Long-term changes in macroinvertebrate communities in streams of Denali National Park, Alaska

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ABSTRACT

Climate change is a major global issue influencing stream ecosystems that may result in changes in invertebrate communities over the long term. Stream ecosystems in subarctic regions receive water from a number of different water sources, making them vulnerable to extreme weather events and warmer air temperature, both potentially affecting freshwater taxa through changing hydrological regimes. Macroinvertebrates were collected every year in 10 streams in Denali National Park (DNP) from 1994 to 2016, except 1997. In a number of streams some taxa in macroinvertebrate communities varied markedly from year to year in terms of abundance and diversity. Large-scale atmospheric patterns (Pacific Decadal Oscillation, North Atlantic Oscillation, Oceanic Niño Index and Pacific-North America) and local climatic variables (e.g. air temperature, precipitation and snowfall) were assessed to see if they affected the persistence and compositional stability of stream macroinvertebrates communities in a changing climate in DNP, Alaska, over this 22 year study period. PDO, NAO and ONI were found to be the large-scale climatic patterns having a direct effect on spring hydrological seasonal regimes, which in turn influenced the stream communities. These patterns also caused warmer spring air temperature at local scales, and linked to other principal environmental variables, created variations in macroinvertebrate persistence and compositional stability. Three distinctive groups of years were evident in a number of the streams during the study period: (1) pre 2005, (2) 2005 to 2008 and (3) post 2008. Rainfall and associated spring floods were the main variables affecting these distinct groups of macroinvertebrate benthic communities. Some Ephemeropteran taxa (e.g. *Baetis* and *Epeorus*) and Plecoptera (*Capnia* and *Doddsia*) showed the capacity to recover from these events during spring. Overall, the findings indicate that the benthos communities in the study streams were extremely sensitive to the effects of local climate drivers, which has wider implications for aquatic environments worldwide.

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Abbreviations / Acronyms

BC	Bray Curtis
ENSO	El Niño South Oscillation
EP-NP	East Pacific-North Pacific
EPT	Ephemeroptera, Plecoptera and Trichopetra
DNP	Denali National Park
IndVal	Value index
J	Jaccard similarity coefficient
Mprecip	Mean total precipitation
Msnow	Mean total snowfall
Mtemp	Mean temperature
NAO	North Atlantic Oscillation
NMDS	Non-metric multidimensional scaling
NOAA	National Oceanic Atmospheric Administration
ONI	Oceanic Niño Index
PCA	Principal component analysis
PC1	Less snow
PC2	Less rainfall
PC3	More rainfall
PC4	Null snow/Negative precipitation
PNA	Pacific/North American
PDO	Pacific Decadal Oscillation
precSD	Precipitation standard deviation
RDA	Redundance Analysis
snowSD	Snow standard deviation
SpringFlood	Spring flood
SpringPrecip	Spring precipitation
SpringTemp	Spring mean temperature

tempSD Temperature standard deviation

U.S.A. United States of America

WintSnow Winter snow

XLSAT Statistical software for excel

1 Introduction

1.0 Introduction

Over the last century, freshwater biodiversity in northern latitude freshwater systems has declined at faster rates than terrestrial biodiversity as a result of climate change (Milner et al., 2009; Múrria et al., 2017). Extreme changes in hydrological regimes continue to have a strong impact in freshwater ecosystems, substantially affecting freshwater biodiversity. Denali National Park (DNP), interior Alaska, was selected in 1991 to develop a Long-term Ecological Monitoring Network in order to provide data on the ecological status of freshwater communities, and trends on the physical and biological resources in DNP in order to protect and preserve their ecosystems (Oakley et al., 2000).

Ten rivers in DNP were chosen as the basis of the monitoring network: Tattler Creek, East Fork Toklat Tributary, Little Stoney Creek, Hogan Creek, Savage River, Sanctuary River, Igloo River, N4, Highway Creek and Moose Creek (see the map in Chapter 2). These 10 streams and rivers were classified by Conn (1998) using TWINSPAN classification based on their macroinvertebrate community similarity into five groups (Table 1.1). Rare taxa with low numbers of individuals were down weighted.

Group 1. Small stable streams

Tattler Creek and East Fork Toklat Tributary. These 1st and 2nd order streams are fed by snowmelt and rain runoff. They have a very stable streambed with close border of vegetation. And they have high production levels of epilithic algal growth with chlorophyll *a*; additionally the inputs of leaves from trees and shrubs serve as food supporting wide diversity taxa, typically dominated by Ephemeroptera, Plecoptera and Chironomidae. Maximum abundance typically exceeds 4500m^2. The main functional feeding group was represented by shredder invertebrates.

Group 2. Spring-fed streams

Little Stoney Creek and Hogan Creek. These 2nd and 3rd order streams are small systems fed by groundwater, having cooler water during summer and warmer water during winter. The constant water flow creates channel stability which allows riparian plants to persist in the close borders. Hence, these streams are relatively productive, supporting high abundance and diversity of macroinvertebrates. The macroinvertebrate community was dominated by Chironomidae and Ephemeroptera with densities exceeding 4000 m^2. The functional feeding group was dominated by scrapers.

Group 3. Streams of the Kantishna area

Moose Creek. A 3rd order stream, possessing a well-developed riparian zone. The primary production is enhanced by its wider channel which allows light infiltration. The average abundance was 3000 individuals m^2, with Chironomidae the dominant taxa, followed by Ephemeroptera and Trichoptera. Scrapers were the group with highest abundance.

Group 4. Larger river systems partially fed by glacier-melt water

Savage River, Sanctuary River and Igloo Creek are 2nd to 4th order systems fed by principally by snow and some glacier-melt. These are relatively productive streams, supporting on average 1500 individuals m^2. Chironomidae was the dominant group in the macroinvertebrate community and collector-gatherers the main functional feeding group.

Group 5. Small, unstable creeks

N4 and Highway Creek were classified as 1st and 2nd order streams and actively migrating channels due to the relatively high gradient. These streams are fed by snowmelt and rain runoff. The average macroinvertebrate densities are 160 individuals m^2, and the primary production was low because the unstable channels restrict algal growth. Thus, scrappers were almost absent, and gatherers were the dominant group.

Table 1.1 Physico-chemical properties of the study streams in Denali National Park during 1995 (adapted from Conn, 1998).

Creek	Lat	Long	Stream Order	Riparian Vegetation on floodplain	Water Source	Stability	Stream Group (see text)	Gradient from source (%)	Catchment (km^2)	Dominant feeding group	Dominant Taxa
Tattler Creek	63.34.04	-149.38.27	1	close border	Snowmelt and rain runoff	High	1	9.6	4.7	Shredder	Ephemeroptera/ Plecoptera/ Chironomidae
East Fork Tolkat Tributary	63.33.50	-149.47.40	2	close border	Snowmelt and rain runoff	Moderate	1	3.8	67.2	Shredder	Ephemeroptera/ Plecoptera/ Chironomidae
Little Stoney Creek	63.27.14	-150.14.17	3	close border	Groundwater	High	2	9.5	1.4	Scrapers	Chironomidae/ Ephemeroptera
Hogan Creek	63.43.41	-149.24.39	2	close border	Groundwater	High	2	2.0	8.9	Scrapers	Chironomidae/ Ephemeroptera
Moose Creek	63.32.03	-150.58.45	3	close border	Variable	High	3	2.1	13.1	Scrapers	Chironomidae/ Ephemeroptera/ Trichoptera
Savage River	63.35.50	-149.47.40	4	Not proximal	Snowpack minor glacier melt	Moderate	4	2.6	89.4	Collector-Gatherers	Chironomidae
Sanctuary River	63.44.22	-149.17.39	3	Not proximal	Snowpack minor glacier melt	Moderate	4	4.4	97.5	Collector-Gatherers	Chironomidae
Igloo Creek	63.35.08	-149.37.10	2	Not proximal	Snowpack	High	4	2.8	13.5	Collector-Gatherers	Ephemeroptera/ Plecoptera/ Chironomidae
N4	63.34.42	-149.37.28	1	Absent	Snowmelt and rain runoff	Low	5	17.4	3.4	Gatherers	Chironomidae
Highway Creek	63.28.13	-150.09.47	2	Absent	Snowmelt and rain runoff	Low	5	6.5	7.6	Gatherers	Chironomidae

The objectives of this long-term (22 years) research network were i) to evaluate the links between regional and local climatic conditions on freshwater stream macroinvertebrate communities and ii) to assess the persistence and compositional stability of stream macroinvertebrate communities in a changing climate in DNP. Developing a better understanding of the resulting physical-biological interactions between climatic conditions and aquatic environments will help us predict how aquatic ecosystems will respond in the future to a changing climate.

1.1 Climatic change in alpine and arctic stream systems

The regional and local weather results from the interaction of solar radiation, ocean circulation patterns, altitude, and large-scale atmospheric patterns (e.g. Pacific Decadal Oscillation, Pacific-North American teleconnection pattern, etc.) (National Oceanic and Atmospheric Administration, 2011). The large -scale atmospheri patterns exhibit negative and positive phases, with interannual to interdecadal time scales (L'Heureux, 2019; Liu & Di, 2017; Mantua et. al., 1997; Mills & Walsh, 2013; National Oceanic and Atmospheric Administration, 2017; North Carolina Climate Office, 2018). Anomalies in the large-scale patterns likely influence air temperature and precipitation in different environments (e.g. tropical, mountain, arctic, etc.), affecting seasonal hydrological regimes (L'Heureux, 2019; Liu & Di, 2017; MDPI, 2020; Mantua et. al., 1997; Mills & Walsh, 2013).

Arctic and alpine environments are complex systems characterized by low air temperature and short growing seasons (Archer et al., 1980). Seasonal hydrological regimes are important in regulating the water supply via precipitation, snowfall, ice melt and permafrost; these being the main water sources to streams (Huss et al., 2017). Highly dependent complex interactions between the source, timing and magnitude of the climatic events in alpine ecosystems have pronounced effects on seasonal regimes in many streams, particularly where snowfall represents the main input to freshwaters (Bunn et al., 2007; Prowse et al., 2006). For rivers at a high altitude and latitude, glaciers may also be important, particularly where they represent the main water source (Cauvy-Fraunié et al., 2015; Jacobsen et al., 2012; Milner et al., 2009). Streams in subarctic regions can be categorized by glacier-melt, snowmelt fed and groundwater-fed streams, all of which have specific habitat conditions (Brittain & Milner, 2001; Hieber et al., 2005; Ward, 2002).

Glacier-melt are streams that emerge from glaciers and are characterized by a maximum temperature ≤ 2°C, usually high turbidity, low in nutrients and large flow fluctuations in summer (reducing primary production). Fish are typically absent, and the zoobenthos is mainly restricted to Chironomidae, particularly of the genus (*Diamesa*). However, when temperatures exceed 2°C, during summer, other dipterans (mainly Simuliidae) and oligochaetes appear (Ward, 2002).

Streams fed by snowmelt occur in unglacierized alpine catchments. The water temperature in these streams is typically between 4-10°C. The habitats in streams fed by snowmelt typically do not show severe flow fluctuations, high turbidity and scarce food resources. Fishes and zoobenthos water specialists (cold-adapted mountain stream species) are present in this environment, including mayflies, stoneflies and caddisflies (Maiolini et al., 2006; Milner et al., 2001; Ward, 2002).

Streams fed by groundwater have stable substratum and cooler and clear water in the summer. Aquatic biota find refugia in the spring sources, emerging along the edge of the river corridor. Thus, the good physical habitat conditions in these environments host diverse aquatic flora and fauna. The zoobenthic community is mainly composed of chironomids, Plecoptera, Ephemeroptera and Trichoptera (Maiolini et al., 2006; Milner et al., 2001; Ward, 2002).

Global warming will alter the timing, magnitude and frequency of water sources and discharge in riverine ecosystems (Milner et al., 2017). Extreme weather events caused by warming air temperature influence precipitation and runoff events, which are occurring at a higher frequency (both at low and high flows) and consequently produce higher sediment transport rates during high flows (Yao et al., 2015). These events have a strong impact on aquatic habitats and their communities (Huss. et al., 2017). In the European Alps, warmer temperature during summer in combination with low rates of snowfall, has led to ice loss of 54% since 1850 and, in 2017 just 4-13% of the ice area in the European Alps remained, according to recent projections (Milner et al., 2017). Hence, stream flow will be more dependent on precipitation events and snow melt rather than glacial runoff in many alpine systems (Milner et al., 2017).

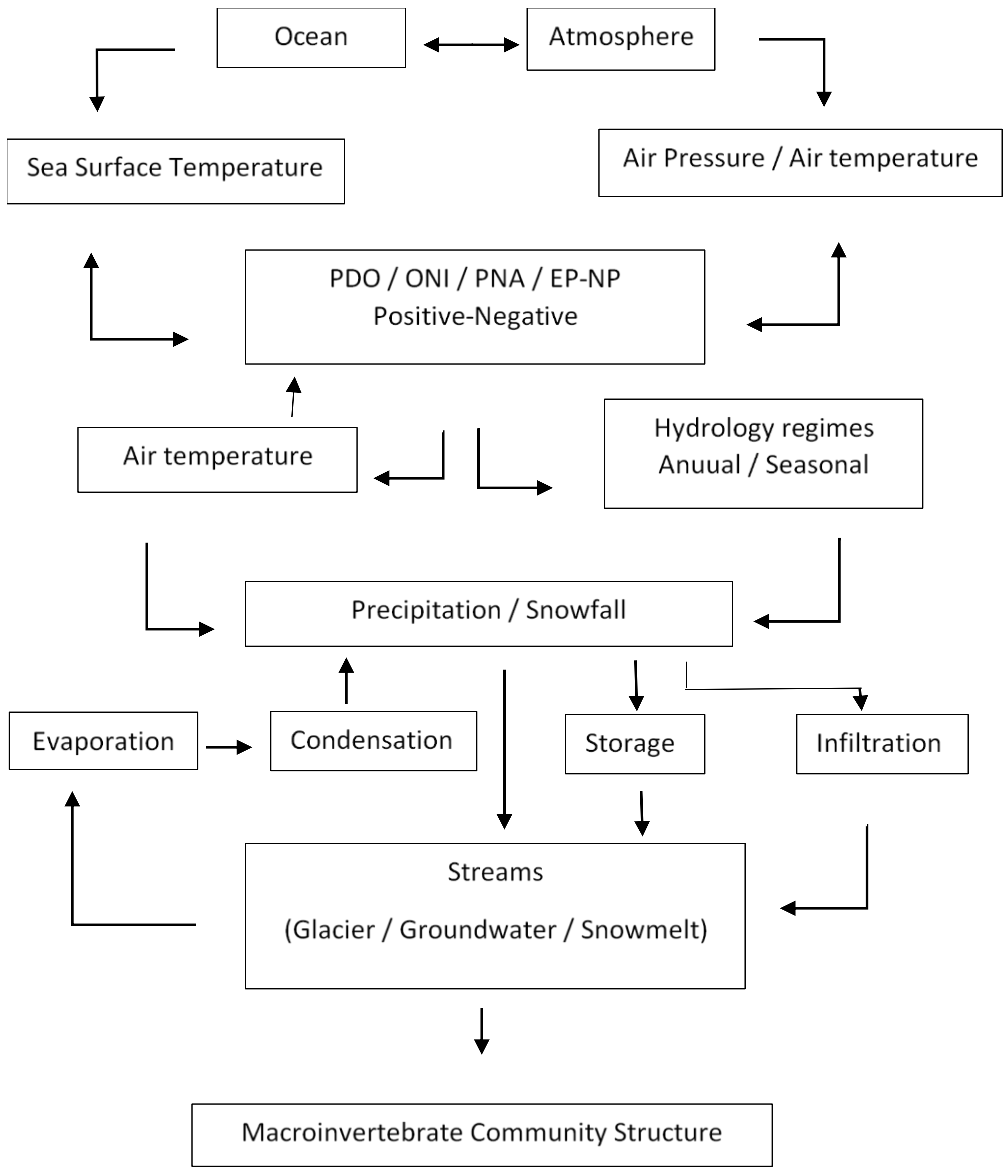

Figure 1.1 Large-scale climatic conditions influencing annual and seasonal hydrological regimes at local scales, and in turn influencing macroinvertebrate community structure.

1.2 Lotic environments in northern latitudes and their macroinvertebrate communities

Freshwater inputs in glacial river systems have important effects on physical (e.g., substrate material -rocks, gravel or sand), chemical (e.g., oxidation, reduction) and biological (e.g., primary production, respiration) properties, as they are associated with the glacial flood pulse (Brown et al., 2014; Pierre et al., 2019; Prowse et al., 2006). Thus, in late spring/early summer, snow and ice melt results in a lateral expansion of the river channel across floodplains, and during that process, melt water mixes with alluvial and hillslope ground water (Brown et al., 2014).

Rivers play a key role in nature as dispersal corridors for species across different trophic levels (Allan et al., 2005; Stoll, et al., 2014; Wrona & Reist, 2005), including rare and endemic macroinvertebrate species (Milner et al., 2009). The atmospheric inputs of precipitation and air temperature into the river system results in the transfer of fluxes through abiotic and biotic elements (Figure 1.1). This in turn affects species community stability (Wrona & Reist, 2005). Through time, species gradually develop physiological and morphological attributes to survive under a set of abiotic conditions, allowing them to adapt to change conditions in space and time (Biggs et al., 2005).

Macroinvertebrate occurrence differs across freshwater ecosystems according to species habitat preferences and their tolerance of environmental conditions, both closely related to environmental heterogeneity along a stream, such as seasonality in flow regimes or frequency discharge disturbance (Heino, 2013; Múrria et al. 2017). Species diversity and composition in glacier-fed rivers might be low due to the harsh habitat conditions (low temperatures $\leq$ 2°C, high turbidity, limited food resources and large flow fluctuations in summer), but as a consequence of the water source shifting from meltwater to groundwater dominated streams, and increasing water temperatures associated to climate change, species diversity will increase in streams located at high latitudes (Cauvy-Fraunié et al., 2015; Lawerence et al., 2010; Milner et al., 2009; Vinke et al., 2015; Ward, 2002). Seasonal environmental changes have a temporal impact in glacial streams, altering channel stability and resulting in seasonal shifts in taxon richness and abundance. During winter, richness and abundance are dependent of the influence and extent of groundwater to the stream (Brittain & Milner, 2001; Milner et al., 2001).

The general spatial longitudinal distribution of macroinvertebrates in glacier-fed streams is mainly determined by water temperature and channel stability; however, the colonization of streams with warm water temperature may be delayed where channel stability is low and specialised taxa of unstable conditions will remain dominant in the community (Brittain & Milner, 2001). Many macroinvertebrate taxa are also dependent on small scale habitats in streams, such as riffles and pools. Pools are habitats characterised by the deepest parts of the stream and low velocity (Buffington et al., 2002), and they are often dominated by shredders (e.g., Limnephilidae; Campell et al., 2012). Riffles are shallow sections of streams characterized by rapid currents, variability in depth, high oxygen concentration, and substrate; this habitat supports the highest diversity of benthic species assemblages (Brown & Brussock, 1991**;** Cook et al., 2018). Riffles are dominated by scrapers, such as mayflies (e.g., *Drunella, Cinygmula, Ephemerella*), and filterers such as Simuliidae, which can be the dominant group in northern alpine streams (Campell et al., 2012; Heino et al., 2005; Hieber et al., 2005; Milner et al., 2001; Vinke et al., 2015).

Macroinvertebrates are an important component of river systems. Their role in freshwaters is crucial in maintaining the structure and functional integrity of aquatic ecosystems. Benthic communities in particular are important as they facilitate energy transfer among trophic levels and transform the physical habitat condition via detritus decomposition and nutrient cycling (Zhang et al., 2014).

1.3 Streams and rivers in Denali National Park, Alaska

Glaciers in Alaska play an important function in rivers system as they contribute significantly to river flow (Jacobsen et al., 2012; Milner et al., 2009); approximately 35% of the runoff is from glaciers.

