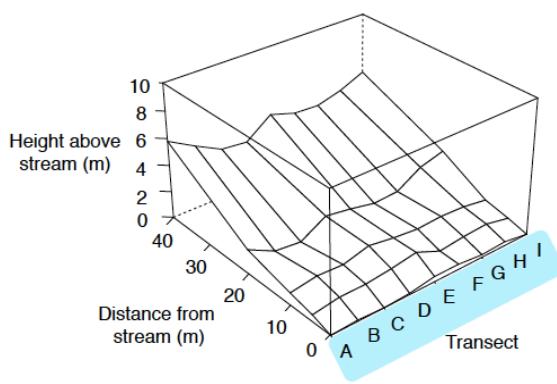
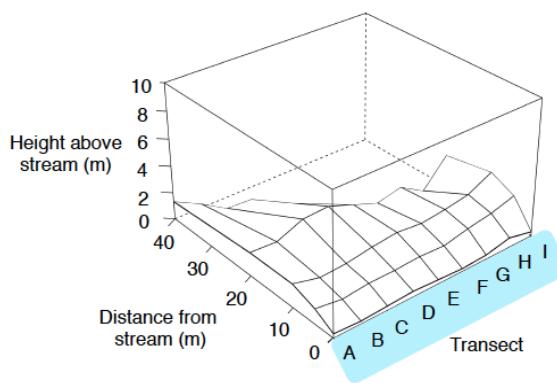
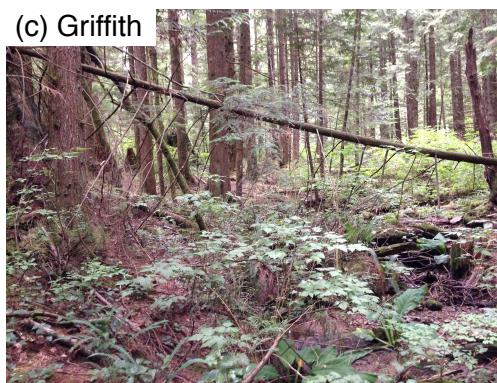
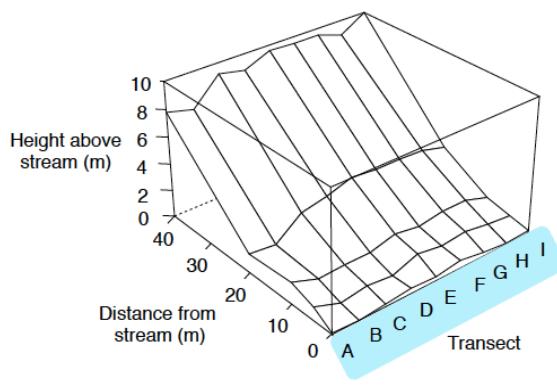
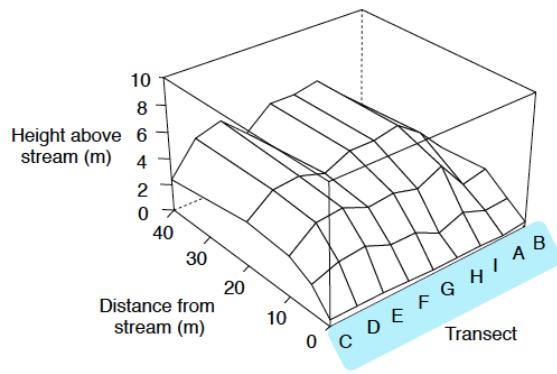
Trial	Parameter	Estimate	SE	z	p	95% CI	RI	# of models
Aug 12 – Nov 12	Intercept	1.445	0.051	28.257	< 0.001	1.345 – 1.545		
	<b>W</b>	<b>0.170</b>	<b>0.049</b>	<b>3.459</b>	<b>&lt; 0.001</b>	<b>0.074 – 0.266</b>	<b>1.00</b>	<b>3 of 3</b>
	<b>N</b>	<b>0.074</b>	<b>0.035</b>	<b>2.105</b>	<b>0.035</b>	<b>0.005 – 0.143</b>	<b>1.00</b>	<b>3 of 3</b>
	D	0.002	0.002	1.161	0.246	-0.001 – 0.005	0.54	2 of 3
	D*W	-0.004	0.002	1.582	0.114	-0.009 – 0.001	0.31	1 of 3
Aug 12 – Aug 13	Intercept	2.560	0.091	27.790	< 0.001	2.380 – 2.741		
	<b>W</b>	<b>0.179</b>	<b>0.067</b>	<b>2.668</b>	<b>0.008</b>	<b>0.048 – 0.311</b>	<b>1.00</b>	<b>3 of 3</b>
	N	0.020	0.067	0.302	0.763	-0.112 – 0.153	0.20	1 of 3
	D	-0.004	0.002	1.786	0.074	-0.009 – 0.000	0.72	2 of 3
Jan 13 – Aug 14	Intercept	1.748	0.051	34.211	< 0.001	1.648 – 1.848		
	<b>W</b>	<b>0.090</b>	<b>0.038</b>	<b>2.324</b>	<b>0.020</b>	<b>0.014 – 0.165</b>	<b>1.00</b>	<b>3 of 3</b>
	N	0.015	0.038	0.387	0.699	-0.061 – 0.091	0.22	1 of 3
	D	0.001	0.001	0.513	0.608	-0.002 – 0.003	0.23	1 of 3
Jun 13 – Jan 14	Intercept	1.449	0.092	15.698	< 0.001	1.268 – 1.630		
	<b>W</b>	<b>0.192</b>	<b>0.095</b>	<b>2.016</b>	<b>0.044</b>	<b>0.005 – 0.379</b>	<b>1.00</b>	<b>5 of 5</b>
	N	0.143	0.090	1.575	0.115	-0.035 – 0.322	0.80	4 of 5
	D	$1.47 \times 10^{-5}$	0.003	0.006	0.996	-0.005 – 0.005	0.67	3 of 5
	<b>W*N</b>	<b>-0.273</b>	<b>0.112</b>	<b>2.421</b>	<b>0.016</b>	<b>-0.494 – -0.052</b>	<b>0.67</b>	<b>3 of 5</b>
	<b>W*D</b>	-0.001	0.004	0.330	0.741	-0.009 – 0.007	0.13	1 of 5
	<b>N*D</b>	0.004	0.004	1.068	0.286	-0.004 – 0.012	0.22	1 of 5

Trial	Parameter	Estimate	SE	z	p	95% CI	RI	# of models
All trials	Intercept	0.035	0.105	0.334	0.739	-0.168 – 0.243		
	<b>W</b>	<b>0.138</b>	<b>0.035</b>	<b>3.993</b>	<b>&lt; 0.001</b>	<b>0.075 – 0.191</b>	<b>1.00</b>	<b>5 of 5</b>
	N	0.039	0.030	1.324	0.185	-0.019 – 0.097	0.53	3 of 5
	D	$-2.61 \times 10^{-4}$	0.001	0.199	0.842	-0.003 – 0.001	0.39	3 of 5
	W*D	-0.003	0.002	1.384	0.166		0.12	1 of 5
	<b>dd</b>	<b><math>3.46 \times 10^{-4}</math></b>	<b><math>1.50 \times 10^{-5}</math></b>	<b>23.055</b>	<b>&lt; 0.001</b>	<b><math>3.16 \times 10^{-4} – 3.75 \times 10^{-4}</math></b>	<b>1.00</b>	<b>5 of 5</b>
	precip	<b>-0.158</b>	<b>0.015</b>	<b>10.638</b>	<b>&lt; 0.001</b>	<b>0.129 – 0.187</b>	<b>1.00</b>	<b>5 of 5</b>

**Malcolm Knapp  
Research Forest**  
Maple Ridge, British Columbia  
Canada



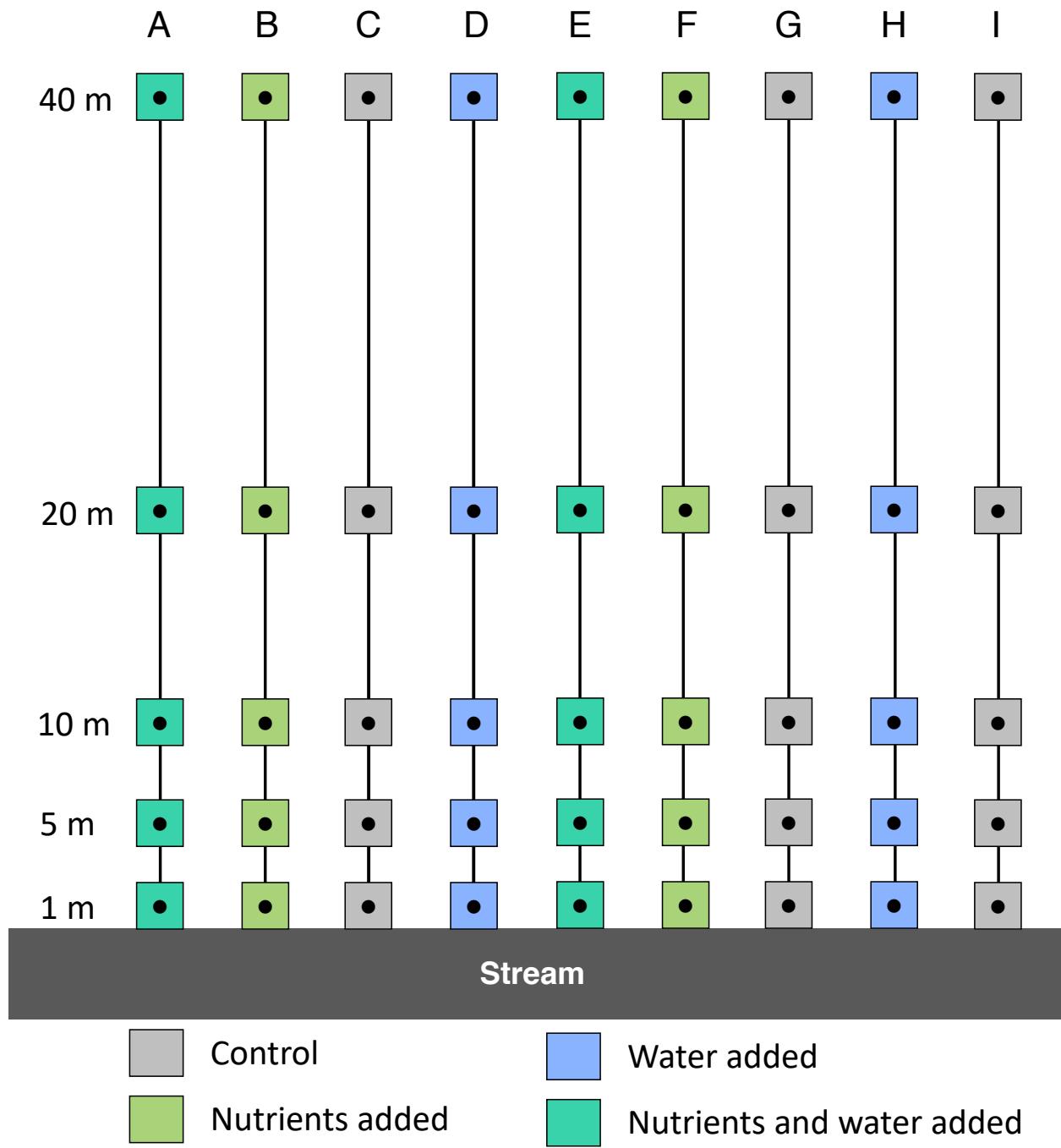
**Figure 3.1** Map of my sites in the Malcolm Knapp Research Forest in Maple Ridge, British Columbia, Canada. Standard UTM, Zone 10 N, 531070.1 E, 5456925.4 N. A more detailed map of the entire stream network with elevation lines can be seen in Appendix C, Fig. C.1. (Outline map of Canada and western USA created by J. Howard at the Stack Overflow Network, stackoverflow.com)



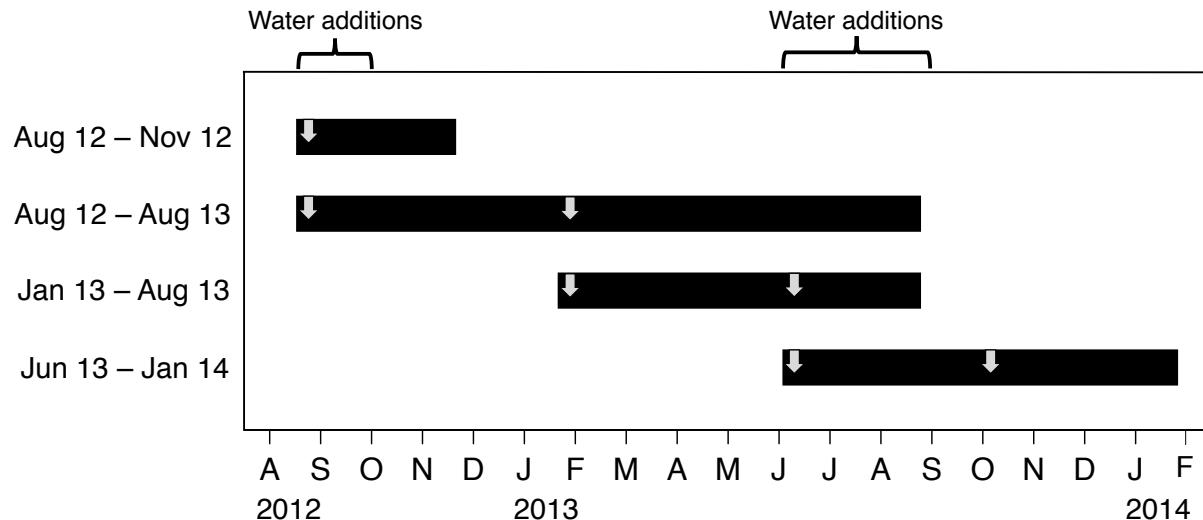
**Figure 3.2** Photographs and 3-dimensional models of the riparian plots at (a) East, (b) GH, (c) Griffith, and (d) Mike Creeks. Note the elevation of the 20 and 40 m portions of transects E through I for Griffith Creek were below the elevation of the stream and are not shown in the model (Photographs taken by T. L. Ramey)



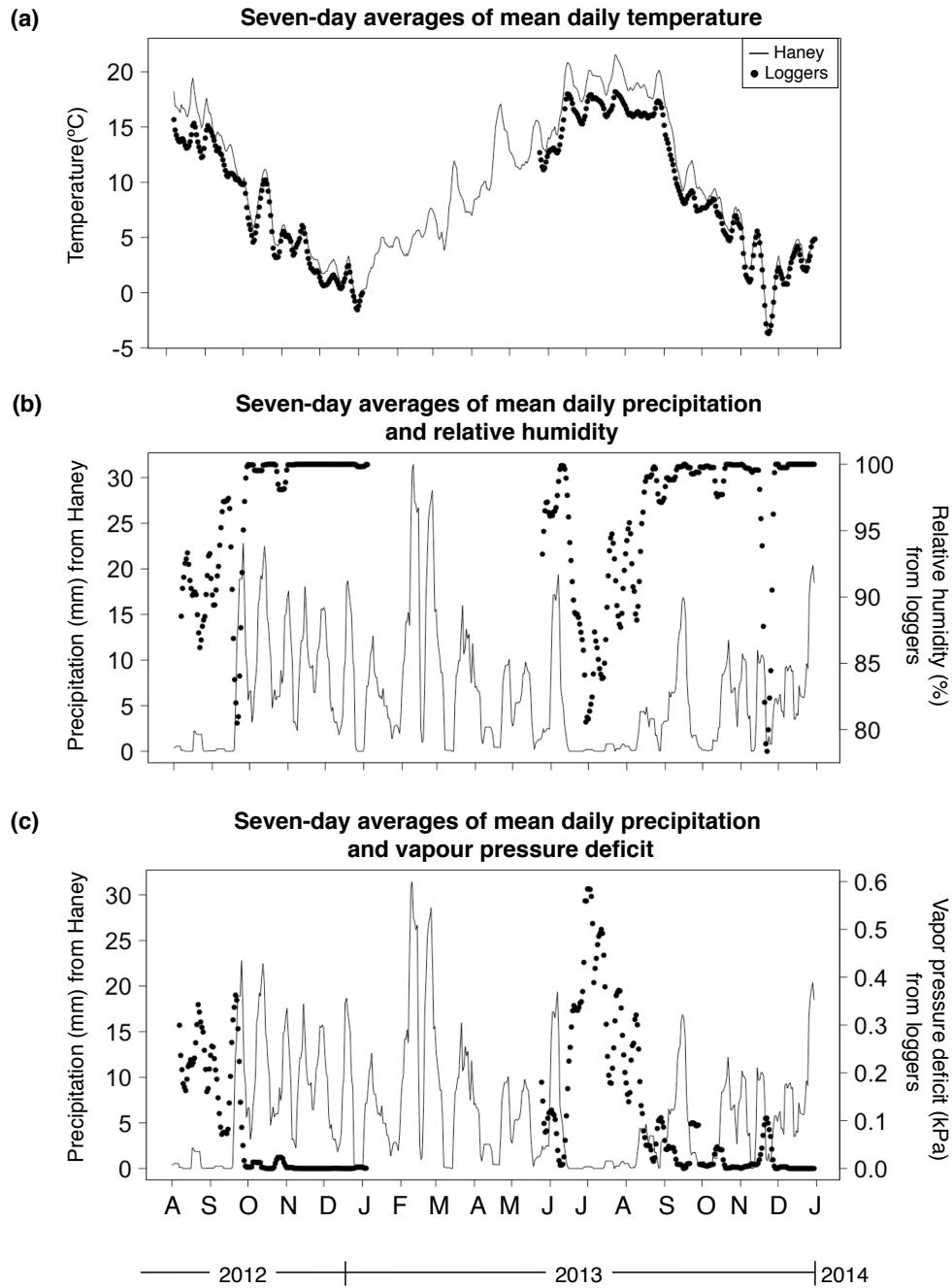
**Figure 3.3** Photographs of (a) East, (b) GH, (c) Griffith, and (d) Mike creeks. All photographs except (c) were taken during the summer dry period between June and August 2013; photograph (c) was taken during winter (between December and February) when stream flow is greater. (Photos a, b, and d taken by T. L. Ramey; photo c taken by J. S. Richardson)



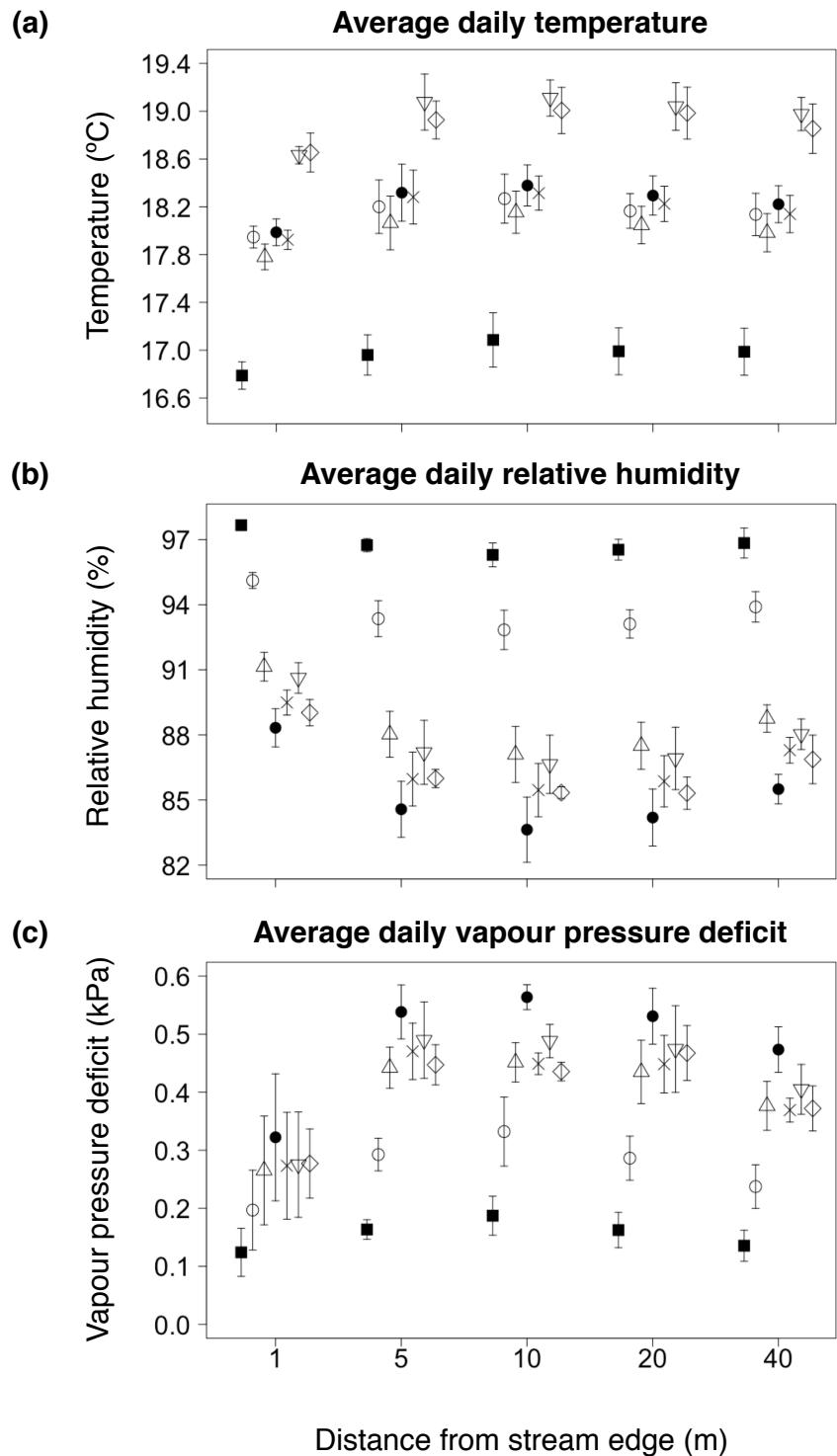
**Figure 3.4** Diagram (drawn to scale) of general site layout located along each headwater stream. Squares represent  $1\text{ m}^2$  stations at which litterbags were placed. Transects are labelled with letters, and colors correspond with treatment type (control, nutrient additions, water additions, nutrient and water additions). Pitfall traps (see Chapter 5) are were also located at stations along each transect; traps are represented by black circles (●).



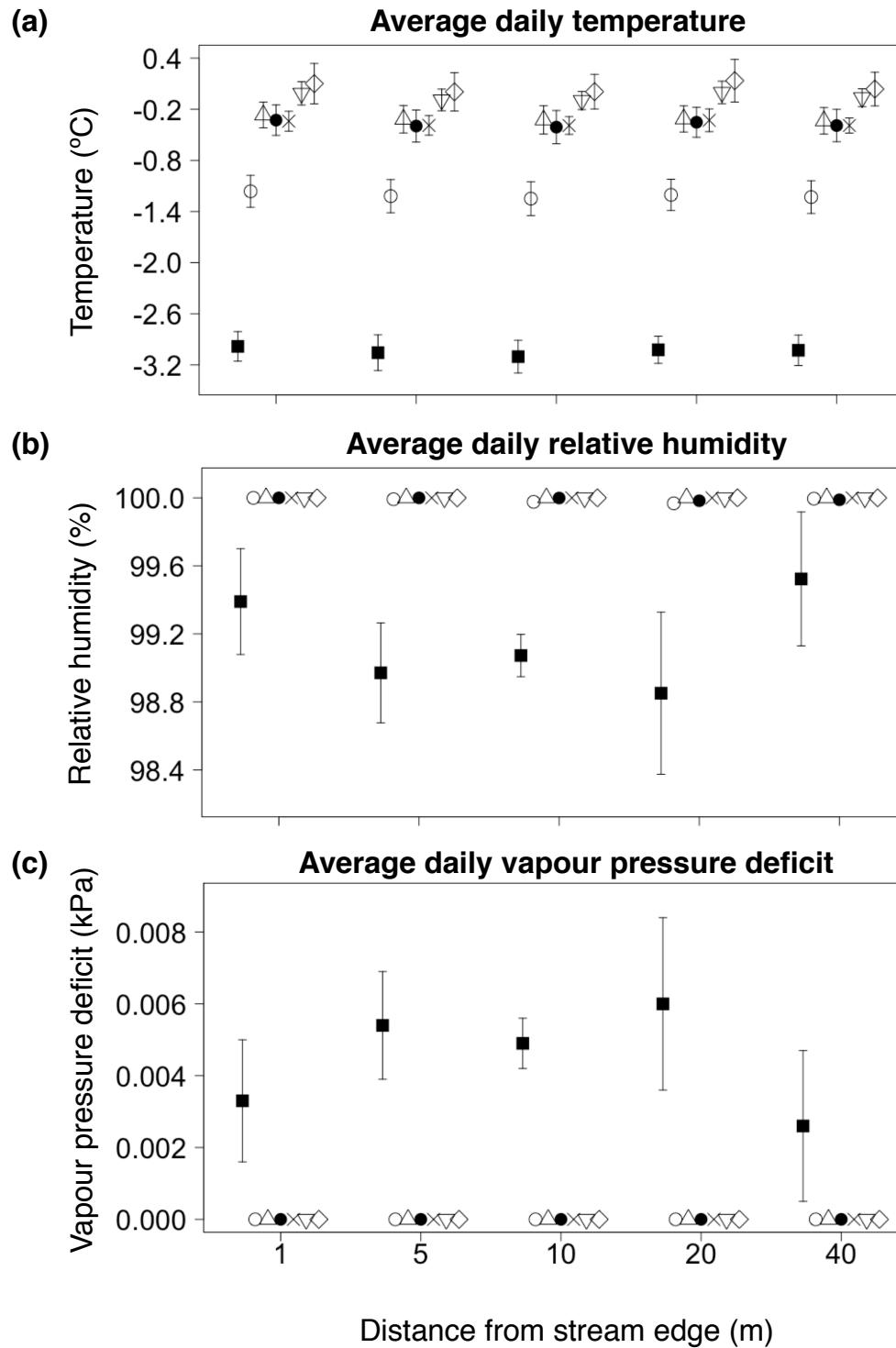
**Figure 3.5** Duration of each red alder litterbag trial. Months are indicated by the first letter of each month, and years are indicated below the month. Periods with water additions are indicated with brackets, and nutrient additions are indicated with arrows.



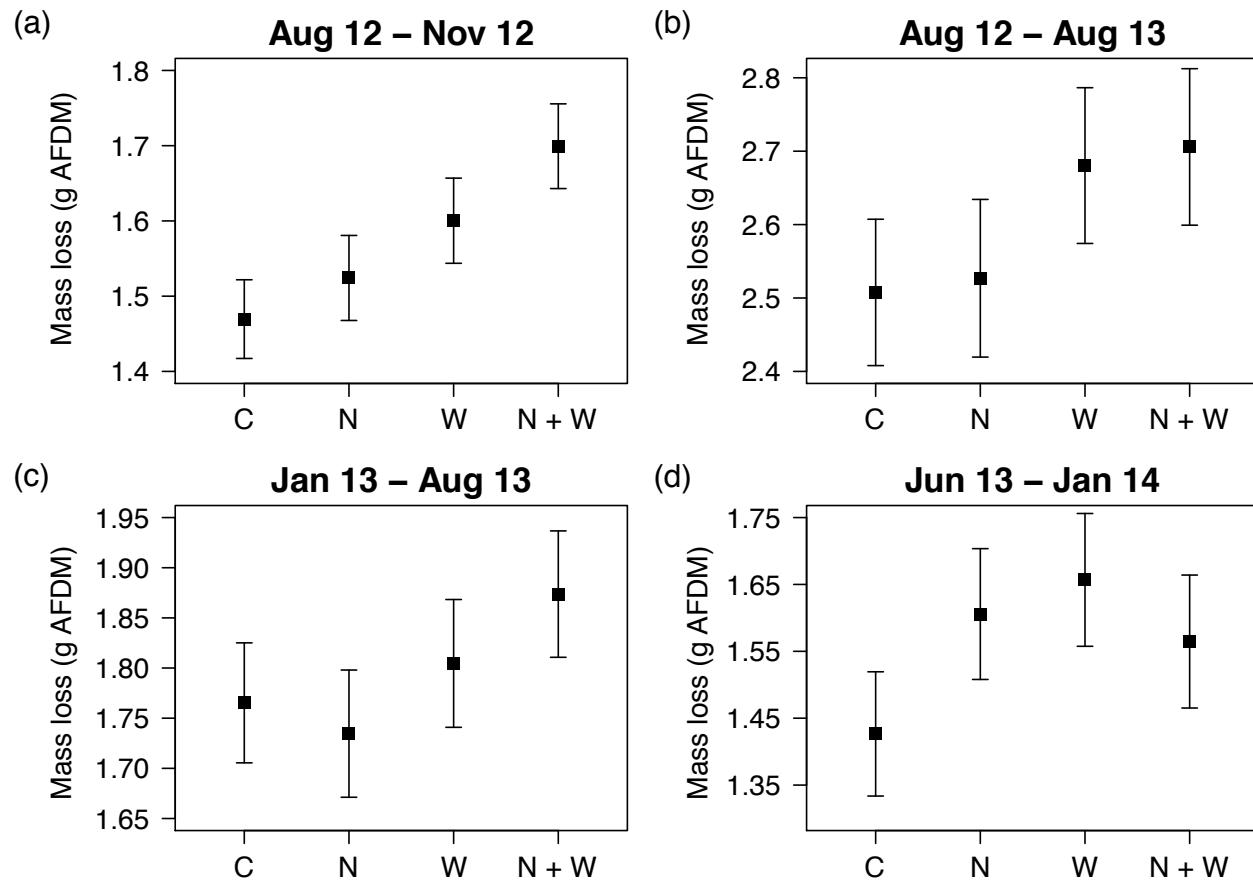
**Figure 3.6** Seven-day moving averages for daily mean air temperature (a) and precipitation (b and c) from measurements taken at the Haney RF weather station in Malcolm Knapp Research Forest (—). Seven-day moving averages for mean daily air temperatures (a), relative humidity (b), and vapour pressure deficit (c) are also included by averaging measurements from 20 HOBO® data loggers at my sites (●). Data from loggers are not continuous as loggers were not in the field during the entire study period. Note logger measurements are offset from Haney measurements as loggers were located within the forest at a higher elevation, whereas the weather station is in an open area without canopy cover. Also note that y-axis values vary for each graph, and the y-axis for relative humidity in (b) does not begin at zero.



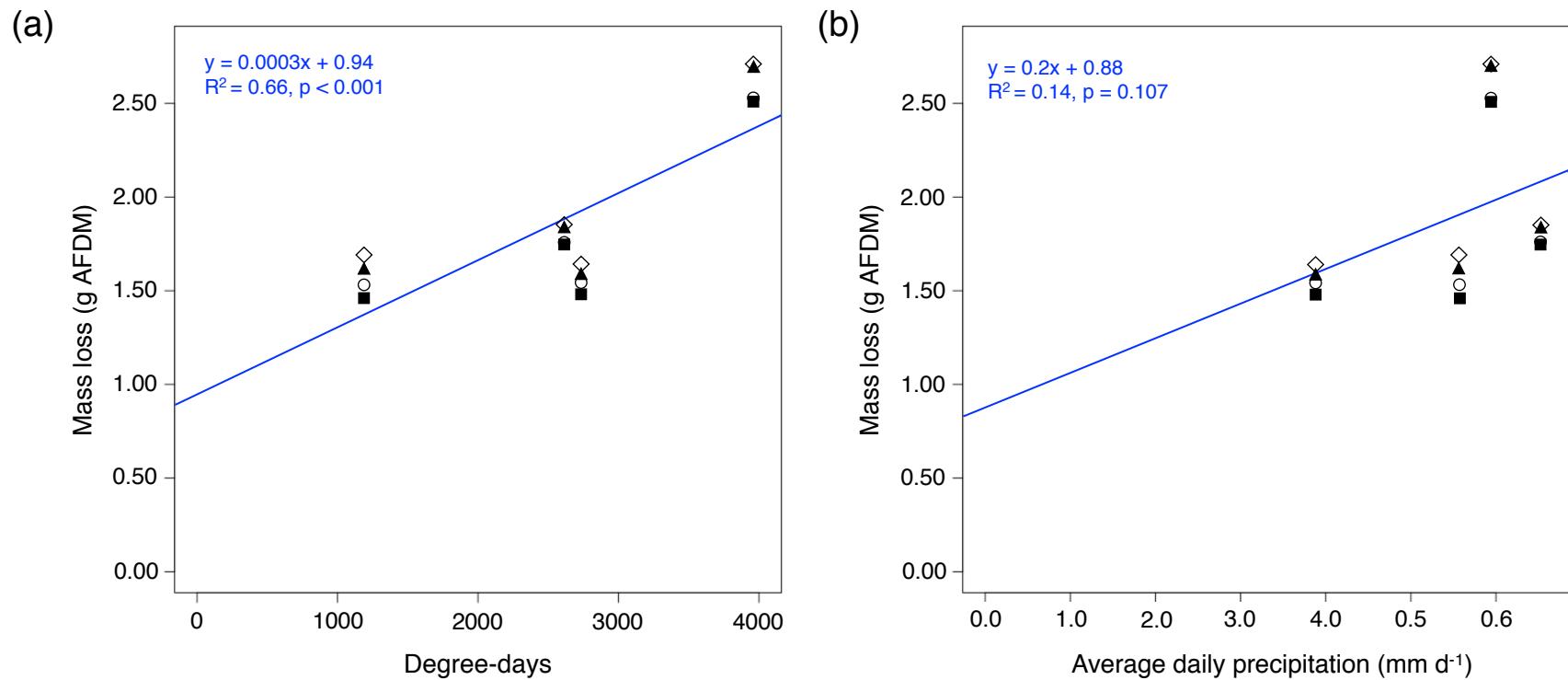
**Figure 3.7** Spatial patterns in daily average (a) air temperature ( $^{\circ}\text{C}$ ), (b) relative humidity (%), and (c) vapour pressure deficit (kPa) with distance from stream for the hottest week in August 2013 using data from data loggers. Symbols represent days: August 4 ( $\blacksquare$ ), 5 ( $\circ$ ), 6 ( $\triangle$ ), 7 ( $\bullet$ ), 8 ( $\times$ ), 9 ( $\nabla$ ), and 10 ( $\diamond$ ). Bars represent  $\pm 1$  S.E. Note that y-axis values vary for each graph, and y-axes in (a) and (b) do not begin at zero.