Global increase in temperature has occurred since at least 1901 (Lindsay & Dahlman, 2018), and surface temperatures during the period 1981-2010 increased on average by 0.38°-0.48°C (Hartfield et al., 2018; Monaham & Fisichelli. 2014; Stroeve et al., 2007). Temperature has increased in US National Parks at an even faster rate, around 0.85°C (1983-2012) (Ritchie, 2018; Monaham & Fisichelli, 2014). According to Monaham & Fisichelli (2014) National Parks should be managed as part of the landscape and not as a different entity as they are also influenced directly (e.g. by scientific, recreation or industrial activities in situ) or indirectly (e.g. by changes in atmospheric circulation, global warming) by anthropogenic activities. The effects of a warming climate in DNP can be dramatic, such as melting glaciers and permafrost, and more frequent fires. These changes alter stream benthic habitat by increasing variability in flow, water temperature, and sediment load, . (National Park Service U.S. Department of the Interior, 2019).

Some streams in DNP are considered glacially dominated systems. Thus, water discharge is seasonally controlled, accumulating beneath glaciers, water melts and is charged with high dissolved solids (Ahearn, 2002). During winter, discharge declines gradually and the rivers run clear (Milner, 2018). The water source in rivers and streams via melting glaciers, melting snow or groundwater springs is strongly influenced by local geology, which determines water chemistry, and processes influencing channel stability within the watershed such as current flow and substrate particle size (National Park Service, 2018).

1.4 Aims and objectives

The primary aim of this study was to examine the effects, in a changing climate, on the persistence and the compositional stability of stream macroinvertebrates communities in DNP, Alaska, over a period of 22 years. To achieve this aim, the relationship between large-scale atmospheric patterns and local climatic conditions was examined, in order to identify the main driving variables affecting aquatic macroinvertebrate communities in the study region. The study objectives were:

- To analyse temporal changes in the persistence and compositional stability of freshwater stream macroinvertebrate communities in ten streams in DNP over a 22-year period.
- To identify the climatic variables driving changes in stream macroinvertebrate communities across this time period.
- To identify the influence of climatic variables in Chironomidae composition specifically from four streams over a 9-year period.

1.5 Thesis structure

Chapter 2 presents the collected climatic and environmental variables that form the basis of the main analyses in the thesis, and the results of the analyses assessing the relationships between the large-scale atmospheric patterns and local climatic variables in DNP. The shift from negative to positive phases and positive to negative phases may have a direct impact on the seasonal climatic conditions at a local scale in DNP, affecting air temperature and hydrological regimes during spring.

Chapter 3 examines the persistence and the compositional stability of the macroinvertebrate communities in the study streams. The influence of the climatic and environmental variables on macroinvertebrate community structure is analysed.

Chapter 4 explores the relationship of large-scale atmospheric patterns (Pacific Decadal Oscillation, Oceanic Niño Index, Pacific-North American, North Atlantic Oscillation) and local climatic conditions in DNP on macroinvertebrate community structure over the study period

In Chapter 5, the influence of different environmental and climatic variables on changes in Chironomidae composition over the 22 year period, across a subset of four streams, is examined.

A discussion of the overall implications of the thesis' findings is provided in Chapter 6, highlighting areas where future research is necessary to advance the results presented here.

2 Study area and climatic variables

2.0 Denali National Park study area

DNP is located between 62° and 64° N in central Alaska, one of the largest national parks in the USA, covering nearly 2.5 million ha (Drazkowski et. al., 2011; Kilkus et. al., 2011; National Park Service U.S. Department of the Interior, 2005). This subarctic and pristine area is dominated by glacial plains, braided streams and permafrost, supporting a large diversity of habitats and organisms (Clark & Duffy. 2006; Kilkus et. al., 2011).

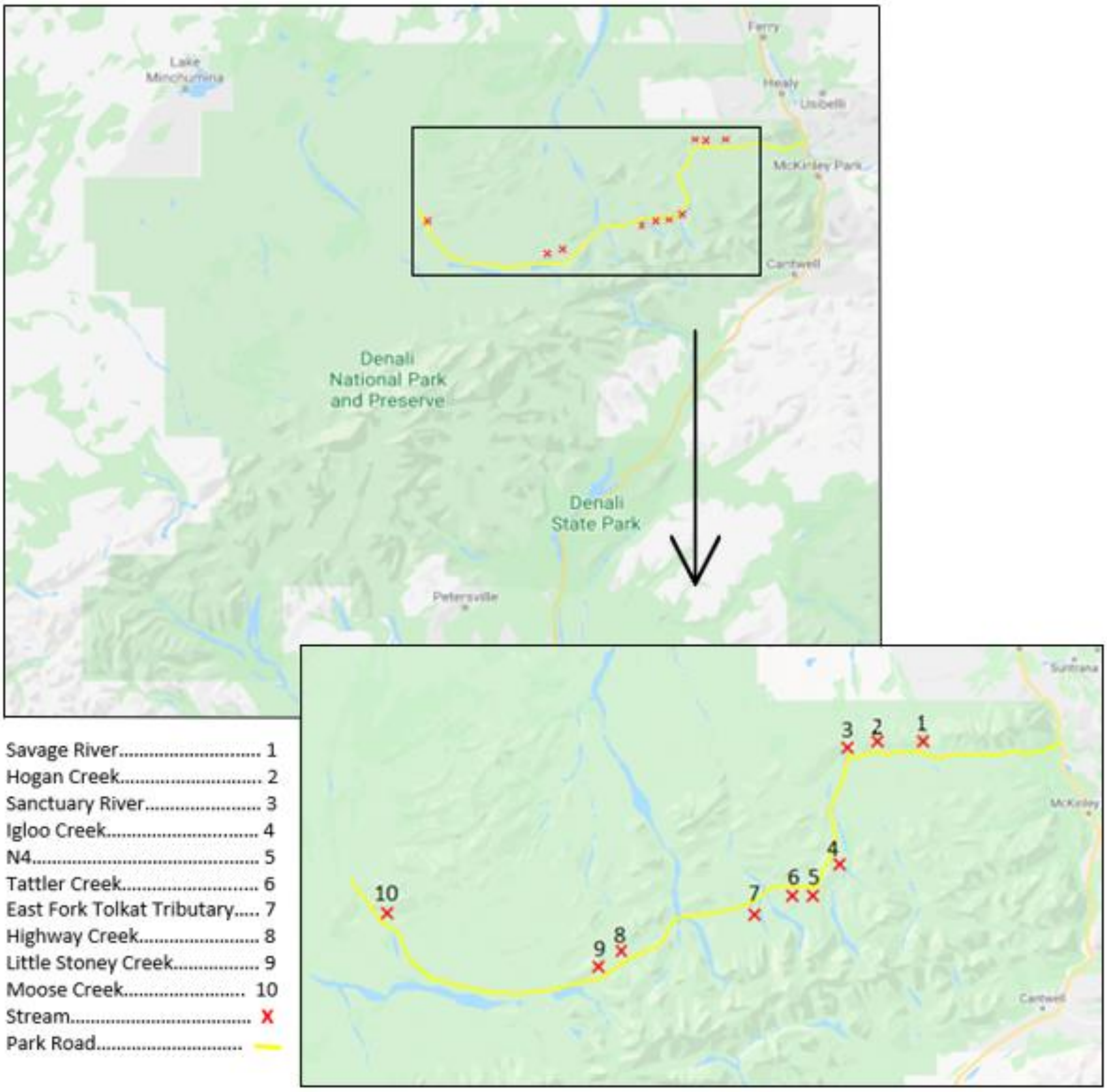

Figure 2.1 Location of streams in Denali National Park (1:2,000,000), Alaska (Google Maps, 2020)

The climate regime in DNP is mainly affected by the ocean and the continental interior (Drazkowski et. al., 2011), resulting in strong seasonal variations in air temperature (Boudreau, 2003), especially during spring, summer and winter. In winter, typical air temperatures are below -4°C, whilst the highest air temperature values are observed during summer exceeding 18°C (Drazkowski et. al., 2011; Wendler & Shulski, 2009).

2.1 Methods

2.1.1 Large scale environmental climatic variables

Five large-scale environmental variables were used in this study, selected for their potential regional and local impact on stream communities in northern latitudes.

(1) The Pacific Decadal Oscillation (PDO) is a recurring ocean-atmosphere climate pattern variation, showing changing periods ranging from about three to seven years, in which changes in the sea surface temperatures and the superficial atmospheric pressure in Pacific Ocean interact resulting in a shift of sea surface from a warm (below average winter temperatures and above average winter precipitation) to a cool (above average winter temperatures and below average winter precipitation) phase (Mantua et. al., 1997; Mills & Walsh, 2013; North Carolina Climate Office, 2018). The PDO shifts from a colder (negative) to a warmer (positive) phase during these cycles.

(2) The East Pacific – North Pacific pattern (EP-NP) is a spring-summer- fall pattern showing positive and negative phases. The positive phase is associated with warm air masses over Alaska increasing surface temperatures, and cold air over the central North Pacific and eastern North America, while the negative phase exhibits

the opposite circulation anomalies in those regions (Liu & Di, 2017; National Oceanic and Atmospheric Administration, 2017; North Carolina Climate Office, 2018).

(3) The Pacific/North American (PNA) teleconnection pattern is characterised by anomalous air mass pressure over the Pacific and North Atlantic, and a correlation between air temperature and precipitation anomalies. PNA has positive and negative phases. The positive phase is characterized by increased precipitation over the eastern U.S.A, and a rise in air temperature over the western U.S.A. In the negative phase, air temperatures tend to decrease (L'Heureux, 2019; North Carolina Climate Office, 2018).

(4) The North Atlantic Oscillation (NAO) consists of differences in sea level pressure between the Subtropical high (Azores, islands located in eastern Atlantic Ocean) and the Subpolar Low (near Iceland), producing positive and negative phases (North Carolina Climate Office, 2018). In the positive phase, the pressure increases over the North Atlantic (wetter pattern), and during the negative phase, the pressure gradient decreases over the North Atlantic (cold air) (North Carolina Climate Office, 2018).

(5) The Oceanic Niño Index (ONI) shows the presence/absence conditions of El Niño (warm) and la Niña (cool) events (NOAA, 2018).

Local weather data (Appendix 2.1) were obtained from McKinley Station (Lat: 63.7175° N, Lon: -148.9692°W) which is the nearest weather station to DNP with full year environmental dataset covering the period from 1994 to 2016 and registered in the National Oceanic Atmospheric Administration (NOAA) (National Oceanic and Atmospheric Administration, 2017). The variables air temperature, rainfall and snowfall were obtained. In addition, from NOAA (2017) the large atmospheric variables, Pacific Decadal Oscillation (PDO), Oceanic Niño Index (ONI), East Pacific / North Pacific Pattern (EP.NP) and Pacific/North American Pattern (PNA) were downloaded. ONI was used in this study instead of the El Niño Southern Oscillation (ENSO) because it incorporates how PNA presence / absence conditions influence the air pressure over the Gulf of Alaska.

2.1.2 Local climatic variables

The environmental data analyses of local climatic variables were as follows (Table 2.1, Appendix 2.2 and 2.3):

(1) Monthly data (from September to August of the following year) of total rainfall, air temperature and total snowfall were collected. The mean and standard deviation of each variable was calculated.

(2) The yearly average from the preceding September through to August for the large-scale metric variables PDO, EP.NP, PNA and ONI was calculated. The monthly period September (preceding year) to August (following year) was used for air temperature, rainfall and snowfall to obtain Mean Temperature (Mtemp), Temperature Standard Deviation (SDtemp), Mean Total Precipitation (Mprec), Snow Standard Deviation (SDsnow), Mean Total Snow (Msnow).

(3) Data for Winter Snowfall (WintSnow) was calculated by summing monthly data from September (preceding year) to April (following year).

(4) Mean Spring Temperature (SpringTemp) and Total Spring Precipitation (SpringPrec) were calculated using monthly data from April and May.

(5) Spring Flood (SpringFlood) was calculated using the number of events with three or more days of heavier than average rain (17.78 – 7.62 cm) from April to July (Weather Atlas, 2019) (Table 2.1).

Table 2.1 Glossary of the acronyms and abbreviation.

Variable	Acronym	Time
Pacific Decadal Oscillation	PDO	Positive/Negative phase 20 to 30 years
East Pacific / North Pacific Pattern	EP-NP	Spring-Summer-Fall pattern
Pacific/North American Pattern	PNA	Autumn, winter and spring
North Atlantic Oscillation	NAO	Difference of atmospheric pressure fluctuation between Icelandic low and Azores High
Oceanic Niño Index	ONI	El Niño en La Niña events in the tropical Pacific
Temperature standard deviation	tempSD	September to August following year
Mean temperature	Mtemp	September to August following year
Mean total precipitation	Mprecip	September to August following year
Precipitation standard deviation	precSD	September to August following year
Snow standard deviation	snowSD	September to August following year
Mean total snowfall	Msnow	September to August following year
Winter snowfall	WintSnow	September to April following year
Winter temperature	Winter temperature	September to April following year
Spring mean temperature	SpringTemp	April and May
Spring mean Precipitation	SpringPrecip	April and May
Spring flood	SpringFlood	number of events with three or more days of heavier than average rain during spring or summer covering April to July

The variables SDprec, Mprec, Wintsnow and Msnow were replaced for PC1, PC2, PC3, PC4 using a PCA analysis to show the correlation between precipitation/snow fall over winter and in general over the year. PC1 which accounted for 87% of the variance was strongly negatively correlated with mean monthly snow, winter snow, and mean total precipitation (PC1=less snow), PC2 was negatively correlated with winter snow, mean total precipitation and precipitation standard deviation (PC2=less rainfall), PC3 was strongly positive correlated with mean total precipitation and precipitation standard deviation (PC3=more rainfall) and PC4 was negatively correlated with mean total precipitation and positive correlated with precipitation standard deviation (Table 2.2).

Table 2.2 Correlations between the four axes of PCA analysis and the four variables used in the PCA: winter snow, mean monthly snow, mean monthly precipitation and precipitation standard deviation. the proportion of variance explained by each PCA axis is provided in the bottom row.

	PC1	PC2	PC3	PC4
WinterSnow	-0.95	0.32	0.03	0
Msnow	-0.96	-0.29	-0.03	0
Mprec	-0.09	-0.28	0.92	-0.27
SDprec	0.10	-0.18	0.97	0.14
Variance explained	87%	9%	3%	<1%

Pearson’s correlation tests were used to ensure there was no substantial multicollinearity between the environmental variables. To reduce the correlation between four of the environmental variables (WintSnow, Msnow, Mprec and SDprec) a Principal Components Analysis was undertaken using these variables and the resultant four orthogonal axes eigenvalues as characteristic values (see Table 2.2). All Pearson’s r values of the final predictors were < 0.7.

2.1.3 Data analysis

The time-series of eight selected local climate environmental variables were then plotted as pairs to observe any co-variation: mean air temperature with total precipitation and total snow (separately), winter temperature and winter air temperature, and spring precipitation with spring temperature and mean spring flood (separately). The time-series of the 4 large-scale atmospheric (EP-NP, PNA, ONI, PDO) patterns from 1994 to 2016 was also plotted to visualise temporal patterns.

To test for relationships between the large-scale atmospheric patterns and local climate variables, a pairwise regression analysis was performed between each large-scale atmospheric pattern (PDO, ONI, PNA, ONI, and EP-N), and each local meteorological variable (tempSD, Mtemp, snowSD, SpringTemp , SpringPrecip, SpringFlood, PC1, PC2, PC3, and PC4) throughout the full-time series. Regressions were used here as it was assumed that the large-scale patterns drove variation in the local climate and not *vice versa*. Additionally, pairwise correlations between all variables were calculated (Table 2.4).

The correlation between the positive and negative phases of the five large scale patterns (PDO, NAO, EP-NP, PNA, and ONI) and the local climate variables (Mtemp, tempSD, snowSD, SpringTemp, springPrec, SpringFlood, PC1, PC2, PC3, and PC4) was undertaken separately. The positive values were filtered for each large-scale pattern, correlating the large-scale pattern with all the local-scale variables. The same process was then repeated for the negative values (data in Appendix 2.4).

2.2 Results

2.2.1 Environmental variables time series

The full set of local climatic pairwise time-series comparisons are provided in Figs. 2.2 – 2.6. The mean air temperature was observed during the years 2000-2001 (Fig. 2.2), whereas the highest precipitation was registered in the years 2015-2016. The pair years 2002-2003 to 2004-2005 showed high air temperatures contrasting with the low precipitation rates registered in the same pair years. The air temperature dropped abruptly during 2012-2013.

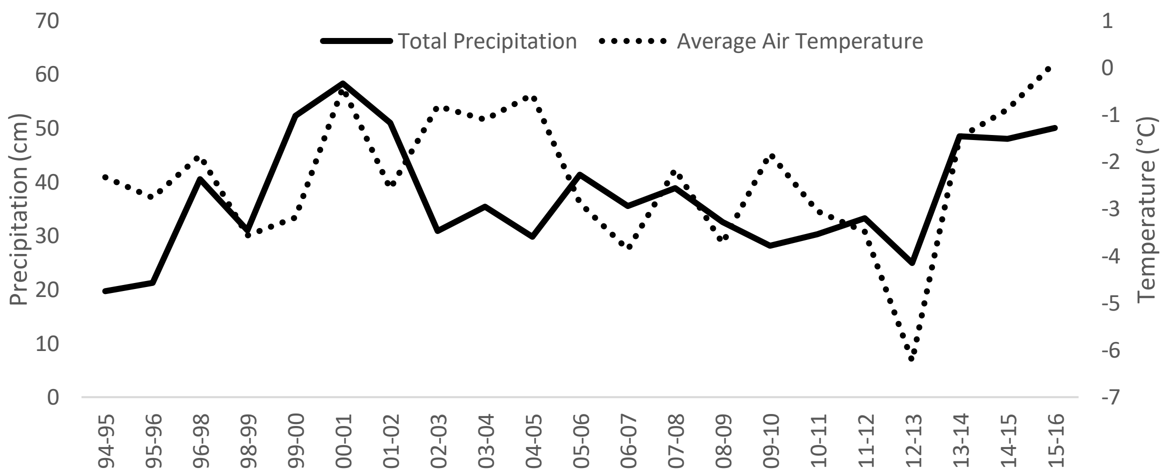

Figure 2.2 Total precipitation and mean air temperature by year pair recorded at McKinley station near DNP from 1994 to 2016.

It is observed in Figure 2.3 that total snow fall during 1999-2000 registered the highest values with a total of 296 cm and the lower values (58.2 cm) was registered during 2002-2003. Overall, snowfall and air temperature showed the highest variability between all pair years, indicating that air temperature has a strong influence on total snowfall. A decrease in snowfall is related to high air temperature showed while an increment in snowfall is associated with low air temperature.

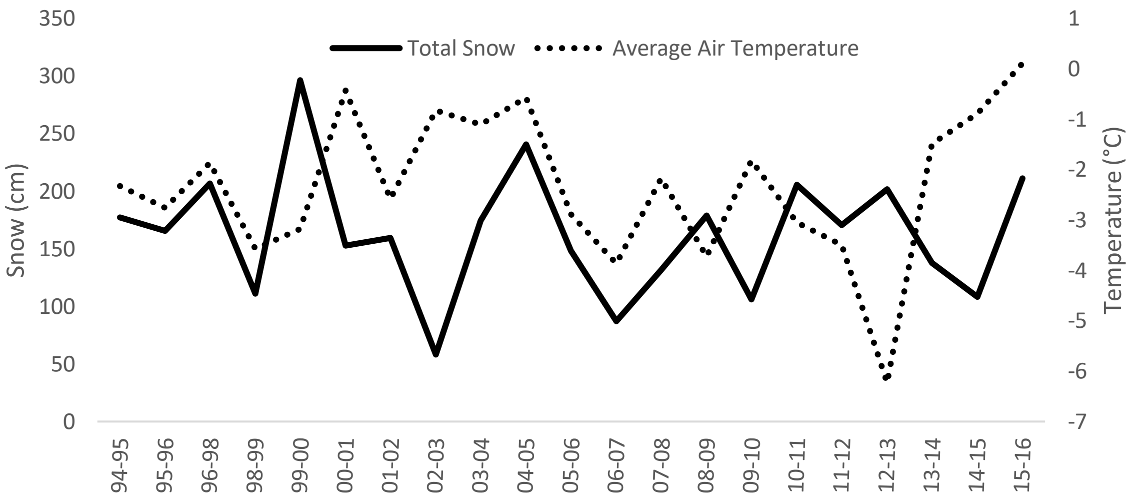

Figure 2.3 Total snow and mean air temperature by pair year recorded in McKinley near station near DNP from 1994 to 2016.

Winter snow showed great variability throughout the period (Figure 2.4). The highest values were registered in 1996-1998 and low air temperature values during the same years. However, winter snow and air temperature values reversed abruptly in 1999-2000, where air temperature increased above 10°C, causing a drop in the amount of snow production. The values of air temperature from following years remained below 0°C supporting constant snow during winter. However, there was only a weak relationship between air temperature and winter snow with a R^2 value of 0.06 (Appendix 2.4).

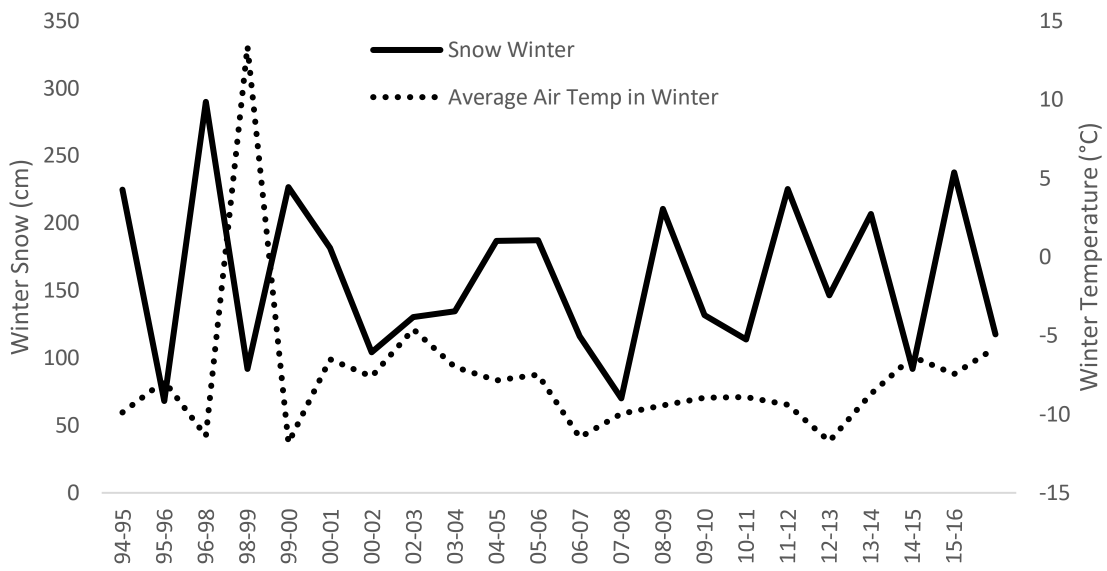

Figure 2.4 Total winter snow and winter air temperature (mean) by pair year recorded at McKinley station near DNP from 1994 to 2016.

Spring precipitation (11.2cm) was highest in 2002 and decreased to <1.2 cm in 2003 when air temperature was also at its lowest (Figure 2.5). Both variables showed a sudden rise again in 2004. On the other hand, 1996 was the year with the lowest spring precipitation (0.13) compared with the following years. The relation between air temperature and precipitation both during spring season is clear, high air temperature values caused low precipitation, while low values in air temperature were associated with an increment in precipitation during spring season. However, the relationship between mean annual air temperature and spring precipitation was weak (R^2 = 0.09).

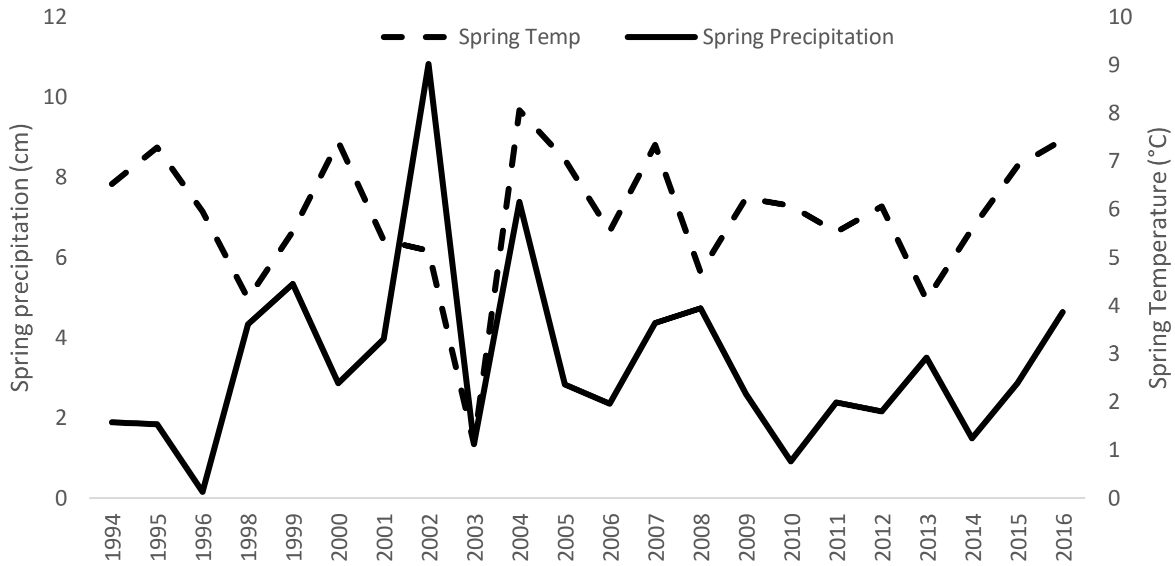

Figure 2.5 Mean spring precipitation and spring air temperature by year recorded at McKinley station near DNP from 1994 to 2016.

Spring Flood and Spring precipitation showed similar trends and showed great variability along the years (Figure. 2.6). Both variables registered the highest values during 2002 where spring precipitation was 9 cm and a spring flood 71.46 cm. Spring precipitation dropped abruptly in 2003, registering 1.12 cm. In addition, in 1996 spring precipitation had the lowest values (0.13 cm). Hence there was a trend that as spring precipitation increased there was a rise in the spring flood The R^2 value was 0.24 (Appendix 2.4) which was the highest value for regression between the local climate variables.

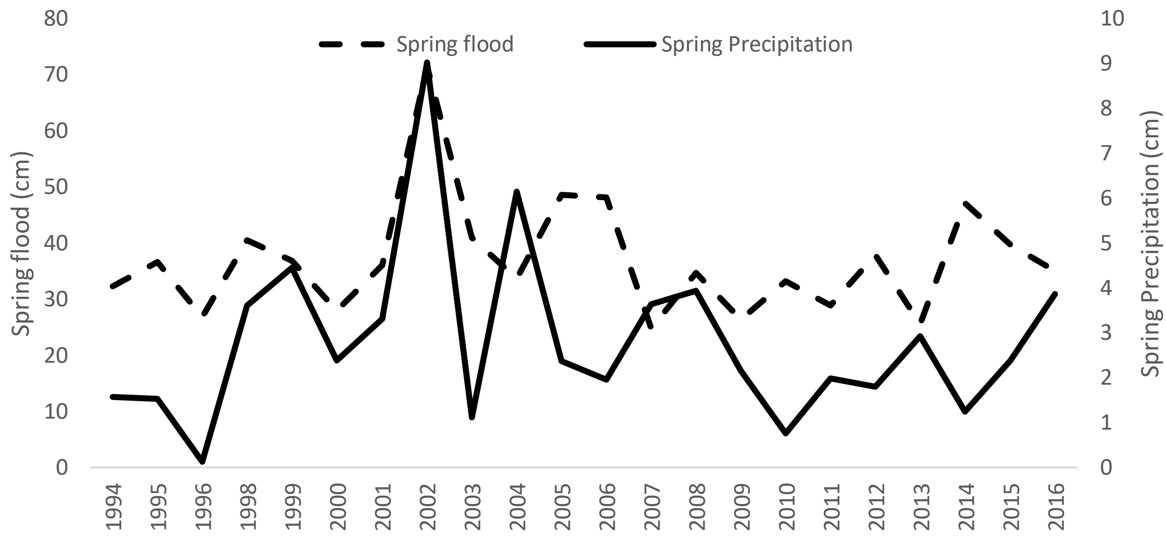

Figure 2.6 Mean spring flood and spring precipitation air temperature by year recorded in McKinley near station to DNP from 1994 to 2016.

The pattern East Pacific / North Pacific had the lowest value in 1994 and the trend since 1995 showed negligible variation (Figure 2.7).

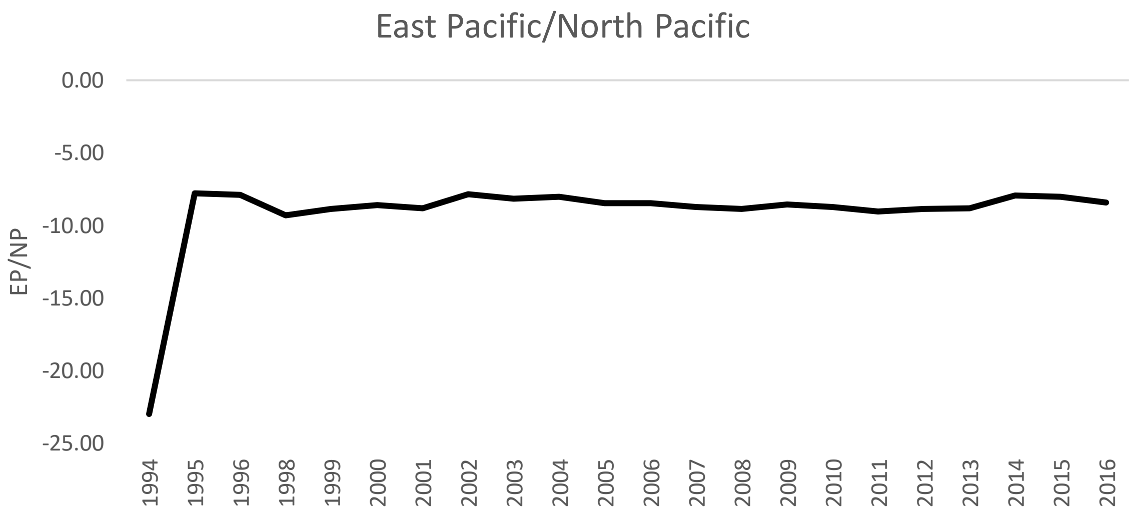

Figure 2.7 Mean yearly EP-NP recorded by NOAA from 1994 to 2016.

The Pacific-North American Oscillation tended towards negative values with the lowest values observed from 1994 to 2004 (Figure 2.8). For the following seven years (2005-2011) the values had a positive trend. Whereas 2013 showed and abrupt decline, almost reaching -2, and resulted in increased rainfall (above normal) in the Western United States.

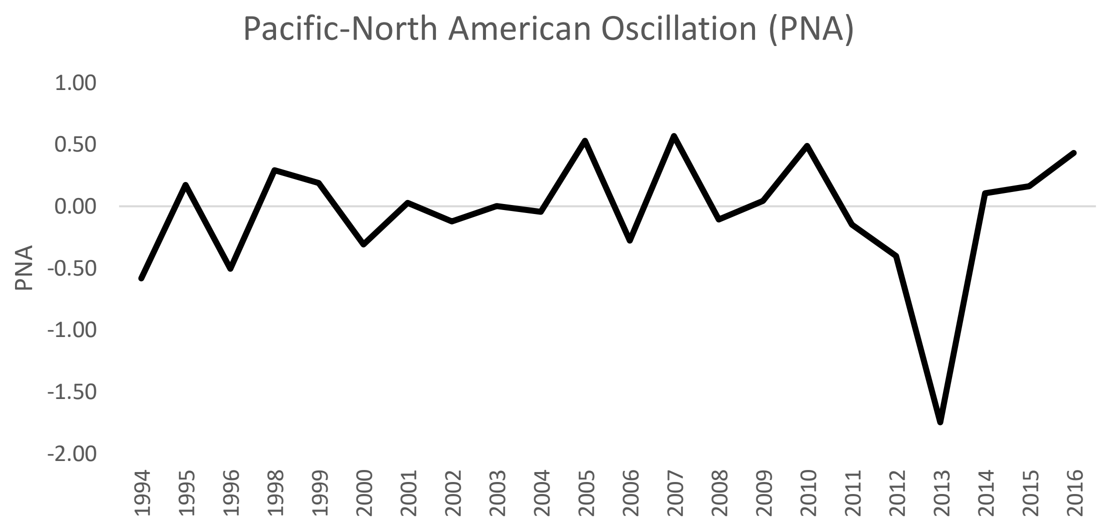

Figure 2.8 Mean yearly PNA recorded by NOAA from 1994 to 2016.

ONI had three negative phases and three positives over the study period. In the first negative phase, the lowest negative value was in 1999, whilst in the second phase there was a reverse phase from negative to positive from 2001 to 2006, that returned negative in 2010 (Figure 2.9). The highest positive value was registered in 2015, which might be considered the beginning of a new positive phase.

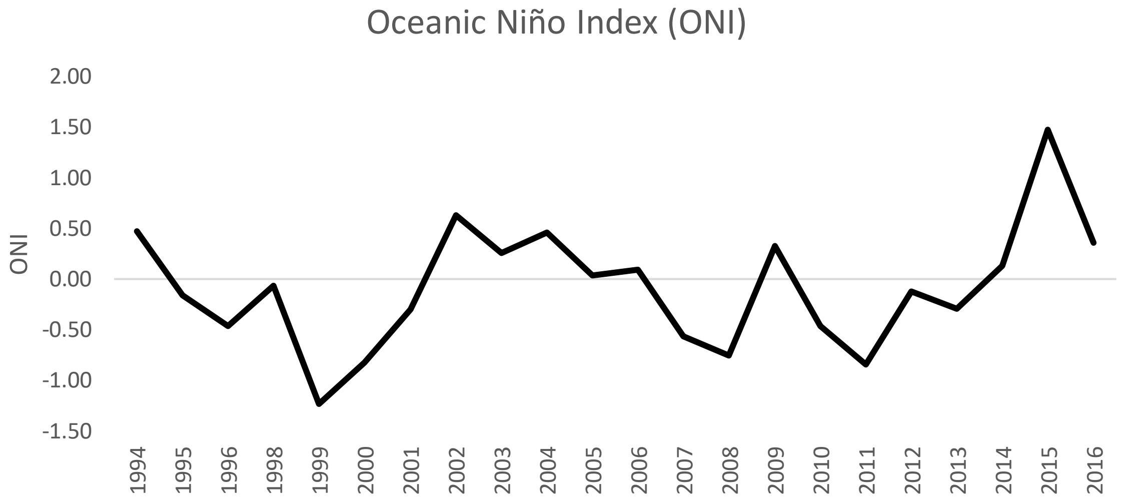

Figure 2.9 Mean yearly ONI recorded by NOAA from 1994 to 2016.

PDO showed over the study period a general trend of negative values, with 1999, 2008 and 2011 having the lowest values (Figure 2.10). However, three distinctive positive values were observed over the study period. The positive values in 1996 preceded the abrupt change to one of the lowest values in 1999. The second peak with positive values was in 2003 is highlighted because this appeared during a negative PDO phase. Finally, the highest positive value was in 2015.

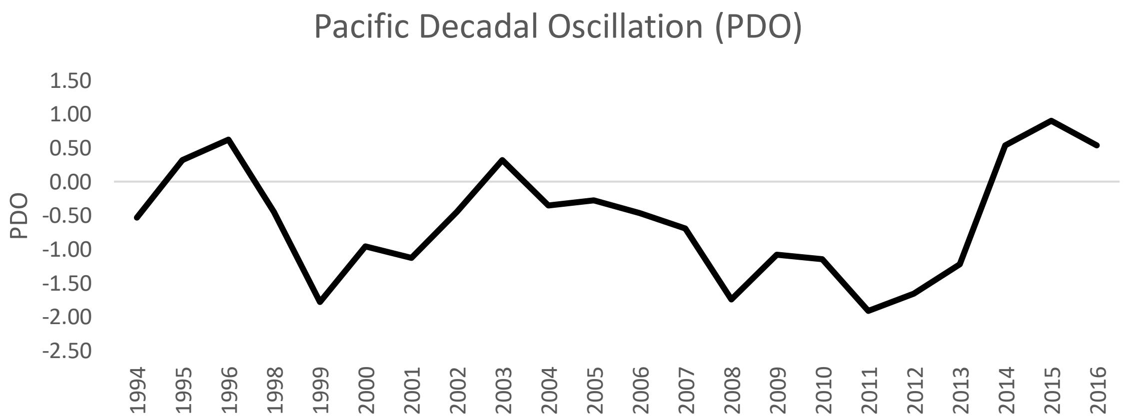

Figure 2.10 Mean yearly PDO recorded by NOAA from 1994 to 2016.

It is observed that the air temperature and rainfall in DNP fluctuated during the study period, where the pair years 1998-1999 recorded low air temperature and low precipitation, while during 2012-2013 there was predominantly low air temperature (Fig. 2.2). Thus, maybe the cool atmospheric conditions resulted in high annual rainfall and snowfall. The opposite effect was observed in 2002-2003, with air temperature increasing in the region and rainfall and snowfall registered low values (Fig. 2.2).

Snow fall during winter might have decreased due to a transition of PNA and ONI from negative to positive during the winter 96-98, resulting in increased air temperature that enhanced rainfall rather than snow precipitation.

2.2.2 Relationships between the large-scale atmospheric patterns and local climate

The observed local climatic annual (mean annual air temperature and mean annual precipitation) and seasonal (spring; temperature and flood, precipitation / winter: snow and temperature) conditions in Interior Alaska were not significantly influenced by the large-scale atmospheric pattern changes (e.g. PDO, ONI, PNA, and EP-NP) as nearly all R^2 values from the regressions were close to zero (Figure 2.11 to 2.17), which indicates no relationship. Dummies (2018) suggested R^2 of 0.70 = strong, R^2 0.50=moderate, R^2 0.30=weak and 0=no relationship. Some relationships with higher (although still weak) values, such as the relationship between PDO and annual temperature, which had an R^2 = 0.34 and a Pearson's r of 0.63 (Figure 2.14).

2.2.3 Relationships between the local climatic variables

All R^2 values obtained from the linear regressions between the local climatic variables (spring flood, spring temperature, spring precipitation, mean annual temperature, mean annual precipitation, winter snow, winter temperature) were low (Table 2.3). The highest R^2 value (0.239) was for the model relating Spring precipitation with spring flood. The full set of pairwise correlations between all variables is provided in Appendix 2.4. All pairwise correlations (of all variable combinations) were less than 0.7.