**Figure 3.8** Spatial patterns in daily average (a) air temperature ( $^{\circ}\text{C}$ ), (b) relative humidity (%), and (c) vapour pressure deficit (kPa) with distance from stream for the winter week in January 2013 using data from data loggers. Symbols represent days: January 13 (■), 14 (○), 15 (△), 16 (●), 17 (×), 18 (▽), and 19 (◇). Bars represent  $\pm 1$  S.E. Points without bars either had standard errors that were too small to be represented or zero.



**Figure 3.9** Average mass loss (g AFDM  $\pm$  1 S.E.) of red alder leaf litter for control litterbags (C) and those receiving treatments (nutrients added—N, water added—W, nutrients and water added—N + W) calculated from the raw data. Trials are: (a) August 2012 to November 2012, (b) August 2012 to August 2013, (c) January 2013 to August 2013, (d) June 2013 to January 2014. Note the y-axes values differ for each trial and do not begin at zero.



**Figure 3.10** Average mass loss (g AFDM) of red alder leaf litter for each treatment (control ■, nutrients added ○, water added ▲, nutrients and water added ◇) in each trial by (a) degree-days and (b) average daily precipitation ( $\text{mm d}^{-1}$ ). Standard error bars were not included due to the close proximity of the points. Magnified versions of these graphs are available in Appendix C, Fig. C.5.

# **Chapter 4: Influence on early-stage mass loss rates of western red cedar litter by experimental manipulation of nutrient and moisture availability near headwater streams**

## **4.1 Synopsis**

My objective for this chapter was to analyze how early-stage mass loss of western red cedar leaf litter responded to nutrient and water additions and varied with distance from the stream edge in riparian forests near four headwater streams. I hypothesized that mass loss of western red cedar leaf litter would be greater with water and nutrient additions compared to litter without these additions (H6 and H7), and greater closer to the stream than further away (H8). I also hypothesized that leaf litter placed in the field for a greater number of degree-days would lose more mass than those in the field for fewer degree-days (H10). I ran three litterbag trials filled with western red cedar leaf litter between January 2013 and January 2014, which varied in duration between four months and one year. Litterbags were placed at five distances from the stream, and were either controls or received one of the following treatments: water addition, nutrient addition, or addition of both water and nutrients. Mass loss for control litterbags was 21% over the January 2013 - January 2014 trial (12 months), 20% for the January 2013 - June 2013 trial (five months), and 15% for the June 2013 – January 2014 trial (eight months). Nutrient additions increased mass loss in western red cedar litter in the June 2013 – January 2014 trial. This trial also showed litterbags located 40 m from the stream edge lost 7% more mass than those located 1 m away. Additions of water during the summer dry period did not increase rates of mass loss. Mass loss increased with the number of degree-days litterbags were in the field, which varied between trials. Mass loss rates of western red cedar responded primarily to nutrient

additions in contrast to red alder, which responded positively to water additions (Chapter 3). This indicates mass loss of western red cedar and red alder are limited by different factors in the same environment. This analysis achieves Objective 4 of my thesis.

## 4.2 Introduction

Western red cedar is a dominant coniferous tree in the forests of the coastal PNW of North America, and is commonly found in mixed stands with western hemlock and Douglas-fir (Minore 1983, Radwan and Harrington 1986, Keenan 1993, Park and Oliver 2015). Like red alder, western red cedar is a main component of riparian forests near small headwater streams throughout southwestern British Columbia, including the Malcolm Knapp Research Forest (Richardson 1992, Mallik and Richardson 2009). It provides frond-like leaf litter to microbes and detritivores in both aquatic and terrestrial habitat, linking nutrient cycles of forest and stream ecosystems (e.g., Cárcamo et al. 2000, Richardson et al. 2004, Hoover et al. 2011). As coniferous forest cover in the coastal PNW can be greater than 60%, conifers like western red cedar often contribute the majority of leaf litter to these food webs (Richardson 1992, Spies et al. 1994). Litter species vary in physical and chemical characteristics such as leaf toughness, lignin and N content, and secondary chemistry such as concentrations of polyphenols (Cornelissen 1996, Trofymow et al. 2002, Hättenschwiler et al. 2005). For example, red alder litter is rich in N and decomposes relatively quickly during early-stage mass loss, whereas western red cedar litter offers greater concentrations of Ca but is more resistant to initial decay (Edmonds 1980, Keenan et al. 1996, Prescott et al. 2000, Matkins 2009). These differences, which also allow each litter species to support different members of the microbial and detritivore communities (e.g., Blair et al. 1990, Bray et al. 2012), may cause their decomposition to be limited by different factors

within the same environment. In this chapter, I examined how the availability of water and nutrients as well as distance from stream limit mass loss of western red cedar leaf litter in headwater riparian forests.

The availability of water through precipitation and soil moisture generally increases decomposition rates of deciduous and coniferous leaf litter by leaching and enhancing microbial activity (Trofymow et al. 2002, Kang et al. 2009, Joly et al. 2016; see Chapter 3, Section 3.2 for further detail). Prescott et al. (1997) noted faster decomposition of litterbags filled with western hemlock and lodgepole pine leaf litter in old-growth western red cedar and western hemlock forests with moist soil surface layers compared to clearcut sites with drier soils. The amount of mass lost due to leaching, though, is generally less for leaves with high lignin concentrations or greater leaf toughness because of their limited ability to absorb water and their lower concentration of water-soluble compounds (Nykvist 1963, Kuiters and Sarink 1986, Taylor and Parkinson 1988, Taylor et al. 1991, Prescott et al. 2000). Western red cedar leaf litter has a low specific leaf area and a small readily leachable fraction (or water-soluble fraction; 5%), and this produces low rates of mass loss through leaching compared to red alder leaves (21%; Harmon et al. 1990). Thus, mass loss of western red cedar is likely to respond positively to water additions in the field, but water may not be the primary limiting factor to its decomposition as seen in red alder (Chapter 4, Section 3.4.2).

The observed effects of endogenous and exogenous nutrient availability on western red cedar litter mass loss has been mixed. Initial concentrations of N and P are generally lower in coniferous than deciduous leaf litter (e.g., Harmon et al. 1990, Kang et al. 2011, Berg and McClaugherty 2014). Litter with a lower nutrient content relative to lignin generally loses mass slower during early-stage decomposition than litter with high nutrient to lignin ratios (Taylor et

al. 1991, Prescott et al. 2000, Zhang et al. 2008). Among coniferous species with high lignin concentrations, decomposition rates can differ due to varying concentrations of endogenous nutrients. Western red cedar leaf litter has low initial concentrations of N and P because red cedar trees are proficient in resorbing nutrients from leaves before senescence: Keenan (1993) found western red cedar trees in coastal British Columbia resorbed 76% N and 82% P before senescence. Though concentrations of lignin are similar between western hemlock (24%) and western red cedar (23.1%; Harmon et al. 1990) leaf litter, the lignin:N ratio is lower in western red cedar (Keenan 1993). Keenan (1993) suggested this difference lead to faster decomposition of hemlock litter ( $k = 0.54 \text{ y}^{-1}$ ) than red cedar ( $k = 0.25 \text{ y}^{-1}$ ) during a litterbag experiment in coastal cedar-hemlock stands on Vancouver Island, BC, Canada. This lower nutrient content combined with a waxy structure makes western red cedar leaf litter a poor-quality food resource for detritivores (Fyles and McGill 1987, Webster and Benfield 1986, Keenan et al. 1996, Richardson et al. 2004), which can result in reduced mass loss rates by detritivore consumption and fragmentation (Cárcamo et al. 2000).

Exogenous nutrients, whether naturally occurring in soils or through additions of fertilizer, can also influence decomposition. Across coniferous ecosystems, Gosz (1981) noted more rapid decomposition of coniferous litter in sites with naturally N-rich soil than in N-poor sites. Applications of exogenous nutrients have shown positive, negative, and neutral effects on coniferous litter mass loss depending on the stage of decomposition examined. Perakis et al. (2012) saw faster decomposition of Douglas-fir leaves in plots fertilized with ammonium nitrate and urea than unfertilized plots within the first year of their litterbag experiment in western Oregon, USA. This effect was reversed after three years, showing slower decomposition on fertilized plots (Perakis et al. 2012). Many studies have examined the effects of fertilizer on the

growth of western red cedar (e.g., Weetman et al. 2003, Blevins et al. 2006, Devine and Harrington 2009), but I could only find one study that analyzed how nutrient additions directly influenced western red cedar leaf litter mass loss (Prescott 1995). Prescott (1995) saw no difference in early-stage mass loss of litterbags filled with a mixture of western hemlock, western red cedar, and Douglas-fir leaf litter in plots fertilized with municipal sewage sludge compared to unfertilized plots in the Malcolm Knapp Research Forest near Maple Ridge, BC, Canada after 18 months in the field. After 36 months, however, decomposition was slower in fertilized plots than unfertilized plots (Prescott 1995). Suppression of mass loss by nutrient additions has been reported for litters with high concentrations of lignin (> 12% lignin; Knorr et al. 2005, Prescott 2005, Prescott 2010, Berg and McClaugherty 2014), usually during late-stage mass loss when litterbags had been in the field for greater than 18 to 24 months (Berg et al. 1987, Carriero et al. 2000, Knorr et al. 2005). This suppression occurs when exogenous N reduces the growth of microbes that produce ligninolytic enzymes, or decreases the abundance or activity of white rot fungi which commonly colonize and degrade high-lignin litters (Carreiro et al. 2000, Frey et al. 2004). Suppression does not generally occur during early-stage mass loss: Knorr et al. (2005) discovered nitrogen additions stimulated decomposition by up to 7% when litter had been decomposing for less than 24 months regardless of litter type (coniferous or deciduous) in their meta-analysis on the effect of nitrogen on litter decomposition in forest, grassland, and tundra ecosystems. As such, western red cedar mass loss could respond positively (as in Knorr et al. 2005) or neutrally (as in Prescott 2005) to nutrient additions during the first twelve months of decomposition.

In riparian zones, western red cedar grows at various distances from the stream edge (Pabst and Spies 1998). It can grow in a variety of habitats and is a flood-tolerant species,

reaching its highest productivity in areas where soils are moist with high concentrations of N and P (Teversham and Slaymaker 1976, Antos et al. 2016). It can also survive in soils of low productivity because it produces leaves that contain low concentrations of N and resorbs a large percentage of foliar N and P before abscission (Keenan et al. 1996, Antos et al. 2016). As previously discussed, distance from the stream edge has been associated with changes in air temperature and moisture (Brosofske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a), soil moisture and nutrient availability (Johnson and Lowe 1985, Shure and Gottschalk 1985, Clinton et al. 2010), canopy cover and vegetation diversity (Day and Monk 1974, Pabst and Spies 1998), and flooding frequency (Johnson and Lowe 1985, Benda et al. 2004, Clinton et al. 2010). These changes can influence leaf litter mass loss rates (Shure et al. 1986, Merritt and Lawson 1980, Peterson and Rolfe 1982, Hutchens and Wallace 2002, Clinton et al. 2010; see Chapter 3, Sections 3.2 and 3.5 for more detail). The majority of studies examining mass loss of leaf litter in riparian habitat have found faster decomposition in litter near the stream than litter placed further inlands (Shure et al. 1986, Merritt and Lawson 1980, Peterson and Rolfe 1982, Hutchens and Wallace 2002). It is currently unknown whether mass loss of western red cedar leaf litter varies with distance from stream.

My objective for this chapter was to determine whether early-stage mass loss of western red cedar leaf litter was limited by the availability of water or nutrients and distance from the stream in riparian forests along headwater streams in southwestern British Columbia. To my knowledge, this is the first study to examine red cedar mass loss in riparian forests. I hypothesized western red cedar leaf litter watered during the summer dry period would lose more mass than un-watered litter (H6). Similarly, I hypothesized that if N and/or P were limiting to decomposition, then western red cedar leaf litter with nutrient additions would lose more mass

than litter without added nutrients (H7). I also hypothesized that red cedar leaf litter located closer to the stream would decompose faster than litter located further away (H8). Given the importance of moisture and temperature to decomposition processes (Zhang et al. 2008, Kang et al. 2009, Prescott 2010), I ran multiple trials that varied in both the duration and season that litterbags were in the field. I hypothesized that western red cedar leaf litter placed in the field for a greater number of degree-days would lose more mass than leaf litter placed in the field for fewer degree-days (H9). This hypothesis does not include precipitation because only two trials that had both water and nutrient additions were used to evaluate it, and the correlation between precipitation and degree-days was 1. This meant only one variable could be used in the analysis. This analysis achieves Objective 4 of my thesis.

## 4.3 Materials and methods

### 4.3.1 Study sites and design

Experiments were conducted using the same sites and transects as well as the same method for applying water and nutrients to litterbags as seen in Chapter 3, Section 3.3.1. Two trials of litterbags were run with water and nutrient treatments (Fig. 4.1): 23 January 2013 to 29 January 2014 (372 days;  $n = 127$ ), and 3 June 2013 to 29 January 2014 (241 days;  $n = 133$ ). A third trial was run between 23 January 2013 to 3 June 2014 (132 days;  $n = 173$ ), however water additions were not made to litterbags in this trial as it ran during the rainy season; in 2013, water was only added to packs between 1 June and 31 August. Nutrient additions were made twice for the January 2013 to January 2014 and June 2013 to January 2014 trial, whereas only one addition was made to litterbags in the January 2013 to June 2013 trial due to its shorter duration (Fig. 4.1). Naturally senesced western red cedar litter was collected from a concrete patio at a

home located in Qualicum, British Columbia on Vancouver Island in October 2012. In British Columbia, western red cedar litterfall peaks in autumn between October and November (Richardson 1992, Keenan et al. 1995). Litter for all trials came from two western red cedar trees in one location and showed little to no visible sign of invertebrate consumption or microbial colonization. It was collected during a single day, and then air-dried for two weeks; green leaves and cones were removed, leaving only brown leaves.

I made a total of 540 litterbags that contained 4 g ( $\pm 0.04$  g) western red cedar leaf litter, and ran 3 trials of 180 litterbags each (four streams  $\times$  nine transects  $\times$  five distances); the final  $n$  was lower for each trial due to the loss of litterbags in the field or damage during processing (see Appendix A for Tables A.6, A.7, and A.8 with litterbag totals by distance and treatment for each trial). Litterbags were 16 cm by 16 cm, with a coarse mesh size of 9 mm that allowed access to larger detritivores; a piece of fine mesh window screen with 1 mm openings was placed in the bag beneath the litter to cover the base of the litterbag and keep litter from falling out (Fig. 4.2). It is possible that this fine mesh may have prevented larger invertebrates that burrow from entering the litterbag from beneath, but they were not restricted from climbing onto the litterbag from the edges. I did not use coverboards over my litterbags as this would have reduced any effects of precipitation and solar radiation that may vary with distance from stream (based on potential changes in % canopy cover or vegetation composition, which I did not measure) and season. The coarse mesh allowed in large amounts of hemlock litter and green western red cedar leaves from the trees at my sites, which had to be removed during processing. This may have also let in additional cedar leaves, however most cedar that fell onto the bags was in large pieces and removed at collection. Though in-site cedar litterfall was random and controlled for using a fully crossed, blocked experimental design, it could have potentially increased the probability of

a type II error. I suggest future studies analyzing conifer leaf litter in field conditions use coverboards to prevent excess litterfall into the litterbags. As with the red alder trials, elevation above stream was left out of models as it was correlated ( $r = 0.51$ ,  $p < 0.001$ ) with distance from stream.

At collection I placed litterbags in 4-L Ziploc bags and froze them at -20°C until processing. I thawed and gently washed the litter after removing it from the mesh litterbags to remove excess soil and invertebrates (including fecal matter). Litter was then dried at 60°C for 72 hours. As in Chapter 3, I did not include the mass of fecal matter in my calculations, which can potentially lead to an overestimation of decomposition rates; therefore, mass loss here refers to loss of litter mass that no longer exists in the form of leaf litter. I calculated initial ash-free dry mass (AFDM) values for undecomposed western red cedar litter by measuring five sets of 4 g dry western red cedar leaf litter that had not been in the field and burned it in a muffle furnace at 500°C for 2.5 hours. I subtracted the ashed weight from the initial weight of the litterbags to determine the ash-free dry mass (AFDM) of each bag and averaged the five values to determine the initial AFDM; this value was  $3.83 \pm 0.01$  g (4% ash). I then calculated the AFDM of the decomposed litterbags from my sites and subtracted this from the initial AFDM to determine the mass loss for each litterbag.

Microclimate variables at each site were tracked and analyzed (see Chapter 3, Fig. 3.6, 3.7, and 3.8). Collection methods and statistical analyses used to determine overall weather patterns and microclimate gradients at my sites using Onset HOBO® Pro v2 data loggers and weather data collected by the Government of Canada at Malcolm Knapp Research forest can be found in Chapter 3, Section 3.2.1 and 3.2.3. These data were also used to determine the total precipitation and number of degree-days for each western red cedar trial. Degree-days were

calculated by counting the number of degrees above 0°C for each day and summing them over each trial period. I chose 0°C as a baseline because it is the temperature below which microbial and invertebrate activity are diminished or stopped (e.g., Block et al. 1990, Uchida et al. 2005).

### 4.3.2 Statistical analysis

All analyses were done in RStudio (Version 1.0.143) using the packages *stats* (V. 3.2.0), *lme4* (V. 1.1-7), *multcomp* (V. 1.4-6) and *MuMin* (V. 1.15.1). I tested my hypotheses that litter with nutrient or water additions (or both) would show greater mass loss than litter without additions (H6 and H7), and that mass loss would be greater closer to the stream than further away (H8) using generalized linear mixed-effects models. Data were normally distributed, and not transformed for this analysis. In global models for each trial, mass loss (g AFDM) was a function of nutrient and water additions, distance from stream, and site as a random factor; the R code was as follows, with asterisks indicating interactions: mass loss ~ nutrients \* water \* distance + (1|site). Similar to my methods for analyzing red alder litter in Section 3.3.2, a series of 16 models were created for the January 2013 to January 2014 and June 2013 to January 2014 trials with water and nutrient additions (see a set of models with all possible combinations of factors in Appendix B, List A). To test my hypothesis that litter in the field for a greater number of degree days would lose more mass than litter in the field for fewer degree days (H9), I created a series of 24 models for the dataset that included data from these two trials together, as well as the number of degree-days for each trial (Appendix B, List C). Because only two trials were included, and only one value of degree days and average daily precipitation existed for each trial, these two variables had a Pearson correlation coefficient (*r*) of 1; as such, both variables could not be included in the models. As degree-day accounts for the duration of each trial and

temperature, I chose to use degree-days in my analysis. I also ran an independent linear regression analysis using values for the average mass loss of western red cedar leaf litter for each treatment in these two trials. A linear model was created for mass loss including only degree-days. An ANOVA was run to determine the significance of the independent relationship between average mass loss and number of degree days. Average mass loss values for each treatment in these trials and their relationship with degree-days were then mapped. Since water was not added during the January to June 2013 trial, five models were created that included all possible combinations of distance and nutrient additions (Appendix B, List D). This trial was not included in the dataset with degree-days because it lacked the watering component.

Models were compared within each trial, with the best model having the lowest AIC value, highest  $w_i$ , and greatest RL. Conditional  $R^2$  values were also calculated for each model (Nakagawa and Schielzeth 2013). I averaged models with  $\Delta AIC \leq 2$  to create an averaged model to determine the RI of each factor for each trial (see Section 3.3.2 for information about thresholds and calculating RI). I also calculated means and standard errors from the raw data to show patterns of mass loss for each treatment. Average mass loss values for each treatment by site and distance for each trial are available in Appendix C, Figs. C.6 and C.7, respectively. Because distance was a significant factor affecting mass loss in the averaged model for the June 2013 to January 2014 trial, I created a generalized linear mixed-effects model where mass loss was a function of distance from stream (as a factor instead of a covariate) and site as a random factor. I then used a post-hoc Tukey test to determine whether differences in mass loss between pairs of distances were significant (see Section 3.3.2 for details on R code for a Tukey test). Statistical significance was determined based on an alpha level of 0.05.

## 4.4 Results

### 4.4.1 Model results for each trial

*January 2013 to January 2014*

Litterbags in this trial were in the field for 3778.5 degree-days, with 360 of 366 days reaching an average daily temperature  $> 0^{\circ}\text{C}$ . Minimum and maximum average daily temperatures during this trial were  $-5.5^{\circ}\text{C}$  (in December 2013) and  $25.0^{\circ}\text{C}$  (in July 2013), respectively. Average mass loss for litterbags without nutrient or water additions was  $2.86 \times 10^{-4}$  g AFDM per degree day. A total of 2048 mm of rain fell during this trial, of which 1880 mm (92%) fell between 23 January to 31 May 2013, and 1 September 2013 and 29 January 2014 (when water additions were not made to litterbags).

Four models were averaged for this trial (Table 4.1). The best model was the null model which included only site as a random factor. The  $w_i$  (0.303) and RL (1.000) of the null model were 1.9 times greater than those of the second-best model ( $w_i = 0.159$ , RL = 0.523). Each model only explained about 1% of variation in the data ( $R^2 = 0.008$  and 0.012, respectively). The averaged model showed water, nutrients, and distance from stream did not significantly influence mass loss of western red cedar leaf litter (Table 4.2). Average mass loss for litter without water or nutrient additions was  $1.08 \pm 0.11$  g AFDM (28% of initial AFDM over 372 days,  $k = 0.0009\text{ d}^{-1}$  or  $0.32\text{ y}^{-1}$ ). Leaf litter with only water additions lost on average  $0.94 \pm 0.10$  g AFDM (25%), and litter with only nutrients additions lost  $0.99 \pm 0.08$  g AFDM (26%); litter with both water and nutrients additions lost  $1.18 \pm 0.10$  g AFDM (31%; Fig. 4.3a). Mass loss values were similar among sites, with leaf litter receiving only nutrients and litter receiving both water and nutrients showing the greatest variation in mass loss (Appendix C, Fig. C.6). Mass loss by treatment for each distance in this trial can be seen in Appendix C, Fig. C.7.

*June 2013 to January 2014*

Litterbags in this trial were in the field for 2734.7 degree-days, with 231 of 241 days reaching an average daily temperature  $> 0^{\circ}\text{C}$ . Minimum and maximum average daily temperatures during this trial were  $-5.5^{\circ}\text{C}$  (in December 2013) and  $25.0^{\circ}\text{C}$  (in July 2013), respectively. Average mass loss for litterbags without nutrient or water additions was  $2.12 \times 10^{-4}$  g AFDM per degree day. A total of 935 mm of rain fell during this trial, of which 768 mm (82%) fell between 1 October and 21 November 2012 (when water additions were not made to litterbags).

Five models were averaged for this trial, with the best model including all fixed factors (water, nutrients, and distance from stream) but no interactions (Table 4.1). The  $w_i$  (0.236) and the RL (1.000) of the best model were 1.3 times greater than those of the second-best model ( $w_i = 0.185$ , RL = 0.787). Models explained between 21 to 23% of variation in the data ( $R^2 = 0.226$  and 0.207, respectively). The averaged model included nutrient additions and distance from stream as significant factors affecting mass loss (Table 4.2). Average mass loss for leaf litter without water or nutrient additions was  $0.58 \pm 0.04$  g AFDM (15% mass loss over 240 days,  $k = 0.0007 \text{ d}^{-1}$  or  $0.25 \text{ y}^{-1}$ ). Leaf litter with only water additions lost on average  $0.67 \pm 0.07$  g AFDM (17%), and litter with only nutrients additions lost  $0.78 \pm 0.07$  g AFDM (20%); litter with both water and nutrients additions lost  $0.83 \pm 0.06$  g AFDM (22%; Fig. 4.3b). Leaf litter with nutrient additions ( $0.81 \pm 0.04$  g AFDM) lost 5% more mass than litter without nutrient additions ( $0.61 \pm 0.04$  g AFDM;  $z = 3.346$ ,  $p < 0.001$ ; Table 4.2). Distance from stream influenced mass loss of litter in this trial ( $z = 2.728$ ,  $p = 0.006$ ; Table 4.2). However, the only significant difference in average mass loss at between distances was for 1 and 40 m: litterbags at 40 m ( $0.81 \pm 0.06$  g AFDM) from the stream lost on average 7% more mass than those at 1 m from the stream ( $0.57$

$\pm 0.07$  g AFDM;  $z = 2.985$ ,  $p = 0.024$ ). Average mass loss was not different between all other distances (Fig. 4.4). East Creek showed lower rates of mass loss compared to other sites, and Griffith Creek showed the greatest level of variation in mass loss among treatments (Appendix C, Fig. C.6). Mass loss by treatment for each distance in this trial can be seen in Appendix C, Fig. C.7.

#### *January 2013 to June 2013 (without water additions)*

Litterbags in this trial were in the field for 1058.6 degree-days, with 130 of 132 days reaching an average daily temperature  $> 0^\circ\text{C}$ . Minimum and maximum average daily temperatures during this trial were  $0.0^\circ\text{C}$  (in January and March) and  $20.5^\circ\text{C}$  (in August), respectively. Average mass loss for litterbags without nutrient or water additions was  $7.27 \times 10^{-4}$  g AFDM per degree day. A total of 1112 mm of rain fell during this trial, of which 1112 mm (100%) fell between 23 January and 31 May 2013. As the trial ended on 3 June, water additions were not made to litterbags.

Three models were averaged for this trial. The null model was the best model, including only site as a random factor (Table 4.1). The  $w_i$  (0.459) and RL (1.000) of the null model were 1.8 times greater than those of the second-best model ( $w_i = 0.259$ , RL = 0.564). Each model only explained about 8% of variation in the data ( $R^2 = 0.078$  and 0.080, respectively). The averaged model showed neither nutrient additions nor distance from stream significantly influenced mass loss (Table 4.2). Average mass loss for leaf litter without nutrient additions was  $0.89 \pm 0.05$  g AFDM (23% mass loss over 132 days,  $k = 0.0020 \text{ d}^{-1}$  or  $0.73 \text{ y}^{-1}$ ). Leaf litter with nutrient additions lost on average  $0.81 \pm 0.05$  g AFDM (or 23%). Mass loss values were generally higher

at GH Creek compared to other sites, and leaf litter at 1 m from the stream showed the greatest variation in mass loss compared to litter further away (Appendix C, Figs. C.8 and C.9).

#### **4.4.2 Model results for dataset including two trials with water additions and the effect degree-days**

Five models were averaged for this dataset, with the best model including nutrients, distance from stream, and degree-days (Table 4.1). The  $w_i$  (0.221) and RL (1.000) of the best model were 1.3 times greater than those of the second-best model ( $w_i = 0.165$ , RL = 0.748). Each model explained 20% of variation in the data ( $R^2 = 0.200$  and 0.190, respectively). Nutrient additions ( $z = 2.396$ ,  $p = 0.017$ ) and degree-days ( $z = 6.283$ ,  $p < 0.001$ ) were significant factors influencing mass loss in the averaged model (Table 4.2). Western red cedar leaf litter with nutrient additions ( $0.95 \pm 0.04$  g AFDM) lost on average 3% more mass than leaf litter without nutrients ( $0.77 \pm 0.04$  g AFDM). The number of degree days was positively related to mass loss of western red cedar leaf litter ( $R^2 = 0.75$ ,  $p = 0.005$ ; Fig. 4.5).

### **4.5 Discussion**

Western red cedar leaf litter lost on average 22% initial mass across all trials ( $k = 0.0007$   $d^{-1}$  or  $0.25$   $y^{-1}$ ). This result is consistent with other studies that have analyzed early-stage mass loss of western red cedar leaf litter. Preston and Trofymow (2000) reported 15% mass loss after 1 year in western red cedar litterbags located across forests in Canada as part of the long-term Canadian Intersite Decomposition Experiment (CIDET) study. Keenan et al. (1996) found 22% mass loss after 1 year for western red cedar litterbags in northern Vancouver Island, British Columbia, Canada. Mass loss occurred more slowly for western red cedar litter than red alder

litter in Chapter 3, which lost 47% mass on average across four trials. The amount of variation explained by western red cedar models varied greatly by trial. Null models explaining only 1 to 8% of variation were the best models for the January 2013 to January 2014 and January 2013 to June 2013 trials, respectively. As such, most of the conclusions drawn below on western red cedar mass loss were based off of results for the June 2013 to January trial; models in this trial explained between 21 to 23% of variation in the data.

The initial ratio of lignin to N in leaf litter is negatively correlated with decomposition rates (Melillo et al. 1982, Moore et al. 1999, Prescott 2005; see Section 4.2 for details), and the high lignin:N ratio of western red cedar (78; Prescott and Preston 1994) has been suggested as the reason for its slow decay (Harmon et al. 1990, Keenan et al. 1995). Rates of processing and consumption by microbes and invertebrate detritivores could have been inhibited by the hard, waxy structure of western red cedar litter, which restricts access to softer interior tissues (Fyles and McGill 1987, Webster and Benfield 1986, Richardson et al. 2004). As litterbags were placed in the forest alongside western hemlock and Douglas-fir trees that produce litter with higher initial %N and lower lignin:N ratios (Keenan 1993, Harmon et al. 1990), microbes and detritivores may have avoided consuming western red cedar litter in favor of hemlock or Douglas-fir litter. Such a preference was seen by Cárcamo et al. (2000) in the millipede *Harpaphe haydeniana*, which is a common detritivore in my sites and an estimated 36% of annual aboveground litter input in coastal forests of the PNW. *Harpaphe haydeniana* preferentially fed on Douglas-fir leaves over western red cedar leaves, and Cárcamo et al. (2000) stated this was likely due to western red cedar's lower nutrient content.

Water additions did not have a significant effect on western red cedar mass loss in either the January 2013 to January 2014 or June 2013 to January 2014 trials. This result rejects my

hypothesis that water additions during the summer months would increase mass loss of western red cedar (H6). Though moisture may be more limited during the summer months when VPD increases and precipitation declines (Fig. 3.6), water was not a limiting factor to decomposition of western red cedar in my trials. This is likely due to the physical and chemical properties of cedar leaves. Cedar has a lower leaf surface area than alder, so cedar leaves may not have retained moisture to the same degree as alder did in litterbags. Because cedar is structurally complex with low proportions of water-soluble compounds such as simple sugars (Prescott et al. 2004), its readily leachable fraction is only about 5% (Harmon et al. 1990). This low proportion of soluble compounds reduces mass loss of western red cedar leaf litter by leaching (McArthur and Richardson 2002, Richardson et al. 2004). Following the loss of soluble compounds from litter, the proportion of recalcitrant material such as lignin increases, which can take years to decay in terrestrial habitats (Harmon et al. 1990, Moore et al. 2000, Trofymow et al. 2002, Berg and McClaugherty 2014). Moisture can promote mass loss by increasing microbial growth and activity (Witkamp 1963, Langhans et al. 2008, Joly et al. 2016), but this higher microbial biomass may offset reductions in litter mass loss due to water additions. Mass loss curves in Zukswert and Prescott (2017) showed a slight pause in mass loss following leaching for leaf litter from eight tree species including western hemlock and Douglas-fir, which could be due to this microbial growth (C. E. Prescott, pers. comm.).

Nutrient additions significantly influenced mass loss for western red cedar in the June 2013 to January 2014 trial. In this trial, litterbags with nutrient additions lost 5% more mass than litterbags without nutrient additions. This result partially supports my hypothesis that nutrient additions would increase early-stage mass loss of western red cedar leaf litter (H7), and suggests that N and/or P may be limiting to decomposition at my sites. However, the addition of nutrients

was not a significant factor influencing mass loss in the other two trials. Nutrients were a significant factor in the model that combined the datasets for the January 2013 to January 2014 and the June 2013 to January 2014 trials, however this is likely because of data from this latter trial. The positive effect of nutrient additions in the June 2013 to January 2014 trial is likely due to increases in microbial and detritivore activity. N and P additions can encourage microbial growth and enzyme production, which leads to the loss of soluble and non-lignified carbohydrates (Berg and Matzner 1997, Carreiro et al. 2000, Hobbie 2000, Perakis et al. 2012). Western red cedar leaf litter has low initial concentrations of N and P (Keenan 1993), and N and P have been reported as limiting to primary productivity in forest soils near my sites in the Malcolm Knapp Research Forest (Feller 1977, Feller and Kimmins 1984). Thus, nutrient additions increased the availability of nutrients to microbes on the forest floor, and potentially enhanced their growth and activity (Berg and Matzner 1997, Carreiro et al. 2000, Hobbie 2000, Perakis et al. 2012). Increased microbial growth could also condition or soften the litter and increase the palatability of western red cedar for invertebrate detritivores (Seastedt 1984, Xiong and Nilsson 1997).