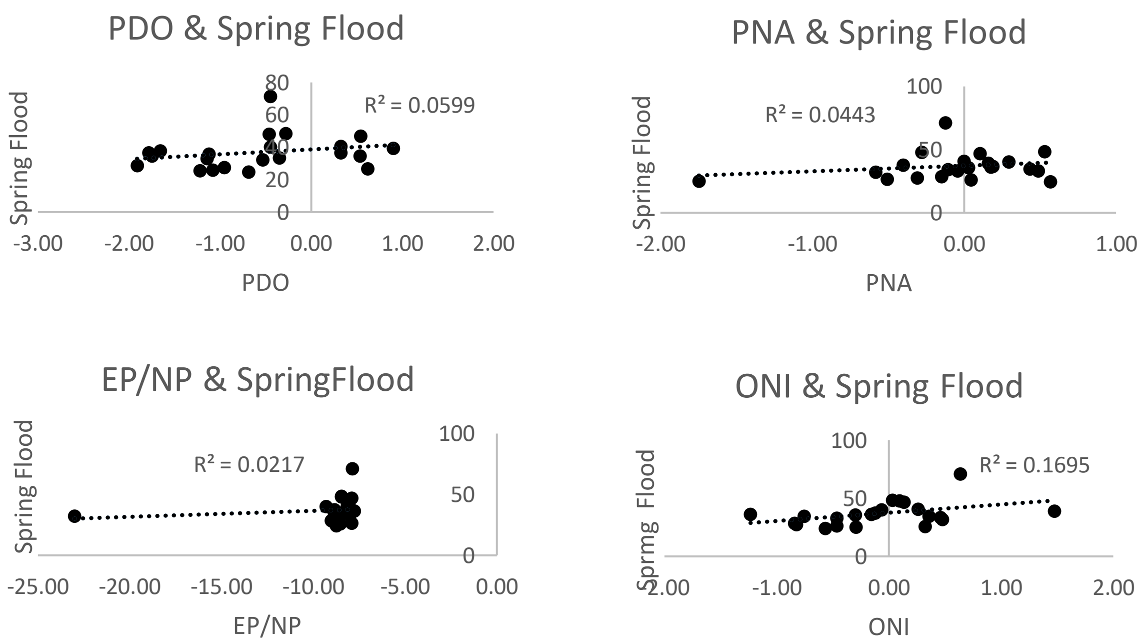

Figure 2.11 Regressions between Spring flood and PDO, ONI, PNA and EP-NP from 1994 to 2016.

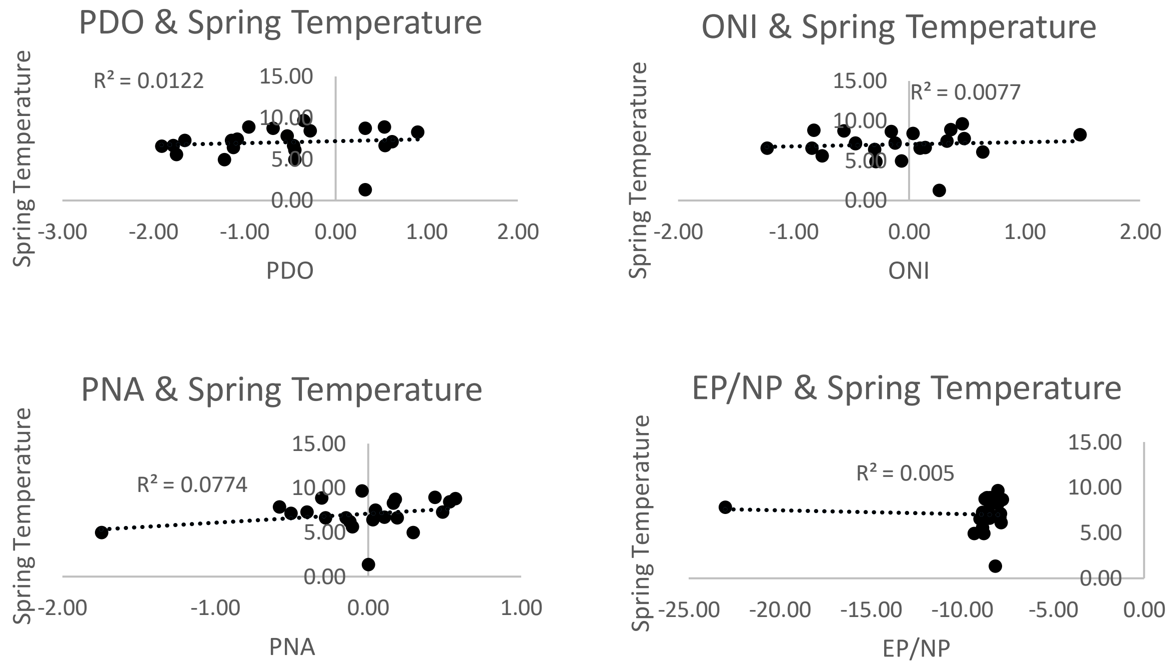

Figure 2.12 Regressions between spring temperature and PSO, ONI, PNA and EP-NP from 1994 to 2016.

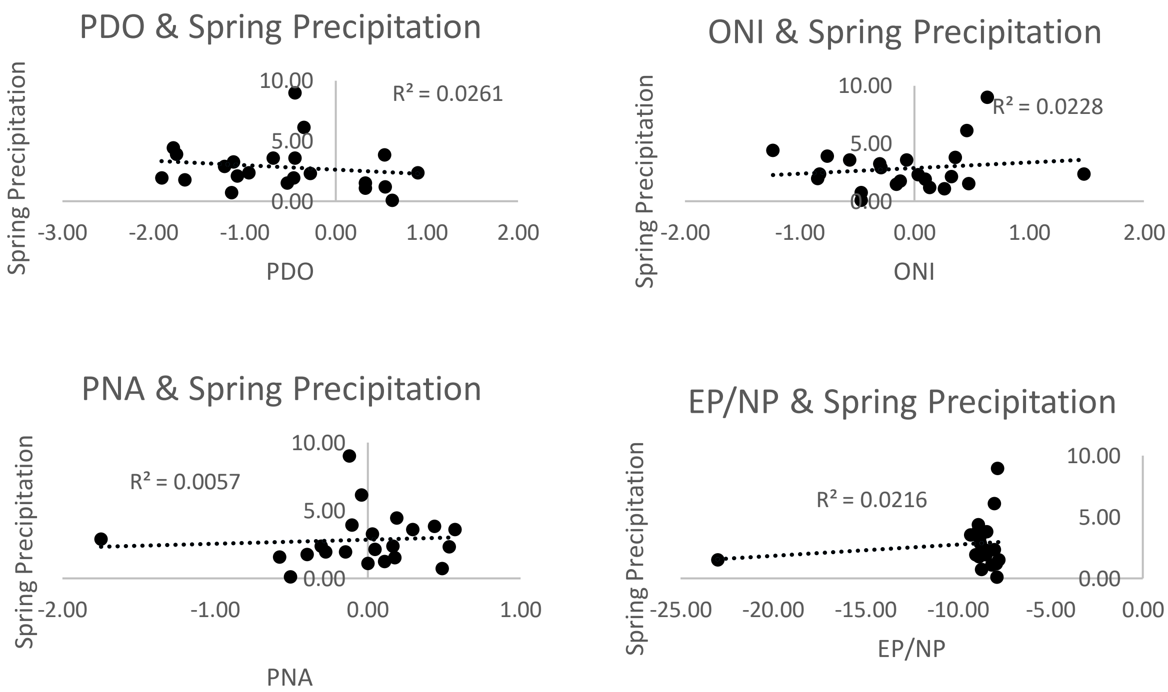

Figure 2.13 Regressions between spring precipitation and PDO, ONI, PNA and EP-NP from 1994 to 2016.

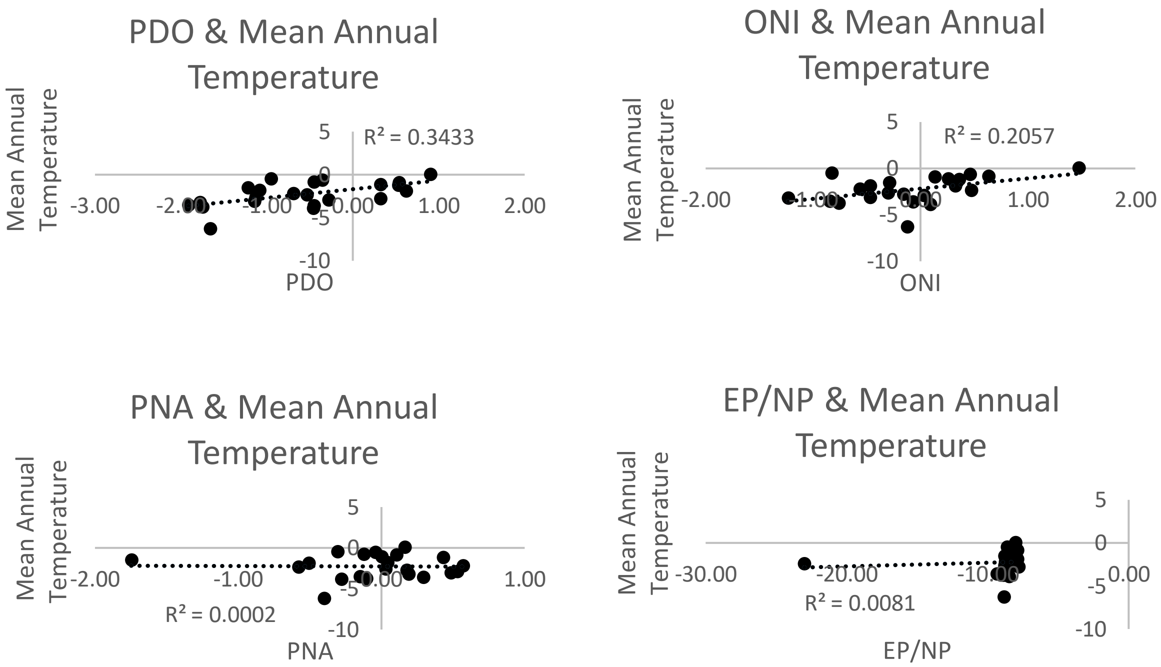

Figure 2.14 Regressions between annual temperature and PDO, ONI, PNA and EP-NP from 1994 to 2016.

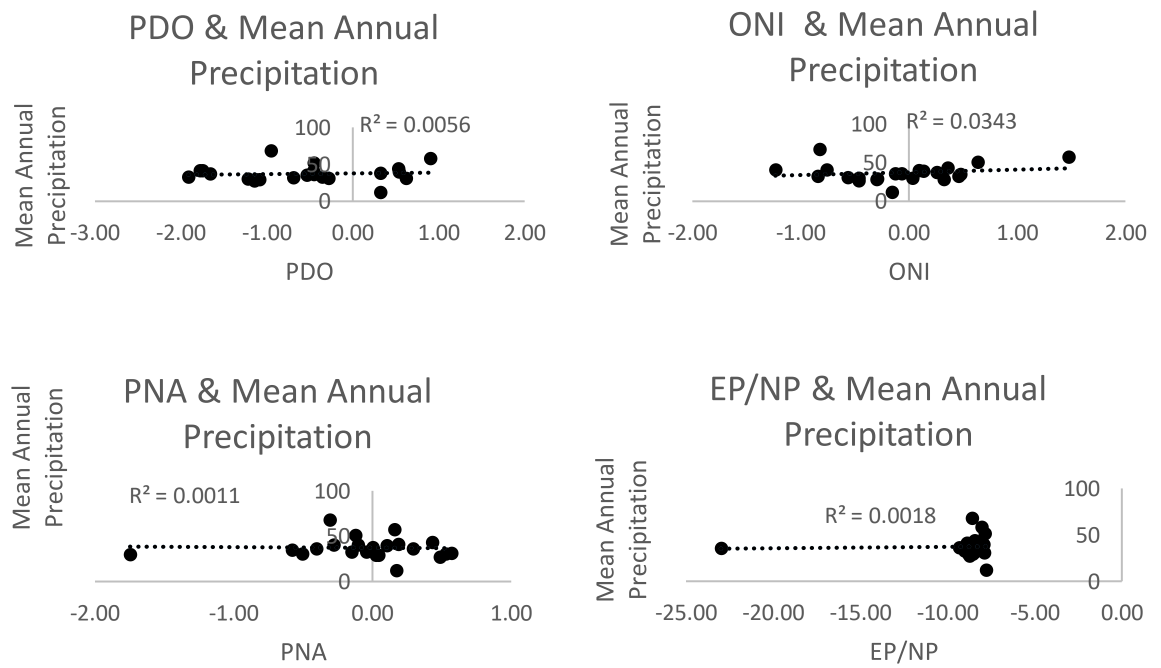

Figure 2.15 Regressions between annual precipitation and PDO, ONI, PNA and EP-NP from 1994 to 2016.

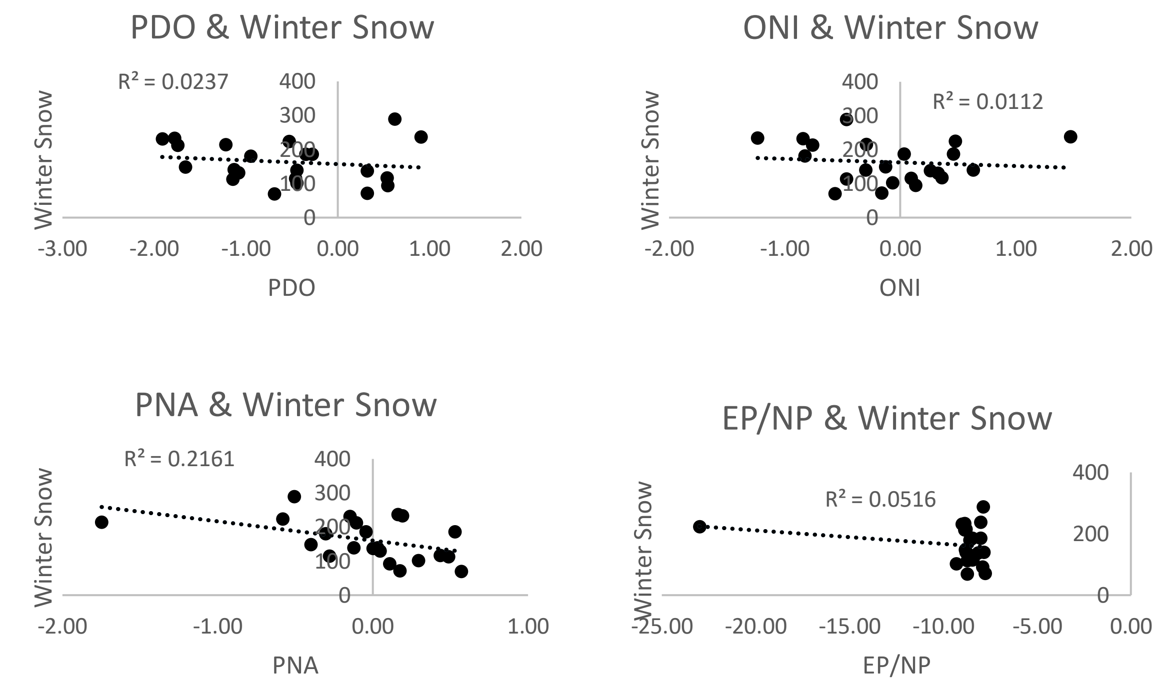

Figure 2.16 Regressions between winter snow and PDO, ONI, PNA and EP-NP from 1994 to 2016.

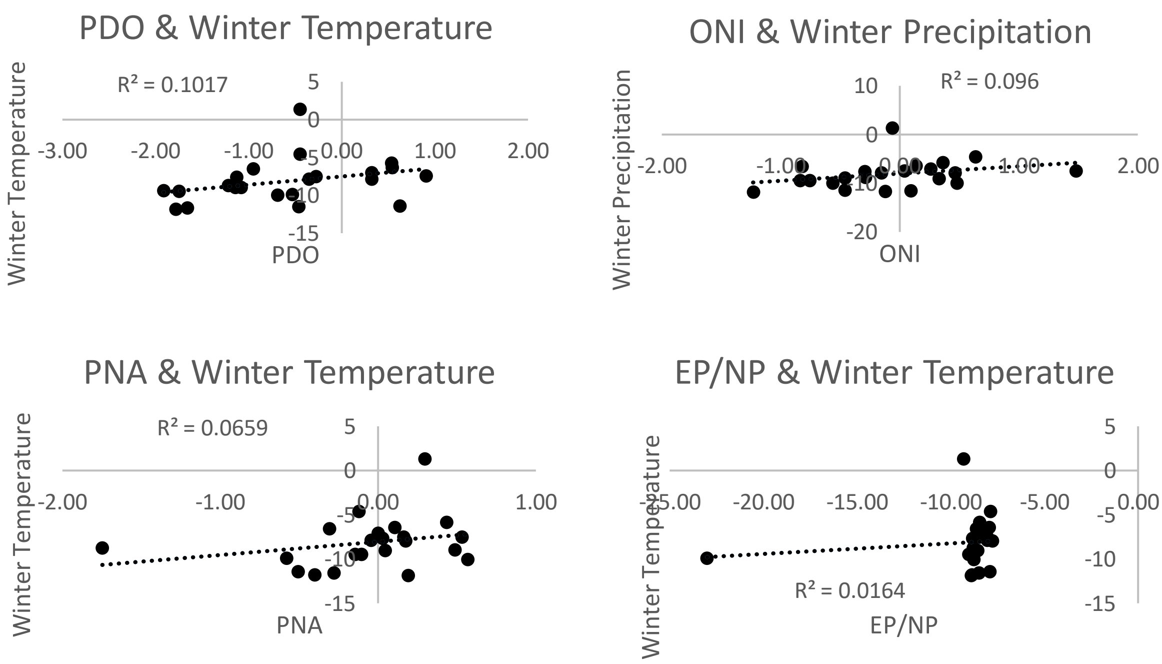

Figure 2.17 Regressions between winter temperature and PDO, ONI, PNA and EP-NP from 1994 to 2016.

Table 2.3 The R2 values of linear regressions between local climatic variables.

Variable	**R2**
Spring Flood - Winter Snow	0.057
Spring Flood - Winter Temperature	0.122
Spring Temperature - Spring Precipitation	0.009
Spring Temperature - Spring Flood	0.039
Spring Precipitation - Spring Flood	**0.239**
Spring Precipitation - Spring Temperature	0.085
MeanAnnualTemperature-Mean AnnualPrecipitation	0.156
MeanAnnual Temperature - Winter Snow	0.008
MeanAnnualTemperature - Winter Temperature	0.101
MeanAnualTemperature - Spring Flood	0.002
MeanAnnualTemperature - Spring Temperature	0.015
MeanAnnualTemperature - SpringPrecipitation	0.049
MeanAnnualPrecipitation - Winter Snow	0.057
MeanAnnualPrecipitation - Winter Temperature	0.042
MeanAnnualPrecipitation - Spring Flood	0.068
MeanAnnualPrecipitation - Spring Temperature	0.001
MeanAnnualPrecipitation - Spring Precipitation	0.087
MeanAnnualPrecipitation - MeanAnnaulTemperature	0.157
Winter Snow - Winter Temperature	0.138
Winter Temperature - Winter Snow	0.057

2.2.4 Positive and negative phases of 5 large-scale atmospheric patterns

The analysis looking at the correlation of these positive and negative phases with local weather conditions showed that local weather often exhibited opposite correlations with the different phases (Table 2.4). Air temperature was positively correlated with a negative phase of PDO, but the correlation was negative with the positive phase of PDO. Seasonal flood during spring showed the opposite correlation pattern with phases of EP-NP; there was a positive correlation with a negative phase of EP-NP and a negative correlation with a positive phase of EP-NP. The same pattern was observed between ONI and PC2, and precipitation during spring with PDO. Seasonal floods during spring were highly positively correlated with NAO in its positive phase, and negatively in its negative phase. A positive correlation was found between a positive phase of ONI with floods, precipitation and air temperature during spring, and they were negatively correlated with ONI in its negative phase. The other local weather variables showing a positive or negative correlation following the phase of the large-scale pattern were precipitation during spring and tempSD with EP-NP, and SnowSD, PC3 and PC4 were positively correlated with PDO in its positive phase, and negatively in its negative phase.

Certain local climatic variables exhibited high correlations with the large-scale atmospheric patterns overall. Rainfall (0.73) and snow (0.74) had a high correlation with ONI in its positive phase. Seasonal flood (0.77) and rainfall (0.69) showed high positive correlation with a positive phase of NAO. PC4 had high positive correlation with PDO and PNA in their positive phase, but were highly negative correlated in their negative phase.

Table 2.4 Pairwise correlation matrix for the local climatic variables and the positive and negative phases of the five large-scale atmospheric pattern variables.

	Mtemp	tempSD	snowSD	SpringTemp	springPrec	SpringFlood	PC1	PC2	PC3	PC4
PDO_Pos.	-0.13	-0.15	0.44	0.05	-0.18	-0.1	0.04	-0.52	0.18	**0.65**
PDO_Neg.	0.37	0.02	-0.13	0.52	0.05	-0.18	0.26	-0.23	-0.23	**-0.65**
NAO_Pos.	-0.08	-0.35	0.36	-0.47	0.53	**0.77**	-0.41	-0.5	**0.69**	0.5
NAO_Neg.	-0.11	0	0.34	-0.39	0.1	-0.15	-0.17	-0.33	0.28	0.21
EP.NP_Pos.	-0.16	0.17	0.12	0.08	0.07	-0.26	0.06	-0.35	-0.24	-0.16
EP.NP_Neg.	0.49	-0.08	-0.28	**0.89**	-0.04	0.27	0.41	-0.52	-0.38	**-0.62**
PNA_Pos.	0.06	-0.31	-0.01	-0.47	**-0.69**	-0.23	0.1	-0.24	-0.34	**0.67**
PNA_Neg.	0.29	-0.03	-0.39	-0.15	-0.32	**-0.69**	0.5	0.1	-0.26	0.15
ONI_Pos.	0.28	-0.47	-0.57	0.34	0.26	0.1	**0.74**	-0.56	**0.73**	0.4
ONI_Neg.	0.49	-0.53	-0.05	-0.2	-0.22	-0.19	0.09	0.22	0.28	0.34

2.3 Discussion

The linear regression models relating large-scale atmospheric patterns with the local climate variables in interior Alaska revealed few significant relationships. However, there was an effect of PDO on annual air temperature, which is in agreement with the results obtained by Papinneau (2001). This suggests that the air temperature anomalies in Alaska may be determined by large-scale atmospheric signals such as PDO; winter temperature at local scales was also affected by ONI and PDO.

However, there was no influence of individual large-scale atmospheric patterns on other local climate variables in DNP, including annual and seasonal rainfall precipitation, snowfall and flooding regimes (Fig. 2.6 -2.9 and Fig. 2.11-2.17). Rather, these local climate variables will be driven by a combination of factors, ranging from the combined effects of multiple broad-scale atmospheric patterns down to finer scale topography, and the interaction with solar radiation and ocean currents, that create the dynamic local weather in interior Alaska (National Oceanic and Atmospheric Administration, 2011).

Of the local climatic variables time series, the only relationship that showed a trend was spring precipitation and spring flood. In sum, air temperature and hydrological regimes are key drivers controlling changes in streams and their habitats, potentially resulting in variation in the macroinvertebrate community. This will be explored in subsequent chapters. The rise in air temperature was followed by a reduction in snow fall, whereas the areas covered with snow and ice increased melting caused floods during spring. In addition, the intensity as well as the time duration of climatic events are altered by climate change (Bradley & Ormerod, 2001), leading to expected warmer winters and floods in streams located in northern latitudes (Puckridge et.al., 2000; Bradley & Ormerod, 2001).

3 Macroinvertebrate community dynamics, persistence and compositional stability from 1994-2016

3.0 Introduction

Freshwater biodiversity at global, regional and local scales is influenced by environmental variables, such as, water temperature and habitat heterogeneity, that influence stream habitat conditions (Jackson & Füreder, 2006; Pace et. al. 2013; Vinke et. al. 2015). Macroinvertebrates in streams across subarctic and arctic areas are sensitive to seasonal environmental conditions and extreme climatic events, which causes changes to community composition (Vinke et. al. 2015). However, the persistence and compositional stability of the macroinvertebrate community within a stream might be greatest with relatively constant environmental conditions or with slow changes over time when the environmental conditions fluctuate slowly through time (Brown et. al. 2005). Persistence in the macroinvertebrate community implies the ability to initially resist disturbance and/or the ability to recover rapidly from a disturbance (resilience); both elements involve adaptation to habitat variability including physiological adjustments, changes in life cycles and the use of refugia. Refugia are typically geographical units with a relative environmental stability than the surrounding landscape providing stable habitats conditions for living organisms, (Brown et. al. 2005; Keppel et.al. 2018; Milner et. al., 2006). Compositional stability reflects the resistance of elements to change with respect to taxa abundance in response to disturbance over time i.e. the less change in relative abundance of taxa over time (Milner et. al. 2006). Hence, in order to understand the mechanisms driving biodiversity patterns it is important to have an appropriate spatial and temporal knowledge of the relationship between species and habitat conditions.

Harsh environmental conditions and severe or unpredictable physical disturbances can cause population losses in stream ecosystems (Bradt et. al. 1999; Jacobsen & Dangles, 2011; Vinke et. al. 2015). Precipitation, temperature, floods, fires, droughts, channel instability (Milner et.al.2006) due in part to anthropogenic activities (Magurran et.al 2010, Milner et.al. 2016) are the most common environmental variables having a strong impact on macroinvertebrate assemblage structure in streams. However, fluctuations in air temperature and precipitation are considered the main drivers influencing physical stream characteristics, as they lead to increasing or decreasing water temperature, water volume and sediment transport (Brown et. al. 2005; Khaliq & Gachon, 2010; Whitfield et.al. 2010; Worthington et. al., 2015).

Long-term datasets are essential to understanding changes taking place in stream macroinvertebrate communities caused by natural or anthropogenic disturbances (Collier 2008, Jackson & Füreder, 2006). Interannual variations in macroinvertebrate populations are affected at different spatial and temporal scales by climatic events causing variations in macroinvertebrate structure (Brown et. al. 2005, Jackson & Füreder, 2006), Therefore, in order to identify variations through time in benthic community composition, reflecting the presence and absence of changes by environmental conditions (Brown et al. 2006; Magurran et al. 2010), samples were collected at the same time every year during the study years.

Biological monitoring conducted in aquatic ecosystems using long-term datasets is important for monitoring water quality and to understand temporal effects on macroinvertebrate community (e.g. functional groups, trophic structure, diversity, stability and persistence) and to isolate the environmental variables causing gradual or abrupt changes in biodiversity (Füreder & Schöner, 2013; Milner et. al., 2006). Taxa belonging to the Ephemeroptera, Plecoptera and Trichoptera (EPT) orders are typically sensitive to disturbances in freshwaters ecosystems, such as water temperature, oxygen content, water velocity and pH, and thus are used as indicators of water quality (Vilenica et.al. 2016). Furthermore, to know and understand the factors affecting macroinvertebrate community in freshwaters, long-term studies are vital in ecological terms, but also for biodiversity conservation purposes (Luoto and Nevalainen, 2015), because changes in species composition provide information about the environmental conditions in aquatic ecosystems (Bradt et. al. 1999).

This long-term study of 10 pristine streams of DNP, Alaska over 22 years (1994-2016) was undertaken to examine the interaction between environmental variables and macroinvertebrate communities, to understand which seasonal or annual climatic events have forced a shift in macroinvertebrate communities.

The objectives of this long-term study were to examine:

(i) the dynamics of the macroinvertebrate communities from 1994 to 2016 and identify key indicator taxa of change, (ii) the persistence and compositional stability of the macroinvertebrate communities (year to year) of the ten streams over the study period, and (iii) the significant environmental variables influencing benthic community change, persistence and compositional stability over time.

3.1 Methods and Data Analysis

As a first step, the abundance of the main taxonomic groups was plotted for each site using bar plots. Indicator species for each stream were then obtained using the IndVal index and applying the approach of Dufrene and Legendre as outlined in Boccard et.al. (2011), which combines species mean abundance and their frequency of occurrence in each stream, using the environmental variables. The years were grouped based on their similar environmental conditions across different streams. Hence, high indicator values or the most prominent species (indicator species) per stream were obtained by combining the large mean abundance from one group of species compared to other group (specificity) and their presence in most years of that group (fidelity).

Macroinvertebrate persistence and compositional stability of macroinvertebrate communities from 10 pristine streams were examined using successive pair years. Jaccard similarity coefficient (J) was used to calculate the persistence of identified taxa. Compositional stability was measure using 1-Bray-Curtis (BC) in order to obtain dissimilarity distances between years. 1-Bray-Curtis was used so that the Jaccard metric and 1-Bray-Curtis varied in the same direction. Both indices take values from 0 to 1, where 0 shows no persistence or compositional stability and 1 represents high persistence/compositional stability (Milner et.al. 2006).

Individual simple regressions were then undertaken linking each local climate variable in turn (Winter Snow, Mean Snow, Spring Temp, Mean Temp, Spring Precip, Spring Flood, Winter Temp, Mean Prec) as outlined in Chapter2 with J and 1-BC, for each site. To undertake a regression analyses to infer the casual relationships between the dependent variable and a collection of independent variables, data must have some of the following assumptions as they are natural variables (not experimental manipulated variables): 1; data must have been collected randomly, 2; all variables have valid values according to the established minimum and maximum values, 3; the explanatory variables should not be colinear to avoid redundancy in the analyses, and 4; variables with many missing values were eliminated (Tabachnick & Fidell, 1996). Hence, in order to infer the causal relationship between species persistence and compositional stability for each stream and environmental data were formatted and these assumptions checked, using Excel.

A time series multiple regression was then performed to analyze the relationship between persistence and stability, and a series of local climatic variables. For each site and the global dataset, a linear regression model with a time series component was fitted using the tslm function in the forecast R package. This linear regression model allows both the response variables and the predictions to be a time series and includes a term ("trend") that models the time trend in the data. The variables used as predictor variables were: mean annual air temperature, snow depth and mean precipitation. The model was fitted twice to these variables, once using persistence as a response and once using composition stability. The persistence and composition stability time series for each site were also plotted along with the climatic time series data to visually inspect the patterns (Appendix 3.6).

3.2 Results

3.2.1 Macroinvertebrate community structure across the long-term record (1994-2016) for 10 streams

3.2.1.1 Assemblage dynamics

Chironomidae showed the highest abundance in the ten streams (typically > 200 /m^2, e.g. Tattler Creek > 328 /m^2, Hogan > 930 /m^2) over the study period (Figs. 3.1-3.10). *Baetis* (Baetidae) was the most abundant mayfly, collected in all streams (Fig. 3.1 to 3.10) with a mean value of 100 individuals per m^2 with the next most abundant *Epeorus* (Heptageniidae) averaging > 50 /m^2, but > 100 per m^2 in Igloo Creek. The most abundant stonefly was *Capnia* (Capniidae) with a mean > 50 /m^2 and the highest abundance in Hogan Creek with a mean of 151 individuals per m^2. Another stonefly *Ostrocerca* (Nemouridae) registered the highest numbers in N4 (> 50 /m^2), followed by Tattler Creek (43 /m^2) and Highway Creek (35 m^2). Tattler Creek supported the highest mean abundance with 265 individuals m^2 followed by Hogan Creek with 131 /m^2. N4 supported the lowest mean abundance at 36 /m^2.

The indicator taxa analysis (Table 3.1) showed that the most common genera over the study period was *Doddsia* (Plecoptera), as highlighted in the global analysis. *Doddsia* was present in six streams, followed by *Dicranota* (Diptera) appearing in two streams. Then, Plecoptera had four different indicator species (*Doddsia*, *Ostrocerca*, *Isoperla* and *Plumiperla*). In Hogan Creek these were *Doddsia* and *Ostrocerca*, in Sanctuary River *Doddsia* and *Isoperla*, and in Savage River *Doddsia* and *Plumiperla*. Diptera were indicators in a number of rivers; *Simullidae* (Highway Creek), *Rhabdomastix* (Sanctuary River), *Dicranota* (Tattler Creek) and *Dicranota, Clinocerinae and Oligochaetae* (East Fork Toklat Tributary). Ephemeroptera, Trichoptera and Annelida showed the lowest number of indicator species in this study.

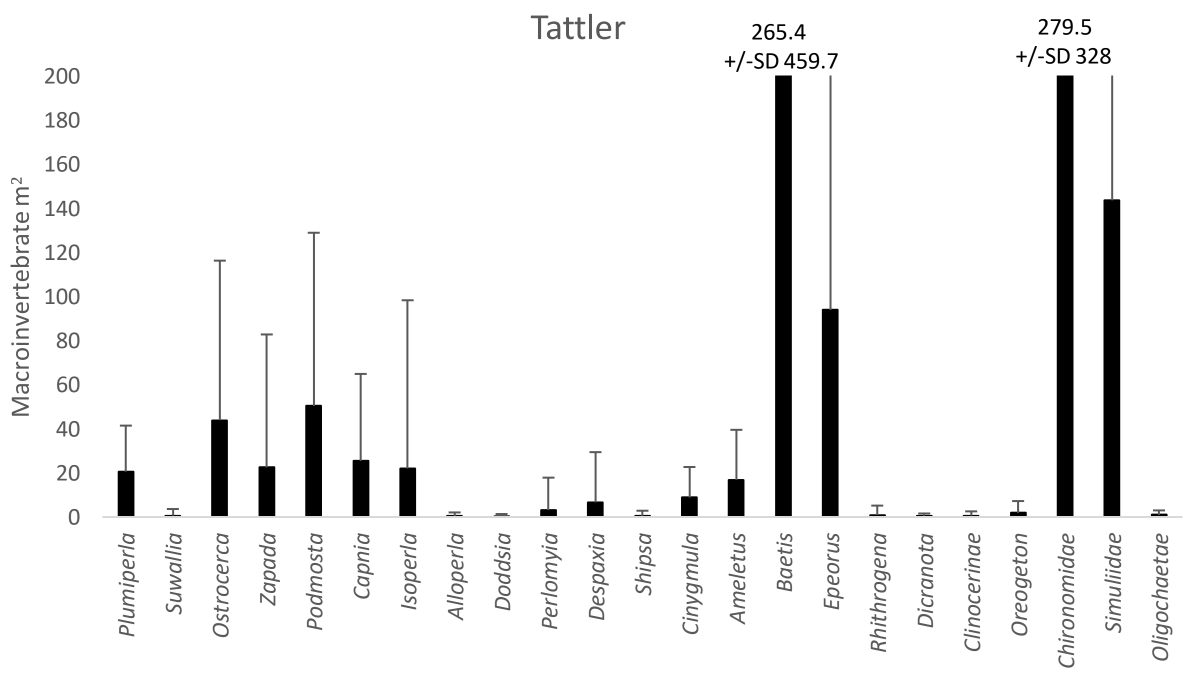

Figure 3.1 Tattler Creek. Macroinvertebrate mean annual abundance (+/- 1SD) from Tattler Creek from 1994 to 2016 (excluding 1997).

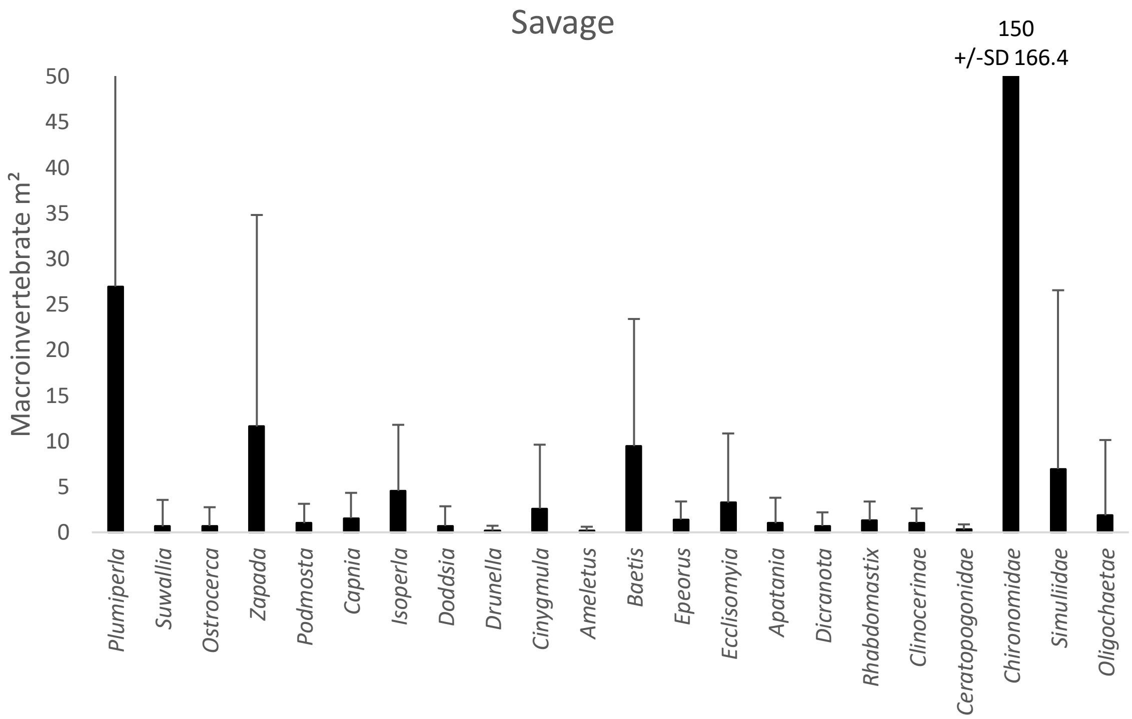

Figure 3.2 Savage River. Macroinvertebrate mean annual abundance (+/- 1sd) from Ravage River from 1994 to 2016 (excluding 1997).

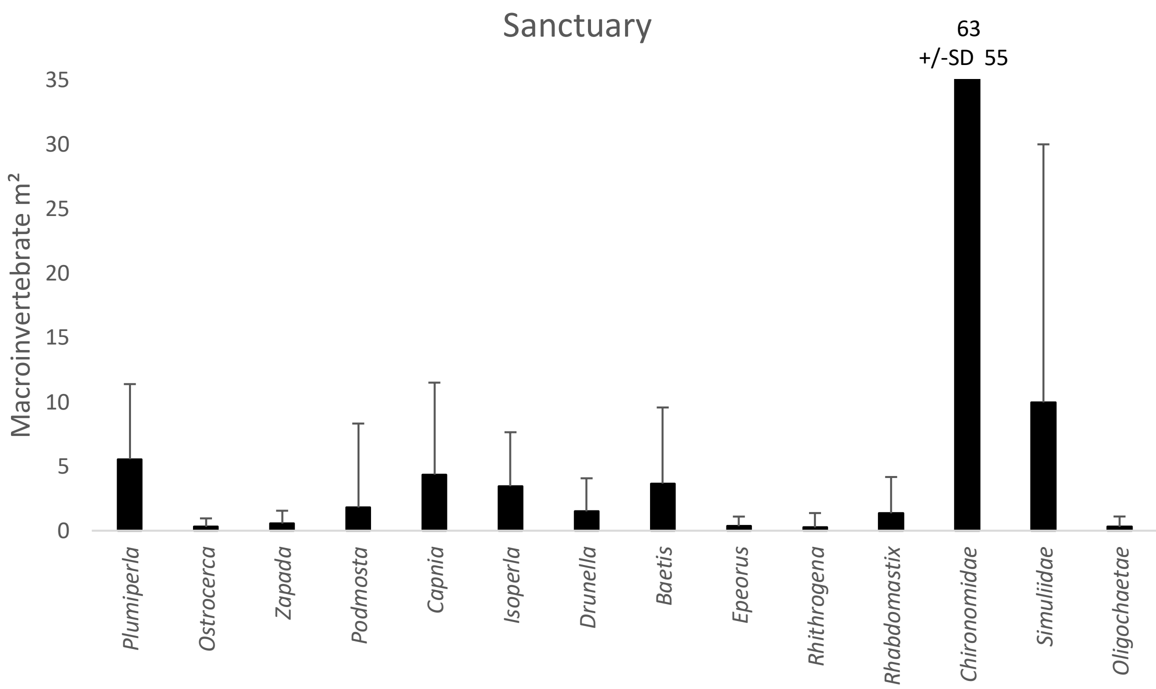

Figure 3.3 Sanctuary River. Macroinvertebrate mean annual abundance (+/- 1SD) from Sanctuary River from 1994 to 2016 (excluding 1997).