The absence of a significant effect of nutrient additions in two of the trials (January 2013 to January 2014 and January 2013 to June 2013) may be due to seasonal differences in precipitation and microbial activity. Winter months in the coastal PNW are also characterized by larger amounts of precipitation than summer months (Feller and Kimmins 1979; see Chapter 3, Fig. 3.6b and c); total precipitation in January 2013 was 238.5 mm, whereas in June it was 123.5 mm). In both of these trials, litterbags were placed in the field and given nutrient additions on 29 January 2013; on that day, 12 mm of precipitation was recorded, followed by 16 mm over the next three days. In comparison, litterbags in the June 2013 to January 2014 trial were placed in

the field and fertilized on 3 June 2013; no precipitation was recorded on that day or the following three days. Additions of crystallized ammonium nitrate and triple superphosphate to the surface of the packs could have been washed into the soil and groundwater before it was utilized by the microbial community. Another possible explanation for why nutrients were not significant factors in the two January trials could be due to lower decomposer activity. In January, the average daily temperature was only 1.4 °C and the activity of microbes and detritivores was likely slowed (e.g., Block et al. 1990, Uchida et al. 2005), compared to the June 2013 to January 2014 trial which began when the average daily temperature was 15.4°C. The neutral effect on nutrient additions in my two winter trials was also seen by Prescott (1995). As N concentrations are positively correlated with the amount of labile C and negatively correlated with lignin content (Taylor et al. 1991), Prescott (1995) suggested nitrogen additions would not increase decomposition rates without concurrent additions of C that can be easily metabolized by microbes. My positive results for the June 2013 to January trial show that this may not always be necessary. It is possible that the significant but small increase (5%) in mass loss during this trial could be a statistically random event. However, water additions significantly increased mass loss in red alder by a similar amount (2 to 5%) in each of the four trials that varied in length. It is therefore unlikely that the increase in mass loss in my June 2013 to July 2014 trial was a random event, and more likely that lower temperatures and precipitation reduced the effectiveness of the nutrient additions.

Distance from the stream edge significantly influenced mass loss of western red cedar in the June 2013 to January 2014 trial, with litterbags at 40 m from the stream losing on average 7% more mass than litterbags at 1 m from the stream. It was not a significant factor in averaged models for the other two trials, or in the combined dataset. This result rejects my hypothesis that

mass loss would occur faster in litterbags closer to the stream than those further upland (H8). It is also unlike results in Chapter 3 as distance from stream had no significant effect on mass loss of red alder leaf litter in the averaged model for each trial (Chapter 3, Table 3.3). Previous research has documented greater mass loss in leaf litter near the stream edge than in litter located further inland (Merritt and Lawson 1980, Peterson and Rolfe 1982, Shure et al. 1986, Hutchens and Wallace 2002), but most of these studies occurred in riparian habitat that was frequently flooded along larger rivers; riparian zones in Hutchens and Wallace (2002) did flood, but bordered second-order streams. As such, results from these studies may not provide a good comparison to results from my experiment.

As flooding was not a factor in my study, my results are most similar to Clinton et al. (2010), who examined red maple decomposition in riparian zones along four first-order streams in western North Carolina, USA. Clinton et al. (2010) found mass loss of litter was faster at 10 and 30 m from the stream than in litter located on the stream edge (0 m). Factors related to decomposition such as microarthropod abundance and soil respiration rate did not vary with distance from stream; soil moisture and nitrate showed a negative association with distance from stream (Clinton et al. 2010). As I did not measure soil moisture or respiration, it is unknown how these factors varied with distance from stream at my sites. However, previous studies in the Malcolm Knapp Research Forest on similar sized streams have found greater soil moisture closer to the stream edge (Feller 1977, Chin 2007). Values for VPD, which can be related to soil moisture (Duff et al. 1997, Sulman et al. 2016), suggest that soil moisture likely did not differ significantly with distance from stream with a possible exception for higher soil moisture at 1 m from the stream edge than further inland (due to significantly lower VPD at 1 m than further away; see Chapter 3, Section 3.4.1). Clinton et al. (2010) suggested differences for

decomposition rates could be due to the patchy and clumped distribution of resources and microarthropods that occur in forest soils. It is currently unclear why my results point to greater decomposition at distances further from the stream. Daily average air temperature was 0.25°C warmer at distances > 1 m from the stream during the summer period (Chapter 3, Section 3.4.1), which may have influenced microbial communities. Yet differences in mass loss of western red cedar litter were only significant between 1 m and 40 m, whereas air temperature was different only between 1 and 10 m and 1 and 20 m; this suggests this small difference in temperature was probably not driving differences in decomposition. Suggestions for future research that may help to identify what factors may be driving effects by distance from stream are provided in Chapter 6, Section 6.4.

The number of degree days in which western red cedar litter was in the field was positively related to mass loss; this supports my hypothesis (H9). This result was also seen in my red alder analysis (Chapter 3, Table 3.3). The longest trial (January 2013 to January 2014) lost the greatest amount of mass and had the highest total number of degree days at 3778.5; in contrast, the June 2013 to January 2014 trial lost the less mass and was in the field for 2737.7 degree days. This result was unsurprising as temperature is positively correlated with early-stage mass loss of coniferous and deciduous leaf litter (Moore et al. 1999, Preston and Trofymow 2000, Zhang et al. 2008, Prescott 2010) due to increasing rates of microbial and detritivore activity (Witkamp 1963, Lloyd and Taylor 1994, Chapin et al. 2002, Gongalsky et al. 2008, Langhans et al. 2008; see Chapter 3, Section 3.5 for more detail). Though average daily precipitation was not included in western red cedar models, it could have played a confounding role in mass loss rates as total precipitation and number of degree -days were positively correlated (see details in Chapter 3, Section 3.3.2). As discussed in the Sections 3.2 and 4.2,

moisture is positively associated with microbial activity on leaves and in soils, and can lead to higher rates of leaching (Trofymow et al. 2002, Kang et al. 2009, Brockett et al. 2012, Joly et al. 2016). Average daily precipitation was a significant factor influencing mass loss in red alder trials as were water additions. Given that water additions were not significant in my western red cedar trials, the effect of precipitation may not have influenced cedar to the same degree.

As western red cedar is a dominant species in moist forests of the coastal PNW, understanding which factors limit the decomposition of its foliar litter is important when considering forest nutrient cycles. Previous research has examined decomposition rates of western red cedar in the field, but few have focused on western red cedar in riparian habitat. This study shows that exogenous nutrient additions can increase rates of western red cedar leaf litter mass loss, but this positive effect may be dependent on temperature, precipitation, and activity levels of microbes and detritivores. My results also show that western red cedar mass loss can vary with distance from the stream edge, though the exact mechanism responsible for this variation is unknown. This study advances our knowledge of factors limiting early-stage decomposition of western red cedar in headwater riparian forests of southwestern British Columbia, and contributes to our broader understanding of factors limiting decomposition processes in riparian zones. Potential directions for future research based on these findings are discussed in Chapter 6, Section 6.4.

**Table 4.1** Comparison of top candidate models for each trial describing ash-free dry mass loss of western red cedar leaf litter as a function of water (W) and nutrient (N) additions, and distance from the bankfull edge (D). An analysis containing data from the two trials that included water additions (the January 2013 to January 2014 trial and the June 2013 to January 2014 trial) also includes the number of degree-days litterbags were in the field (dd). All models include site as a random factor. Interactions are indicated with an asterisk (\*). Results for each model include Akaike Information Criterion (AIC), change in Akaike Information Criterion relative to the best model ( $\Delta\text{AIC}$ ), Akaike weight ( $w_i$ ), relative likelihood (RL), and conditional  $R^2$ .

Trial	Model	df	AIC	$\Delta\text{AIC}$	$w_i$	RL	$R^2$
Jan 13 – Jan 14	<b>Null</b>	<b>3</b>	<b>217.538</b>	<b>0.000</b>	<b>0.303</b>	<b>1.000</b>	<b>0.008</b>
	N	4	218.833	1.295	0.159	0.523	0.012
	W	4	219.475	1.937	0.115	0.380	0.009
	D	4	219.533	1.995	0.112	0.369	0.008
Jun 13 – Jan 14	<b>N + W + D</b>	<b>6</b>	<b>72.117</b>	<b>0.000</b>	<b>0.236</b>	<b>1.000</b>	<b>0.226</b>
	N + D	5	72.597	0.480	0.185	0.787	0.207
	W*D + N + W + D	7	72.833	0.715	0.165	0.699	0.234
	W*N + N + W + D	7	73.825	1.708	0.100	0.426	0.227
	N*D + N + W + D	7	74.040	1.923	0.090	0.382	0.226
Jan 13 – Jun 13 <sup>a</sup>	<b>Null</b>	<b>3</b>	<b>220.264</b>	<b>0.000</b>	<b>0.459</b>	<b>1.000</b>	<b>0.078</b>
	N	4	221.411	1.146	0.259	0.564	0.080
	D	4	222.252	1.988	0.170	0.370	0.078
Combined trials <sup>b</sup>	<b>N + D + dd</b>	<b>6</b>	<b>342.734</b>	<b>0.000</b>	<b>0.221</b>	<b>1.000</b>	<b>0.200</b>
	N + dd	5	343.316	0.581	0.165	0.748	0.190
	N + W + D + dd	7	343.667	0.933	0.139	0.627	0.204
	N + W + dd	6	344.333	1.598	0.099	0.450	0.194
	N*W + N + W + D + dd	8	344.411	1.676	0.096	0.432	0.208

<sup>a</sup> Water additions were not made in the January 2013 to June 2013 trial.

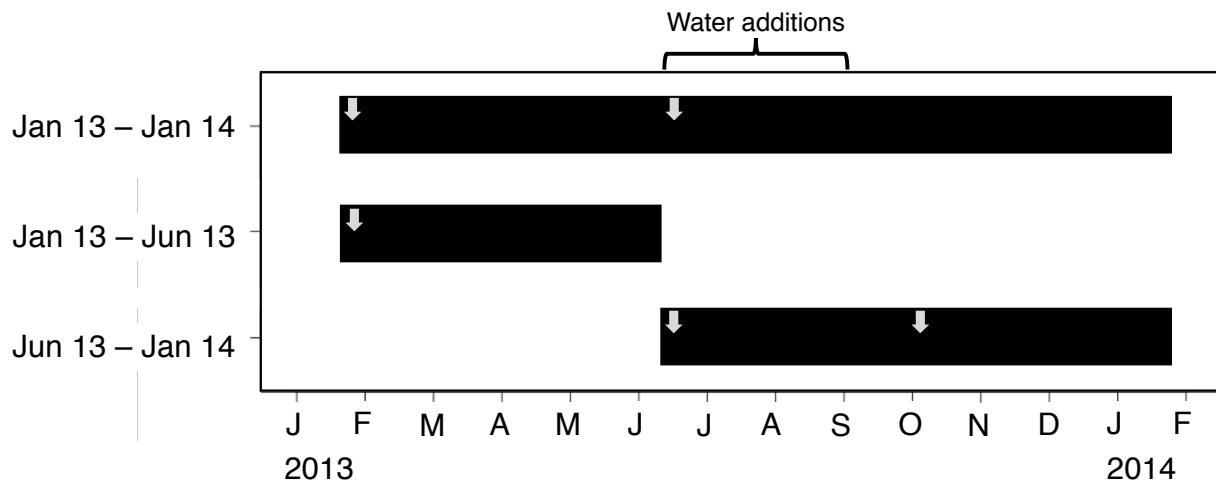
<sup>b</sup> “Combined trials” includes data from the January 2013 to January 2014 trial and the June 2013 to January 2014 trial. The January 2013 to June 2013 trial was not included because it lacked water additions.

**Table 4.2** Average parameter estimates (mass loss g AFDM) with standard errors (SE) for the top models of each western red cedar trial. Significant parameters are in bold. Parameter terms are water additions (W), nutrient additions (N), distance from the bankfull edge (D), and number of degree-days litterbags were in the field (dd). Abbreviations include standard error (SE), 95% confidence interval (CI), the relative importance (RI) of each parameter, and the number of models each parameter is in for each trial. Interactions are indicated with an asterisk (\*).

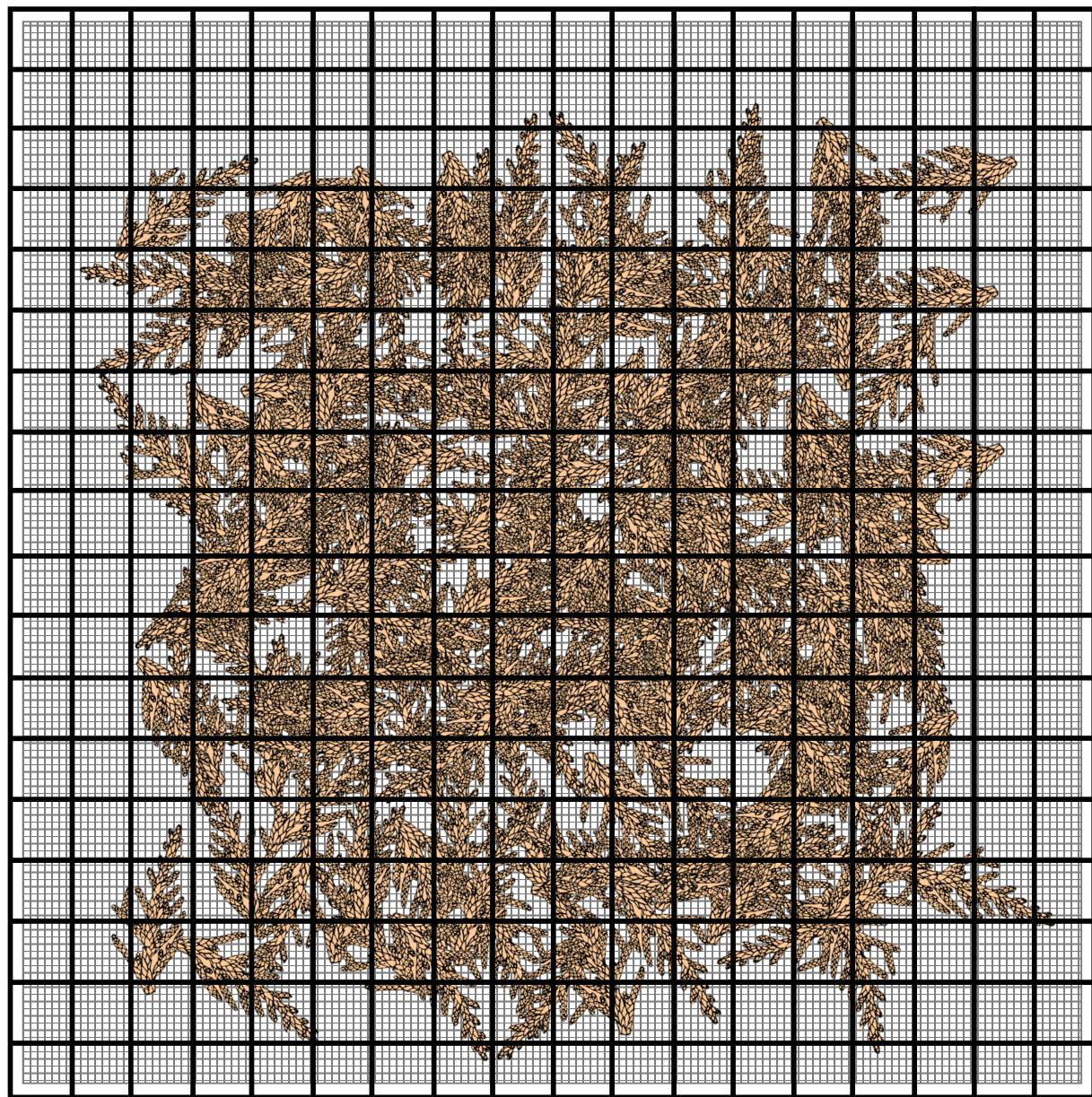
Trial	Parameter	Estimate	SE	z	p	95% CI	RI	# of models
Jan 13 – Jan 14	Intercept	1.037	0.069	14.991	< 0.001	0.901 – 1.173		
	N	0.083	0.098	0.835	0.404	-0.112 – 0.278	0.22	1 of 4
	W	0.025	0.098	0.249	0.803	-0.170 – 0.220	0.16	1 of 4
	D	$2.63 \times 10^{-4}$	0.004	0.073	0.942	-0.007 – 0.007	0.16	1 of 4
Jun 13 – Jan 14	Intercept	0.487	0.073	6.629	< 0.001	0.343 – 0.631		
	N	<b>0.201</b>	<b>0.059</b>	<b>3.346</b>	<b>&lt; 0.001</b>	<b>0.083 – 0.318</b>	<b>1.00</b>	<b>5 of 5</b>
	W	0.105	0.069	1.513	0.130	-0.031 – 0.242	0.76	4 of 5
	D	<b>0.006</b>	<b>0.002</b>	<b>2.728</b>	<b>0.006</b>	<b>0.002 – 0.010</b>	<b>1.00</b>	<b>5 of 5</b>
	N*W	-0.057	0.105	0.536	0.592	-0.265 – 0.151	0.13	1 of 5
	N*D	-0.001	0.004	0.275	0.783	-0.008 – 0.006	0.12	1 of 5
	W*D	-0.004	0.004	1.126	0.260	-0.011 – 0.003	0.21	1 of 5
Jan 13 – Jun 13 <sup>a</sup>	Intercept	0.840	0.077	10.872	< 0.001	0.689 – 0.991		
	N	0.062	0.067	0.919	0.358	-0.071 – 0.195	0.29	1 of 3
	D	$2.63 \times 10^{-4}$	0.002	0.109	0.913	-0.004 – 0.005	0.19	1 of 3
Combined trials <sup>b</sup>	Intercept	-0.344	0.187	1.834	0.067	-0.709 – 0.025		
	N	<b>0.152</b>	<b>0.063</b>	<b>2.396</b>	<b>0.017</b>	<b>0.030 – 0.275</b>	<b>1.00</b>	<b>5 of 5</b>
	W	0.040	0.067	0.599	0.549	-0.089 – 0.172	0.46	3 of 5
	D	0.003	0.002	1.604	0.109	-0.001 – 0.007	0.63	3 of 5
	dd	$3.34 \times 10^{-4}$	$5.30 \times 10^{-5}$	<b>6.283</b>	<b>&lt; 0.001</b>	$2.30 \times 10^{-4} – 4.39 \times 10^{-4}$	<b>1.00</b>	<b>5 of 5</b>
	N*W	0.125	0.111	1.117	0.264	-0.094 – 0.343	0.13	1 of 5

<sup>a</sup> Water additions were not made in the January 2013 to June 2013 trial.

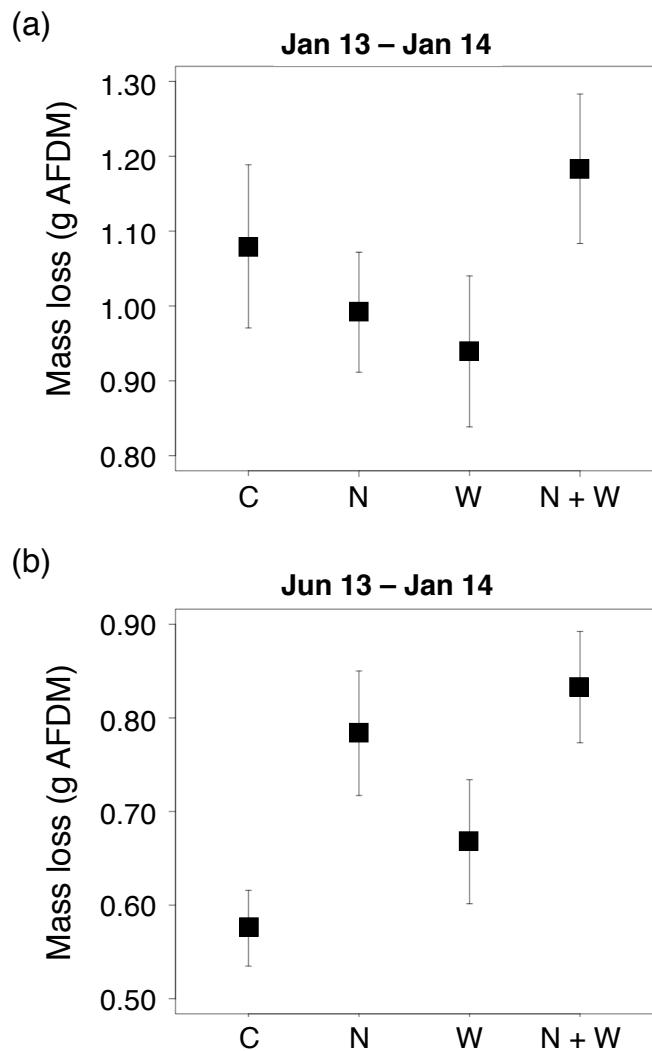
<sup>b</sup> “Combined trials” includes data from the January 2013 to January 2014 trial and the June 2013 to January 2014 trial. The January 2013 to June 2013 trial was not included because it lacked water additions.



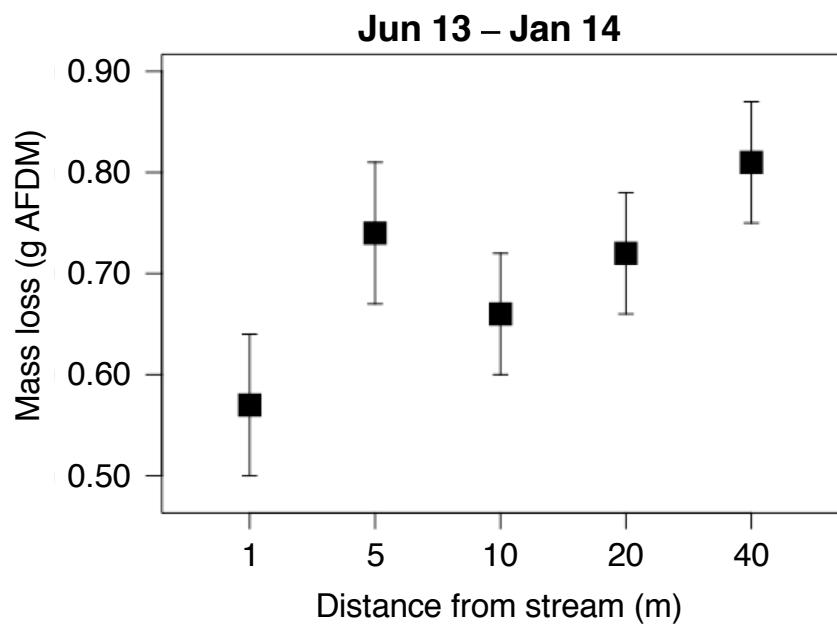
**Figure 4.1** Duration of each western red cedar litterbag trial. Months are indicated by the first letter of each month, and years are indicated below the month. The period with water additions is indicated with a bracket, and nutrient additions are indicated with gray arrows.



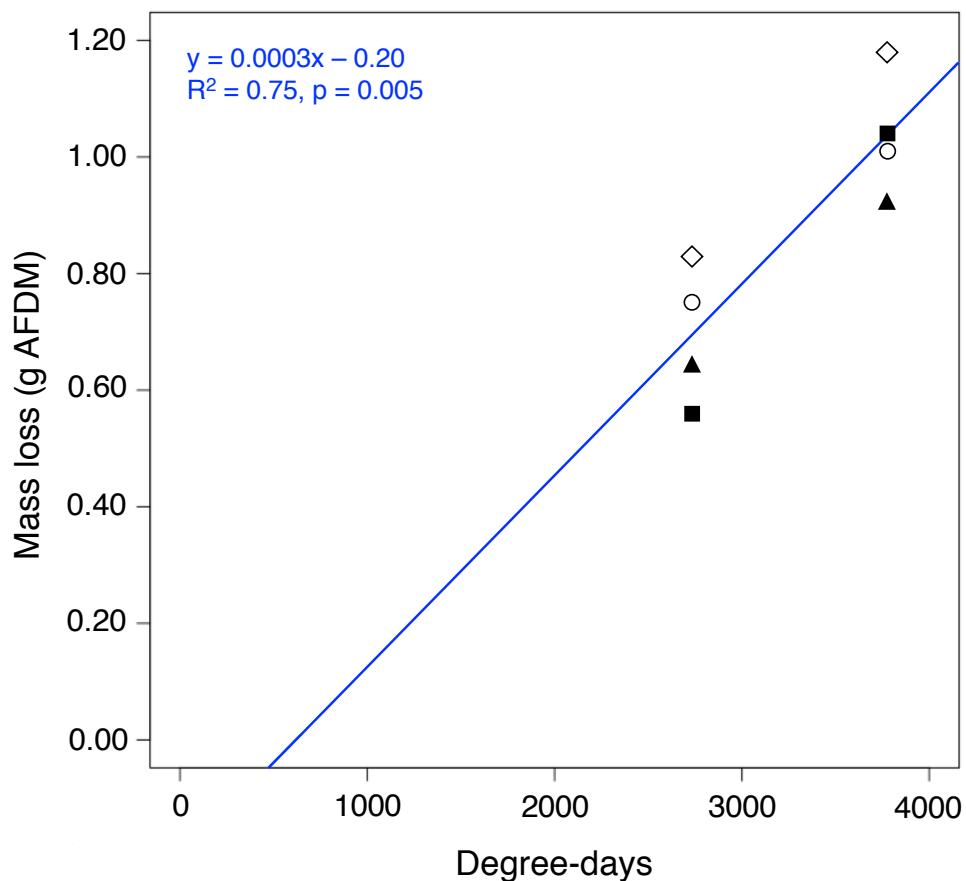
**Figure 4.2** Top view of coarse mesh (9 mm) western red cedar litterbag. The fine mesh (1 mm) window screen was inserted into the litterbag beneath the cedar leaves. This diagram is drawn to scale. (Cedar leaf drawing by the Michigan Department of Natural Resources, MI, USA)



**Figure 4.3** Average mass loss (g AFDM  $\pm$  1 S.E.) of western red cedar leaf litter for each treatment (control—C, nutrients added—N, water added—W, nutrients and water added—N + W) calculated from the raw data. Trials are: (a) January 2013 to January 2014, (b) June 2013 to January 2014. Note the range of mass loss values differs for each trial, and the y-axes do not begin at zero.



**Figure 4.4** Average mass loss (g AFDM  $\pm$  1 S.E.) of western red cedar leaf litter during the June 2013 to January 2014 trial by distance from stream (m). Average mass loss between 1 m and 40 m was significant ( $z = 2.985$ ,  $p = 0.024$ ); differences between all other distances were not significant. Note y-axis does not begin at zero.



**Figure 4.5** Average mass loss (g AFDM) of western red cedar leaf litter for each treatment (control ■, nutrients added ○, water added ▲, nutrients and water added ◇) by degree-days in the January 2013 to January 2014 and June 3013 to January 2014 trials. Standard error bars were not included due to the close proximity of the points.

# **Chapter 5: Abundance and diversity of terrestrial riparian invertebrates near headwater streams in southwestern British Columbia**

## **5.1 Synopsis**

My objective for this chapter was to determine whether water, nutrients, and distance from stream influence the abundance and taxonomic richness of terrestrial invertebrates in riparian zones near headwater streams. I hypothesized that (1) traps at watered stations or those with nutrient additions would show greater invertebrate abundance and taxonomic richness than traps at stations without water or nutrients (H10 and H11), and (2) traps closer to the stream edge would show greater invertebrate abundance and taxonomic richness than those further from the stream (H12). Invertebrate species often vary in their phenology and peak activity periods. I therefore hypothesized that invertebrate abundance and community composition in traps would vary with the month of capture (H13). At the same four headwater sites described in Chapters 3 and 4, I placed five pitfall traps along each transects (45 traps per site, with a total of 180 traps across sites) that either remained as controls or were treated with one of the following: nutrient additions, water additions, or additions of both nutrients and water. A subset of this collection was analyzed that included data from one control transect and one transect for each treatment (for a total of 20 traps per site, and 80 traps total). Three collections were made (in June, July, and August 2013), and a total of 240 samples were examined from these collections. I analyzed trap abundance and taxonomic richness for three groups of invertebrates: (1) all captured taxa, (2) common taxa with a relative abundance > 1%, and (c) beetle taxa. Coarser analyses were also completed for invertebrate orders and beetle families. Traps captured 1,256 individuals from 67 taxa; spiders from the families Cybaeidae and Linyphiidae, ants from the genus *Myrmica*, and

the beetle families Carabidae and Staphylinidae were the most abundant taxa. Fewer individuals were captured in traps with nutrient additions compared to those without nutrients when all 67 taxa were analyzed together. A greater number of invertebrate orders were captured per trap in July and August than in June. A similar pattern was seen for the number of individuals and taxa captured per trap for 23 common taxa. In contrast, beetles showed fewer individuals, total taxa, and families captured per trap in August compared to June and July. Distance from stream and water additions did not significantly influence trap abundance or taxonomic richness for any invertebrate groups. This analysis identified a suite of invertebrate taxa active in the riparian zones near headwater streams in southwest British Columbia, and demonstrated applications of exogenous nutrients can potentially decrease invertebrate abundance. It also highlighted seasonal differences in invertebrate abundance and taxonomic richness in riparian zones.

## 5.2 Introduction

Once described as “the little things that run the world” (Wilson 1987), invertebrates play substantial roles in ecosystems across the globe. They perform ecosystem functions such as decomposition and soil aeration; they also contribute to supporting and regulating ecosystem services such as pollination and water filtration that sustain human populations (Prather et al. 2013). Terrestrial invertebrates are important components of riparian habitats not only because they perform ecosystem functions, but they represent a major link between basal resources and higher trophic levels of food webs in both aquatic and terrestrial ecosystems (e.g., Nakano and Murakami 2001, Kawaguchi et al. 2003, DeBano and Wooster 2004, Baxter et al. 2005, Hagar et al. 2012, Richardson and Sato 2015, Kautza and Sullivan 2016). Many terrestrial invertebrates are sensitive to small changes in factors such as air temperature, soil moisture, and vegetation or

leaf litter composition (e.g., Thiele 1977, Bohac 1999, Ellis et al. 2001, Herrera and Dudley 2003, Rainio and Niemelä 2003, Yanahan and Taylor 2014). This sensitivity has made them good indicators of riparian habitat quality and restoration success (e.g., Williams 1993, Carton et al. 2003, McCluney and Sabo 2014, Maceda-Viega et al. 2016, Maoela et al. 2016, Ralston et al. 2017). Anthropogenic activities such as river regulation, water withdrawals, and forest harvesting (Nilsson and Berg 2000, Tockner and Stanford 2002, Poff et al. 2011, González et al. 2017, Stella and Bendix 2019) can lower water tables and alter riparian microclimate gradients, causing shifts in the abundance and distribution of invertebrates (e.g., Paetzold et al. 2008, Rykken et al. 2007a, Rykken et al. 2011, Kautza and Sullivan 2015) and potentially affect the ecosystem functions riparian invertebrates support. In order to effectively manage and conserve riparian habitat, we need to first understand what mechanisms influence the abundance and diversity of riparian invertebrate communities. In this chapter, I examined how the availability of water and nutrients as well as distance from stream influence ground-dwelling invertebrate communities in headwater riparian forests.

Moisture availability is one mechanism that may contribute to patterns in abundance and diversity of riparian invertebrate communities in headwater forests in southern British Columbia. Moist soils or litter layers and increased RH in riparian zones provide habitat for hygrophilous species (e.g., Antvogel and Bonn 2001, Henshall et al. 2011, Rykken et al. 2011, Allen 2016). In exposed riverine sediments along the River Elbe in northern Germany, soil moisture was a primary factor influencing the composition and distribution of carabid beetle communities (Antvogel and Bonn 2001). Moist riparian zones can also offer refuge from desiccation during periods with low precipitation and high temperatures. Wenninger and Fagan (2000) examined wolf spider assemblages in riparian habitats along natural and regulated portions of the Salt

River in Arizona, USA during hot and dry conditions in June and July. They determined that wolf spider abundance was more related to greater soil moisture and lower air and surface soil temperatures than prey availability during this time (Wenninger and Fagan 2000). In western Oregon, Rykken et al. (2007b) found a unique riparian assemblage of terrestrial invertebrates within 1 m of the stream edge at 15 first- and second-order streams that was associated with cool, moist conditions created by the stream between May and October when annual precipitation declines. Moist soils are also associated with higher microbial biomass and activity (Baldrian et al. 2010, Brockett et al. 2012), which can influence the abundance and composition of invertebrates that graze on microbial biofilms in soil and litter (e.g., Zimmer and Topp 1999). These benefits associated with elevated moisture may therefore lead to greater abundance and diversity of terrestrial invertebrates at locations with water additions during the summer dry period compared to un-watered locations.

The availability of nutrients in the environment may also influence patterns in abundance and diversity of forest floor invertebrates. Inorganic nutrient additions, especially those high in N, can increase plant biomass and root exudates, which are food resources for soil microbes, microarthropods, and phytophagous invertebrates (Wang et al. 2015). Berch et al. (2009) observed greater numbers of mites (Acari: Oribatida and Prostigmata) in soils under fertilized spruce (*Picea* spp.) forests compared to unfertilized forest soils in the interior of British Columbia, Canada, which corresponded to increases in tree growth and fine root length. Nutrient additions can also increase litter production and microbial growth on leaf litter, enhancing its nutrient content and palatability for detritivorous invertebrates (Seastedt 1984, Berg and Matzner 1997, Xiong and Nilsson 1997, Carreiro et al. 2000, Hobbie 2000, Perakis et al. 2012). Greater numbers of springtails (Collembola) have been recorded in agricultural fields fertilized with

ammonium nitrate due to N-stimulated microbial growth in soils (Sticht et al. 2006). Detritivore species richness was positively related to the rate of N addition in grasslands due to an increase in litter biomass (Haddad et al. 2000). Greater numbers of phytophagous and detritivorous invertebrates can subsequently attract higher numbers of predators (e.g., Haddad et al. 2000, Sullivan and Sullivan 2018). To my knowledge, a study analyzing invertebrate abundance and taxonomic richness in response to nutrient additions in riparian habitat has not been done. As nutrient additions are used to enhance primary production of western hemlock-western red cedar forests in British Columbia, determining how invertebrate communities respond to nutrient additions provides an opportunity to better understand how riparian communities function.