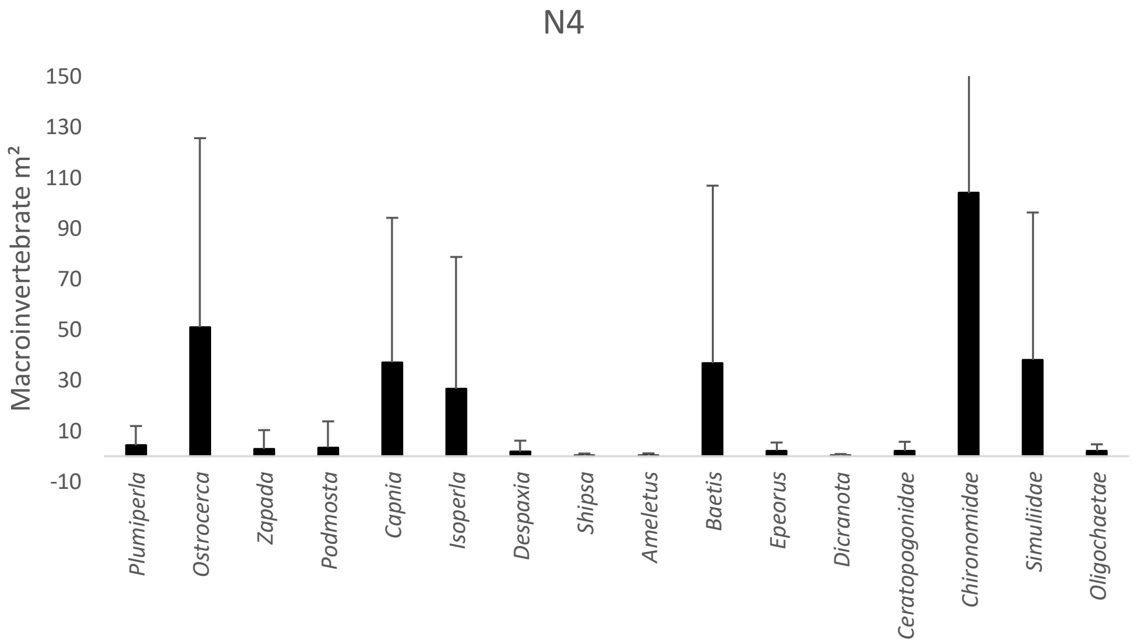

Figure 3.4 N4. Macroinvertebrate mean abundance (+/- 1sd) from n4 from 1994 to 2016 (excluding 1997).

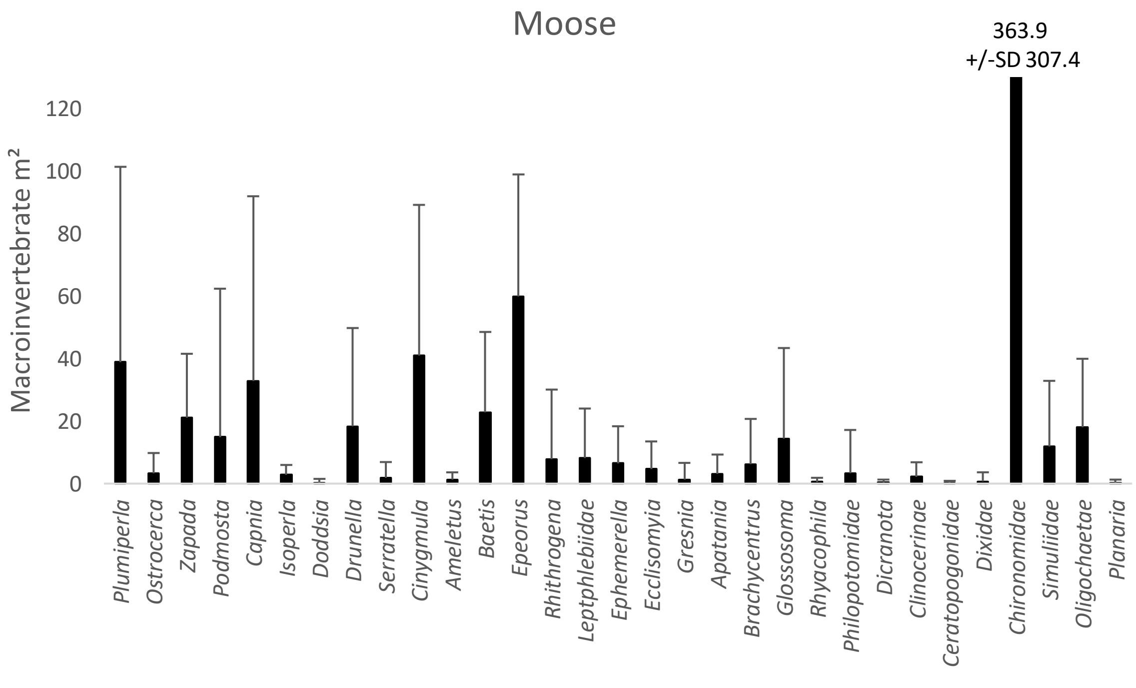

Figure 3.5 Moose Creek. Macroinvertebrate mean annual abundance (+/- 1sd) from Moose Creek from 1994 to 2016 (excluding 1997).

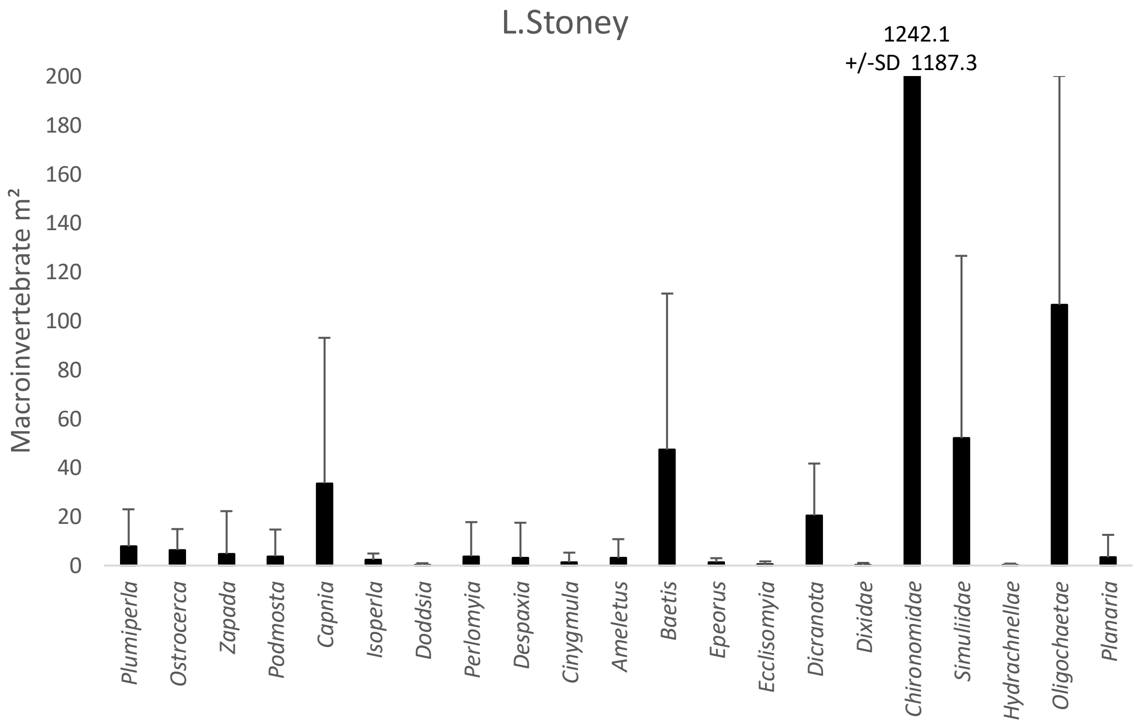

Figure 3.6 Little Stoney Creek. Macroinvertebrate mean annual abundance (+/- 1sd) from L. Stoney Creek from 1994 to 2016 (excluding 1997).

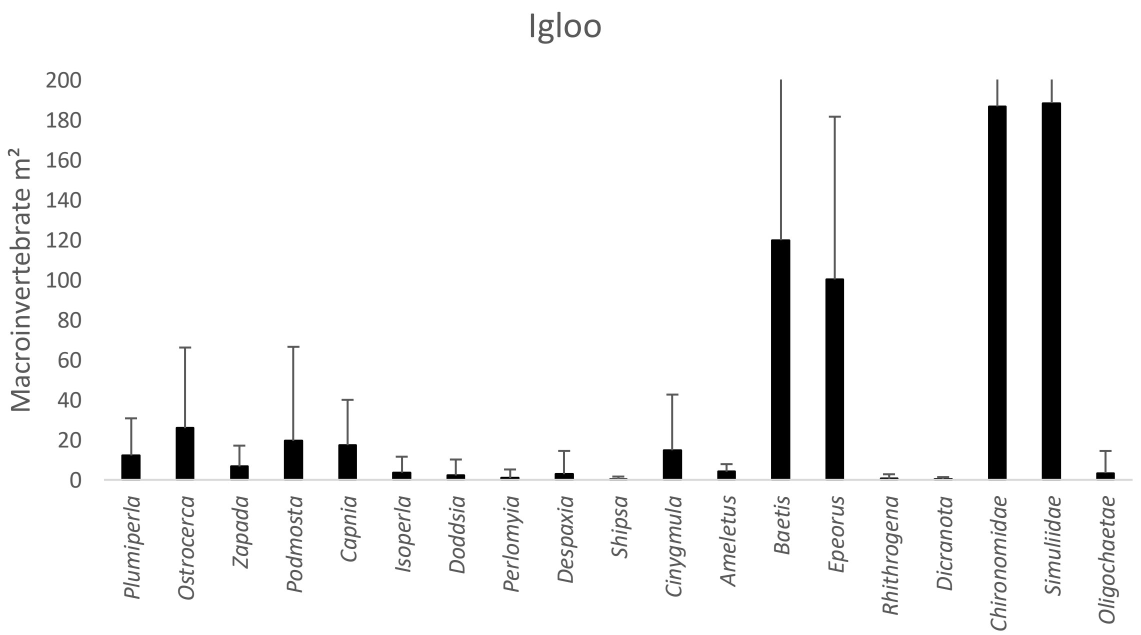

Figure 3.7 Igloo Creek. Macroinvertebrate mean annual abundance (+/- 1sd) from Igloo Creek from 1994 to 2016 (excluding 1997).

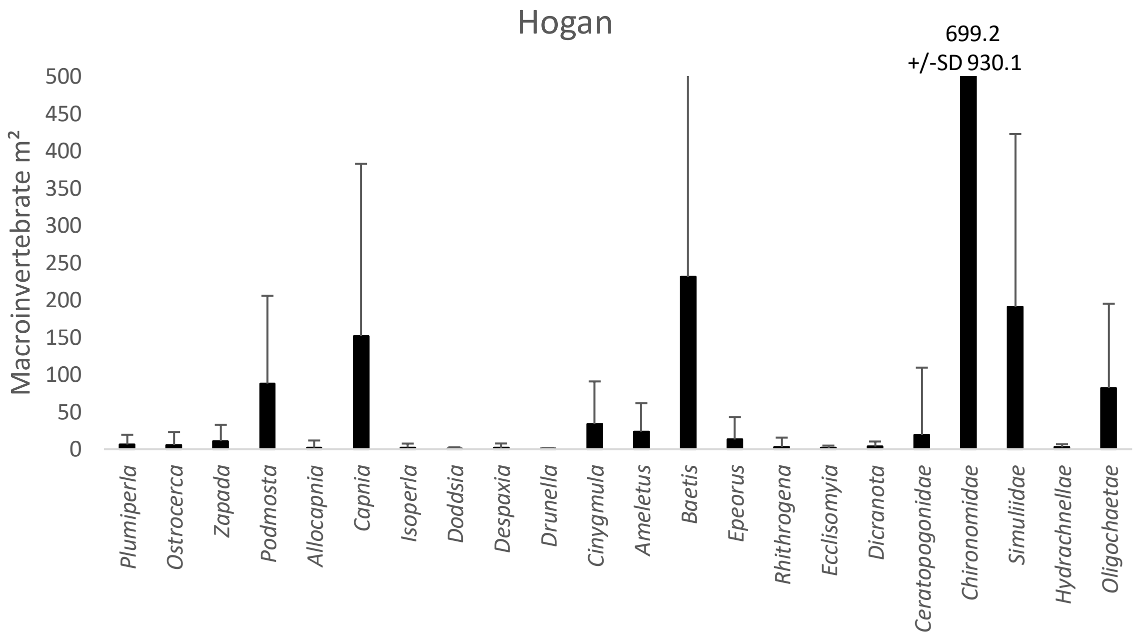

Figure 3.8 Hogan Creek. Macroinvertebrate mean annual abundance (+/- 1sd) from Hogan Creek from 1994 to 2016 (excluding 1997).

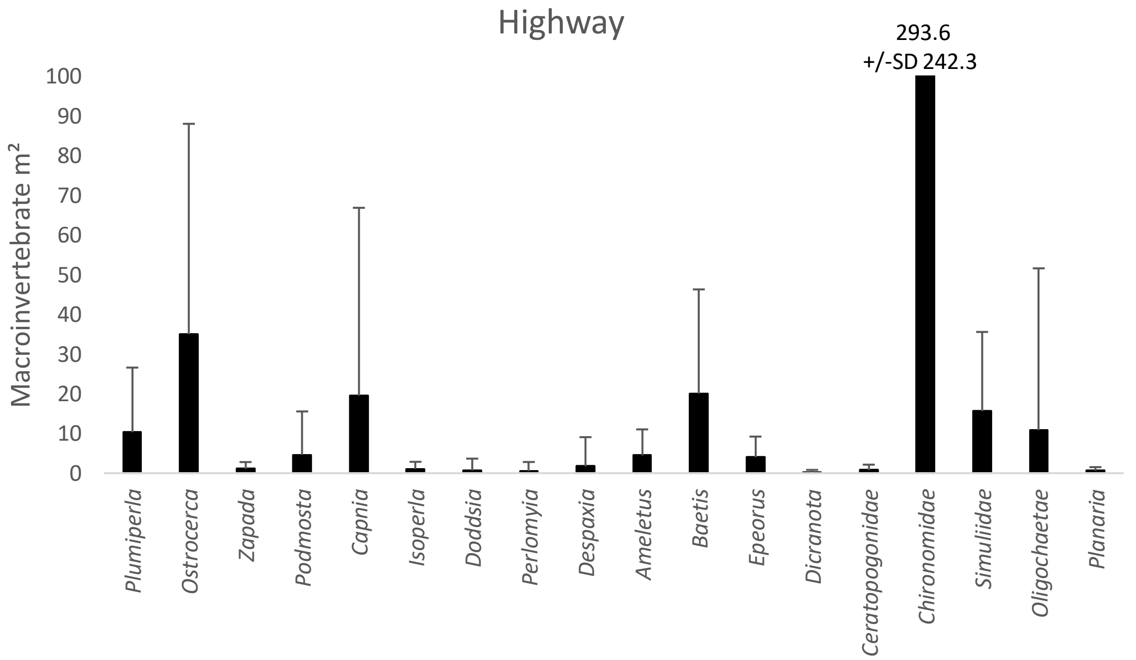

Figure 3.9 Highway Creek. Macroinvertebrate mean annual abundance (+/- 1sd) from Highway Creek from 1994 to 2016 (excluding 1997).

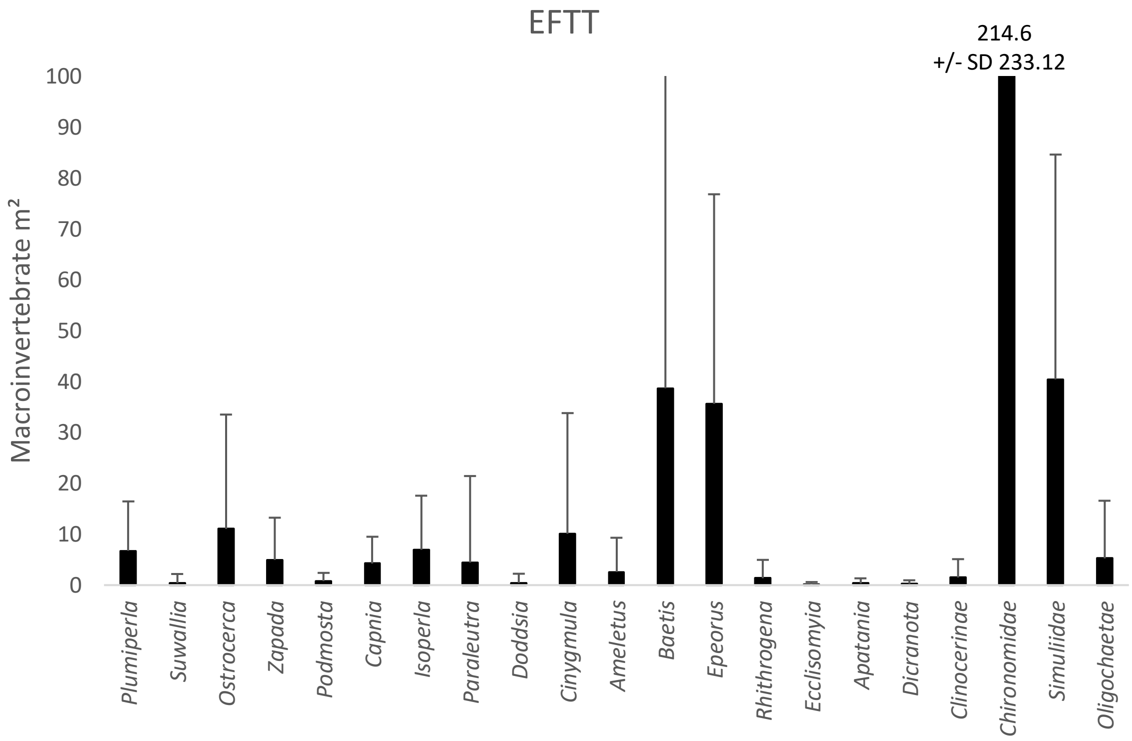

Figure 3.10 East Fork Tolkat Tributary. Macroinvertebrate mean annual abundance (+/- 1SD) from EFTT from 1994 to 2016 (excluding 1997)

Table 3.1 Indicator genera/families per each stream using IndVal index. (/) no indicator taxa were selected. Dufrene and Legendre approach (Boccard et.al. 2011).

Stream	**Ephemeroptera**	**Plecoptera**	**Trichoptera**	**Diptera**
East Fork Tolkat Tributary	/	*Doddsia*	/	*Dicranota,* Clinocerinae, Oligochaetae
Highway Creek	/	/	/	Simullidae
Hogan Creek	/	*Doddsia, Ostrocerca*	/	/
Igloo Creek	/	*Doddsia*	/	/
Little Stoney Creek	/	/	*Ecclisomyia*	/
Moose River	*Ephemerella*	/	/	/
N4	/	/	/	/
Sanctuary River	*Drunella*	*Doddsia, Isoperla*	/	*Rhabdomastix*
Savage River	/	*Doddsia. Plumiperla*	/	/
Tattler Creek	/	/	/	*Dicranota*
Global	/	*Doddsia*	/	/

3.2.1.2 Community persistence and stability

In the analysis of the 10 streams (Fig. 3.11 and 3.12), the years with the highest persistence (J=1) were between 2010 and 2011, and the lowest persistence (J=0.56) was for the pair year 2006-2007. Overall, the persistence varied widely among the ten streams (Fig. 3.11-3.22). However, the global analysis showed that the highest mean values over the year pairs between 2010 and 2014 and the lowest mean values were registered in the pair years 2002-2003 and 2006-2007 (Fig. 3.11). The creeks that showed the highest overall mean values of J were Tattler Creek (0.67 range 0.27 to 0.93), Igloo Creek (0.72 range 0.5 to 0.91) and East Fork Tolkat Tributary (0.66 range 0.33 to 1) (Figs. 13, 19 and 22). The lowest mean persistence was recorded for Savage River with a mean J = 0.46 (range 0.16 to 0.81) and Sanctuary River with a mean of J = 0.47 (range 0.14 to 0.81) (Fig. 3.14 and 3.15).

Similarly, compositional stability in the 10 streams showed the highest value (1-BC=1) in the year pair 2010-2011 and the lowest (1-BC = 0.56) between 2006-2007 (Fig. 3.11). The same 3 streams also showed the highest mean compositional stability; Igloo Creek (0.82; 0.66 to 0.95) Hogan Creek (0.76; 0.46 to 0.96) and East Fork Tolkat Tributary (0.77; 0.47 to 1), but also Tattler Creek (0.78; 0.42 to 0.94) (Fig. 3.12). Savage River had the lowest compositional stability with a mean 1-BC = 0.60 (range 0.28 to 0.87). The compositional stability varied over the time for the ten streams. The highest compositional stability (Fig. 3.11) was observed in different consecutive pair years (Fig.3.11-3.22) from 2010-2011 to 2013-2014, except for 1998-1999 registered in Savage (Fig. 3.2). The lowest compositional stability occurred at different pair years, for East Fork Tolkat Tributary, Savage River, Hogan Creek, Highway Creek and Tattler Creek it occurred in 2007-2008. Igloo and N4 had three consecutive pair years with low compositional stability from 2000-2001 to 2003-2004, whilst for Sanctuary was in 2004-2005, Moose 2005-2007, 2007-2009 and L. Stoney 2002-2003.

Finally, it was observed that persistence and compositional stability does not follow similar patterns in Savage River and Highway Creek. In Savage River, from the pair year 2008-2010 to 2010-2011 compositional stability increased but persistence decreased (Fig. 3.14). Highway, during the year pairs 2006-2007 and 2007-2008 showed an increase in persistence but a decrease in compositional stability (Fig. 3.21).

Table 3.2 Descriptive R2 values for models relating community persistence (Jaccard similarity) /compositional stability (1 -Bray-Curtis distances) to local environmental variables (see appendix 3.1).

Stream	Winter Snow cm		Mean Snow cm (annual)		Spring Temp °C		Mean Temp °C (annual)		Spring Precip cm		Spring Flood		Winter Temp °C		Mean Prec cm (annual)	
	J	1-BC	J	1-BC	J	1-BC	J	1-BC	J	1-BC	J	1-BC	J	1-BC	J	1-BC
Global	0.0480	0.0730	0.0570	0.2670	0.0150	0.0120	0.0000	0.0020	**0.3940**	**0.3670**	0.0950	**0.9500**	0.0470	0.0810	0.0040	0.0790
Esat Fork Tolkat Tributary	0.0100	0.1050	0.0590	0.0540	0.1430	0.1340	0.0900	0.0750	0.3570	0.3790	0.0060	0.0030	0.0580	0.0560	0.1170	0.0840
Little Stoney Creek	0.2100	0.2400	0.1110	0.1450	0.0660	0.0740	0.0280	0.0250	0.3720	0.3710	0.1290	0.1690	0.0060	0.0160	0.0050	0.0010
Moose River	0.0220	0.0390	0.0190	0.0380	0.0820	0.0930	0.0000	0.0010	0.2970	0.2640	0.0020	0.0001	0.3850	0.4700	0.0210	0.0100
N4	0.0300	0.0450	0.0030	0.0040	0.0890	0.1130	0.0040	0.0010	0.2410	0.2490	0.0440	0.0320	0.0220	0.0150	0.1560	0.1630
Santuary River	0.0020	0.0070	0.0010	0.0050	0.0070	0.0030	0.0150	0.0180	0.3890	0.3610	**0.9590**	0.1630	0.0005	0.0000	0.0040	0.0010
Savage River	0.0080	0.0090	0.0080	0.0050	0.1810	0.0250	0.0270	0.0140	0.1290	0.0720	0.0770	0.0260	0.1150	0.2330	0.0010	0.0110
Highway Creek	0.1220	0.0310	0.1560	0.0250	0.0090	0.0030	0.1270	0.0420	0.0000	0.0370	0.0290	0.0009	0.0080	0.0100	0.1430	0.0460
Hogan Creek	0.0050	0.0090	0.0040	0.0080	0.0070	0.0070	0.0580	0.0520	0.1100	0.1500	0.0070	0.0012	0.0120	0.0090	0.0080	0.0120
Igloo Creek	0.0990	0.1070	0.0030	0.2480	0.0330	0.0280	0.0330	0.0610	0.0850	0.0920	0.0260	0.0190	0.0640	0.0620	0.4310	0.0900
Tattler Creek	0.0350	0.0300	0.0470	0.0420	0.1420	0.1190	0.0470	0.0260	0.0320	0.0240	0.0001	0.0015	0.0096	0.0160	0.0040	0.0080

Table 3.3 Descriptive R2 values for models relating community persistence (Jaccard similarity) /compositional stability (1 -Bray-Curtis distances) to four large-scale environmental variables.

Stream	PDO		ONI		PNA		EP-NP	
	J	BC	J	BC	J	BC	J	BC
Global	0.0180	0.0160	0.0490	0.0003	**0.116**	**0.113**	0.046	0.038
East Fork Tolkat Tributary	0.053	0.048	0.047	0.053	0.009	0.015	0.132	0.121
Little Stoney Creek	0.0008	0.002	0.014	0.043	0.0004	0.002	0.008	0.015
Moose River	0.003	0.0007	0.009	0.011	0.19	0.227	0.01	0.004
N4	0.056	0.032	0.0004	0.006	0.001	0.003	7.00E-11	0.0008
Sanctuary River	**0.627**	**0.726**	0.234	0.015	0.102	0.117	0.007	0.006
Savage River	0.003	0.069	0.005	0.088	0.295	0.004	0.013	0.011
Highway Creek	0.123	0.016	0.002	0.026	0.205	0.193	0.105	5.00E-06
Hogan Creek	0.01	0.004	0.009	0.011	0.149	0.145	0.004	0.012
Igloo Creek	0.031	0.021	0.002	7.00E-06	0.056	0.043	0.098	0.095
Tattler Creek	0.044	**0.787**	3.00E-05	0.001	0.185	0.163	0.008	0.011

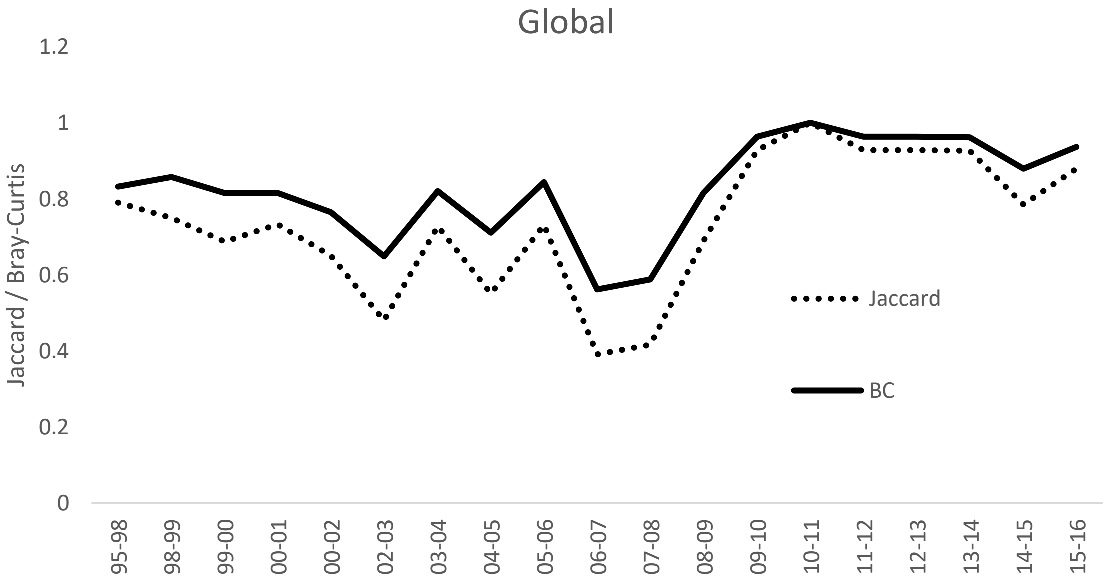

Figure 3.11 Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs for all streams.

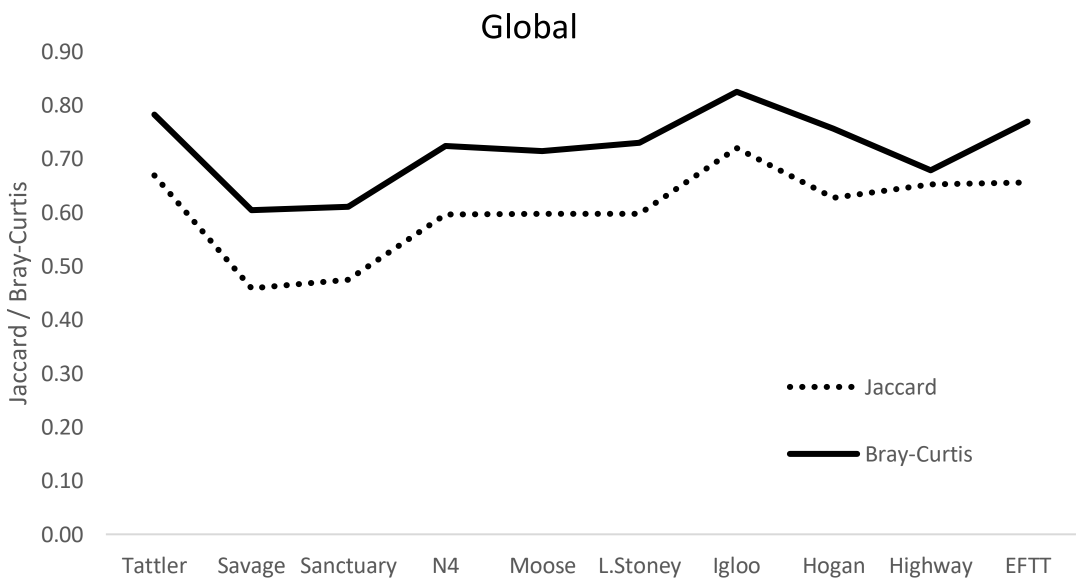

Figure 3.12 Mean global persistence (Jaccard) and mean stability (1-Bray-Curtis) of the macroinvertebrate community between year pairs from 1994 to 2016.

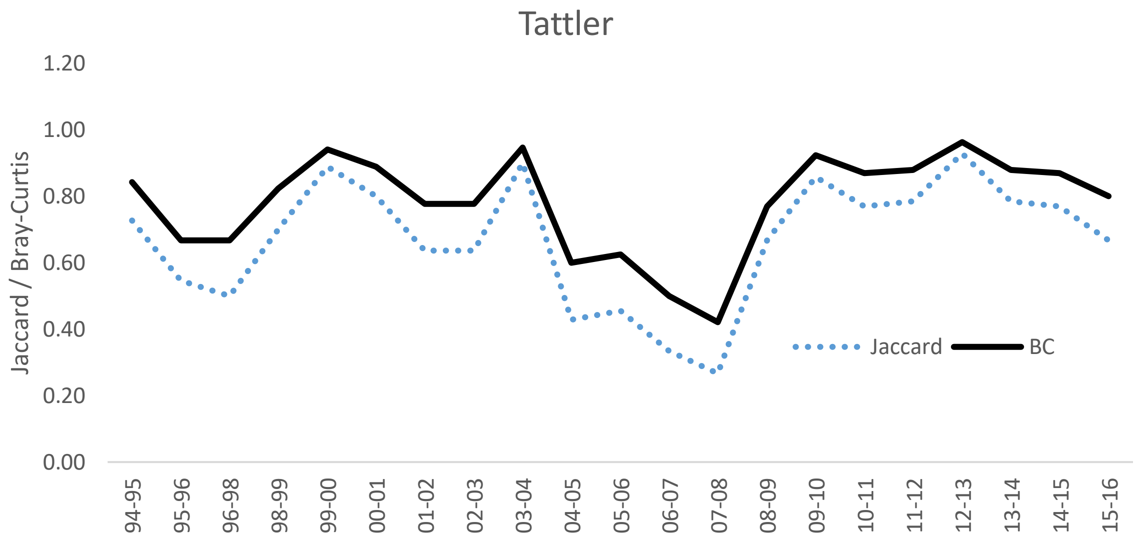

Figure 3.13 Tattler Creek. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

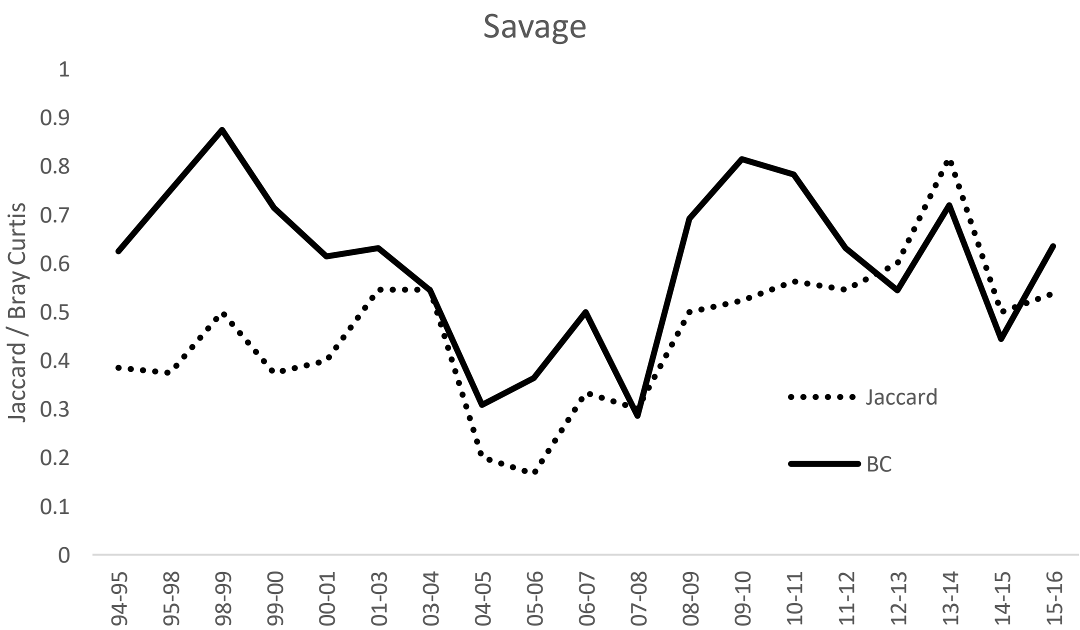

Figure 3.14 Savage River. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

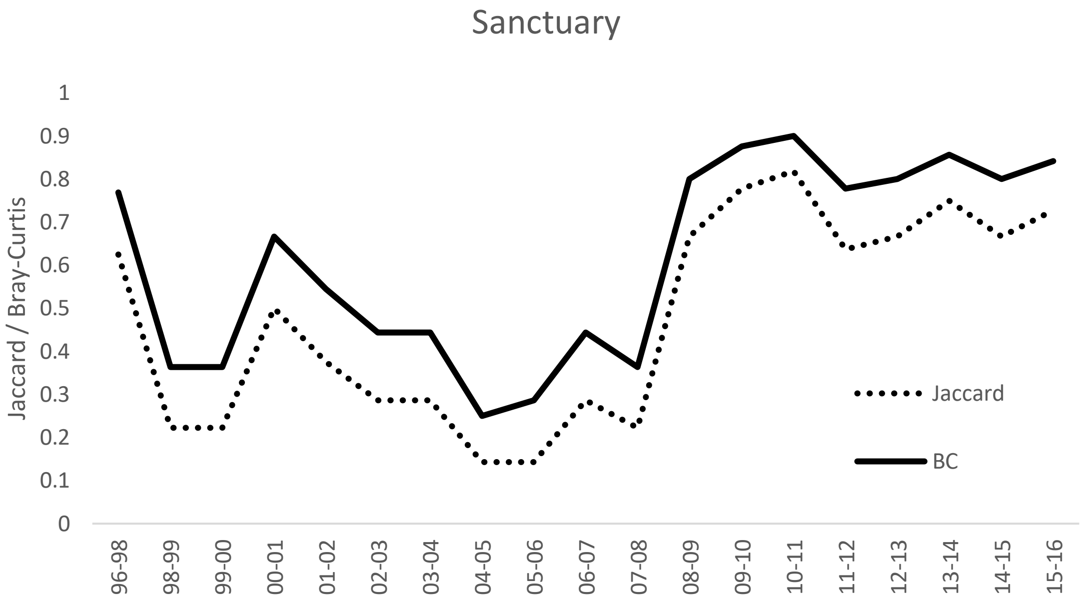

Figure 3.15 Sanctuary River. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

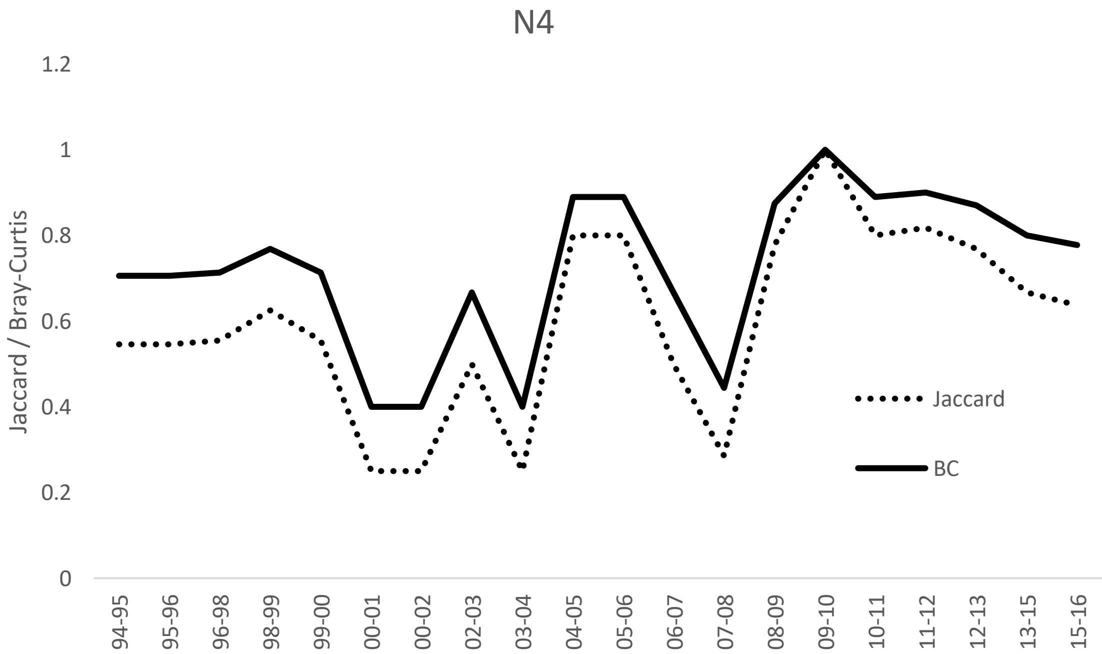

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Figure 3.16 N4. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