Distance from stream is often associated with changes in air and soil moisture, vegetation composition, flooding frequency, soil nutrient content, and substrate type (Day and Monk 1974, Johnson and Lowe 1985, Brosofske et al. 1997, Pabst and Spies 1998, Nierenberg and Hibbs 2000, Benda et al. 2004, Lite et al. 2005). As terrestrial invertebrates are sensitive to changes in these factors (e.g., Thiele 1977, Bohac 1999, Ellis et al. 2001, Herrera and Dudley 2003, Rainio and Niemelä 2003, Rykken et al. 2007a, Yanahan and Taylor 2014), their abundance and diversity can differ laterally across the riparian zone. On exposed gravel bars along the River Severn in the southern UK, Bates et al. (2007) noted differences in the abundance and community composition of carabid and elaterid beetles with distance from stream; these differences were associated with changes in vegetation cover and flooding frequency. In northwestern Oregon, USA, Hagar et al. (2012) found greater numbers of terrestrial arthropods at the banks of six headwater streams (0.3 to 3.4 m wide) compared to 50 m away, and attributed this to lateral differences in vegetation community composition. DeVito and Formanowicz (2003) examined the density of the riparian wolf spider *Pirata sedentarius* near a small, 2 to 3 m

wide stream in western New York, USA, and determined spider density declined with distance from stream due to lateral declines in soil moisture. At the same creek, DeVito et al. (2004) noted the proportional abundance of three wolf spider species (*Pardosa fuscula*, *Pardosa lapidicina*, and *Pirata sedentarius*) changed with distance from stream based on lateral differences in soil moisture across the riparian zone and differences in desiccation resistance between species. The availability of emergent aquatic insects can also lead to greater number of predaceous terrestrial invertebrates like carabid beetles and web-building spiders close to the stream edge than further away (e.g., Hering and Plachter 1997, Kato et al. 2004, Paetzold et al. 2005). Thus, invertebrate abundance and diversity may be higher at distances closer to the stream than further away in riparian zones near headwater streams in coastal British Columbia.

My objective for this chapter was to determine how the availability of water, nutrients and distance from the stream (alone or in combination) influence ground-dwelling invertebrate abundance and taxonomic richness in riparian forests along four headwater streams in southwestern British Columbia. I focused on headwater streams because they comprise the majority of stream network lengths (Meyer and Wallace 2001, Gomi et al. 2002, Benda et al. 2004) in this region, and because the majority of studies on riparian invertebrates focus on large, alluvial floodplain rivers; much less is known about headwater riparian communities (see LeSage et al. 2005, Rykken et al. 2007b, Foster and Ziegler 2013 for some exceptions). I hypothesized that traps located at watered stations and stations with nutrient additions would show greater abundance and taxonomic richness than traps at un-watered stations and stations without nutrients (H10 and H11). I also hypothesized abundance and taxonomic richness would be higher in pitfall traps closer to the stream than further away (H12). I was also interested in how invertebrate abundance and taxonomic richness varies with month of capture. Previous studies

have documented changes in invertebrate abundance in late summer and shifts in community composition between summer months (e.g., Brenner 2000, LaBonte 2002, Rykken et al. 2011). I sampled invertebrates once a month for three months, and based on these prior studies, I hypothesized that invertebrate abundance and community composition would vary with month of capture (H13). This analysis achieves Objective 5 of my thesis.

## 5.3 Materials and methods

### 5.3.1 Study sites and design

This study was conducted between June and August 2013 at the University of British Columbia's Malcolm Knapp Research Forest. Details on the climate, dominant vegetation, and history of this forest, and sites can be found in Chapter 3, Section 3.3.1, as I collected invertebrate samples at the same four sites as those previously described in Chapters 3 and 4. Pitfall traps were placed at all five distances along all nine transects at each site, and collections were made from each trap over three months. Along each transect, one trap comprised of two 532 mL plastic cups were placed 1, 5, 10, 20, and 40 m from the stream and dug into the soil so edges were level with the soil surface. One cup was placed in the soil and not removed until the end of the study to limit disturbance to the soil, while the other cup was placed inside the other and easily removed when trapping invertebrates. I placed 30 cm by 30 cm plywood covers about 15 cm above each trap, held up by three dowels surrounding the cups to exclude rain and prevent arboreal invertebrates from falling into traps. Roughly 100 mL of Prestone® Low Tox Antifreeze was added to each cup to euthanize and preserve invertebrates. As small vertebrates such as shrews and salamanders were present at my sites, I placed an inverted 89 mL paper cup with a small hole into each trap to prevent bycatch while still capturing small invertebrates; this

“island” method has not been used previously to my knowledge, but proved useful for eliminating bycatch of shrews and most amphibians as the inverted cup provided a ledge from which animals could reach the edge of the cup and exit the trap (Fig. 5.1). Each transect was randomly assigned to one of four treatments: control, addition of nutrients, addition of water, and addition of both nutrients and water. Nutrient and water additions were made to the soil surrounding each trap following the methods outlined in Chapter 3, Section 3.3.1. Full details on data collected on air temperature and RH at each distance for each site using 20 Onset HOBO® Pro v2 data loggers can be found in Chapter 3, Section 3.4.1.

Three collections were made during my study. Traps were activated with antifreeze for one week during each collection period, followed by a few weeks when traps were deactivated so as not to deplete invertebrate communities at each site. Collection periods in 2013 were as follows: June 10 – 17, July 9 – 16, and August 14 – 21. Upon collection, I filtered samples into high-density polyethylene plastic jars using a 250 µm sieve; those invertebrates retained on the sieve were stored in 70% ethanol. I focused my analyses on ground-dwelling mesofauna (0.1 – 2 mm) and macrofauna (> 2 mm), with emphasis on arthropods, gastropods, and annelids (Swift et al. 1979). Springtails (Collembola) and mites (Acari) were not enumerated in this study. These two subclasses are important members of the decomposer microfauna community, however they can account for up to 95% of total arthropod abundance in litter and soil layers (Hardings and Stuttard 1974, Maraun and Scheu 2000, Rusterholz et al. 2014). Because their abundance was far greater than any of the other arthropod and gastropod taxa I collected in my traps, their inclusion would have skewed abundance and diversity analyses. Excluding springtails and mites allowed for comparisons with similar terrestrial invertebrate community analyses by LeSage et al. (2005), Rykken et al. (2007b), and Foster and Ziegler (2013) along headwater streams, and multiple

studies along larger streams (e.g., Lambeets et al. 2008, Henshall et al. 2011, Januschke et al. 2011, King et al. 2014), all of which focused on mesofauna and macrofauna. Using a sieve size of 250 µm, I was able to capture minute beetles such as the beetle genus *Acrotrichis* (Ptiliidae, < 1 mm) and *Enicmus cordatus* (Latridiidae, 1.5 mm), but generally exclude microfauna such as nematodes. I made all identifications to the lowest taxonomic level possible, using taxonomic keys (e.g., Forsyth 2004, Burke et al. 2011) and consulting with local experts for confirmations; levels ranged from species or genus (carabid beetles) to family (spiders in Cybaeidae and Linyphiidae) and order (Opiliones and Pseudoscorpiones). I focused only on ground-dwelling terrestrial taxa, removing aerial adult insects such as mosquitos, stoneflies, bees, and wasps from the analysis; because caterpillars are ground-dwelling, they were included. I also removed slugs from my analysis as they were attracted to the paper cup islands in my traps and were often found partially consuming them.

### 5.3.2 Statistical analysis

Due to the large number of invertebrate samples collected (720 across three months) and time constraints related to processing both litterbags and invertebrate samples, analyses in this chapter are based on a subset of the collected data. I randomly chose one control transect and one transect of each treatment type (nutrients added, water added, and both nutrients and water added) at each site for the analysis. Data from collections along these transects were compiled across months and used for the final analysis. A total of 177 samples were used for this analysis (3 were lost due to accidental drying of the samples in faulty collection jars).

All statistical analyses were done in R Studio (Version 1.0.143) using the packages *glmmTMB* (V. 0.8.3.3), *graphics* (V. 3.4.3), *MuMIn* (V. 1.15.1), *stats* (V. 3.2.0), and *vegan* (V.

2.4-6). To test my hypotheses that water and nutrient additions would increase the abundance and taxonomic richness of invertebrates (H10 and H11), and that abundance would vary with month of capture (H12), created generalized linear mixed-effects models. Model selection followed the same methods using AIC as stated in Chapter 3, Section 3.3.2. Water and nutrient additions, month of capture, and distance from stream were fixed effects. A series of 24 models was created that included every combination of factors and their interactions, and every model included site as a random factor (see Appendix B, List E for a set of models).

Distance from stream was set as a factor with two levels: (1) 1 m from the stream edge, and (2) > 1 m from the stream edge. The decision to include distance from stream as a factor in models was made after a comparison between factor and covariate versions showed that AIC and  $R^2$  values were similar between model sets. In addition, fewer models were averaged for each group when distance was set as a factor (due to a lower number of models with  $\Delta AIC < 2$ ). I also determined how distance from stream interacted with treatments and noted distance had no significant effect on control traps when distance was a factor (see Appendix C, Fig. C.10 for an example of the nutrients-distance interaction). I therefore decided to use distance from stream as a factor in the models. The delineation between 1 m and > 1 m was based on multiple studies that have shown either higher abundance or a unique community composition of invertebrates at the stream edge compared to distances further inland (between 5 to 70 m; e.g., Rykken et al. 2007b, Burdon and Harding 2008, Hagar et al. 2012).

I divided the data into three separate groups for analysis: (1) all taxa collected, (2) common taxa which each had a relative abundance of > 1%, to effectively eliminated any effects of rare taxa (this 1% cutoff is commonly used to classify statistically rare species; e.g., Farina 1997, Hua et al. 2014), and (3) all beetle taxa, as I identified beetles as among my most abundant

taxa. Beetle taxa are among the most commonly trapped mesofauna and macrofauna in terrestrial riparian invertebrate surveys and make up a large percentage of riparian invertebrate abundance, diversity, and biomass (e.g., Famenau et al. 2002, Herrera and Dudley 2003, Rykken et al. 2007b, Moody and Sabo 2017). They are also sensitive to environmental changes (e.g., Ellis et al. 2001, Rainio and Niemelä 2003, Rykken et al. 2007a). Two sets of models (for total individuals and total taxa caught per trap per week) were created for each group, resulting in a pair of results for each of the three groups listed above. As data were counts of individuals and taxa, distributions were analyzed using histograms to determine whether Poisson or negative binomial distributions should be specified in the models (Chen et al. 2011). I did not indicate zero-inflation for any of the models as they were not over-dispersed and zeros in the count data are true zeros; this is because I identified individuals to the lowest taxonomic classification possible based on my ability and consultation with experts, and sampling methods were consistent across sites (Zuur et al. 2009). I also examined model results for total number of invertebrate orders and beetle families per trap per week, which increased the coarseness of the data to highlight potential patterns that could be obscured by the large number of identified taxa. Analyses at the order level have been useful for determining how the invertebrate community as a whole responds to changes in soil moisture, vegetation structure, and litter cover (e.g., Derraik et al. 2005, Doxon et al. 2011, Cameron and Leather 2012). Model selection was performed using AIC to determine which factors and/or interactions had significant effects on the abundance and taxonomic richness per trap per week of each group (see methods for model selection in Chapter 3, Section 3.3.2). Conditional R<sup>2</sup> values were also calculated for each model; these are considered pseudo-R<sup>2</sup> values due to my use count data with Poisson and negative binomial distributions (Nakagawa et al. 2017). Pseudo-R<sup>2</sup> values can only be compared between

models of the same data that predict the same dependent variable; they were calculated using the *my\_rsq* function in the *glmmTMB* package. I averaged models with  $\Delta\text{AIC} \leq 2$  to create an averaged model to determine the RI of each factor for each trial (see Section 3.3.2 for information about thresholds and calculating RI). Significant effects were depicted graphically using treatment means and standard errors calculated from the raw data, with differences between groups described as percentages in the Results (Section 5.4). Statistical significance was determined based on an alpha level of 0.05.

I also used canonical correspondence analyses (CCAs) to test my hypothesis that trap community composition of the groups would change with month of capture (H13). CCAs were completed in RStudio using the package *vegan*. One community matrix was created with counts for each taxon within a dataset, and matrix was created for the environmental variables associated with that taxa (month and site), which is used to constrain the ordination. I then used the *cca* function to run the CCA of the model where the community matrix is a function of month (R code example: `cca. Model<-cca(community. Matrix ~ Month, data=environmental. Matrix)`). Plots were made using the *plot* function for the model of the ordination, showing where taxa (“sp”) and months (“cn”) lie on the ordination plane by using the display argument (R code example: `plot(cca.model, display=c("sp","cn"))`). Because I had specific hypotheses about the effects of water, nutrients, distance from stream, and month of capture on pitfall trap abundance and taxonomic richness, and I used models to test these hypotheses with CCAs to visualize trap community composition by month, I did not include non-metric multidimensional scaling in my analysis.

## 5.4 Results

I collected 1,254 individual animals of 67 taxa in 177 traps (Table 5.1). The most abundant taxa included spiders in the family Linyphiidae (165 individuals, relative abundance of 13%) and Cybaeidae (71, 6%), beetles in the families Carabidae (144) and Staphylinidae (175), crickets in the family Rhaphidophoridae (97, 8%), and ants of the genus *Myrmica* (80, 6%). Coleoptera was the most abundant order, with 416 individuals captured (33% of total catch) and 14 families represented. Araneae (236, 19%), Hymenoptera (only Formicidae; 103, 8%), and Diplopoda (93, 7%) were also abundant. Capture rates of snails were low ( $n = 59$ , 5%), with *Ancotrema sportella* (19) and *Vespericola columbianus* (17) accounting for 32% and 29% of all snails, respectively.

### 5.4.1 Models for abundance and richness of all invertebrate taxa collected and invertebrate orders

Six models were averaged to determine which factors influenced the average number of individuals captured per trap per week (Table 5.2). The best model included only nutrient additions. The  $w_i$  (0.156) and RL (1.000) of the best model was 1.2 times those of the second-best model, which included nutrient additions and distance from stream ( $w_i = 0.127$ , RL = 0.811). All six models explained on average 10% of the variation in the data. The averaged model showed fewer individuals captured per trap per week at stations with nutrient additions ( $\bar{x} = 5.2 \pm 0.3$  individuals) compared to stations without nutrients ( $\bar{x} = 5.7 \pm 0.3$  individuals;  $z = 2.068$ ,  $p = 0.039$ ; Table 5.3). The number of individuals captured per trap per week at control stations and those with water and nutrient treatments can be seen in Fig. 5.2a.

Seven models were averaged to determine which factors influenced the average number of taxa captured per trap per week (Table 5.2). The best model included only nutrient additions. The  $w_i$  (0.185) and RL (1.000) of the best model was 1.3 and 1.2 times greater than  $w_i$  (0.185) and RL (0.824), respectively, of the second-best model including nutrient additions and month of capture. All six models only explained on average 4% of the variation in the data. The averaged model showed no significant effects by any factors on average number of taxa captured per trap per week (Table 5.3).

Models were also run at a coarser level with invertebrate order richness per trap. Three models were averaged to determine which factors influenced the average number of invertebrate orders captured per trap per week (Table 5.2). The best model included nutrient additions. The  $w_i$  (0.423) and RL (1.000) of the best model was 2.6 times greater than the second-best model, which included nutrient additions, water additions, and month of capture ( $w_i = 0.185$ , RL = 0.842). All three models explained on average 12% of variation in the data. The averaged model showed fewer orders captured per trap per week at stations with nutrient additions ( $\bar{x} = 2.8 \pm 0.1$  orders) compared to stations without nutrient additions ( $\bar{x} = 3.4 \pm 0.2$  orders;  $z = 2.481$ ,  $p = 0.013$ ; Table 5.3). The average number of orders captured per trap per week at control stations and those with water and nutrient treatment can be seen in Fig. 5.2b. Lower numbers of centipedes (Geophilomorpha), ants (Hymenoptera), caterpillars (Lepidoptera), woodlice (Oniscidea), and barklice (Psocoptera) were captured in traps at stations with nutrient additions (Appendix C, Fig. C.11). A greater number of orders were captured per trap per week in July ( $\bar{x} = 3.2 \pm 0.2$  orders;  $z = 2.350$ ,  $p = 0.019$ ) and August ( $\bar{x} = 3.6 \pm 0.2$  orders;  $z = 3.580$ ,  $p < 0.001$ ) than in June ( $\bar{x} = 2.6 \pm 0.2$  orders; Table 5.3; Fig. 5.3a). Coleoptera, Diplopoda and Oligochaeta showed greater numbers of total individuals captured during June and July; Orthoptera,

Pseudoscorpiones, and Psocoptera were more abundant in traps during August (Appendix C, Fig. C.12). Month influenced community composition ( $\chi^2 = 0.1538$ ,  $F = 5.518$ ,  $p = 0.001$ ); captures of Oligochaeta were associated with June, whereas Psocoptera was associated with August (Fig. 5.4a).

#### 5.4.2 Models for abundance and taxonomic richness of common taxa

Common taxa represented 85% of all collected taxa (bold text in Table 5.1); here I refer to individuals of these taxa as common individuals. Three models were averaged to determine which factors influenced the average number of common individuals captured per trap per week (Table 5.2). The best model included nutrient additions, distance from stream, and month of capture. The  $w_i$  (0.220) and RL (1.000) of the best model was 1.2 times greater than the second-best model, which included nutrient additions and month of capture ( $w_i = 0.185$ , RL = 0.842). All three models explained on average 13% of variation in the data. The averaged model showed fewer common individuals captured per trap per week at stations with nutrient additions ( $\bar{x} = 4.2 \pm 0.3$  individuals) compared to stations without nutrients ( $\bar{x} = 4.8 \pm 0.3$  individuals;  $z = 2.353$ ,  $p = 0.019$ ; Table 5.3). The average number of common individuals captured per trap per week at control stations and those with water and nutrient treatment can be seen in Fig. 5.2c. A greater number of individuals were captured per trap per week in August ( $\bar{x} = 4.9 \pm 0.3$  individuals;  $z = 2.350$ ,  $p = 0.019$ ) than in June ( $\bar{x} = 4.0 \pm 0.3$  individuals; Table 5.3; Fig. 5.3b).

Five models were averaged to determine which factors influenced the average number of common taxa captured per trap per week (Table 5.2). The best model included nutrient additions and month of capture. The  $w_i$  (0.223) and RL (1.000) of the best model was 1.4 times that of the second-best model, which included only month of capture ( $w_i = 0.162$ , RL = 0.728). All three

models explained on average 7% of variation in the data. The averaged model showed greater number of common taxa captured per trap per week in July ( $\bar{x} = 3.4 \pm 0.2$  taxa;  $z = 2.317$ ,  $p = 0.020$ ) and August ( $\bar{x} = 3.5 \pm 0.2$  taxa;  $z = 2.655$ ,  $p = 0.008$ ) than in June ( $\bar{x} = 2.8 \pm 0.2$  taxa; Table 5.3; Fig. 5.3c). Ordination indicated month influenced trap community composition ( $\chi^2 = 2.718$ ,  $F = 4.994$ ,  $p = 0.001$ ); the worm family Enchytraeidae and the beetle *Enicmus cordatus* were associated with June and July, respectively (Fig. 5.4b).

#### 5.4.3 Models for abundance and richness of beetle taxa and families

Five models were averaged to determine which factors influenced the average number of beetle individuals captured per trap per week (Table 5.2). The best model included only month of capture ( $w_i = 0.244$ , RL = 1.000). The second-best model included water additions and month of capture ( $w_i = 0.233$ , RL = 0.958); values of  $w_i$  and RL were similar between these two models. All five models explained on average 8% of variation in the data. The averaged model showed fewer beetle individuals captured per trap per week in August ( $\bar{x} = 1.1 \pm 0.1$  individuals;  $z = 3.577$ ,  $p < 0.001$ ) than in June ( $\bar{x} = 2.2 \pm 0.2$  individuals; Table 5.3; Fig. 5.3d).

Six models were averaged to determine which factors influenced the average number of beetle taxa captured per trap per week (Table 5.2). The best model included water additions and month of capture ( $w_i = 0.229$ , RL = 1.000). The second-best model included only month of capture ( $w_i = 0.212$ , RL = 0.958); values of  $w_i$  and RL were similar between these two models. All five models explained on average 10% of variation in the data. The averaged model showed fewer beetle taxa captured per trap per week in August ( $\bar{x} = 0.9 \pm 0.1$  taxa;  $z = 3.722$ ,  $p < 0.001$ ) than in June ( $\bar{x} = 1.6 \pm 0.1$  taxa; Table 5.3; Fig. 5.3e). *Omus dejearni* and *Pterostichus* spp. in the family Carabidae, and the subfamilies Aleocharinae and Tachyporinae in the family

Staphylinidae were more abundant in traps during June and July, whereas the carabid *Scaphinotus angusticollis* was more abundant in traps during August (Appendix C, Fig. C.13). Ordination confirmed that month influenced trap community composition ( $\chi^2 = 0.585$ ,  $F = 2.890$ ,  $p = 0.001$ ). The appearance of *S. angulatus*, *S. marginatus*, and *Cychrus tuberculatus* in traps was associated with June, and *Leistus ferruginosus* was associated with August (Fig. 5.5a). Further associations between taxa and month can be seen in Fig. 5.5a, however, many taxa were represented by a single individual or single instance of capture (such as Silphidae with six individuals in one trap) during the associated months and therefore may not represent a true association.

Models were also run at a coarser level for beetle family richness per trap. Four models were averaged to determine which factors influenced the average number of beetle families captured per trap per week (Table 5.2). The best model included water additions and month of capture. The  $w_i$  (0.236) and RL (1.000) of the best model was 1.3 times that of the second-best model, which included only month of capture ( $w_i = 0.187$ , RL = 0.792). All four models explained on average 7% of variation in the data. The averaged model showed fewer beetle families captured per trap per week in August ( $\bar{x} = 0.8 \pm 0.1$  families;  $z = 2.495$ ,  $p = 0.013$ ) than in June ( $\bar{x} = 1.2 \pm 0.1$  families; Table 5.3; Fig. 5.3f). Month influenced trap community composition ( $\chi^2 = 0.244$ ,  $F = 3.336$ ,  $p = 0.001$ ) with a strong association seen between Latridiidae and July (Fig. 5.5b). Like the ordination with beetle taxa, associations between families and months can be seen in this Fig. 5.5b, but many of these families are represented by a single individual or a single capture event and may not represent a true association.

## 5.5 Discussion

The abundance and taxonomic richness of ground-dwelling invertebrates captured in riparian forests near small headwater streams of British Columbia were primarily influenced by the addition of nutrients and month of capture. Additions of water and distance of traps from the bankfull edge of the stream did not significantly influence abundance or taxonomic richness in pitfall traps. My analysis of terrestrial riparian communities adds to the limited body of previous studies that characterize ground-dwelling terrestrial invertebrate communities near small headwater streams (Brenner 2000, DeVito and Formanowicz 2003, Devito et al. 2004, Rykken et al. 2007a, Hagar et al. 2012, Ziegelmtrum and Foster 2013, Sullivan et al. 2019b). It is also the first study, to my knowledge, to experimentally determine how invertebrate abundance and taxonomic richness responded to manipulations of water and nutrients in headwater riparian zones.

The majority of the captured taxa were highly mobile predators, with linyphiid spiders, carabid beetles, and staphylinid beetles showing the highest relative abundance. Linyphiid spiders often disperse by wind using strands of silk (called ballooning) over distances of several metres or even kilometres if wind conditions are suitable (Holland et al. 1999, Holland et al. 2002, Thomas et al. 2003, Schmidt and Tscharntke 2005). The majority of carabid and staphylinid beetles are highly active predators, capable of traveling several metres and consuming the equivalent of their own mass in prey daily (Thiele 1977, Lövei and Sutherland 1996, Brenner 2000, Bess et al. 2002, Steward et al. 2018). Taxa captured in my traps were similar to those captured during previous riparian studies in the coastal Pacific Northwest. Brenner (2000) examined riparian beetle communities near a third-order stream in the H. J. Andrews Experimental Forest in western Oregon, and captured many beetles in the subfamily

Aleocharinae (Staphylinidae), and the genera *Catops* (Leiodidae) and *Pterostichus* (Carabidae). Rykken et al. (2007b) examined invertebrate communities along 15 first- to second-order streams in the H. J. Andrews Experimental Forest, and caught large numbers of the carabids *Scaphinotus angusticollis* and *Pterostichus* spp., the millipede *Harpaphe haydeniana*, the snail *Ancotrema sportella*, and spiders in the genus *Cybaeus*. However, the most abundant taxon in Rykken et al. (2007b) was the wolf spider *Pardosa dorsalis*, which was not collected in my study.

Water additions did not statistically influence invertebrate abundance or taxonomic richness in pitfall traps for any group. This finding rejects my hypothesis that pitfall traps at watered stations would show greater abundance and taxonomic richness than traps at un-watered stations (H6). Precipitation in June and July 2013 was lower than monthly averages based on climate normals for the region (Appendix C, Figure C.2), VPD was elevated during this time (Fig. 3.6c), and previous research in the Malcolm Knapp Research Forest determined soil moisture is generally lowest (< 18% volumetric water content) between mid-June and mid-August (Chin 2007). This information suggests that water additions likely increased suitable habitat for species that are prone to desiccation during summer periods by creating moist soils. Water additions were only made to stations once a week and soil moisture was not measured at stations between watering events, the duration of the water's effect on soil moisture (whether it was hours or days) is unknown. It is possible that water infiltrated the soils and was either quickly taken up by plants or moved through the permeable top soil (Leach 2014) into lower soil layers, and thus did not significantly influence surface-dwelling arthropods. It is also possible that the majority of species I captured, most of which were highly mobile, may not have responded to such small-scale ( $1 \text{ m}^2$ ) manipulations in moisture availability (see Chapter 6,

Section 6.4 for further detail). A similar result was seen by Chikoski et al. (2006), who examined terrestrial invertebrate communities in experimentally watered grass, shrubland, and forest plots within an aspen stand in Saskatchewan, Canada. They saw no effect of weekly water additions on the abundance of larger, more mobile taxa such as spiders, beetles, and centipedes; only mites and springtails showed greater abundance in watered plots (Chikoski et al. 2006). Liu et al. (2017) also found increases in springtail abundance with water additions in grassland soils in the western Gansu Province, China. It is therefore possible that water additions did influence the invertebrate communities at my sites (such as mites and springtails), but not the assemblage I examined.

The application of nutrients had a negative effect on the average total number of individuals caught per trap and the number of invertebrate orders per trap. It should be noted that these models had low predictive power, explaining on average 11% of variation in the data. This finding rejects my hypothesis that pitfall traps at stations with nutrient additions would capture greater numbers of individuals and greater numbers of taxa than traps at stations without nutrients (H7). This decline in trap abundance may be due to behavioural avoidance of fertilized plots or death of individuals in fertilized plots. Nitrogen-rich fertilizers can depress invertebrate communities in soils with high amounts of organic matter such as those in temperate forests (Edwards 1984). Negative effects of exogenous nutrients on invertebrate individuals and populations may occur directly from contact with the crystallized nutrients and its toxic compounds (Bünemann et al. 2006, Gomiero 2013, Roberts 2014), or indirectly through changes in soil conditions. Adding crystallized nutrients during periods with low precipitation and drier soils can increase the total concentration of dissolved solids in the soil, increasing osmotic pressure (Lohm et al. 1977). This reaction increases the salt content of the soil and can reduce

the activity or even cause death in invertebrates that are sensitive to increases in soil osmotic pressure, or taxa without hard, protective exoskeletons such as earthworms (Blake 1961, Lohm et al. 1977, Springett and Syers 1984). Inorganic compounds such as ammonium nitrate have been shown to decrease the wet biomass of the earthworm *Lumbricus terrestris* (Lumbricidae) and abundance of the springtail *Folsomia caliginosa* (Isotomidae) in microcosms (Sandor et al. 2016). Applications of ammonium nitrate also reduced the survival and growth rate of Colorado potato beetle larvae (*Lepinotarsa decemlineata*; Chrysomelidae; Veverka and Oliberius 1987). Long-term use of nitrogenous fertilizers can also lower soil pH and reduce survival and reproduction in earthworms (Edwards and Lofty 1977, Ma et al. 1990).

The reason for declines in invertebrate abundance and order richness at stations with nutrient additions are unclear. Applications of nutrients at my sites were limited to five 1<sup>2</sup> m stations per site and were infrequent, with nutrient additions made on 3 June 2013 and the first collection of invertebrates occurring on 10 June 2013. Subsequent collections were made in July and August with no additional applications of nutrients. Nutrients had been added to the same plots in August 2012 and January 2013 as part of my red alder experiments in Chapter 3. Because of the infrequent and spatially-restricted nature of my nutrient additions, negative effects due to changes in soil pH that typically occur with repeated fertilization (Edwards and Lofty 1977, Ma et al. 1990) are unlikely compared to potential toxic effects from direct contact with the crystalized compounds on or dissolved in the soil. Yet differences in the number of individuals and order richness between traps with nutrients and without, though statistically significant, were low: traps at stations with nutrients caught on average one less individual and one less invertebrate order per trap per week than traps at stations without nutrients. This suggests that invertebrate death directly due to contact with the fertilizer was unlikely, though as

most species were highly mobile and treated stations were spatially limited recolonization from surrounding habitat could have hidden this lethal effect. Behavioural avoidance could potentially occur if nutrient additions reduced or altered the abundance and composition of soil microarthropods or microbial communities (e.g., Traeseder 2008), though I could not test this as soil communities were not analyzed. As I did not track individuals who had contact with crystallized nutrients or hand-search areas surrounding pitfall traps for dead invertebrates, I cannot say whether declines in abundance were due to death of individuals or avoidance of fertilized sites. Potential experiments to determine which crystallized compound produced declines in trap abundance, and whether declines could be limited by dissolving compounds before addition to stations, are suggested in Chapter 6, Section 6.5.4.

Distance from stream edge did not influence the abundance or diversity of taxa in traps for any group. This result rejects my hypothesis that invertebrate abundance and taxonomic richness would be greater with 1 m of the stream edge than > 1 m away (H8). This hypothesis was based on previous studies that have shown greater terrestrial invertebrate abundance at the stream edge stream compared to in forest 50 m away (Hagar et al. 2012), and changes in invertebrate community composition and distribution associated with microclimate gradients extending from the stream into riparian habitat (Wenninger and Fagan 2000, Rykken et al. 2007b). As discussed in Chapter 3 (Section 3.5), there was a difference in the magnitude of changes in microclimate parameters observed in Oregon by Rykken et al. (2007a) and this study. Rykken et al. (2007a) reported an increase in air temperature 5.4°C and a decrease in RH by 25% between 1 and 20 m from the stream edge, whereas I found air temperatures increased by 0.25°C and RH decreased by 3% on average between 1 m from the stream edge and distances further inland (Chapter 3, Section 3.4.1). This small difference in riparian microclimate could help to

explain why distance from stream did not influence terrestrial invertebrate abundance and diversity at my sites, especially considering most captured taxa were highly mobile.

Riparian invertebrate abundance and diversity was influenced by month at my sites; this finding supports my hypothesis (H13). The number of invertebrate orders and common taxa caught per trap per week increased between June and August, and trap community composition varied by month. Beetle abundance and taxonomic richness in my pitfall traps was greater in June and July than in August, a pattern that was also seen by Niemelä et al. (1992) and Brenner (2000). Differences in the abundance and composition of invertebrate communities over time often occur due to seasonal changes in temperature (Barlow 1973, Koskela 1979, Moeed and Meads 1985). As temperatures rise, the metabolism of poikilothermic organisms including invertebrates increases, allowing for greater periods of activity (Koskela 1979). For example, Niemelä et al. (1994) reported the abundance and species richness of boreal forest floor spiders in southern Finland was greater in early summer (May to June) when precipitation was higher compared to late autumn (September to November). Foster and Claeson (2011) found millipede community composition changed seasonally in riparian forests of western Washington due to differences in precipitation and air and soil temperatures. The abundance of spiders, ants, centipedes, millipedes, and beetles in pitfall traps in forests of the Orongorongo Valley, New Zealand, were all positively related to temperature (Moeed and Meads 1985). Seasonal changes in temperature and precipitation can also cause fluctuations in primary production, litterfall, and canopy coverage also occur which indirectly influences invertebrate communities (e.g., Bultman and Uetz 1982, Ziesche and Roth 2008).

Differences between taxa in desiccation tolerance (Rykken et al. 2011), seasonal activity (Koskela 1979, Moeed and Meads 1985), and phenology (e.g., Gilbert 1957, Rivard 1964,

Framenau et al. 2002) can also result in variable capture rates between months, which are often related to temperature. The majority of Aleocharinae, a subfamily of Staphylinidae, were captured in June and July and showed a marked decrease in abundance in August (Fig. C.13). This is likely due to changes in seasonal flight activity: Koskela (1979) recorded greater flight activity of Aleocharinae in southern Finland during summer when temperatures were elevated and daylight was longer compared to autumn (Koskela 1979). In contrast, total abundance of *Scaphinotus angusticollis* in traps was much greater in August than June or July (Fig. C.13). In western Oregon, Rykken et al. (2011) noted the movement of *S. angusticollis* in a riparian buffer adjacent to a clear-cut was restricted to cool, moist portions of the buffer. It is possible that increasing precipitation and decreasing VPD in August compared to June and July could have provided more suitable conditions to this species, leading to greater activity levels and higher capture rates. These results suggest that monthly differences in temperature and moisture, and subsequent effects on activity of invertebrate species, contribute to the patterns of invertebrate abundance and diversity in headwater riparian zones.

It is important to note that models in my analysis explained only a small portion of variation in the data, ranging from 2.7% to 13%. Though nutrient additions significantly influenced invertebrate abundance and taxonomic richness in pitfall traps, these data suggest there are other untested factors which influence these invertebrate community parameters. Previous analyses have identified habitat heterogeneity, microhabitat diversity, vegetation composition, sediment size, and the availability of emergent aquatic insects as factors influencing the abundance, distribution, and diversity of riparian invertebrate communities (e.g., Hering and Plachter 1997, Framenau et al. 2002, Kato et al. 2004, Sadler et al. 2004, Jähnig et al. 2009, Januschke et al. 2011; see Chapter 2 for more details). This does not diminish the

significance of nutrient additions even though their effect was small, but demonstrates the complex and often interacting factors that influence invertebrate communities in riparian zones. It also highlights the need for future experimental research that address multiple mechanisms and tests their relative importance and possible interactions.

This study examined the abundance and diversity of ground-dwelling invertebrate taxa in riparian forests near headwater streams. Though previous studies have described the relationship between distance from stream and moisture availability with invertebrate abundance and diversity, this study was the first to determine how riparian invertebrates respond to direct manipulations of water and nutrients in riparian zones to my knowledge. My results provide a baseline census of ground-dwelling invertebrate taxa in headwater riparian zones in this region. They also create a basis for future research that may identify which inorganic compounds used in forest fertilization negatively influence riparian invertebrate taxa, and whether changes in abundance result from behavioural avoidance or death of invertebrates. Suggestions for future research based on these results are provided in Chapter 6, Section 6.5.

**Table 5.1** Taxa identified in pitfall traps, organized by phylum, class, and order. Number of individuals found (*n*), relative abundance (%), and number of traps in which they were found are also given. Taxa were considered common when their relative abundance > 1%, and are noted with bold text.

Phylum	Class or Subclass	Order or Suborder	Family or Subfamily	Species	<i>n</i>	Relative abundance	Number of traps
Arthropoda	Arachnida	Araneae	<b>Cybaeidae</b>		71	5.65	54
			<b>Linyphiidae</b>		165	13.14	104
		Archaeognatha	<b>Machilidae</b>		18	1.43	17
		<b>Opiliones</b>			21	1.67	21
		Pseudoscorpiones	<b>Chthoniidae</b>		38	3.03	35
			Neobisidae		3	0.24	3
	Insecta	Coleoptera	Carabidae	<i>Cychrus tuberculatus</i>	6	0.48	4
				<i>Leistus ferruginosus</i>	7	0.56	7
				<b><i>Omus dejeani</i></b>	14	1.11	11
				<i>Promecognathus crassus</i>	1	0.08	1
				<b><i>Pterostichus</i> spp.</b>	47	3.74	33
				<i>Scaphinotus angulatus</i>	8	0.64	7
				<b><i>Scaphinotus angusticollis</i></b>	53	4.22	38
				<i>Scaphinotus marginatus</i>	8	0.64	7
				<i>Lioon simplicipes</i>	1	0.08	1
			Curculionidae	<i>Dyslobius verrucifer</i>	2	0.16	2
				<i>Otiorhynchus singularis</i>	3	0.24	2
				<i>Rhyncolus</i> spp.	7	0.56	7
				<i>Steremnius carinatus</i>	7	0.56	5
				<i>Steremnius tuberosus</i>	3	0.24	3
				<i>Sthereus horridus</i>	3	0.24	3

Phylum	Class or Subclass	Order or Suborder	Family or Subfamily	Species	n	Relative abundance	Number of traps
			Cryptophagidae		2	0.16	2
			Elateridae	<i>Agriotes lineatus</i>	1	0.08	1
				<i>Corymbitodes pygmaeus</i>	1	0.08	1
			Ischaliidae	<i>Ischalia vancouverensis</i>	1	0.08	1
			Latridiidae	<b><i>Enicmus cordatus</i></b>	15	1.19	13
			Leiodidae	<i>Agathidium</i> spp.	1	0.08	1
				<b><i>Catops</i> spp.</b>	17	1.35	10
				<i>Leiodes</i> spp.	10	0.80	2
			Monotomidae	<i>Rhizophagus</i> spp.	1	0.08	1
			Ptiliidae	<i>Acrotrichis</i> spp.	2	0.16	2
			Pyrochroidae	<i>Dendroides ephemerooides</i>	1	0.08	1
			Silphidae	<i>Nicrophorus</i> spp.	6	0.48	1
			Staphylinidae				
			<b>Aleocharinae</b>		117	9.32	71
			Micropeplinae	<i>Micropeplus</i> spp.	2	0.16	1
			Omalinae		11	0.88	10
			Oxytelinae	<i>Syntomium</i> spp.	1	0.08	1
			Pselaphinae		1	0.08	1
			Quediina	<i>Quedius</i> spp.	4	0.32	4
			Scaphidiinae	<i>Scaphisoma castaneum</i>	1	0.08	1
			Scydmaeninae	<i>Lophioderus</i> spp.	6	0.48	6
				<i>Scydmaenus</i> spp.	1	0.08	1
			Staphylininae	<i>Staphylinus</i> spp.	4	0.32	4
			<b>Tachyporinae</b>		27	2.15	22

Phylum	Class or Subclass	Order or Suborder	Family or Subfamily	Species	n	Relative abundance	Number of traps
			Zopheridae	<i>Phelopsis porcata</i>	1	0.08	1
			Unknown larvae		12	0.96	11
		Hymenoptera	Formicidae	<i>Camponotus</i> spp.	4	0.32	3
				<i>Lasius</i> spp.	19	1.51	10
				<i>Myrmica</i> spp.	80	6.37	52
		Lepidoptera	Geometridae		11	0.88	10
			Unknown larvae		2	0.16	2
		Orthoptera	<b>Rhaphidophoridae</b>		97	7.72	69
		<b>Psocoptera</b>			49	3.90	34
Chilopoda	<b>Geophilomorpha</b>				36	2.87	29
	Hemiptera		<b>Aphidae</b>		26	2.07	23
Diplopoda	<b>Julida</b>				51	4.06	38
		Polydesmida	Polydesmidae		7	0.56	5
			Xystodesmidae	<i>Harpaphe haydeniana</i>	34	2.71	27
		Polyzoniida	Hirudisomatidae	<i>Octoglena anura</i>	1	0.08	1
Malacostraca	Isopoda		Oniscoidea <sup>1</sup>		12	0.96	8
Mollusca	Gastropoda	Stylommatophora <sup>2</sup>	Haplotrema	<i>Ancotrema sportella</i>	19	1.51	18
				<i>Haplotrema vancouverense</i>	2	0.16	2
			Polygyridae	<i>Vespericola columbianus</i>	17	1.35	17
			Pristilomatidae	<i>Pristiloma</i> spp.	5	0.40	4
			Punctidae	<i>Punctum randolphi</i>	8	0.64	8
			Vertiginidae	<i>Columella endentula</i>	6	0.56	6
				<i>Vertigo columbiana</i>	2	0.16	2
Annelida	Oligochaeta	Haplotauxida	<b>Enchytraeidae</b>		31	2.47	17

<b>Phylum</b>	<b>Class or Subclass</b>	<b>Order or Suborder</b>	<b>Family or Subfamily</b>	<b>Species</b>	<b><i>n</i></b>	<b>Relative abundance</b>	<b>Number of traps</b>
		Lumbricina <sup>3</sup>			3	0.24	3

<sup>1</sup> Superfamily

<sup>2</sup> Clade

<sup>3</sup> Suborder

**Table 5.2** Comparison of top candidate models describing total number of individuals or taxa a function of water (W) and nutrient (N) additions, distance from the stream edge (D), and month of capture (M) for all taxa, common taxa only, and beetle taxa only. All models include site as a random factor. Interactions are indicated with an asterisk (\*). Results for each model include Akaike Information Criterion (AIC), change in Akaike Information Criterion relative to best model ( $\Delta\text{AIC}$ ), degrees of freedom (df), Akaike weight ( $w_i$ ), relative likelihood (RL), and conditional  $R^2$ .

	Model distribution	Model	df	AIC	$\Delta\text{AIC}$	$w_i$	RL	$R^2$
<b>All taxa</b>								
Total individuals	Poisson	N	3	<b>1269.344</b>	<b>0.000</b>	<b>0.156</b>	<b>1.000</b>	<b>0.093</b>
		N + D	4	1269.762	0.419	0.127	0.811	0.103
		N + M	5	1270.190	0.846	0.102	0.655	0.101
		N + D + M	6	1270.554	1.210	0.085	0.546	0.111
		N + W	4	1270.765	1.421	0.077	0.491	0.092
		N + W + D	5	1271.195	1.851	0.062	0.396	0.103
Total taxa	Poisson	N	3	<b>1004.096</b>	<b>0.000</b>	<b>0.145</b>	<b>1.000</b>	<b>0.034</b>
		Null	2	1004.532	0.436	0.117	0.804	0.027
		N + M	5	1004.671	0.575	0.109	0.750	0.046
		M	4	1005.090	0.994	0.088	0.608	0.038
		N + W	4	1005.355	1.259	0.077	0.533	0.035
		W	3	1005.781	1.685	0.062	0.431	0.028
		N + W + M	6	1005.959	1.863	0.057	0.394	0.046
Order richness	Poisson	N + M	5	<b>880.355</b>	<b>0.000</b>	<b>0.423</b>	<b>1.000</b>	<b>0.123</b>
		N + W + M	6	882.294	1.940	0.160	0.379	0.123
		N + D + M	6	882.353	1.999	0.156	0.368	0.123

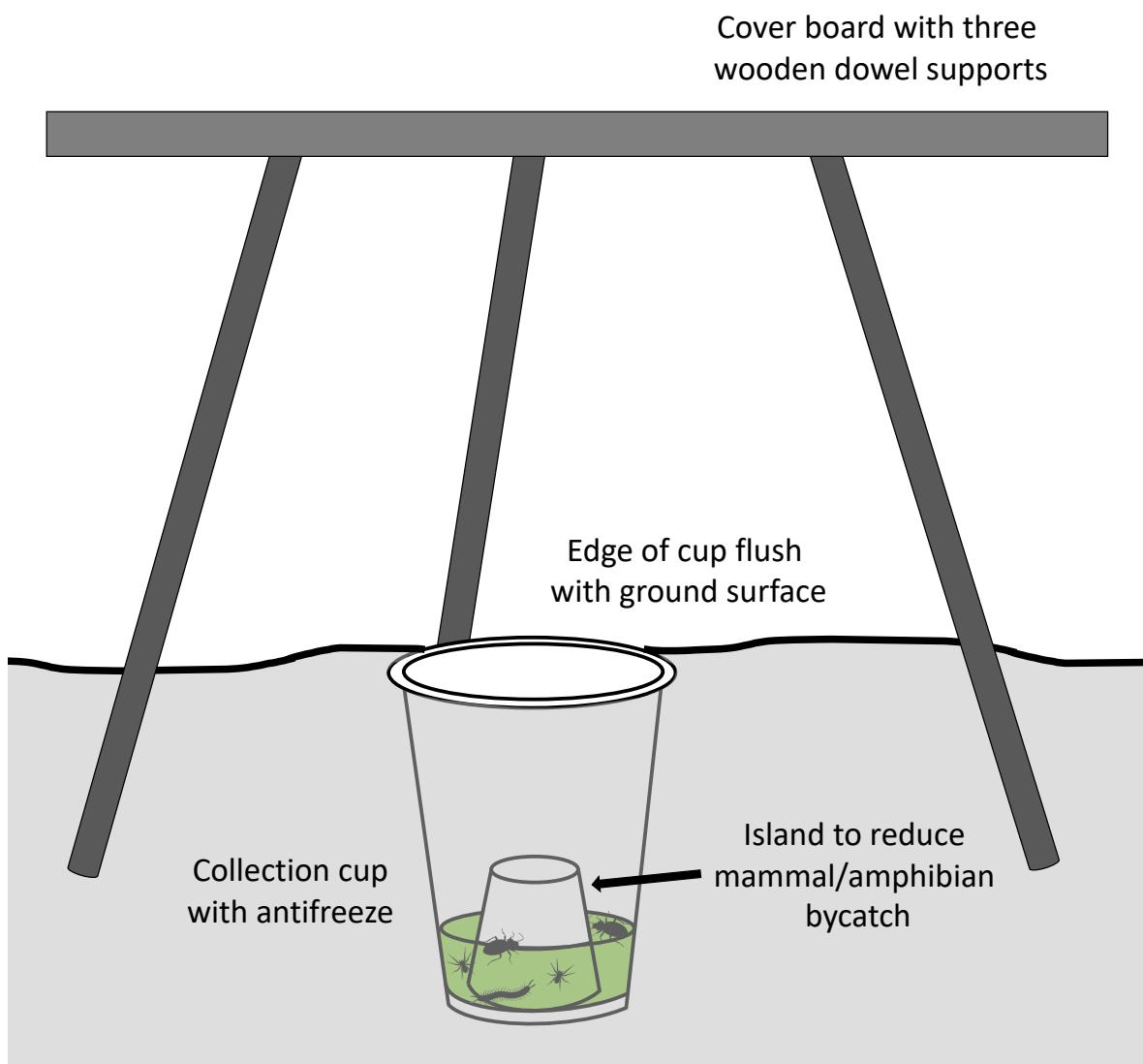
	Model distribution	Model	df	AIC	$\Delta\text{AIC}$	$w_i$	RL	$R^2$
<b>Common taxa</b>								
Total individuals	Poisson	<b>N + D + M</b>	<b>6</b>	<b>1181.738</b>	<b>0.000</b>	<b>0.220</b>	<b>1.000</b>	<b>0.131</b>
		N + M	5	1182.084	0.345	0.185	0.842	0.123
		N + W + D + M	7	1183.479	1.741	0.092	0.419	0.132
Total taxa	Poisson	<b>N + M</b>	<b>5</b>	<b>930.794</b>	<b>0.000</b>	<b>0.223</b>	<b>1.000</b>	<b>0.075</b>
		M	4	931.428	0.634	0.162	0.728	0.064
		N + W + M	6	932.134	1.339	0.114	0.512	0.078
		N + D + M	6	932.592	1.798	0.091	0.407	0.076
		W + M	5	932.757	1.963	0.084	0.375	0.066
<b>Beetle taxa</b>								
Total individuals	Negative binomial	<b>M</b>	<b>5</b>	<b>847.535</b>	<b>0.000</b>	<b>0.244</b>	<b>1.000</b>	<b>0.078</b>
		W + M	6	847.621	0.086	0.233	0.958	0.088
		W + D + M	6	849.394	1.859	0.096	0.395	0.078
		N + W + M	7	849.503	1.969	0.091	0.374	0.088
		N + M	6	849.523	1.988	0.090	0.370	0.077
Total taxa	Poisson	<b>W + M</b>	<b>5</b>	<b>693.438</b>	<b>0.000</b>	<b>0.229</b>	<b>1.000</b>	<b>0.101</b>
		M	4	693.597	0.159	0.212	0.924	0.091
		W + D + M	6	695.179	1.741	0.096	0.419	0.103
		N + W + M	6	695.198	1.760	0.095	0.415	0.102
		D + M	5	695.330	1.892	0.089	0.388	0.093
		N + M	5	695.364	1.925	0.088	0.382	0.092

	Model distribution	Model	df	AIC	$\Delta\text{AIC}$	$w_i$	RL	$R^2$
Family richness	Poisson	<b>W + M</b>	<b>5</b>	<b>600.602</b>	<b>0.000</b>	<b>0.236</b>	<b>1.000</b>	<b>0.068</b>
		M	4	601.069	0.467	0.187	0.792	0.055
		D + W + M	6	602.487	1.885	0.092	0.390	0.069
		N + W + M	6	602.526	1.924	0.090	0.382	0.068

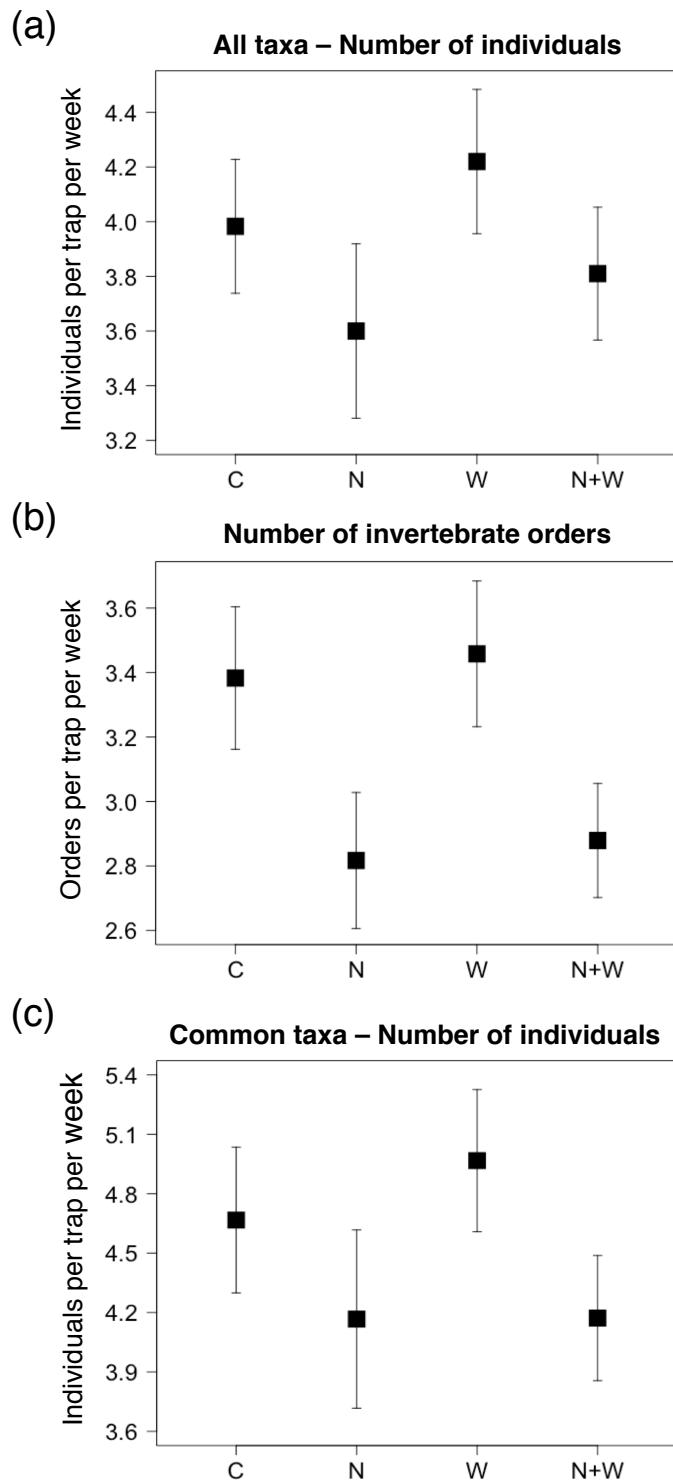
**Table 5.3** Average parameter estimates (mass loss g AFDM) with standard errors (SE) of the top models for total individuals or taxa of all taxa, common taxa only, and beetle taxa only. Significant parameters are in bold. Parameter term abbreviations are water additions (W), nutrient additions (N), distance from stream edge (D), and month of capture (M). The relative importance (RI) of each model and the number of models the parameter is in for each trial is given. Interactions are indicated with an asterisk (\*).

	Parameter	Estimate	SE	z	p	RI	# models
<b>All taxa</b>							
Total individuals							
	Intercept	1.657	0.105	15.766	<0.001		
	N	<b>-0.117</b>	<b>0.057</b>	<b>2.068</b>	<b>0.039</b>	<b>1.00</b>	<b>6 of 6</b>
	W	0.043	0.056	0.754	0.451	0.23	2 of 6
	D (>1 m)	0.091	0.073	1.244	0.213	0.44	3 of 6
	M (Jul)	0.111	0.070	1.575	0.115	0.29	2 of 6
	M (Aug)	0.106	0.070	1.505	0.132	0.29	2 of 6
Total taxa							
	Intercept	1.344	0.087	15.474	<0.001		
	N	-0.103	0.066	1.548	0.122	0.58	4 of 6
	W	0.056	0.066	0.854	0.393	0.29	3 of 6
	M (Jul)	0.138	0.082	1.678	0.093	0.37	3 of 6
	M (Aug)	0.124	0.082	1.509	0.131	0.37	3 of 6
Order richness							
	Intercept	1.026	0.102	9.983	<0.001		
	N	<b>-0.184</b>	<b>0.074</b>	<b>2.481</b>	<b>0.013</b>	<b>1.00</b>	<b>3 of 3</b>
	W	0.018	0.073	0.244	0.807	0.21	1 of 3
	D (>1 m)	0.003	0.092	0.035	0.972	0.20	1 of 3
	M (July)	<b>0.223</b>	<b>0.094</b>	<b>2.350</b>	<b>0.019</b>	<b>1.00</b>	<b>3 of 3</b>
	M (Aug)	<b>0.331</b>	<b>0.092</b>	<b>3.580</b>	<0.001	<b>1.00</b>	<b>3 of 3</b>
<b>Common taxa</b>							
Total individuals							
	Intercept	1.387	0.116	11.880	<0.001		
	N	<b>-0.145</b>	<b>0.061</b>	<b>2.353</b>	<b>0.019</b>	<b>1.00</b>	<b>3 of 3</b>
	W	0.031	0.061	0.506	0.613	0.17	1 of 3
	D (>1 m)	0.121	0.080	1.503	0.133	0.61	2 of 3
	M (Jul)	0.138	0.077	1.781	0.075	1.00	3 of 3
	M (Aug)	<b>0.195</b>	<b>0.076</b>	<b>2.549</b>	<b>0.011</b>	<b>1.00</b>	<b>3 of 3</b>

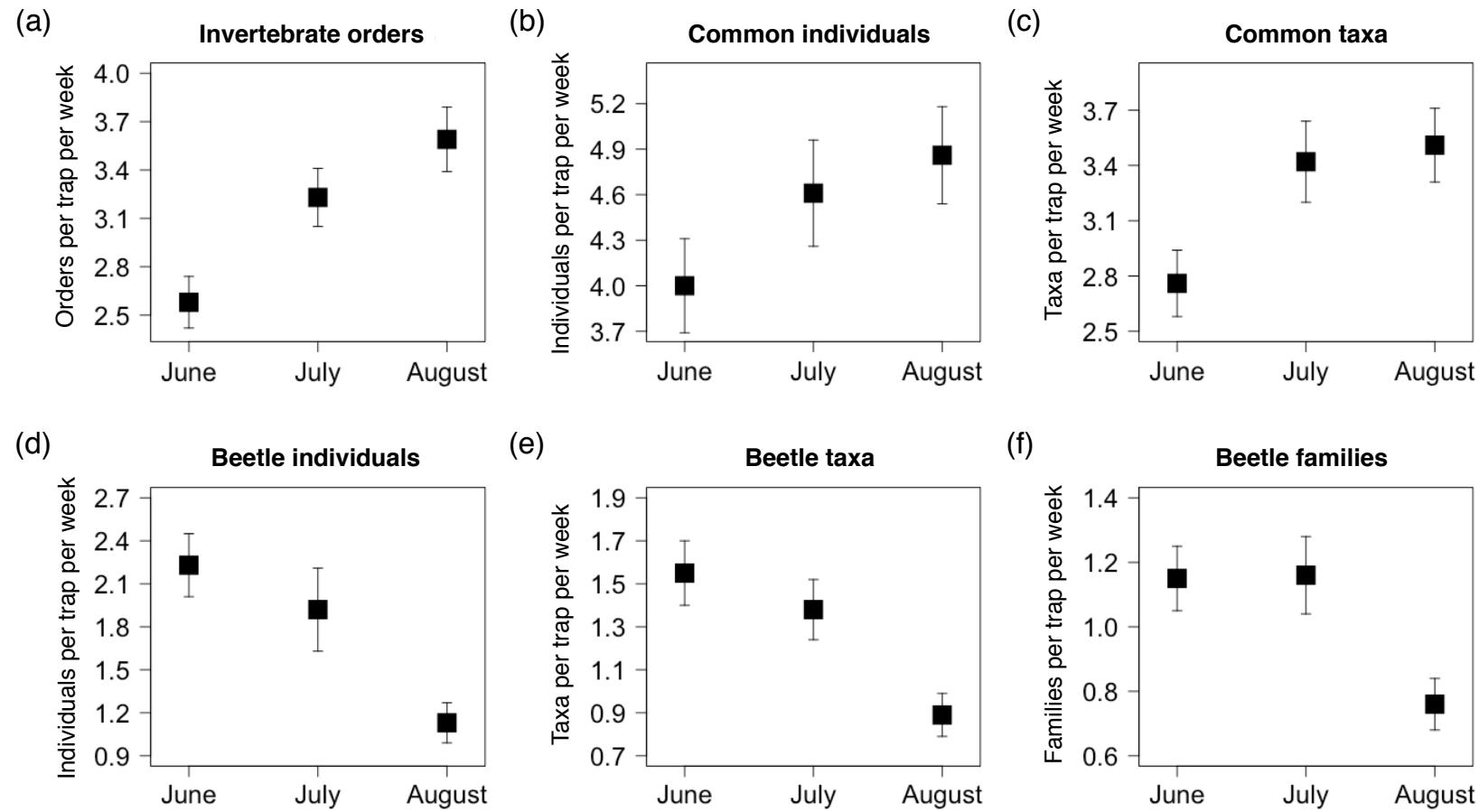
Total taxa	Intercept	1.034	0.095	10.820	<0.001		
	N	-0.117	0.072	1.611	0.107	0.62	3 of 5
	W	0.059	0.072	0.811	0.417	0.29	2 of 5
	D (> 1 m)	0.041	0.092	0.446	0.656	0.13	1 of 5
	<b>M (Jul)</b>	<b>0.213</b>	<b>0.091</b>	<b>2.317</b>	<b>0.020</b>	<b>1.00</b>	<b>5 of 5</b>
	<b>M (Aug)</b>	<b>0.242</b>	<b>0.091</b>	<b>2.655</b>	<b>0.008</b>	<b>1.00</b>	<b>5 of 5</b>
<b>Beetle taxa</b>							
Total individuals	Intercept	0.752	0.145	5.166	<0.001		
	N	-0.015	0.133	0.109	0.913	0.12	1 of 5
	W	0.182	0.132	1.373	0.170	0.42	2 of 5
	D (> 1 m)	0.060	0.168	0.355	0.722	0.24	2 of 5
	M (Jul)	-0.193	0.153	1.259	0.208	1.00	5 of 5
	<b>M (Aug)</b>	<b>-0.609</b>	<b>0.169</b>	<b>3.577</b>	<b>&lt;0.001</b>	<b>1.00</b>	<b>5 of 5</b>
Total taxa	Intercept	0.375	0.129	2.894	0.004		
	N	0.056	0.115	0.484	0.628	0.22	2 of 6
	W	0.170	0.116	1.459	0.144	0.51	3 of 6
	D (> 1 m)	0.075	0.148	0.506	0.613	0.22	2 of 6
	M (Jul)	-0.117	0.132	0.885	0.376	1.00	6 of 6
	<b>M (Aug)</b>	<b>-0.559</b>	<b>0.150</b>	<b>3.722</b>	<b>&lt;0.001</b>	<b>1.00</b>	<b>6 of 6</b>
Family richness	Intercept	0.064	0.144	0.443	0.658		
	N	0.035	0.128	0.273	0.785	0.14	1 of 4
	W	0.202	0.129	1.559	0.119	0.68	3 of 4
	D (> 1 m)	0.055	0.164	0.335	0.738	0.14	1 of 4
	M (Jul)	0.008	0.148	0.057	0.955	1.00	4 of 4
	<b>M (Aug)</b>	<b>-0.416</b>	<b>0.166</b>	<b>2.495</b>	<b>0.013</b>	<b>1.00</b>	<b>4 of 4</b>



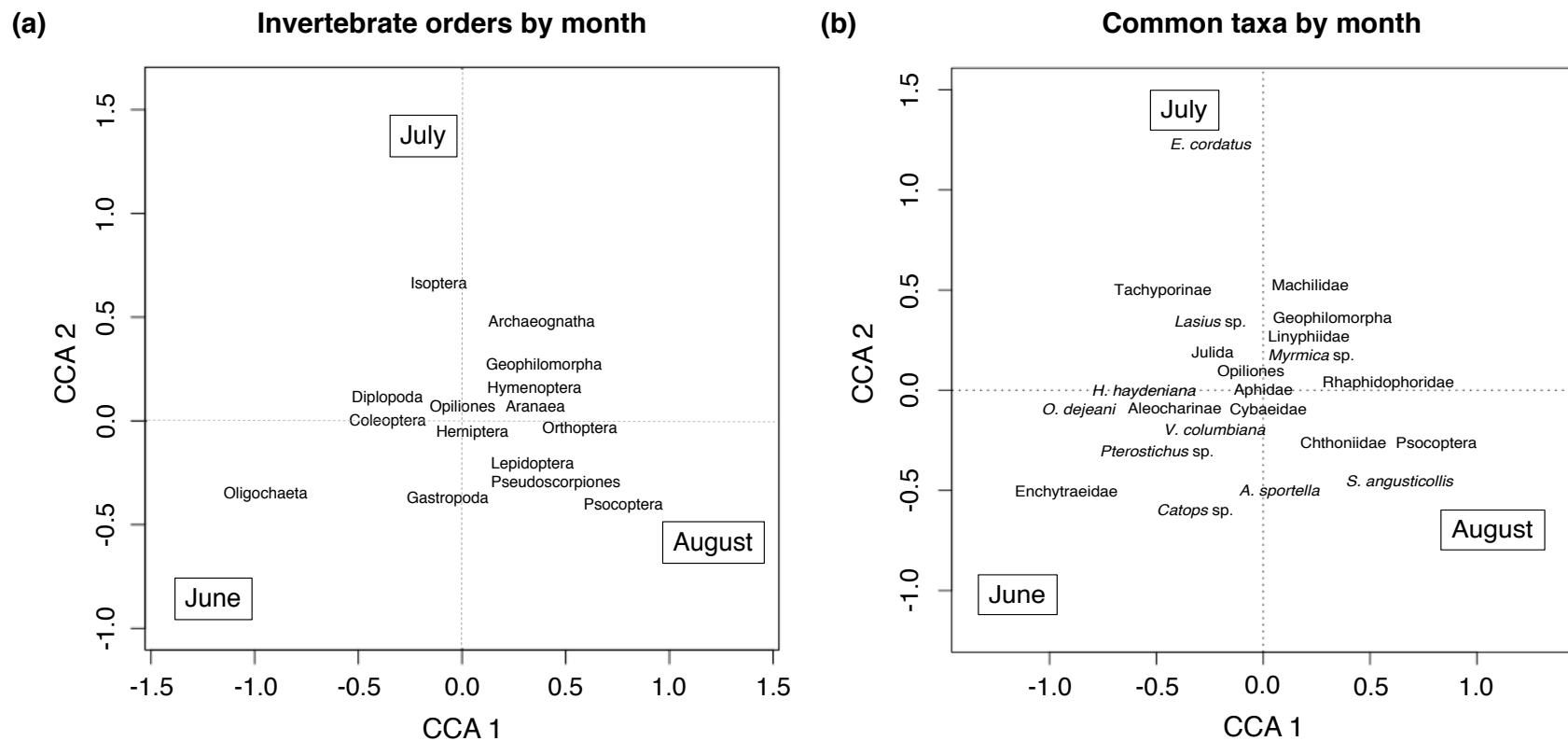
**Figure 5.1** Diagram of pitfall trap setup (drawn to scale). The cover board was perched 15 cm above the collection cup. A total of 20 pitfall traps with this design were placed at each site. Note that the collection cup and portions of the wooden dowel supports were underground (soil is shaded).



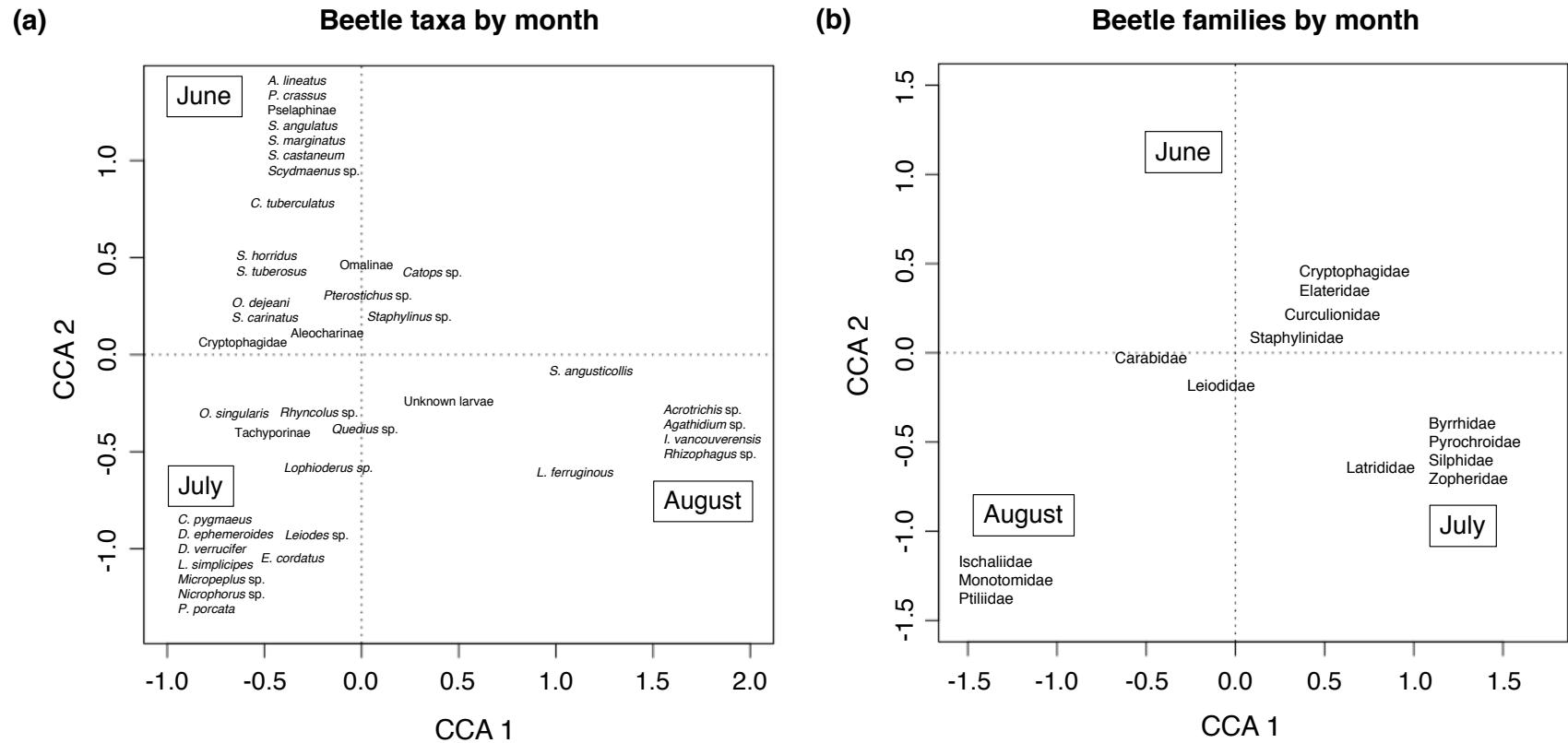
**Figure 5.2** Average ( $\pm 1$  S.E.) number of individuals captured per trap per week for (a) all captured invertebrate taxa, (b) invertebrate orders, and (c) common taxa for each treatment. Treatments are: control (C), nutrient additions (N), water additions (W), water and nutrient additions (N+W). Averages are across sites and months, and calculated from the raw data. Note y-axis values differ for each graph and do not begin at zero.



**Figure 5.3** Average ( $\pm 1$  S.E.) number of orders, taxa, or families caught per trap by month for (a) all invertebrate orders, (b and c) common taxa, and (d, e and f) beetle taxa. Note y-axes differ for each graph and do not begin at zero.



**Figure 5.4** Canonical correlation analysis (CCA) for (a) invertebrate orders and (b) common taxa by month. Names of taxa and months are centered over their CCA coordinates on graphs. Full species names can be seen in Table 5.1.



**Figure 5.5** Canonical correlation analysis (CCA) for (a) beetle taxa and (b) beetle families by month. Names of taxa and months are centered over their CCA coordinates on graphs. Full species names can be seen in Table 5.1.

## **Chapter 6: Main findings, implications, and future directions**

### **6.1 Overview**

The aim of my thesis was to experimentally determine how moisture, nutrients, and distance from stream limit rates of leaf litter decomposition and patterns of terrestrial invertebrate abundance and diversity in riparian zones near headwater streams. This was accomplished by fulfilling five main objectives in Chapters 2 through 5.

**Objective 1** was to review the mechanisms specific to riparian areas that are possible contributors to the diversity of riparian invertebrates. I accomplished this objective through a literature review in Chapter 2, which identified and discussed the following five mechanisms: disturbance by flooding and drying events, elevated nutrient and water availability, microclimate gradients, heightened microhabitat diversity and primary production, and unique food resources. I also discussed how these mechanisms change with distance from the stream (lateral gradients) and position within a catchment (longitudinal gradients). **Objective 2** was to experimentally determine whether water, nutrients, or distance from stream (alone or in combination) limit early-stage mass loss of red alder leaf litter in riparian forests surrounding headwater streams in the mesic, coastal climate of southwestern British Columbia. This objective was achieved in Chapter 3 by conducting four red alder litterbag trials where litter was placed between 1 and 40 m from the stream edge, and treated with water, nutrients, or both at four headwater riparian sites. **Objective 3** was to measure small-scale differences in air T, RH, and VPD at five distances between 1 and 40 m from the stream edge, and to determine whether these factors varied with distance from stream during winter and summer periods. I accomplished this objective in Chapter 3 by using data loggers to monitor these three microclimate parameters during winter

(December 2012 to January 2013) and summer (July to August 2013). **Objective 4** was to experimentally determine whether water, nutrients, or distance from stream (alone or in combination) limit early-stage mass loss of western red cedar leaf litter in riparian forests surrounding headwater streams in the mesic coastal climate of southwestern British Columbia. This objective was achieved in Chapter 4 by conducting three western red cedar litterbag trials using a design similar to my red alder experiment, where litter was placed between 1 and 40 m from the stream edge, and treated with water, nutrients, or both at four headwater, riparian sites. **Objective 5** was to experimentally determine whether terrestrial invertebrate abundance, taxonomic richness, and community composition are influenced by water, nutrients, distance from stream, or month of capture (alone or in combination). This objective was accomplished in Chapter 5 by capturing ground-dwelling invertebrates in pitfall traps between June and August 2013 using the same design and treatments as Chapters 3 and 4.

## 6.2 Main findings

Water additions were the primary factor influencing red alder leaf litter mass loss in Chapter 3. Water additions increased mass loss from 2 to 5% across all four trials. Additions of water were only made during the summer season when precipitation levels were lowest, and loggers at my sites recorded higher average daily air temperatures and lower average daily RH during this period (Chapter 3, Figure 3.6). Calculated values of VPD were also higher during this period. The effect size of water additions on red alder mass loss was smaller than I had anticipated, though I did not have any quantitative predictions as no previous study had examined the role of experimental watering in red alder decomposition. Zukswert and Prescott (2017) quantified mass loss through leaching, but this was determined by soaking leaves for 24

hours—my leaves were never inundated. Clein and Schimel (1994) and Schimel et al. (1999) examined the effect of weekly water additions during summer months on paper birch litter in a birch forest near Fairbanks Alaska, but they only examined microbial biomass and respiration, not mass loss rates. Even though the effect size of water additions was small, this result demonstrates that water is a limiting factor to red alder leaf litter decomposition during the drier summer months at my sites. It also shows that water additions can affect rates of decomposition even in a mesic ecosystem that receives on average 2900 mm of precipitation annually (Kiffney and Richardson 2010).

Nutrient additions increased mass loss of western red cedar leaf litter by 7% during the June 2013 to January 2014 trial in Chapter 4. The other two trials, which differed in duration and began in January 2013 when nutrient additions coincided with high precipitation and low average daily temperatures, showed no effect of nutrient additions on mass loss. Several studies have analyzed western red cedar leaf litter decomposition (Harmon et al. 1990, Keenan 1993, Keenan et al. 1996, Bryant et al. 1998, Moore et al. 1999, Preston and Trofymow 2000, Trofymow et al. 2002, Parton 2007), but there are no studies to my knowledge that have examined red cedar mass loss in riparian forests. In addition, my experiment and that of Prescott (1995) appear to be the only two studies which examined the direct effects of nutrient additions on western red cedar leaf litter mass loss. The positive result of nutrients on mass loss in my June 2013 to January 2014 trial was in contrast to Prescott (1995), who saw no effect of nutrient additions on a mix of western red cedar, western hemlock, and Douglas-fir leaf litter within the first 18 months of decomposition. My study is the first to suggest that nutrient additions may increase western red cedar early-stage mass loss, though this effect is likely dependent on

seasonal differences in temperature, precipitation, and activity levels of microbial and detritivore communities (see Chapter 4, Section 4.5 for details).

In Chapter 5, nutrient additions were associated with lower abundance of invertebrates and lower numbers of invertebrate orders collected in pitfall traps between June and August 2013. Water additions and distance from stream did not influence invertebrate abundance or taxonomic richness in my pitfall trap experiment. A few studies have examined terrestrial invertebrate diversity in riparian habitat near low-order or headwater streams (see Rykken et al. 2007b, Foster and Claeson 2011, Hagar et al. 2012, Foster and Ziegelmuth 2013). My analysis adds to this body of literature on terrestrial invertebrate communities in headwater riparian zones, and is the first to my knowledge to determine how these riparian invertebrate communities respond to experimental manipulations of water and nutrient availability.

I also examined the degree to which temperature, RH and VPD change with distance from stream, and whether these differences vary seasonally. In contrast to results reported by Brossofske et al. (1997) in coastal Washington and Rykken et al. (2007a) in western Oregon, gradients in air temperature, RH and VPD were not detected at my sites. I discovered only small differences between 1 m from the stream and distances further inland. Summer average daily air temperature and VPD (July to August 2013) were 0.3°C and 0.14 kPa lower, respectively, and average daily RH was 3% greater, at 1 m than distances further inland. During winter (December 2012 and January 2013), average daily air temperature at 1 m was 0.1°C higher than distances further away. These results do not show gradual gradients in microclimate parameters with distance from stream as seen in other studies (Brossofske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a), but they do still show that headwater streams can influence riparian

microclimate, even if that influence is spatially restricted to within 1 m from the stream edge and change seasonally.

The results of my experiments reveal which factors limit decomposition rates of leaf litter for two tree species, both of which are common to riparian zones near headwater streams in the coastal Pacific Northwest and integral to riparian nutrient cycles in this region (Richardson 1992, Keenan et al. 1993, Hibbs and Bower 2001, Edmonds and Tuttle 2010, Jackrel and Wooton 2014). These results also offer a detailed look at the variety of invertebrate taxa occupying headwater riparian zones and how these taxa respond to small-scale manipulations of nutrients and water. This thesis advances our understanding of headwater riparian zones and contributes to the broader picture of variation in leaf decomposition in riparian areas and terrestrial diversity along river networks.

## 6.3 Ecological implications

### 6.3.1 Climate change and forest harvesting may influence rates of decomposition

Decomposing red alder leaf litter rapidly releases high amounts of N into coniferous riparian soils, enhancing the availability of mineralizable N to microbial communities and plants (Lavery et al. 2004, Edmonds and Tuttle 2010). As red alder is a N-fixing species, it can increase soil N content (Binkley et al. 1992, Binkley et al. 1994, Compton et al. 2003, Perks et al. 2012) and can return nitrogen to the soil in large quantities through its leaf litter: average returns of N in red alder stands through litterfall reach approximately  $100 \text{ kg ha}^{-1} \text{ y}^{-1}$  (Tarrant et al. 1969, Gessel and Turner 1974, Radwan et al. 1984), whereas coniferous stands only return about  $36 \text{ kg ha}^{-1} \text{ y}^{-1}$  (Tarrant et al. 1969). Primary production is limited by N and P in western red cedar-western hemlock forests of coastal southern British Columbia (Tarrant 1951, Feller 1977, Feller

and Kimmins 1984, Prescott et al. 1993a). Conifer leaf litter is generally lower in N than red alder and releases N slowly during decomposition (Harmon et al. 1990, Perakis et al. 2012). Red alder growing in riparian conifer stands can influence nutrient cycles by contributing immediate releases of N during early-stage decomposition of its leaf litter (Lavery et al. 2004, Edmonds and Tuttle 2010, Perakis et al. 2012). This N can add to total mineralizable N in forest soils and be assimilated by plants in N-limited soils (Lavery et al. 2004, Edmonds and Tuttle 2010, Perakis et al. 2012).

In Chapter 3, I discovered that water is a limiting factor to decomposition of red alder leaf litter in headwater riparian zones during the summer period. Potential implications of this result for nutrient cycling in coniferous, riparian forests exist in light of climate change and forest harvesting. The effects of climate change in regulating red alder decomposition is unclear. Climate projections for the coastal PNW predict an increase in mean annual precipitation over the next century (Romero-Lankoa et al. 2014). Total precipitation for each trial positively influenced mass loss of red alder leaf litter in my experiments, so projected increases in mean annual precipitation for this region could increase annual mass loss rates of red alder litter (see Zhang et al. 2008, Portillo-Estrada et al. 2016 for a general overview on the effect of mean annual precipitation on leaf litter decomposition). But climate models also predict longer periods in summer without rain, with an increased potential for summer droughts as summer maximum temperatures are expected to rise (Romero-Lankoa et al. 2014). Lower snowfall and earlier peak flows from snowmelt, combined with higher evaporation of moisture from soils, are likely to reduce water availability in riparian zones during summer (Bennett et al. 2012, Romero-Lankoa et al. 2014). Lower water availability during future summer periods and increasing frequency of summer droughts are likely to decrease decomposition rates of red alder leaf litter during this

period, though this decrease may be small as watering increased mass loss by only 2 to 5% across the four trials in my experiment. As red alder leaf litter is a good source of mineralizable N (Lavery et al. 2004, Edmonds and Tuttle 2010, Perakis et al. 2012), changes in its decomposition caused by declines in summer moisture could influence N cycling in riparian systems where alder grows during this period (see Santonja et al. 2015 and Zhou et al. 2018 for examples of reductions in precipitation influencing litter decomposition N dynamics). Though these predictions are based on my results, climate change can also cause variability in factors such as atmospheric CO<sub>2</sub>, air and soil temperature, and microbial or detritivore activity which could all influence decomposition rates (e.g., Chen et al. 2001, Rouifed et al. 2010, Ott et al. 2012). Future studies will need to take these factors and their potential interactions into account to determine how climate change scenarios will influence red alder decomposition and its role in N cycling in riparian systems.

Red alder decomposition may also be influenced by forest harvesting. Clearcutting forests or creating large patch cuts can reduce RH and increase solar radiation, surface soil temperature, air temperature, and wind velocity in riparian areas (Brosofske et al. 1997, Rykken et al. 2007a, Moore et al. 2005). For example, clearcut floodplain, hardwood forests showed higher soil temperatures and lower moisture in the top 15 cm of soil compared to partial cut and uncut stands in eastern Texas, USA. This loss of soil moisture can influence leaf litter decomposition. Prescott (1997) documented slower decomposition of western hemlock and lodgepole pine leaf litter in clearcut forests compared to litter placed in old growth stands on Vancouver Island in British Columbia, Canada. This difference was attributed to lower surface soil moisture in clearcuts during summer months (Prescott 1997). There are cases of increased soil moisture following clearcutting due to lower rates of transpiration and greater infiltration of

precipitation in open patches (Hetherington 1987, Adams et al. 1991, Moore et al. 2005), with subsequent increases in mass loss of aspen litter due to leaching (Prescott et al. 2000). However, greater infiltration could also result in higher moisture in deeper soil near groundwater flow paths, and not necessarily in surface soils. This was the case in Edwards and Ross-Todd (1983), who measured drier soils at 3 cm below the ground surface but wetter soils at 15 cm deep in clearcut hardwood forests in Tennessee, USA. Therefore, effects of forest harvesting on moisture availability in riparian zones during summer months will depend on local factors such as soil permeability, depth to groundwater, and size of the harvested patches.

### **6.3.2 Forest fertilization and effects on western red cedar decomposition and riparian invertebrate abundance**

According to my results from Chapter 4, mass loss rates of western red cedar leaf litter may be either enhanced or unaffected at forest sites where nutrient additions have been added to improve primary productivity. Ammonium nitrate and triple superphosphate are inorganic compounds that are commonly used as fertilizers in cedar-hemlock forests in the coastal PNW (Miller and Tarrant 1983, Barclay and Brix 1984, Weetman et al. 1989, Binkley et al. 1999, Bennet et al. 2003). Based on the results from my June 2013 to January 2014 trial, it is possible that early-stage mass loss of western red cedar litter could occur more rapidly in managed forests where these compounds have been applied, potentially leading to faster rates of nutrient mineralization (Gosz 1981, Vitousek et al. 1982). Nutrient additions may also lead to lower rates of western red cedar during late-stage decomposition. Studies examining late-stage decomposition of coniferous litter treated with nutrient additions found slower rates of late-stage mass loss after 18 months (Berg et al. 1982, Berg et al. 1987, Gill and Lavender 1983, Berg and

Tamm 1991, Prescott 1995, Knorr et al. 2005). As my decomposition trials only lasted between five and 12 months, it is possible that negative effects of nutrient additions on late-stage western red cedar leaf litter decomposition could have occurred if my trials had lasted for longer periods, as was seen by Prescott (1995). As with red alder, slower rates of western red cedar decomposition could lead to higher carbon storage in fertilized coniferous riparian forests.

The fertilization of managed riparian forests may also negatively influence terrestrial invertebrate communities based on my results. The lower abundance of invertebrates in pitfall traps at stations with nutrient additions is consistent with previous studies: lower abundances of enchytraeid and lumbricid worms (Huhta 1967, Marshall 1974, Lohm et al. 1977), nematodes (Sohlenius and Wasilewska 1984), springtails and mites (Lohm et al. 1977) have been documented in coniferous forests treated with inorganic fertilizers. Declines in invertebrate abundance with nutrient additions may reduce the rates of ecosystem functions they provide (Prather et al. 2013). However, reductions in invertebrate abundance in previous studies were generally short-lived (one to two years; Huhta et al. 1964, Lohm et al. 1977), with some studies even showing a general increase in invertebrate abundance two to three years after nutrient additions were made due to a greater pool of resources from increased primary productivity and litterfall (Huhta et al. 1964, Lohm et al. 1977). Thus, nutrient additions in riparian forests may cause short-term reductions in terrestrial invertebrate abundance, but this effect is not likely to last and may even be reversed over time.

The number of invertebrate orders was also lower in traps at stations with nutrient additions compared to stations without nutrients. Geophilomorpha (centipedes), Hymenoptera (ants), Isopoda, and Lepidoptera (caterpillars) were captured less often at stations with nutrient additions than stations without nutrients. If declines in invertebrate orders that were negatively

affected by nutrient additions in my study occurred in forests fertilized with ammonium nitrate and triple superphosphate, the ecological functions these orders provide could be negatively affected. Centipedes and ants are soil-dwelling predators that contribute to soil mixing and aeration, and herbivorous caterpillars grow into pollinating butterflies and moths (Prather et al. 2013). Isopods fragment and consume leaf litter, distributing faecal pellets with high levels of bacteria and fungi through litter layers on the forest floor and contribute to nutrient cycling (Hassall et al. 1987). Declines in ecosystem functions due to the changes in the abundance of the orders may be unlikely, though, as other invertebrate orders that perform similar functions showed no difference in abundance in pitfall traps with or without nutrient additions in my study. For example, snails (Gastropoda) and millipedes (Diplopoda) fragment and consume leaf litter, and worms (Oligochaeta) mix soils through their movement (Cárcamo et al. 2000, De Oliveira et al. 2010, Prather et al. 2013); these three orders showed similar abundances in pitfall traps with and without nutrient additions. This functional redundancy in the invertebrate community may therefore buffer the ecosystem functions they provide from the potential consequences of anthropogenic nutrient additions (Lawton and Brown 1993, Rosenfeld 2002). We should continue to examine how different fertilization practices influence forest invertebrate communities, and track changes in abundance and diversity along with any changes in the rate of functions they perform to limit potential negative consequences of fertilization regimes (see Section 6.5.4 for details).

### **6.3.3 Minimal effects of distance from stream on leaf litter decomposition and riparian microclimate**

The significance of distance from stream in explaining mass loss of leaf litter and invertebrate abundance and diversity in my experiments differed from previous studies. Distance from stream was included in generalized linear mixed-effects models for red alder and western red cedar mass loss, as well as pitfall trap abundance and diversity. The only significant effect by distance across all of these experiments occurred in the June 2013 to January 2014 western red cedar trial. Mass loss of western red cedar leaf litter was 7% greater at 40 m than 1 m from the stream edge, a result that was contrary to what I hypothesized based on previous studies (Merritt and Lawson 1980, Peterson and Rolfe 1982, Shure et al. 1986, Hutchens and Wallace 2002). Distance from stream did not influence invertebrate abundance or diversity as was seen in other studies (Devito et al. 2004, Kato et al. 2004, Bates et al. 2007, Rykken et al. 2007b, Hagar et al. 2012). My results and these previous studies' results show that there is variability in the response of terrestrial invertebrate communities to distance from stream. When compared to Rykken et al. (2007a, b), my results also show variability in the extent of headwater riparian microclimates and the response of riparian invertebrates to moisture availability within geographic regions like the coastal PNW. Many studies describing climate change and its potential effects on hydrology, vegetation, or wildlife (including invertebrate) distributions often treat the coastal PNW as a homogenous region (e.g., Mote et al. 2003, Mote and Salathé 2010, Wu et al. 2012, Rogers et al. 2015, Vano et al. 2015). Such studies are useful for visualizing potential long-term trends across the region, but do not recognize the local differences that can influence ecosystem functions and wildlife communities in riparian zones (e.g., Sheridan et al. 2003, Rykken et al. 2007b). Forest managers often use criteria like rates of nutrient cycling, the presence of microclimate gradients,

and the presence or absence of wildlife to determine whether riparian buffers are effective in reducing the impact of forest harvesting on riparian and stream communities (e.g., Brosowske et al. 1997, Cockle and Richardson 2003, Rykken et al. 2007a, Rykken et al. 2011). By identifying factors that are limiting to rates of ecological processes or patterns in the abundance and diversity of wildlife, we can recognize how these rates or patterns vary geographically, which ultimately advances our understanding of how these ecosystems function.

## 6.4 Limitations

This thesis provides evidence that water and nutrient availability, and possibly distance from stream, can influence decomposition rates and invertebrate communities in headwater riparian zones. However, generalization of the results to all riparian areas is not prudent. Rates of environmental functions are often context-dependent. Riparian areas occur across the globe, in tundra, temperate forests, tropical rainforests, and in desert regions. The influence of factors such as moisture and nutrient availability on decomposition and nutrient cycling or invertebrate diversity and abundance will depend on regional climate, local geography, and size of the waterbody (e.g., Malanson 1993, Williams 2006, García-Palacios et al. 2013, García-Palacios et al. 2016, Tiegs et al. 2019). Because of this heterogeneity, conclusions from this thesis should be limited to small-order or headwater riparian zones in temperate forests.

Litterbags, which are simple and inexpensive to construct, have been used over the past 80 years for analyzing the decomposition of leaf litter (Falconer et al. 1933, Bocock and Gilbert 1957, Wider and Lang 1982, Kampichler and Bruckner 2009), but there are some issues with their use that should be considered. Confined leaf litter can trap moisture between leaves, leading to greater mass loss than unconfined litter (Virzo De Santo et al. 1993, Hutchinson et al. 1990).

Fragmentation of leaves from handling during setup and removal from sites is also more likely with litterbags made from larger mesh (Bradford et al. 2002); this type of loss can be limited through careful handling and ensuring that every litterbag goes through the same assembly and collection processes in the laboratory and the field, as was done in this study. Greater mass loss of litter through fragmentation or removal by invertebrates can also occur in litterbags with a larger mesh size, and this larger mesh does not generally retain small litter fragments (< 8 mm in my experiments) which could be weighed and included in mass loss calculations (Bradford et al. 2002, Prescott 2010). These issues can lead to potential overestimation of mass loss that may not accurately reflect decomposition trends of unconfined litter (Wider and Lang 1982). However, large mesh litterbags were the most appropriate method for measuring mass loss based on my research questions. The advantage of large mesh is more of the litter in each bag is exposed to ambient conditions such as precipitation, the additions of water and nutrients, and is available to a wider array of detritivorous taxa (Bradford et al. 2002). Because of these benefits, Lecerf (2017) suggested that litterbags made with larger mesh provide a more realistic approximation of decay rates than litterbags with finer mesh. Additionally, my study examined mass loss of leaf litter in a field setting, and loss of mass through fragmentation or consumption by invertebrates is part of the natural decomposition process (Anderson 1973, Bokhorst and Wardle 2013). The inclusion of small litter fragments or invertebrate faeces in mass loss calculations is important when determining the role of invertebrates in decomposition or determining the fate of foliar C or N in decomposing leaves (e.g., Bradford et al. 2002, Prescott 2010), but these questions were beyond the scope on my research.

As with litterbags, pitfall traps also are used with certain caveats. Pitfall traps are a commonly used method of sampling invertebrate populations in terrestrial environments as they

are efficient, inexpensive, and useful for capturing large numbers of individuals and taxa (Spence and Niemelä 1994, Ward et al. 2001). When compared with hand-searches, pitfall traps reflect similar patterns in community composition and can capture greater total numbers of invertebrates (Lin et al. 2005). However, such traps tend to capture large-bodied, fast-moving taxa (Spence and Niemelä 1994, Zaller et al. 2015). Given the 1 m<sup>2</sup> size of the treated stations at each trap location, and the 5 m distances between transects, it is possible that such mobile species may have merely been captured while wandering through my sites and thus did not reflect significant, small-scale effects of water or distance from stream. Yet it is also possible that my sites did offer ample resources and sampled individuals were spending the majority of time there. Sampling by sweep netting or vacuuming (Doğramacı et al. 2011, Anderson et al. 2013) would complement the passive sampling used in this study and by Rykken et al. (2007b). Such active sampling, when used in conjunction with experimental manipulations like water and nutrient additions, would provide a more comprehensive survey of the invertebrate community in headwater riparian zones, and may reveal whether the abundance and diversity of smaller and less mobile taxa are influenced by water and nutrient additions to a greater degree than larger, more mobile invertebrates.

Lastly, the spatial scale of my experiment may have influenced the small degree to which water and nutrient additions affected invertebrate communities in my analyses. Mass loss of leaf litter is highly dependent on local conditions; as such, 40 m by 40 m plots and water and/or nutrient additions to 1 m<sup>2</sup> stations were an appropriate scale for the study of decomposition. But in my pitfall trap experiment, most captured invertebrate taxa were highly mobile and their movements may have overwhelmed my small-scale manipulations. For example, Rykken et al. (2011) estimated the wingless snail-eating carabids *Scaphinotus angusticollis* (a common species

in my traps) and *S. marginatus* move 10 to 19 m daily in riparian forests. Thus, weekly water additions to 1 m<sup>2</sup> stations may have been on too small a scale to influence the distribution of mobile species that can move several metres per day, and may be why I saw no significant effect of water additions on terrestrial invertebrate abundance or diversity. As previously mentioned, active sampling using sweep netting or vacuuming (or even taking soil cores) can target smaller, less mobile taxa which may respond to such small-scale differences in water and nutrient availability.

## 6.5 Key questions for future research

### 6.5.1 Changes in terrestrial riparian invertebrate communities along lateral and longitudinal gradients in a river network

My literature review (Chapter 2) identified two areas of research on factors limiting riparian invertebrate diversity that need to be addressed: (1) the effect of gradients in nutrient availability on invertebrate productivity and diversity; and (2) the occurrence and extent of microclimate gradients in larger floodplains. Riparian zones are often described as nutrient sinks and chemical buffers for stream habitat (Gregory et al. 1991, Naiman and Décamps 1997), and as such, investigations into how nutrients directly or indirectly alter invertebrate diversity should be pursued. How might invertebrate communities change as streams become larger and alluvial deposition expands, thereby potentially increasing the availability of nutrients and heterogeneity of resources? If there are cases where nutrient availability decreases with distance from the stream, do herbivore or detritivore communities subsequently decrease with distance from stream because of potentially lower primary productivity and lower quality food resources?

Further research on microclimate gradients in riparian zones is also needed. Most of the current literature on riparian microclimate focuses on either small, first- to third-order streams (e.g., Brosowske et al. 1997, Moore et al. 2005) or descriptions of extreme conditions on exposed gravel bars of larger rivers (e.g., Wenninger and Fagan 2000, Bates et al. 2007, Tonolla 2010, Steward et al. 2011). It is unclear how microclimate gradients change with increasing stream size, landscape position, and across regional climates; it is also currently unknown whether lateral gradients in microclimate along larger rivers are linear. Larger rivers with heterogeneous floodplains may have more complex, patchy microclimates that do not necessarily produce linear gradients in parameters such as soil moisture or air temperature. Gravel bars can experience strong winds and high daytime temperatures (Henshall et al. 2011); periodic inundation often creates vegetation zonation, which generates various associated microhabitats for multiple species (e.g., Antvogel and Bonn, Bates et al. 2007, Lambeets et al. 2009). A few studies documenting microclimate parameters on exposed riverine sediments along larger rivers suggest these parameters do not exist as linear gradients extending from the stream (Antvogel and Bonn, Bates et al. 2007, Lambeets et al. 2009). Research that details how microclimate parameters like soil moisture, air temperature, solar radiation and wind velocity in floodplains of larger rivers, as well as whether nutrients exist as lateral gradients through floodplains, are needed to help determine how these parameters differ in riparian habitat along larger rivers compared to small streams. Further work on nutrient availability and microclimate gradients across floodplains and throughout the river network will help clarify how these mechanisms work to assemble and maintain unique invertebrate assemblages in the riparian zone.

## **6.5.2 Terrestrial riparian invertebrates, climate change, and invasive species**

There are several other research avenues in riparian invertebrate ecology related to climate change, land use, and invasive species. Climate change is predicted to increase the frequency and intensity of disturbances such as drought events in many regions of the world (Kundzewicz et al. 2007). As rivers dry because of drought, microclimate gradients may become more spatially restricted, as may the extent of riparian plant communities. Dry riverbeds can be novel habitat to riparian species that shift their range when waters recede (Corti and Datry 2016). However, dry riverbeds can also support communities that differ from those in the riparian zone (Steward et al. 2011), and they can even be distinct among riparian communities with different hydrological regimes (Moody and Sabo 2016). One question to consider in areas where dry riverbeds support terrestrial communities that are distinct from the riparian community is to what extent these riverbed communities interact with their riparian counterparts, and what this interaction looks like when flooding occurs and the riverbed becomes uninhabitable or when flows recede. Similarly, as riparian plant communities can respond to the changing water regimes (Nilsson and Svedmark 2002), we should also consider how invertebrate assemblages are linked to vegetation composition and community dynamics through time and space. This latter question also relates to changes brought about by land use, such as forest harvesting and stream bank modification. Increasing urbanization or agricultural activities that withdraw water from the ecosystem can also cause differences in riparian plant community composition, which may result in changes to riparian invertebrate communities (Santos 2010). Therefore, mechanisms supporting unique riparian communities are likely to be altered with climate and land-use change, and we should be monitoring these changes.

As climates and land use change, we should also further consider how riparian invertebrate communities will respond to the arrival of invasive species. Some researchers have begun to investigate how changes to riparian plant communities, such as the introduction of the giant reed *Arundo donax* (e.g., Maceda-Viega et al. 2016), have influenced terrestrial riparian invertebrates. Invasive plants can directly affect invertebrate communities by altering the microclimate around streams, changing the structure of riparian soils or leaf-litter layers, and providing leaves of varying quality for terrestrial herbivores and detritivores (Maceda-Viega et al. 2016). Other changes can be more indirect, such as how the abundance of an invasive clam in streams and their subsequent mortality events have provided a benefit to terrestrial scavengers (Novais et al. 2015). The occurrence of invasive species in both terrestrial and aquatic communities is expected to rise with climate change (Nilsson and Berg 2000, Tockner and Stanford 2002, Poff et al. 2011, González et al. 2017, Stella and Bendix 2019), and I therefore suggest continued monitoring in both aquatic and riparian habitats to develop and test hypotheses on how these changes influence riparian invertebrate communities and potential implications for their restoration.

### **6.5.3 Assessing the mechanisms contributing to leaf litter mass loss by water and nutrient additions**

It is clear from my data that water additions during the summer dry period increased mass loss in red alder leaf litter, but the mechanisms by which water enhanced mass loss remains unclear. In the literature, water generally increases decomposition rates by increasing leaching and microbial activity (e.g., Nykvist 1963). Leaching can cause approximately 10% mass loss of red alder leaves over 24 hours (Zukswert and Prescott 2017), and previous research has shown

that leachate can stimulate microbial activity in soils below, leading to further mass loss (Polunin 1984, Xiong and Nilsson 1997, Nielsen and Ball 2015, Datry et al. 2018). As microbial activity was not monitored in my experiments, there are several questions that future research can address based on my results. First, does watering riparian soils during the summer dry period increase microbial biomass and activity? This question analyzes the role of only water in promoting microbial activity during periods when precipitation is low, temperatures are elevated, and VPD increases (see Figure 3.6), all of which may reduce soil moisture. It would also assess background levels of soil microbial activity during this period. Field experiments with red alder could ask whether watered red alder leaf litter supports greater microbial biomass during the summer dry period compared to un-watered leaf litter. In addition, field or laboratory microcosm experiments using riparian soils could ask whether red alder leachate stimulates microbial growth and respiration in underlying soils compared to water additions without leachate. These questions would be able to test the hypothesis that water increases mass loss of red alder litter by enhancing microbial respiration.

An indirect mechanism by which water may increase red alder mass loss is by increasing consumption and fragmentation by detritivores due to higher microbial growth (Seastedt 1984, Xiong and Nilsson 1997, Cárcamo et al. 2000). Invertebrate abundance and diversity in red alder litterbags were not assessed in my study. Field experiments using red alder leaf litterbags could test whether litter watered during the summer dry season supports higher numbers of detritivorous invertebrates compared to un-watered litter. Laboratory feeding trials like that of Cárcamo et al. (2000) might examine whether detritivorous invertebrates prefer consuming litter that had been previously conditioned in the field with water additions during the summer over conditioned, un-watered litter. When combined with investigations into the effect of watering on

microbial biomass, these questions would help to determine if water increases mass loss indirectly by increasing detritivore activity.

Western red cedar litter primarily responded to nutrient additions, though this was only in the June 2013 to January 2014 trial. Nutrient additions likely increase mass loss by enhancing microbial activities in the soil (Berg and Matzner 1997, Carreiro et al. 2000, Hobbie 2000, Perakis et al. 2012). In my experiment with western red cedar leaf litter, N and P were added in combination, and as such I am unable to say whether one or both increased mass loss. Additionally, I did not monitor microbial biomass or detritivorous invertebrate abundance on western red cedar leaf litter in my study so I cannot say whether nutrients increased mass loss through microbial or invertebrate activity. Future experiments should examine the effects of each element on red cedar mass loss, and whether microbial biomass and respiration respond to nutrient additions. Does western red cedar leaf litter mass loss respond positively to additions of only N or only P? Does varying the ratio of N:P influence the rate of red cedar mass loss? Is microbial biomass and respiration higher on western red cedar leaf litter with nutrient additions than litter without nutrient additions? Collecting data on microbial biomass throughout the trial may also help confirm whether pauses in mass loss following leaching seen by Zukswert and Prescott (2017) are due to increased growth of microbial communities (as suggested by C.E. Prescott). Finally, is detritivore abundance higher in litter with nutrient additions compared to litter without nutrient additions? These questions could help to disentangle whether N or P is driving increases in mass loss for litter with nutrient additions, and to determine whether nutrients increase mass loss directly via microbial activity and indirectly via detritivore consumption.

It was unclear why western red cedar leaf litter lost 7% more mass at 40 m from the stream than 1 m in my June 2013 to July 2014 trial. This result is in contrast to the majority of decomposition studies in riparian habitat. Greater soil moisture and nutrient availability have been documented closer to the stream edge in riparian habitat (Shure and Gottschalk 1985, Groffman et al. 1992, Lite et al. 2005, Clinton et al. 2010, Weibel et al. 2011), and these differences are potential drivers of greater decomposition in litter near the stream than further away (Merritt and Lawson 1980, Peterson and Rolfe 1982, Shure et al. 1986). Previous studies in the Malcolm Knapp Research Forest on similar-sized streams to my sites have documented higher moisture in soils at the stream edge than further away (Feller 1977, Chin 2007), but lateral gradients in soil nutrients have not been examined. One suggestion for future research is to determine whether differences in soil N and P occur between soils near the stream edge and those further away near headwater streams in this region. Additionally, future studies should determine whether western red cedar leaf litter placed at greater distances from the stream edge show higher microbial biomass and respiration than litter placed at the stream edge. If differences in soil nutrient availability and microbial activity on red cedar leaf litter occur with distance from stream, this could help to explain why mass loss was greater in western red cedar litter located 40 m from the stream than 1 m in my study.

Future research on decomposition in riparian zones should also investigate how geographic differences in riparian microclimate influence mass loss of leaf litter. Microclimate gradients did not exist across riparian zones at my headwater sites, and distance from stream was not a significant factor for most of my litter trials. At sites where distinct and gradual microclimate gradients extending from the stream edge into the riparian zone have been documented (Brosofske et al. 1997, Danehy and Kirpes 2000, Rykken et al. 2007a), I would

hypothesize that there would be higher rates of decomposition closer to the stream edge.

However, these previous studies did not consider decomposition, so this hypothesis has not yet been tested at these sites. Examining decomposition in multiple riparian headwater sites across the coastal PNW would provide determine how this ecosystem function varies geographically in a region that is often characterized as homogenous (e.g., Mote et al. 2003, Mote and Salathé 2010, Wu et al. 2012, Rogers et al. 2015, Vano et al. 2015).

Changes in the distribution of soil microarthropods and detritivores with distance from stream may also influence leaf litter decomposition rates. Clinton et al. (2010) studied mass loss of red maple leaf litter near small streams in North Carolina, USA, and observed faster mass loss in leaf litter placed at 10 and 30 m from the stream than in leaf litter placed on the stream bank. After ruling out potential effects of soil moisture and nutrients on decomposition with distance from stream, they suggested differences in mass loss could be due to the patchy and clumped distribution of resources and microarthropods that occur in forest soils (Clinton et al. 2010). Based on the results from my experiment, future studies could ask: Are the abundance and diversity of soil microarthropods and detritivores greater at 40 m from the stream edge than 1 m? Does detritivorous invertebrate abundance differ on litter placed close to the stream than litter placed further away? Distance from stream can also be associated with changes in variables including canopy cover, solar radiation, and vegetation composition (e.g., Day and Monk 1974, Pabst and Spies 1998, Moore et al. 2005), so future research should also determine how these characteristics vary with distance and include them in models for leaf litter decomposition to evaluate their effect. Decomposing leaves in laboratory microcosms with soils sampled at different distances from the stream may help to determine whether characteristics of the soil itself or in situ parameters like vegetation composition are influencing patterns in mass loss with

distance from stream (see Prescott 1996 for microcosm design used to examine the influence of soils from different forest types on the decomposition of leaf litter).

#### **6.5.4 Effects of nutrient additions on invertebrate abundance and order richness**

My results showed that pitfall traps at stations with nutrient additions collected fewer individuals per trap than pitfall traps at stations without nutrients, though the effect size was small, but why nutrients reduced invertebrate trap abundance is unclear. One of the first questions that future studies should ask is whether this decline in abundance resulted from the death of individuals that made contact with the fertilizer or whether they merely avoided stations with nutrient additions. It is possible individuals were not lost from the community, but merely elsewhere in the site. The following questions should be examined based on my results: Do declines in pitfall trap abundance occur at stations treated with only ammonium nitrate or only triple superphosphate? This question can help determine whether each compound is associated with declines in abundance or if one compound is driving the decline. Second, do declines in invertebrate abundance stem from the death of individuals or behavioural avoidance of plots with nutrient additions? Treating larger plots ( $> 1 \text{ m}^2$ ) with either ammonium nitrate, triple superphosphate, or both and using both pitfall traps and hand searching methods could help determine the reason for a decline in pitfall trap abundance and which compound may be responsible. Finally, are declines in invertebrate abundance greater in plots treated with dry crystallized compounds compared to those treated with dissolved compounds? If invertebrates avoid stations with nutrient additions because crystallized nutrients are toxic or increase osmotic pressure in the soil (Blake 1961, Lohm et al. 1977, Springett and Syers 1984, Büinemann et al. 2006, Gomiero 2013, Roberts 2014), additions of dissolved compounds to plots may limit

declines in abundance. These questions could help determine whether each compound is detrimental to riparian invertebrate communities, and whether the method of application can limit declines in invertebrate abundance.

### **6.5.5 Final thoughts**

My thesis determined how water and nutrient additions and distance from stream influence mass loss rates of leaf litter and patterns of invertebrate abundance and diversity in headwater riparian areas. These suggested directions for future research offer pathways to expand our knowledge of how these mechanisms operate in riparian zones. Such research will enhance our understanding of riparian ecology and the factors contributing to the diversity of riparian communities and the ecosystem functions they perform. It will also reveal how geographic and climatic differences influence how rates of decomposition respond to differences in moisture and nutrient availability, or the extent to which microclimate gradients occur in riparian zones and how these gradients influence decomposition rates and invertebrate communities. Given the importance of riparian zones to wildlife and humans alike, and their globally threatened status due to anthropogenic activity and changing climates, this research provides information that resource managers and conservation biologists can use to better understand the functions and their limiting factors in these unique ecosystems.

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## Appendix A: Tables

This appendix presents a series of tables that provide information on physical aspects of my four study sites as well as numbers of litterbags by treatment and distance from stream analyzed for Chapters 3 and 4.

**Table A.1** Average elevation above stream and standard error (SE) by distance from bankfull edge of stream across all four sites.

Distance (m)	Elevation above stream (m)	SE
1	0.3	0.0
5	1.2	0.1
10	2.0	0.2
20	2.6	0.2
40	4.0	0.7

**Table A.2** Average elevation above stream and standard error (SE) by distance from bankfull edge of stream for each site.

Site	Distance (m)	Elevation above stream (m)	SE
East	1	0.4	0.0
	5	2.0	0.2
	10	3.7	0.3
	20	4.5	0.3
	40	4.1	0.6
GH	1	0.2	0.1
	5	0.7	0.1
	10	1.2	0.1
	20	2.8	0.3
	40	9.0	0.3
Griffith	1	0.3	0.1
	5	1.3	0.1
	10	1.8	0.2
	20	1.7	0.2
	40	-1.8	0.6
Mike	1	0.2	0.1
	5	0.8	0.1
	10	1.1	0.1
	20	1.5	0.2
	40	4.6	0.3

**Table A.3** Number of red alder litterbags per treatment for each trial.

Treatment	Aug 2012 – Nov 2012	Aug 2012 – Aug 2013	Jan 2013 – Aug 2013	June 2013 – Jan 2014
Control	54	52	52	53
Nutrients added	36	36	38	38
Water added	37	39	38	36
Nutrients and water added	36	36	38	34

**Table A.4** Number of red alder litterbags per distance from stream for each trial.

Distance from stream (m)	Aug 2012 – Nov 2012	Aug 2012 – Aug 2013	Jan 2013 – Aug 2013	June 2013 – Jan 2014
1	34	34	35	33
5	32	33	36	31
10	31	32	27	33
20	32	35	32	31
40	34	29	36	33

**Table A.5** Number of red alder litterbags per treatment and distance per trial.

Treatment	Distance from stream (m)	Distance			June 2013 – Jan 2014
		Aug 2012 – Nov 2012	Aug 2012 – Aug 2013	Jan 2013 – Aug 2013	
Control	1	12	11	11	12
	5	11	9	12	11
	10	10	11	7	10
	20	10	12	10	10
	40	11	9	12	10
Nutrients added	1	8	7	8	7
	5	8	8	8	7
	10	6	7	7	8
	20	6	7	7	8
	40	8	7	8	8
Water added	1	7	8	8	7
	5	7	8	8	8
	10	8	8	7	7
	20	8	8	7	6
	40	7	7	8	8
Nutrients and water added	1	7	8	8	7
	5	6	8	8	5
	10	7	6	6	8
	20	8	8	8	7
	40	8	6	8	7

**Table A.6** Number of western red cedar litterbags per treatment per trial.

Treatment	Jan 2013 – Jan 2014	Jan 2013 – Jun 2013	Jun 2013 – Jan 2014
Control	32	57	44
Nutrients added	29	39	27
Water added	33	37	30
Nutrients and Water added	33	40	32

**Table A.7** Number of western red cedar litterbags per distance from stream for each trial.

Distance from stream (m)	Jan 2013 – Jan 2014	Jan 2013 – Jun 2013	Jun 2013 – Jan 2014
1	22	34	26
5	26	35	24
10	25	34	29
20	29	35	25
40	25	35	29

**Table A.8** Number of western red cedar litterbags per treatment and distance from stream for each trial.

Treatment	Distance from stream (m)	Jan 2013 – Jan 2014	Jan 2013 – Jun 2013	Jun 2013 – Jan 2014
Control	1	3	11	7
	5	6	12	9
	10	6	11	9
	20	9	11	7
	40	8	12	12
Nutrients added	1	6	8	8
	5	6	8	4
	10	5	8	5
	20	7	8	5
	40	5	7	5
Water added	1	7	7	5
	5	7	8	6
	10	6	7	7
	20	7	8	7
	40	6	7	5
Nutrients and water added	1	6	8	6
	5	7	7	5
	10	8	8	8
	20	6	8	6
	40	6	9	7

## Appendix B: Models

This appendix includes:

- **List A:** A set of 16 models used in my statistical analysis for both red alder and western red cedar litterbag trials (Lists A and B).
- **List B:** A set of 40 models for the dataset including all four red alder litterbag trials, in addition to the number of degree-days litterbags were in the field and average daily precipitation for each trial.
- **List C:** A set of 24 models for the dataset including two western red cedar litterbag trials with water additions, and the number of degree-days litterbags were in the field.
- **List D:** A set of five models used for the January 2013 to June 2013 western red cedar trial that did not include water additions.
- **List E:** A set of 24 models used in my analysis of invertebrate abundance and diversity.

**List A)** Set of generalized linear mixed-effects models included in litterbag mass loss analysis for each red alder and western red cedar trial. Asterisks indicate interactions between variables. Nutrient and water additions were set as factors, and indicated by either 0 (no addition made) or 1 (addition made) in the data. Distance from stream was either 1, 5, 10, 20, or 40 m, and was a covariate in the model. Sites included East, GH, Griffith, and Mike Creeks, and site was included as a random factor in all models. Formatting follows generalized linear mixed-effects model notation in R Studio. Models were identical between trials. The dependent variable is mass loss (g AFDM).

1. *Global model:* Nutrients\*Water\*Distance + Nutrients \*Water + Nutrients \*Distance +Water\*Distance + Nutrients + Water + Distance + (1|site)
2. Nutrients \*Water + Nutrients \*Distance +Water\*Distance + Nutrients + Water + Distance + (1|site)
3. Nutrients \*Water + Nutrients \*Distance + Nutrients + Water + Distance + (1|site)
4. Nutrients \*Water + Water\*Distance + Nutrients + Water + Distance + (1|site)
5. Nutrients \*Distance + Water\*Distance + Nutrients + Water + Distance + (1|site)
6. Nutrients \* Water + Nutrients + Water + Distance + (1|site)
7. Nutrients \*Distance + Nutrients + Water + Distance + (1|site)
8. Water\*Distance + Nutrients + Water + Distance + (1|site)
9. Nutrients + Water + Distance + (1|site)
10. Nutrients + Water + (1|site)
11. Nutrients + Distance + (1|site)
12. Water + Distance + (1|site)
13. Nutrients + (1|site)
14. Water + (1|site)
15. Distance + (1|site)
16. *Null model:* 1 + (1|site)

**List B)** Set of generalized linear mixed-effects models included in litterbag mass loss analysis for the dataset that included all red alder trials. Asterisks indicate interactions between variables. Nutrient and water additions were set as factors, and indicated by either 0 (no addition made) or 1 (addition made) in the data. Distance from stream was either 1, 5, 10, 20, or 40 m, and was a covariate in the model. Degree-days and average daily precipitation for a trial are noted as “dd” and “precip”, respectively. No interactions were included with precip. Sites included East, GH, Griffith, and Mike Creeks, and site was included as a random factor in all models. Formatting follows generalized linear mixed-effects model notation in R Studio. Dependent variable is mass loss (g AFDM).

1. *Global model:* Nutrients\*Water\*Distance + Nutrients\*Water + Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + dd + precip + (1|site)
2. Nutrients\*Water + Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + dd + precip + (1|site)
3. Nutrients\*Water + Nutrients\*Distance + Nutrients + Water + Distance + dd + precip + (1|site)
4. Nutrients\*Water + Water\*Distance + Nutrients + Water + Distance + dd + precip + (1|site)
5. Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + dd + precip + (1|site)
6. Nutrients\* Water + Nutrients + Water + Distance + dd + precip + (1|site)
7. Nutrients\*Distance + Nutrients + Water + Distance + dd + precip + (1|site)
8. Water\*Distance + Nutrients + Water + Distance + dd + precip + (1|site)
9. Nutrients + Water + Distance + precip + dd + (1|site)
10. Nutrients + Water + Distance + dd + (1|site)
11. Nutrients + Water + Distance + precip + (1|site)
12. Nutrients + Water + dd + precip + (1|site)
13. Nutrients + Distance + dd + precip + (1|site)
14. Water + Distance + dd + precip + (1|site)
15. Nutrients + Water + Distance + (1|site)
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17. Nutrients + Water + precip + (1|site)
18. Nutrients + Distance + dd + (1|site)
19. Nutrients + Distance + precip + (1|site)
20. Nutrients + dd + precip + (1|site)
21. Water + Distance + dd + (1|site)
22. Water + Distance + precip + (1|site)
23. Water + dd + precip + (1|site)
24. Distance + dd + precip + (1|site)
25. Nutrients + Water + (1|site)
26. Nutrients + Distance + (1|site)
27. Nutrients + dd + (1|site)
28. Nutrients + precip + (1|site)
29. Water + Distance + (1|site)
30. Water + dd + (1|site)
31. Water + precip + (1|site)

- 32. Distance + dd + (1|site)
- 33. Distance + precip + (1|site)
- 34. dd + precip + (1|site)
- 35. Nutrients + (1|site)
- 36. Water + (1|site)
- 37. Distance + (1|site)
- 38. dd + (1|site)
- 39. precip + (1|site)
- 40. *Null model:* 1 + (1|site)

**List C)** Set of generalized linear mixed-effects models included in litterbag mass loss analysis for the dataset that included all red alder trials, and the dataset for western red cedar that included the January 2013 to January 2014. Asterisks indicate interactions between variables. Nutrient and water additions were set as factors, and indicated by either 0 (no addition made) or 1 (addition made) in the data. Distance from stream was either 1, 5, 10, 20, or 40 m, and was a covariate in the model. The number of degree-days (dd) litterbags were in the field was also included as a covariate. No interactions were included with precip. Sites included East, GH, Griffith, and Mike Creeks, and site was included as a random factor in all models. Formatting follows generalized linear mixed-effects model notation in R Studio. Dependent variable is mass loss (g AFDM).

1. *Global model:* Nutrients\*Water\*Distance + Nutrients\*Water + Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + dd + (1|site)
2. Nutrients\*Water + Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + dd + (1|site)
3. Nutrients\*Water + Nutrients\*Distance + Nutrients + Water + Distance + dd + (1|site)
4. Nutrients\*Water + Water\*Distance + Nutrients + Water + Distance + dd + (1|site)
5. Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + dd + (1|site)
6. Nutrients\* Water + Nutrients + Water + Distance + dd + (1|site)
7. Nutrients\*Distance + Nutrients + Water + Distance + dd + (1|site)
8. Water\*Distance + Nutrients + Water + Distance + dd + (1|site)
9. Nutrients + Water + Distance + dd + (1|site)
10. Nutrients + Water + Distance + (1|site)
11. Nutrients + Water + dd + (1|site)
12. Nutrients + Distance + dd + (1|site)
13. Water + Distance + dd + (1|site)
14. Nutrients + Water + (1|site)
15. Nutrients + Distance + (1|site)
16. Nutrients + dd + (1|site)
17. Water + Distance + (1|site)
18. Water + dd + (1|site)
19. Distance + dd + (1|site)
20. Nutrients + (1|site)
21. Water + (1|site)
22. Distance + (1|site)
23. dd + (1|site)
24. *Null model:* 1 + (1|site)

**List D)** List of generalized linear mixed-effects models included in litterbag mass loss analysis for the western red cedar trial January 2013 to June 2013. Water additions were not made in this trial. Asterisks indicate interactions between variables. Nutrient additions were set as a factor, and indicated by either 0 (no addition made) or 1 (addition made) in the data. Distance from stream was either 1, 5, 10, 20, or 40 m, and was a covariate in the model. Sites included East, GH, Griffith, and Mike Creeks, and site was included as a random factor in all models. Formatting follows generalized linear mixed-effects model notation in R Studio. Dependent variable is mass loss (g AFDM).

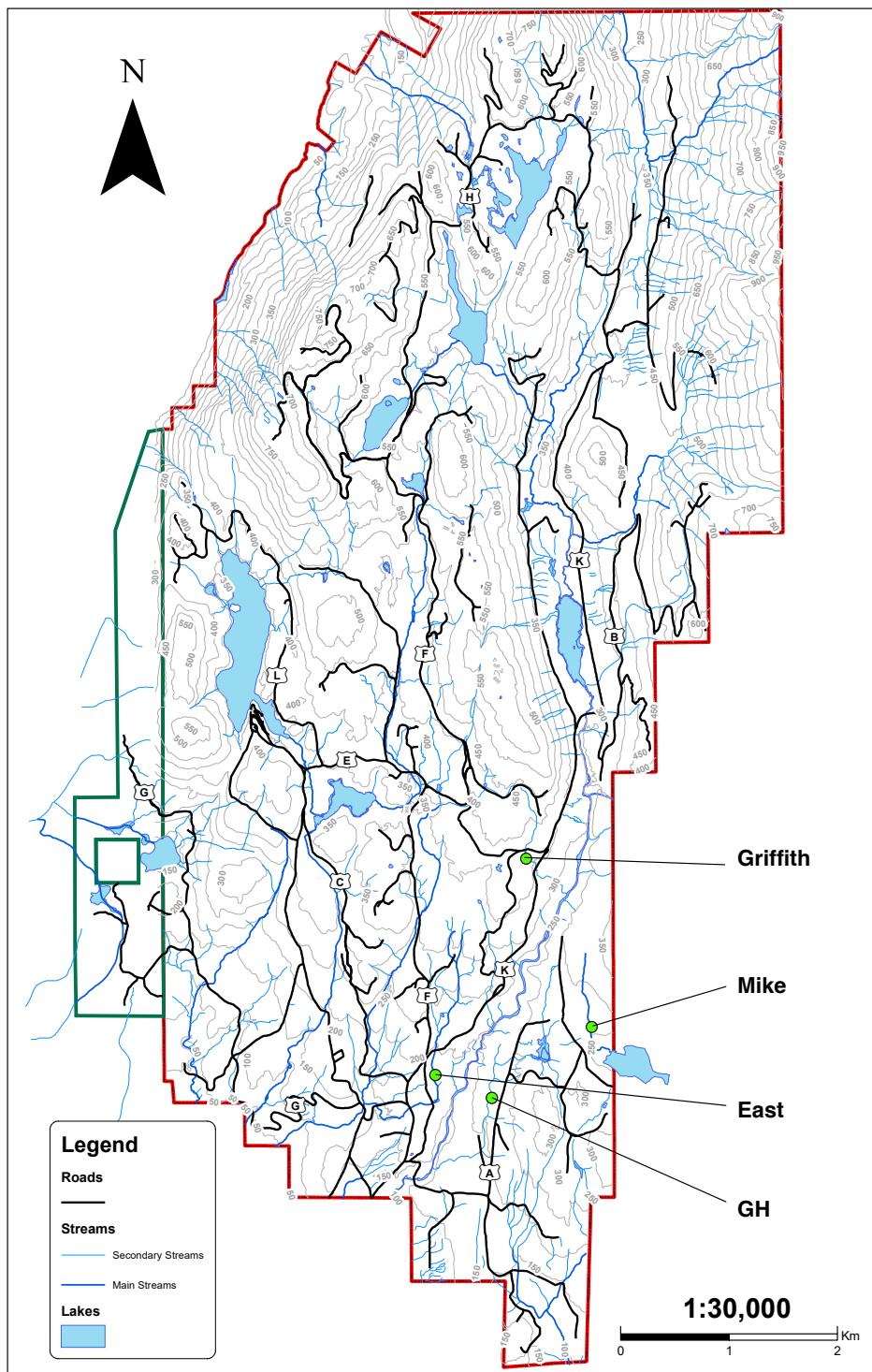
1. *Global model:* Nutrients \* Distance + Nutrients + Distance + (1|Site)
2. Nutrients + Distance + (1|Site)
3. Nutrients + (1|Site)
4. Distance + (1|Site)
5. *Null:* 1 + (1|Site)

**List E)** Set of generalized linear mixed-effects models included taxon abundance and richness analyses for each group. Asterisks indicate interactions between variables. Nutrients and water additions were set as factors, and indicated by either 0 (no addition made) or 1 (addition made) in the data. Distance from stream was either 1, 5, 10, 20, or 40 m, and was a covariate in the models. Months included June, July, and August; no interactions with Month were included in models. Sites included East, GH, Griffith, and Mike creeks, and site was included as a random factor in all models. Formatting follows generalized linear mixed-effects model notation in R Studio. Models were identical between groups, with models for invertebrate orders and beetle families following the same model format below. Dependent variables are number of individuals per trap or number of taxa per trap.

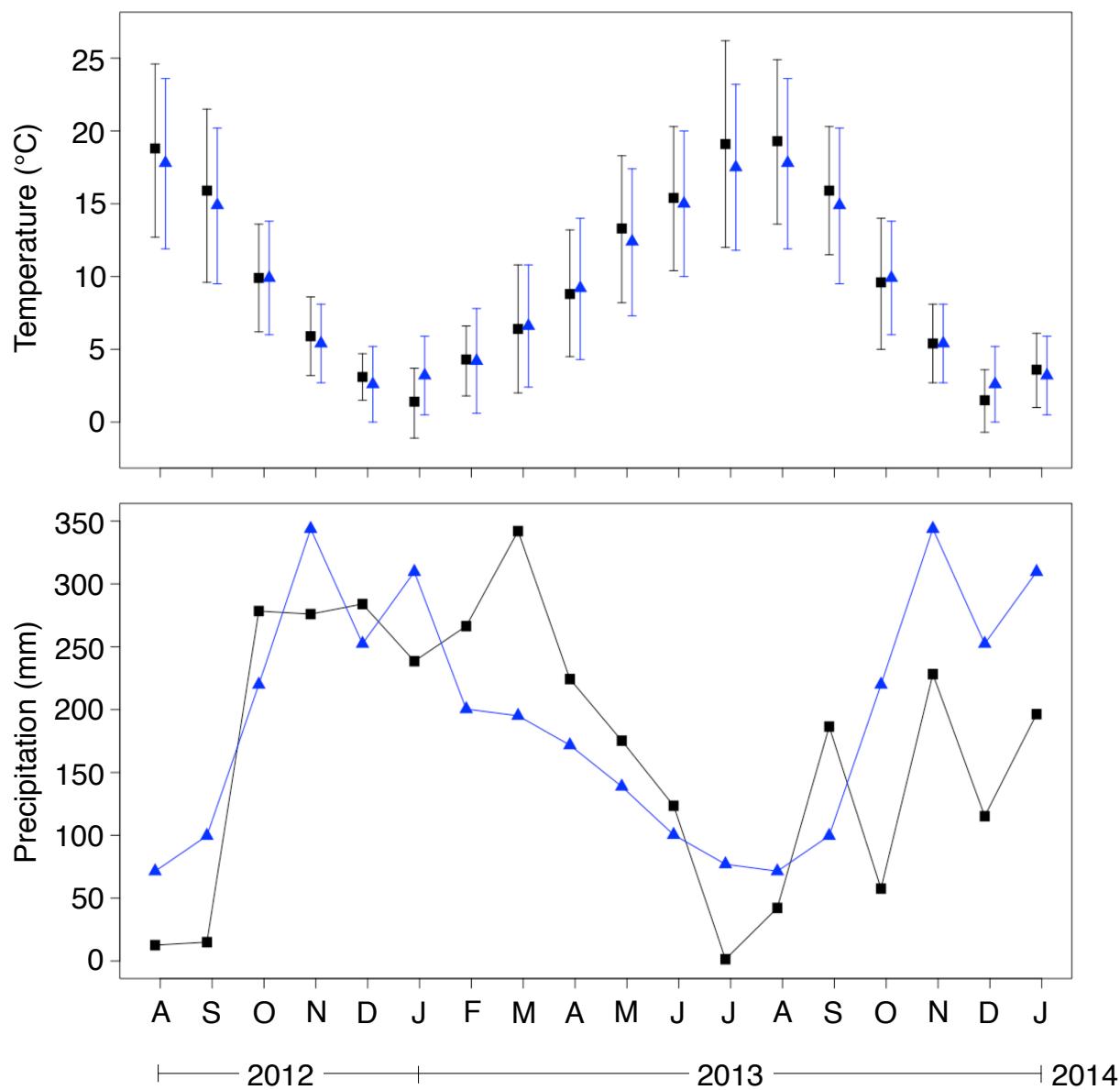
1. *Global model:* Nutrients\*Water\*Distance + Nutrients\*Water + Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + Month + (1|site)
2. Nutrients\*Water + Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + Month + (1|site)
3. Nutrients\*Water + Nutrients\*Distance + Nutrients + Water + Distance + Month + (1|site)
4. Nutrients\*Water + Water\*Distance + Nutrients + Water + Distance + Month + (1|site)
5. Nutrients\*Distance + Water\*Distance + Nutrients + Water + Distance + Month + (1|site)
6. Nutrients\* Water + Nutrients + Water + Distance + Month + (1|site)
7. Nutrients\*Distance + Nutrients + Water + Distance + Month + (1|site)
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9. Nutrients + Water + Distance + Month + (1|site)
10. Nutrients + Water + Distance + (1|site)
11. Nutrients + Water + Month + (1|site)
12. Nutrients + Distance + Month + (1|site)
13. Water + Distance + Month + (1|site)
14. Nutrients + Water + (1|site)
15. Nutrients + Distance + (1|site)
16. Nutrients + Month + (1|site)
17. Water + Distance + (1|site)
18. Water + Month + (1|site)
19. Distance + Month + (1|site)
20. Nutrients + (1|site)
21. Water + (1|site)
22. Distance + (1|site)
23. Month + (1|site)
24. *Null model:* 1 + (1|site)

## **Appendix C: Figures**

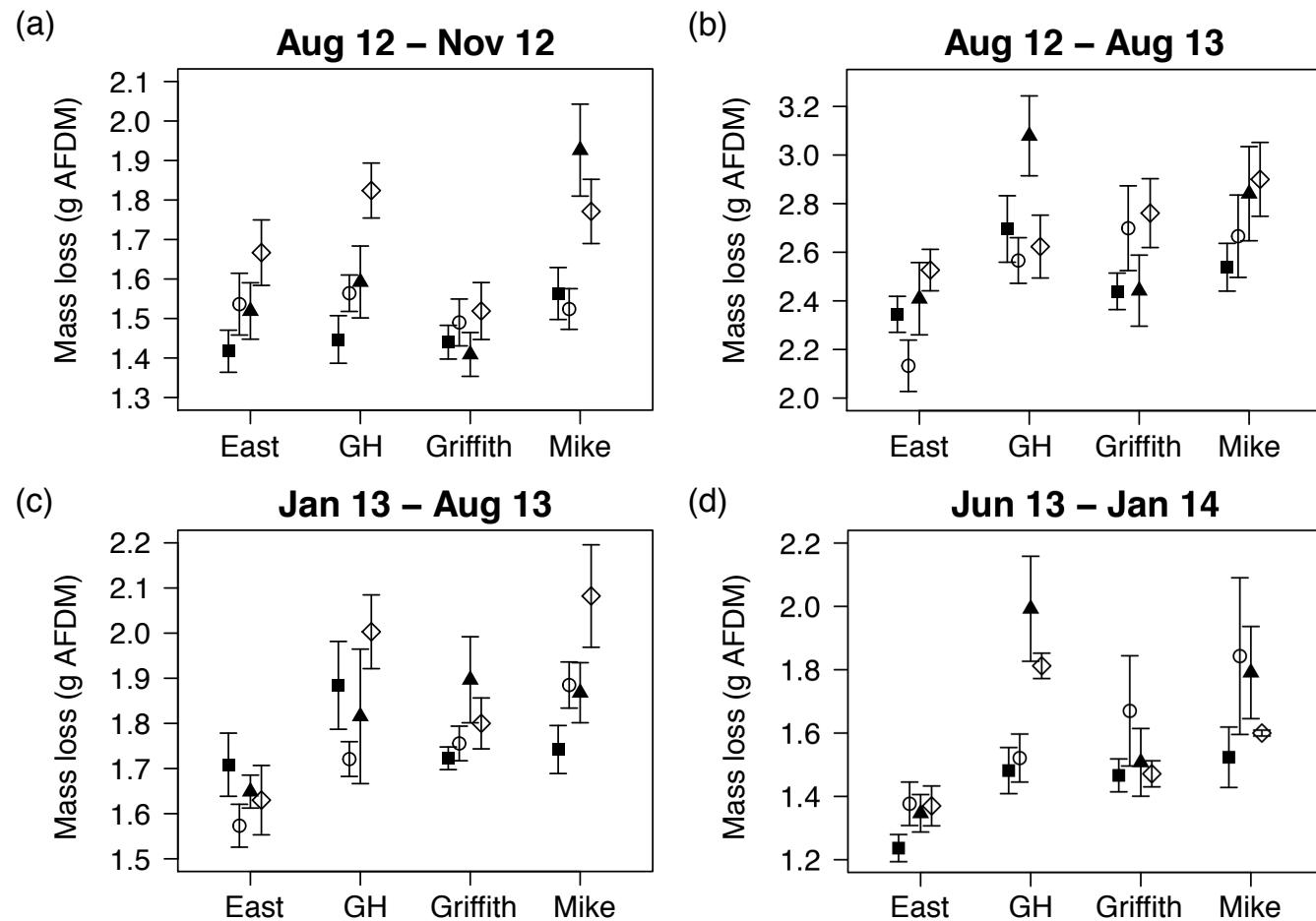
This appendix presents a series of figures that provide supporting information for Chapters 3, 4, and 5. These figures provide information on physical aspects of my four study sites, mass loss of red alder and western red cedar litterbags by site and distance from stream, and numbers of invertebrate taxa captured in pitfall traps by month.



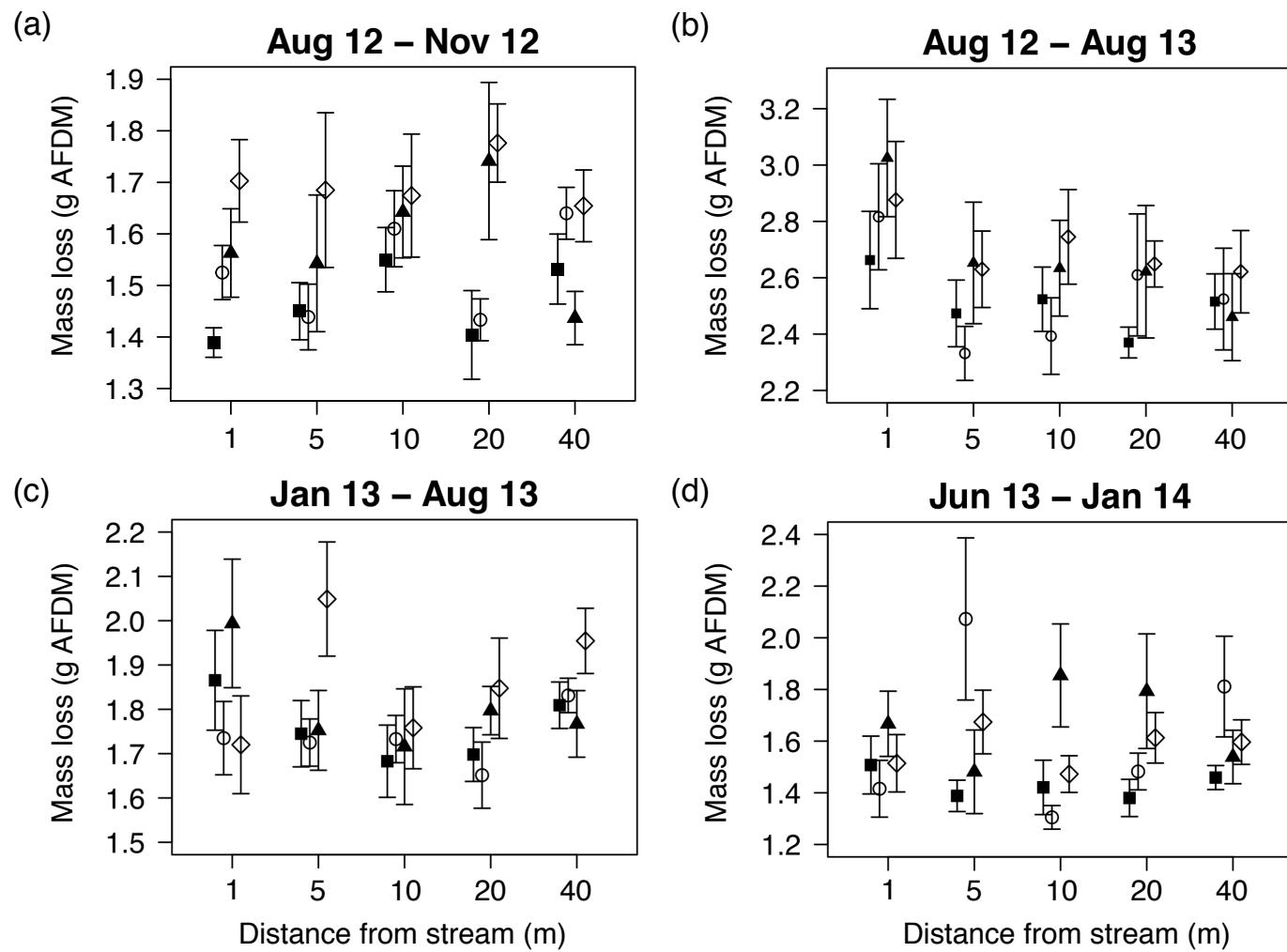
**Figure C.1** Detailed map of my four sites (East, GH, Griffith, and Mike creeks) within the Malcolm Knapp Research Forest in Maple Ridge, British Columbia, Canada. Gray lines show elevation (M.A.S.L.). Red lines show the boundary of the research forest.



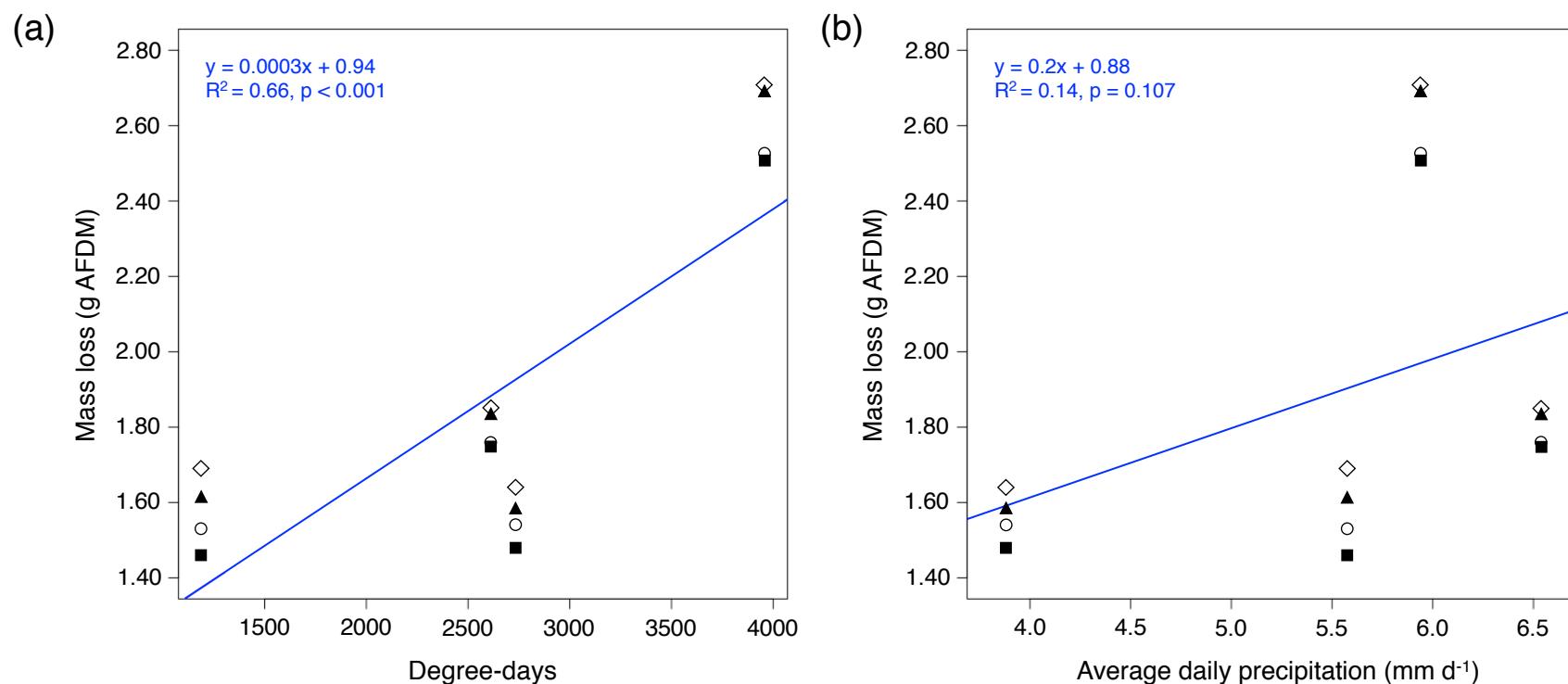
**Figure C.2** Average daily temperature ( $^{\circ}\text{C}$ , with bars representing average maximum and minimum daily temperatures) and average total precipitation (mm) recorded at the Haney RF weather station in the Malcolm Knapp Research Forest. Black squares (■) and lines (—) are data recorded during my study period between August 2012 and January 2014. Blue triangles ( $\blacktriangle$ ) and lines (—) are climate normals for 1981 to 2010 recorded at the Haney RF weather station.



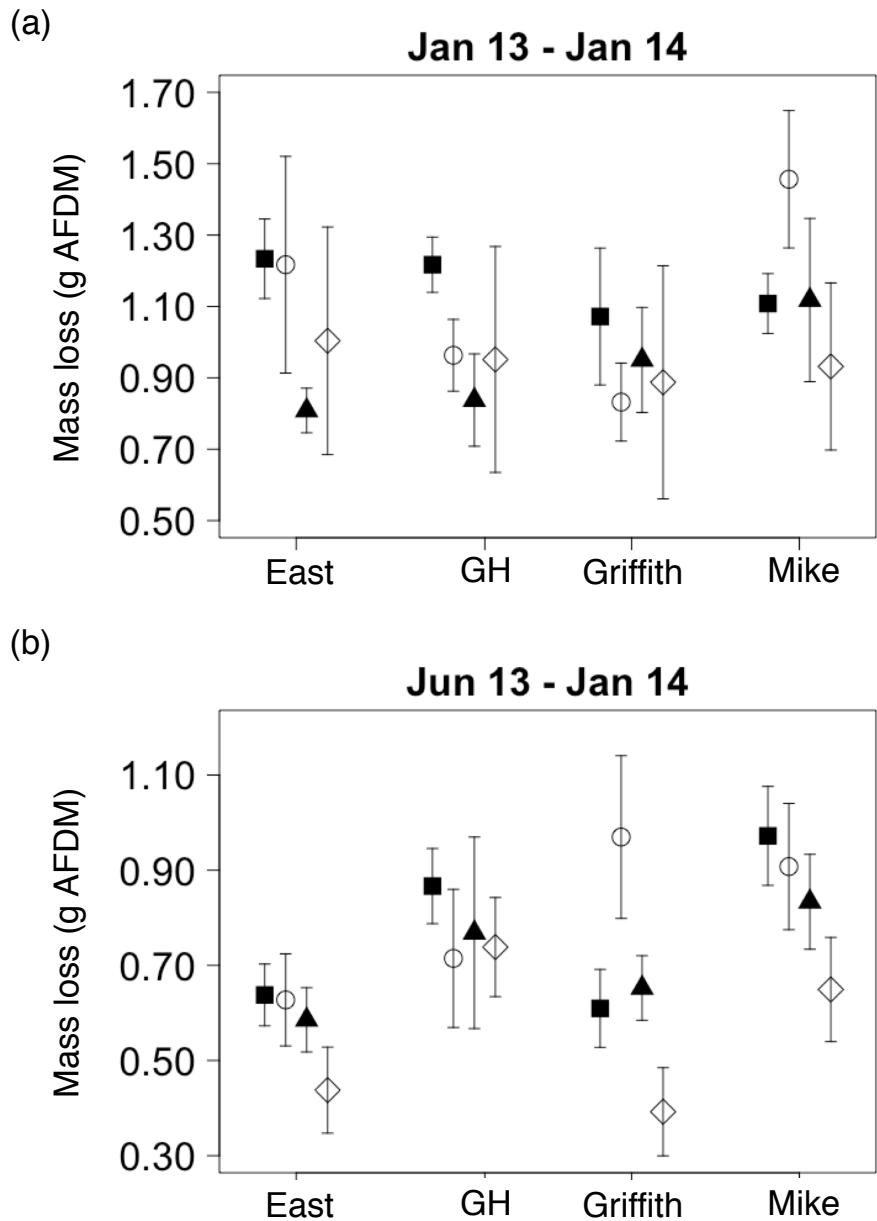
**Figure C.3** Average mass loss (g AFDM  $\pm$  1 S.E.) of red alder leaf litter by treatment (control ■, nutrients added ○, water added ▲, nutrients and water added ◇) for each site in each trial calculated from the raw data. Trials are: (a) August 2012 to November 2012, (b) August 2012 to August 2013, (c) January 2013 to August 2013, (d) June 2013 to January 2014. Note the range of mass loss values differs for each trial, and y-axes do not begin at zero.



**Figure C.4** Average mass loss (g AFDM  $\pm$  1 S.E.) of red alder leaf litter by treatment (control ■, nutrients added ○, water added ▲, nutrients and water added ◇) for each distance from stream edge in each trial calculated from the raw data. Trials are: (a) August 2012 to November 2012, (b) August 2012 to August 2013, (c) January 2013 to August 2013, (d) June 2013 to January 2014. Note the range of mass loss values differs for each trial, and y-axes do not begin at zero.



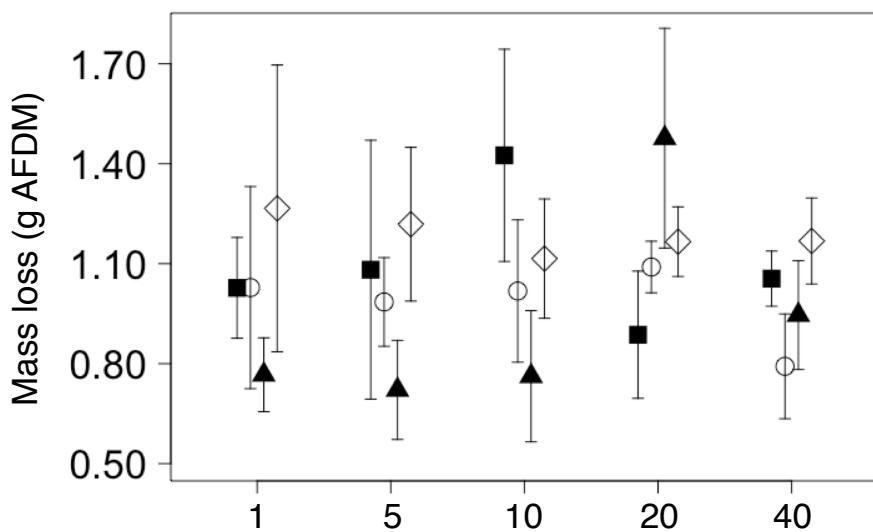
**Figure C.5** Magnified view of average mass loss (g AFDM) of red alder litterbags by treatment (control ■, nutrients added ○, water added ▲, nutrients and water added ◇) as a function of (a) degree-days and (b) average daily precipitation (mm d<sup>-1</sup>) in each trial. Standard error bars were not included due to the close proximity of the points. Note x- and y-axes do not begin at zero.



**Figure C.6** Average mass loss (g AFDM  $\pm$  1 S.E.) of western red cedar leaf litter by treatment (control ■, nutrients added ○, water added ▲, nutrients and water added ◇) for each site in each trial calculated from the raw data. Trials are: (a) January 2013 to January 2014, (b) June 2013 to January 2014. Note the range of mass loss differs for each trial, and y-axes do not begin at zero.

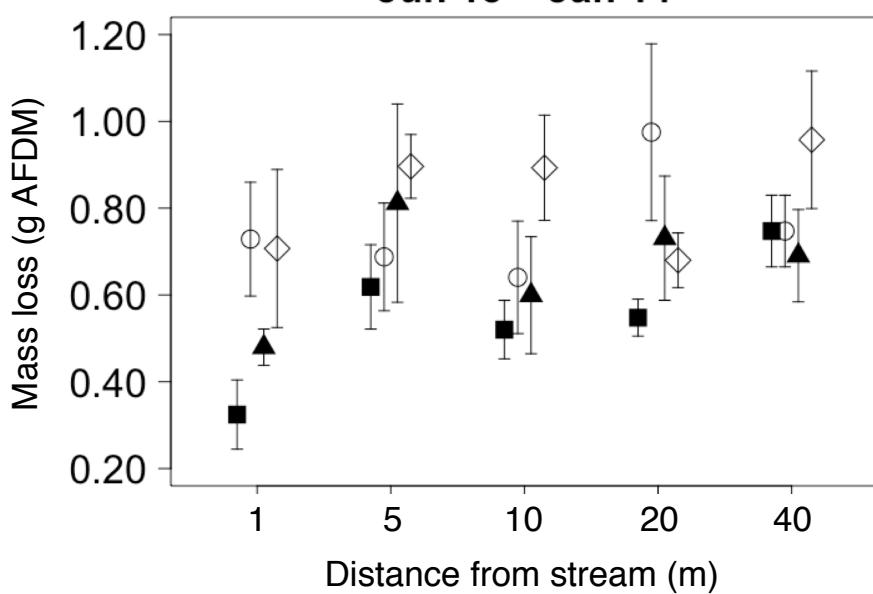
(a)

Jan 13 – Jan 14

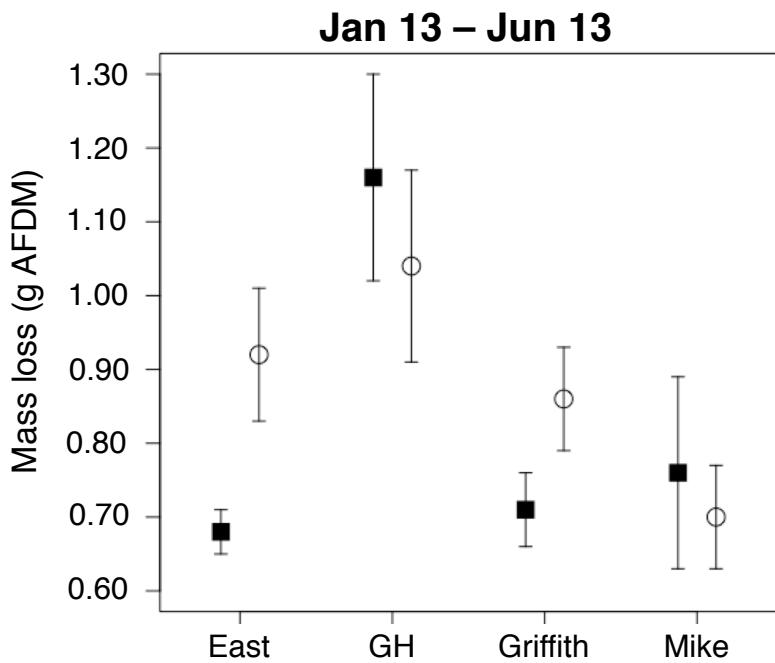


(b)

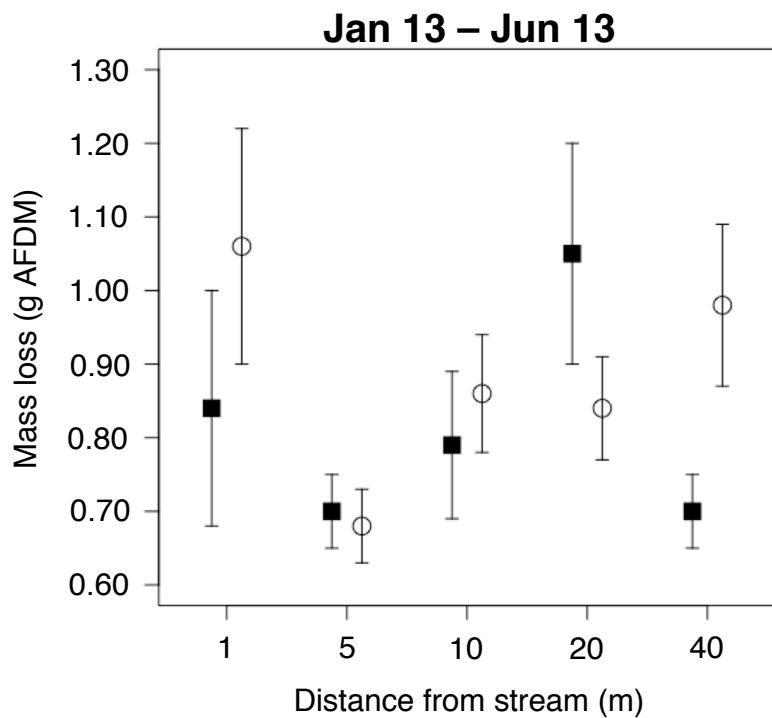
Jun 13 – Jan 14



**Figure C.7** Average mass loss (g AFDM  $\pm$  1 S.E.) of western red cedar leaf litter by treatment (control ■, nutrients added ○, water added ▲, nutrients and water added ◇) for each distance from stream edge in each trial calculated from the raw data. Trials are: (a) January 2013 to January 2014, (b) June 2013 to January 2014. Note the range of mass loss differs for each trial, and y-axes do not begin at zero.

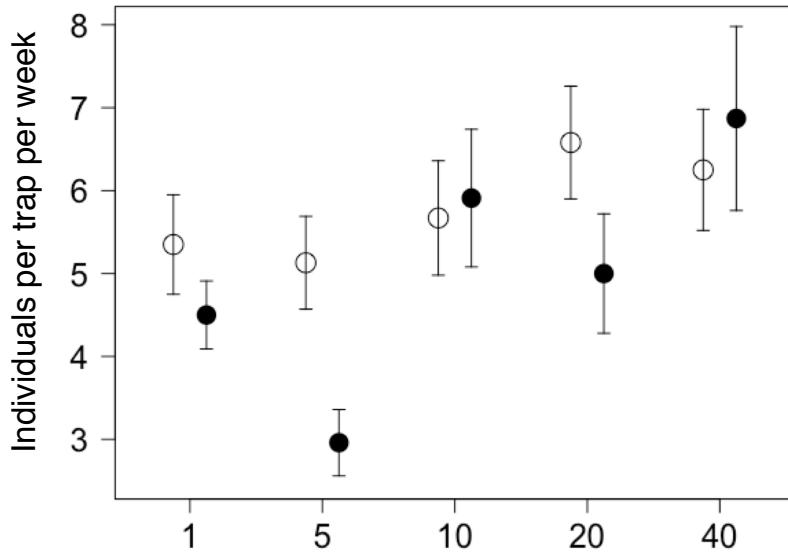


**Figure C.8** Average mass loss (g AFDM  $\pm$  1 S.E.) of western red cedar leaf litter for litterbags without nutrient additions (■) and with nutrient additions (○) for each site in the January 2013 to June 2013 trial. Average values were calculated from the raw data. Note the y-axis does not begin at zero.

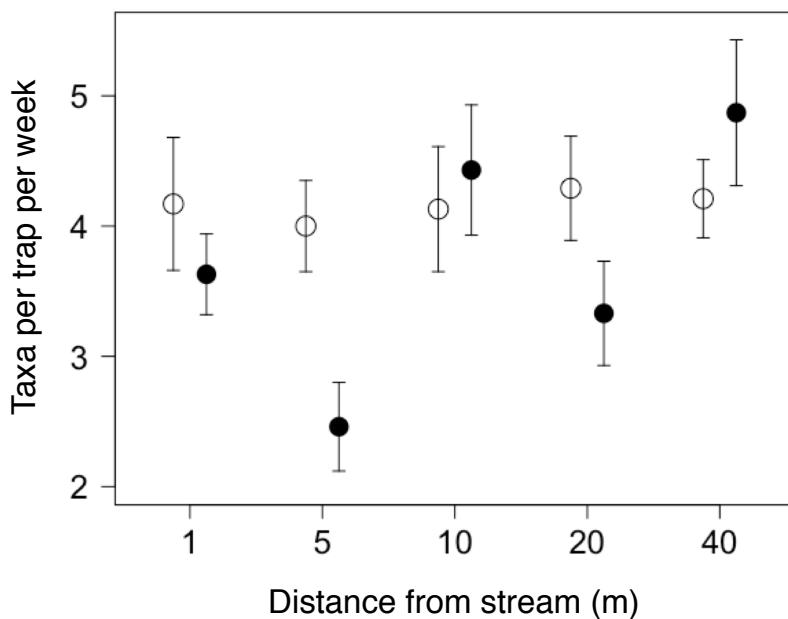


**Figure C.9** Average mass loss (g AFDM  $\pm$  1 S.E.) of western red cedar leaf litter for litterbags without nutrient additions (■) and with nutrient additions (○) for each distance from stream in the January 2013 to June 2013. Average values were calculated from the raw data. Note the y-axis does not begin at zero.

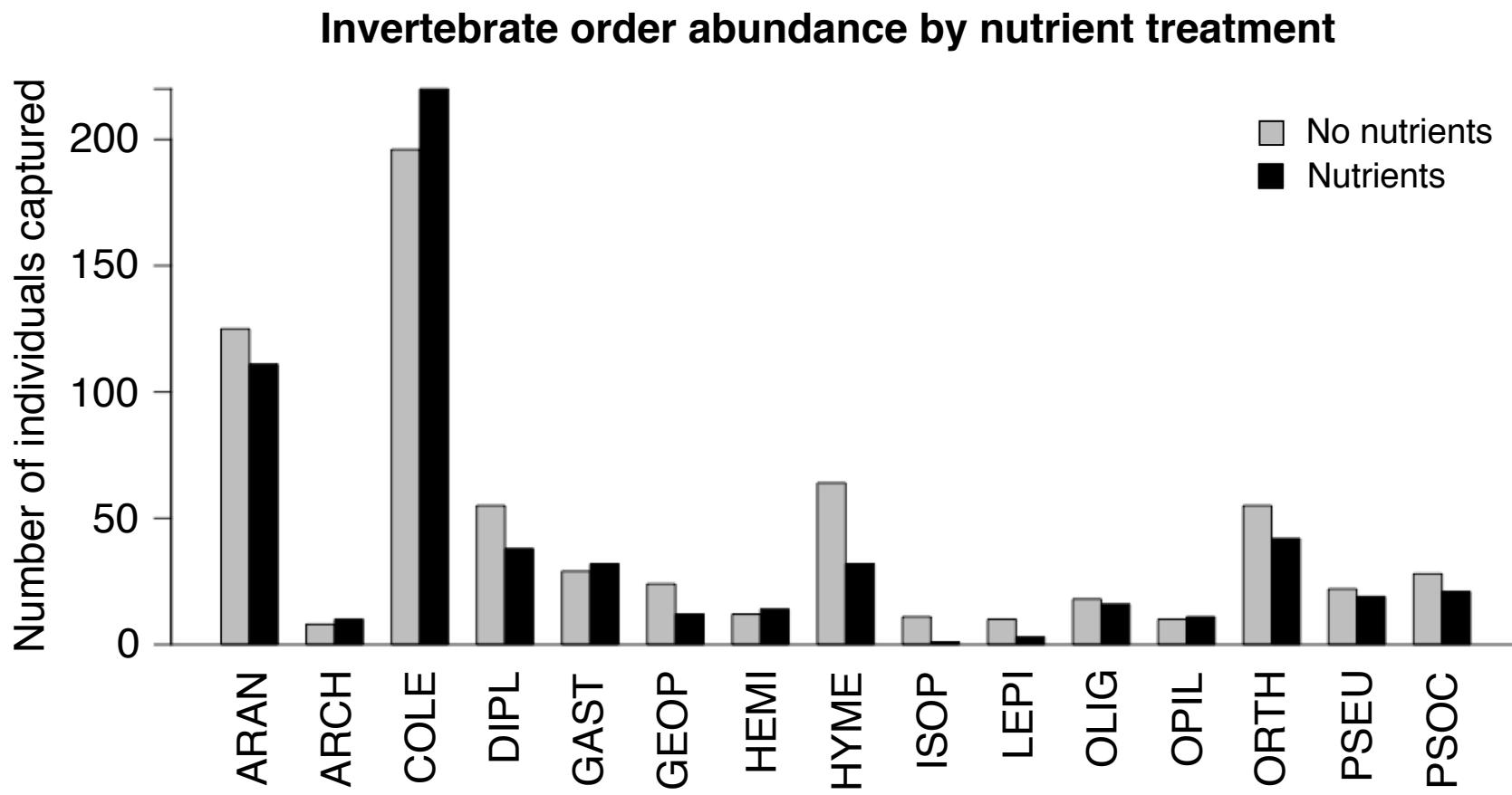
(a)

**Total individuals**

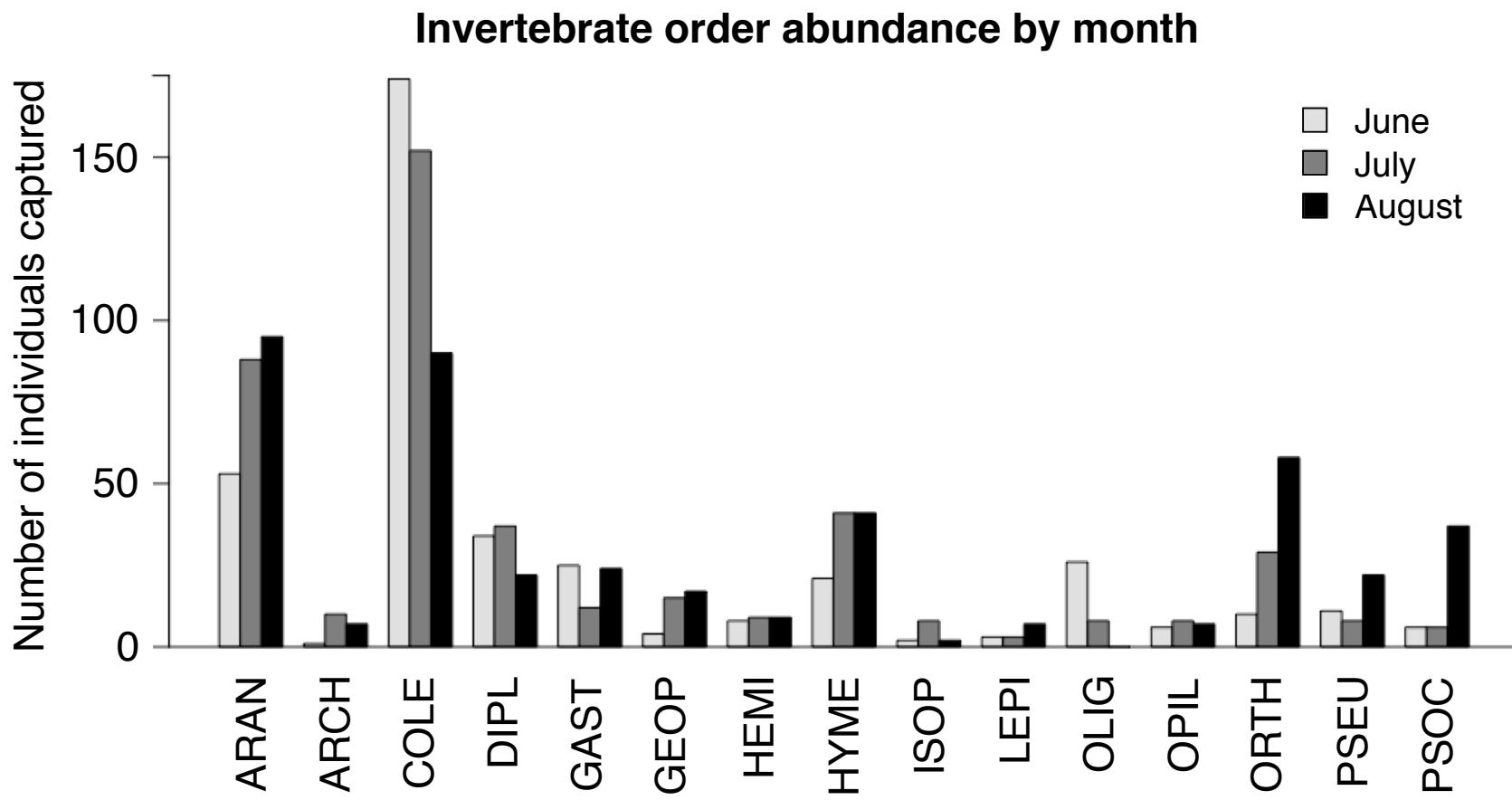
(b)

**Total taxa**

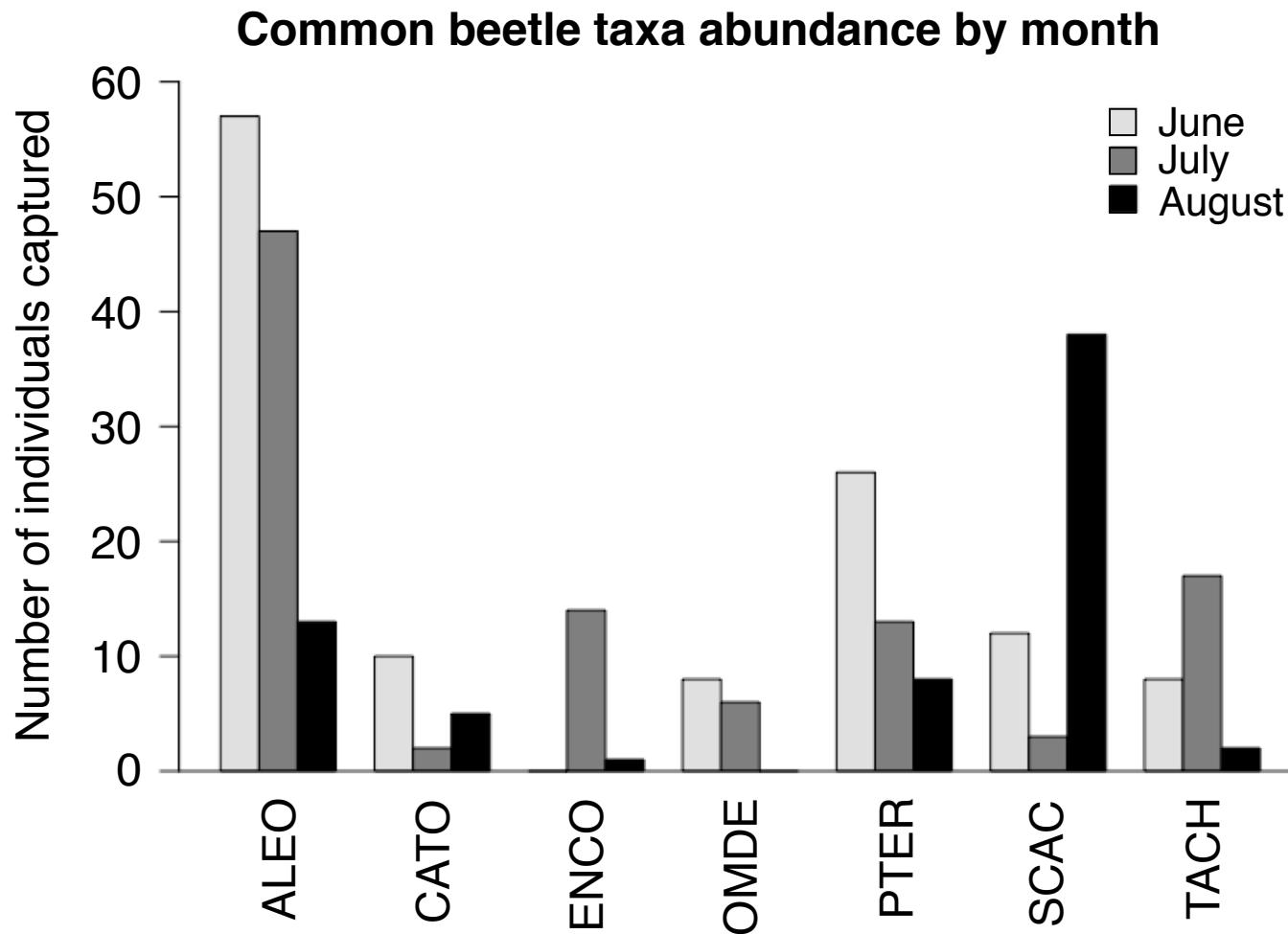
**Figure C.10** Mean  $\pm$  1 S.E. of (a) total individuals per trap per week and (b) total taxa per trap per week for all captured taxa at control stations (○) and those receiving nutrients (●). The interaction between nutrients and distance was not significant ( $p = 0.06$ ) for this group when distance was a covariate. Note y-axes values differ for each graph and do not begin at zero.



**Figure C.11** Number of individuals captured by invertebrate order in traps with and without nutrient additions. Abbreviations for invertebrate orders: Araneae (ARAN), Archaeognatha (ARCH), Coleoptera (COLE), Diplopoda (DIPL), Gastropoda (GAST), Geophilomorpha (GEOP), Hemiptera (HEMI), Hymenoptera (HYME), Isopoda (ISOP), Lepidoptera (LEPI), Oligochaeta (OLIG), Opiliones (OPIL), Orthoptera (ORTH), Pseudoscorpiones (PSEU), Psocoptera (PSOC).



**Figure C.12** Number of individuals captured by invertebrate order in each month. Abbreviations for invertebrate orders: Araneae (ARAN), Archaeognatha (ARCH), Coleoptera (COLE), Diplopoda (DIPL), Gastropoda (GAST), Geophilomorpha (GEOP), Hemiptera (HEMI), Hymenoptera (HYME), Isopoda (ISOP), Lepidoptera (LEPI), Oligochaeta (OLIG), Opiliones (OPIL), Orthoptera (ORTH), Pseudoscorpiones (PSEU), Psocoptera (PSOC).



**Figure C.13** Number of individuals caught by common beetle taxa (with relative abundances > 1%) in each month. Abbreviations for beetle taxa: Aleocharinae (ALEO), *Catops* spp. (CATO), *Enicmus cordatus* (ENCO), *Omus dejani* (OMDE), *Pterostichus* spp. (PTER), *Scaphinotus angusticollis* (SCAC), Tachyporinae (TACH).