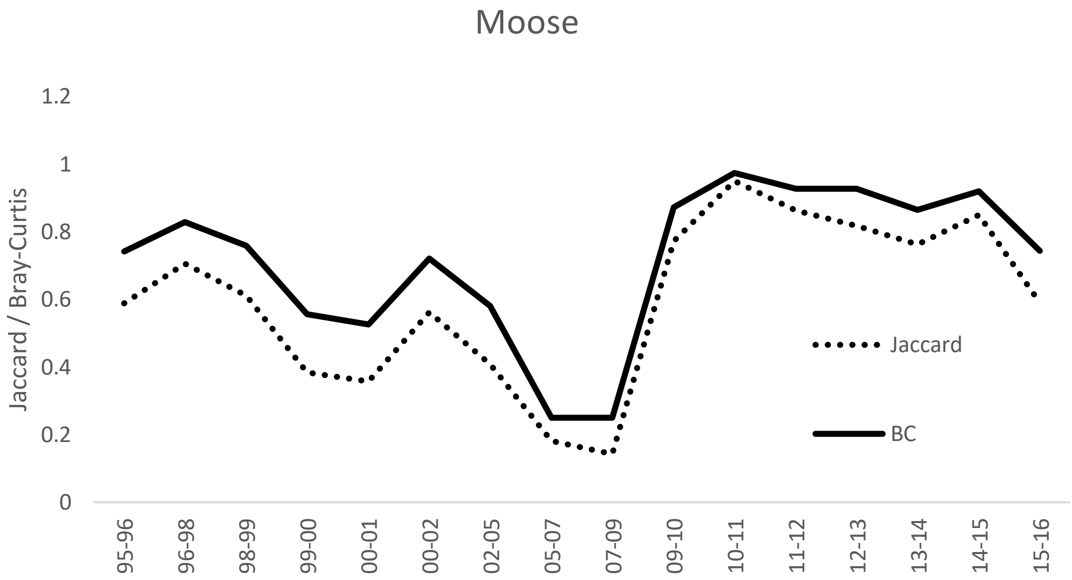


Figure 3.17 Moose Creek. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

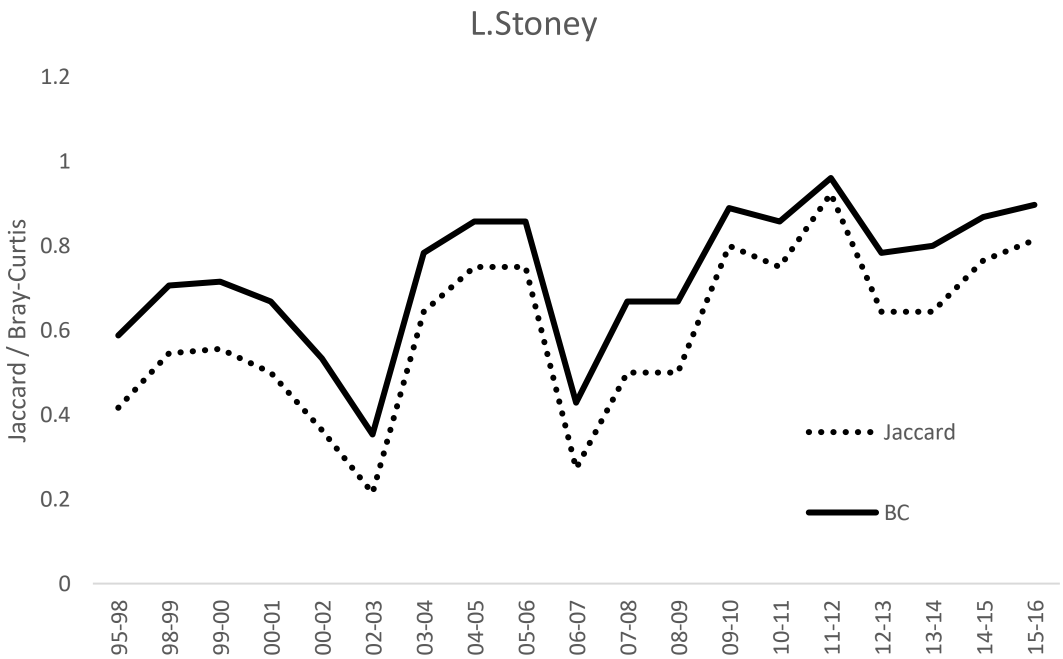


Figure 3.18 Little Stoney Creek. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

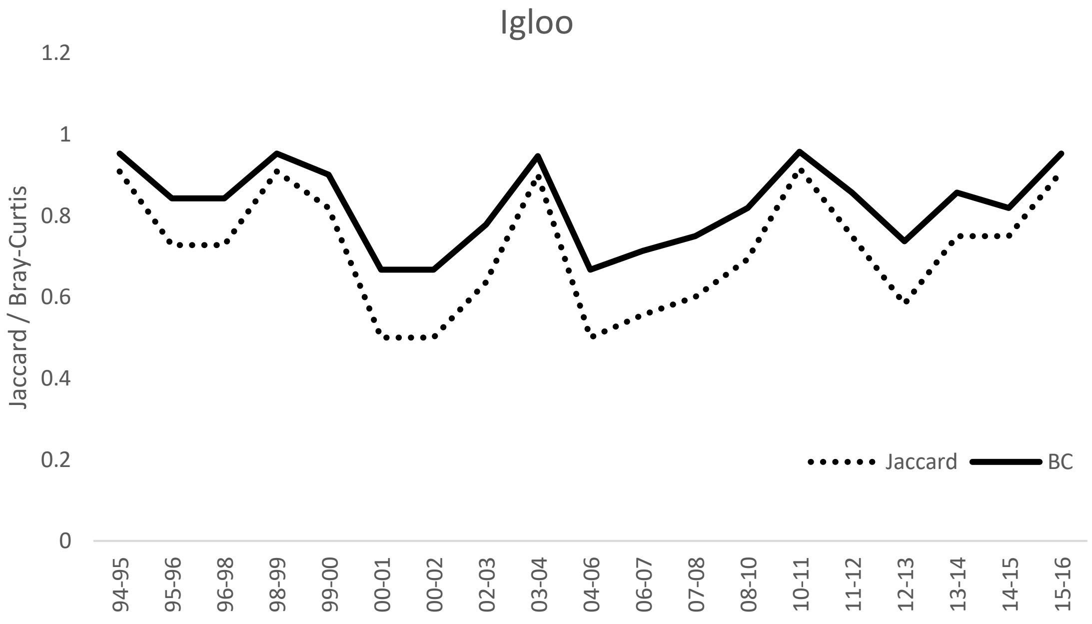


Figure 3.19 Igloo Creek. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

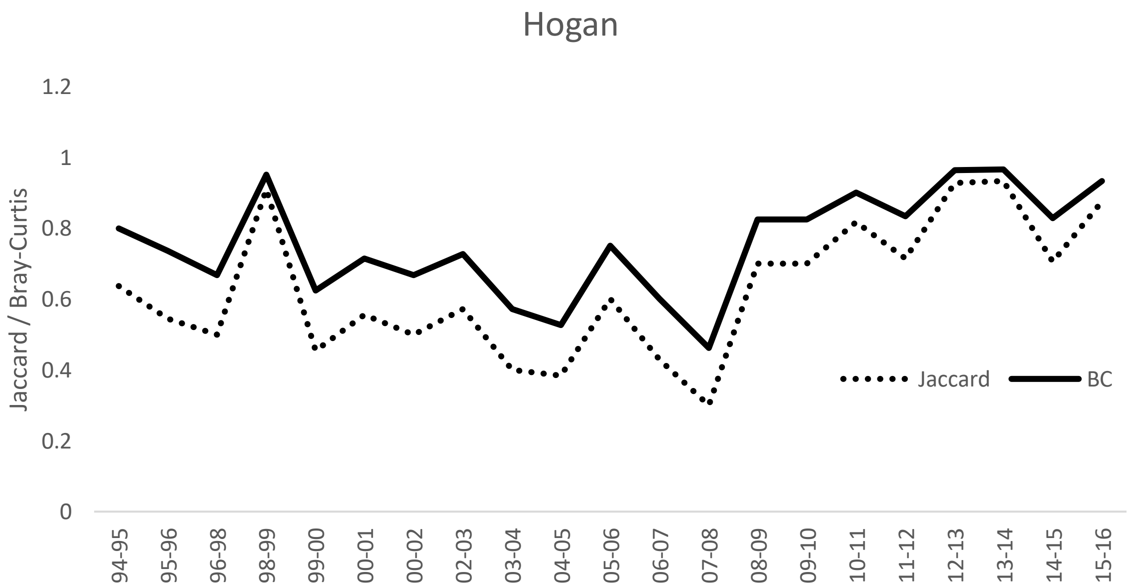


Figure 3.20 Hogan Creek. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

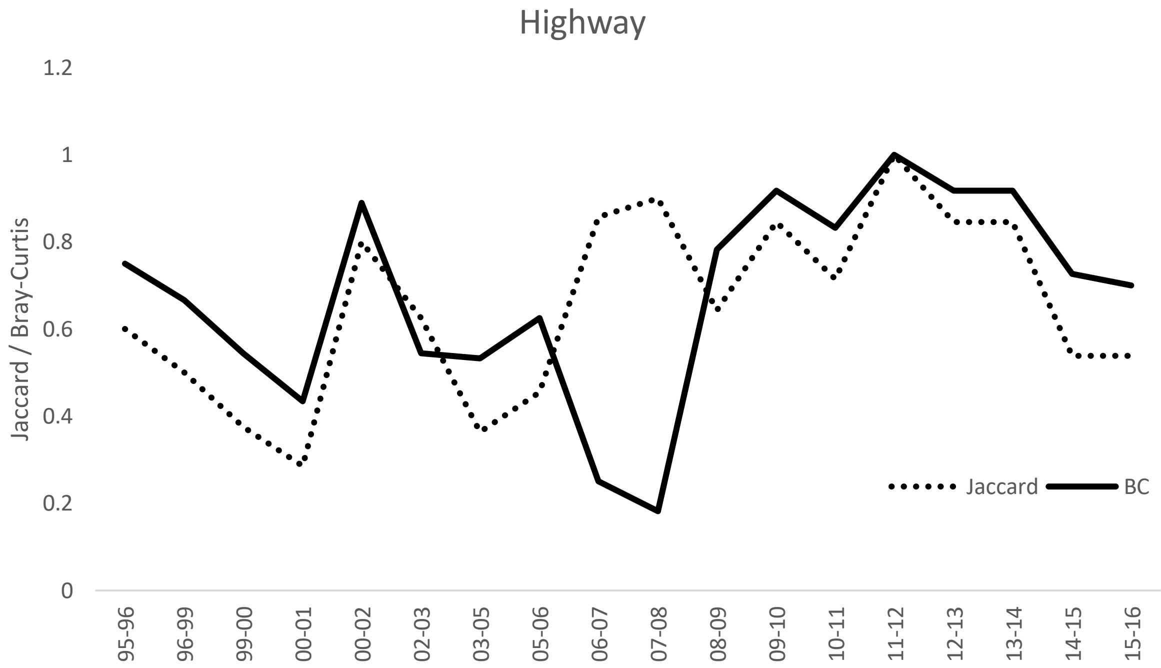


Figure 3.21 Highway Creek. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

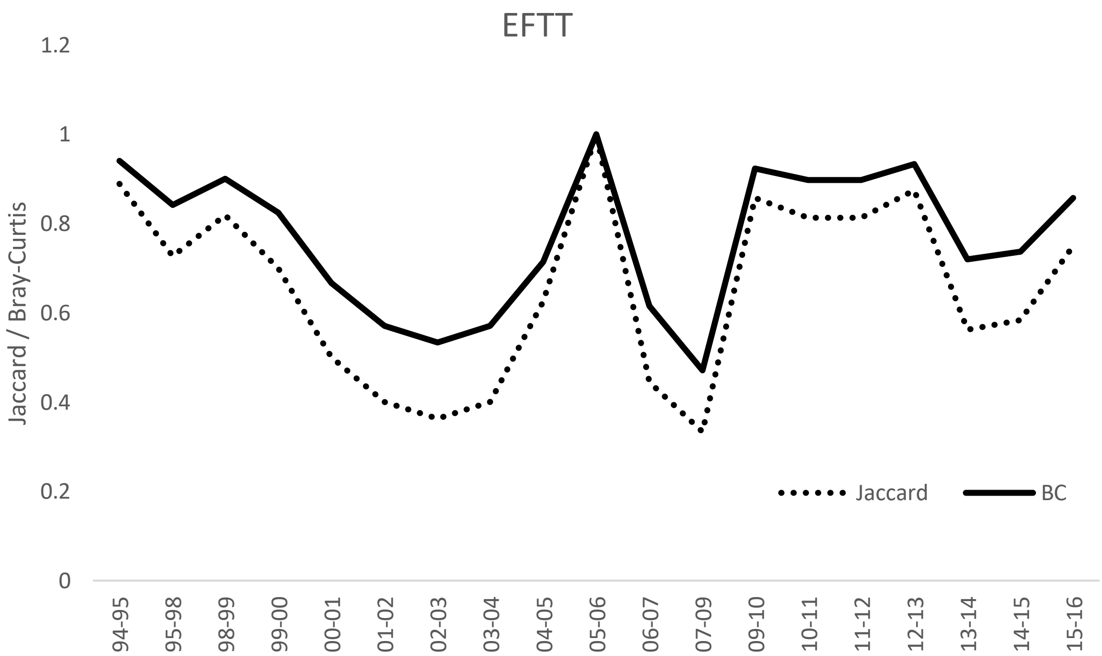


Figure 3.22 East Fork Tolkat Tributary. Community persistence (Jaccard similarity) and compositional stability (1-Bray-Curtis distance) between year pairs from 1994 to 2016.

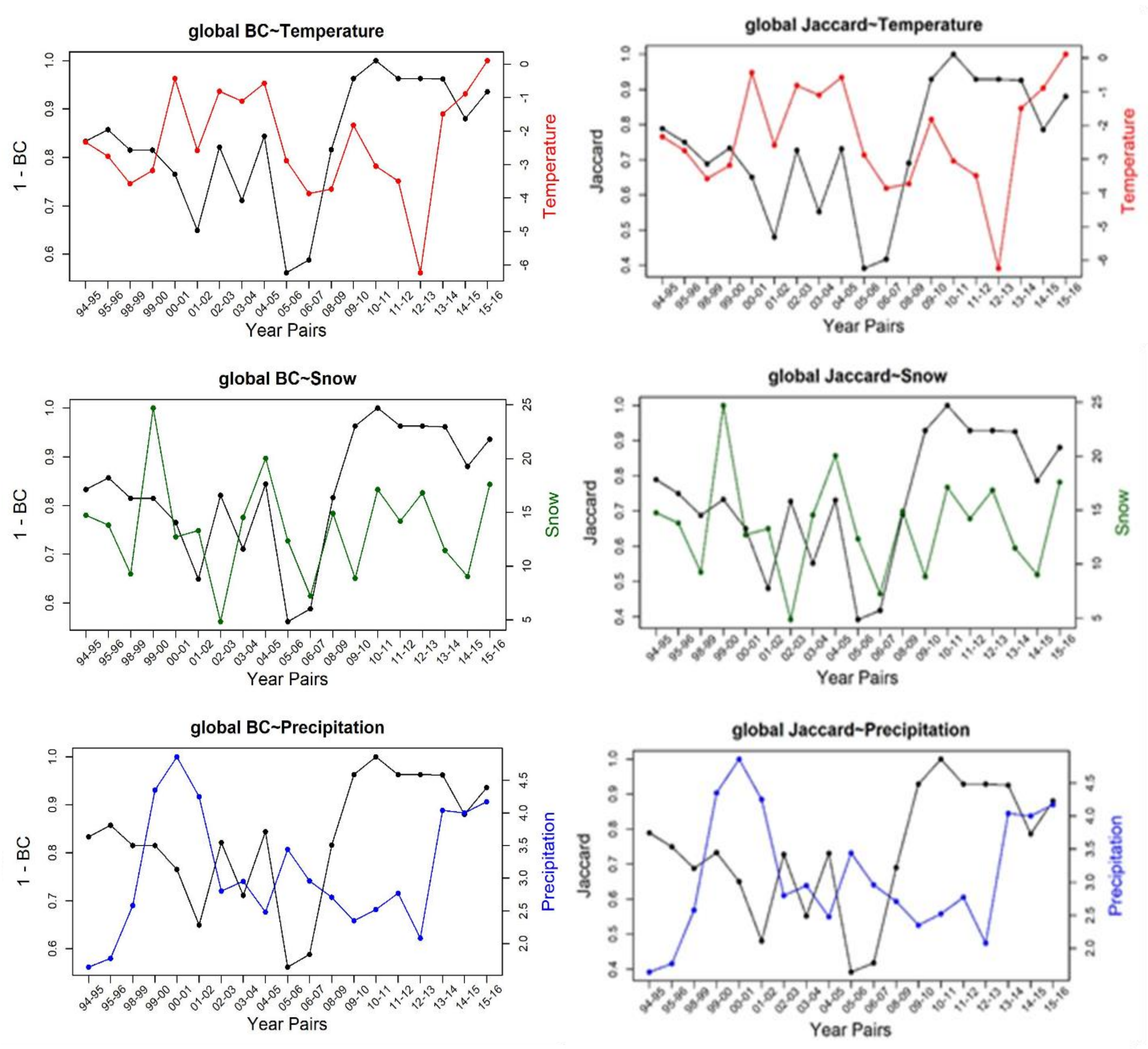


Figure 3.23 All stream (Global) results of the time-series linear regression, using Jaccard (persistence) and 1-BC (compositional stability) as the response variables and three local environmental variables (total annual air temperature, total snow, and total annual precipitation). See Table 3.2.

3.2.1.3 Macroinvertebrate community structure and environmental variables

In relation to the simple regression models, the global analysis revealed that for community persistence the two variables with the highest relative R^2 values were spring precipitation (0.39) from local climatic variables and PNA (0.12) from the large-scale atmospheric patterns, but the relationship was not strong, according to the model coefficients, where 0.70 = strong, 0.50=moderate, 0.30=weak and 0=no relationship (Dummies. 2018).(Table 3.2 and 3.3).

For the individual streams, there was only weak relationships between persistence and the local environmental variables. The R^2 values showing the highest range are those described below. The macroinvertebrate community persistence decreased with increased spring precipitation as observed in East Fork Tolkat Tributary (R^2 = 0.36), Moose Creek (R^2 = 0.30), N4 (R^2 = 0.24) and Sanctuary River (R^2 = 0.39). Increasing total annual precipitation resulted in a decrease in the macroinvertebrate community persistence in N4 (R^2=0.15). Increasing total annual air temperature showed a decrease in persistence community in Highway Creek (R^2=0.12). Community persistence in East Fork Tolkat Tributary (R^2=0.14) and Tattler Creek ($R^{2=}$0.14) increased with the effects of spring air temperature (Appendix 3.3 and 3.4).

Compositional stability of the macroinvertebrate community across all streams (global) also generally only had weak relationships with the environmental variables. The highest relative value was spring precipitation (R^2 = 0.37) (Table 3.2). However, the East Fork Tolkat Tributary (0. 38), L. Stoney Creek (0. 37) and Sanctuary River (0. 36), followed by Moose Creek and N4 with R^2 = 0.26 and R^2 = 0.25 respectively (Table 3.2), where the streams showing low compositional stability values when spring precipitation increased. In addition, increased spring flooding had great influence on compositional stability as indicated by the global results (R^2 = 0.95) reducing the compositional stability. With regard to the large scale variables compositional stability was highly influenced by PDO in Sanctuary River (R^2 = 0.73) and Tattler Creek (R^2 = 0.79), whilst the impact in compositional stability in Moose Creek (R^2 = 0.23) and Highway Creek (R^2 = 0.19) was mainly related to the PNA but the relationship was not strong (Table 3.3). The global analysis showed that total winter snowfall ($R^2 = 0.07$) had a negligible effect on the composition stability.

In regard to the time-series regression analyses, the all streams time trend plot (Fig. 3.23) shows the relationship between persistence and stability with three local climate variables: annual mean air temperature (temp), total snow depth (snow), and total mean precipitation (prec). Total mean precipitation was almost a significant driver of persistence ($p = 0.07$) and compositional stability ($p = 0.06$). The p values for some individual streams was significant for certain local climate variables (Appendix 3.4 and Appendix 3.6). Highway Creek, in the persistence analysis showed significant p values for air temperature (0.05) and snow (0.04). The snow depth was a significant driver of persistence in Igloo Creek and total mean precipitation was a significant driver of persistence in N4. The compositional stability analysis showed that snow depth was a significant driver of Little Stoney Creek ($p = 0.04$) and Igloo ($p = 0.03$). Precipitation was the main driver of compositional stability ($p = 0.01$) in N4.

In addition, the three local climatic variables used in the time series analysis were not significant drivers of persistence and compositional stability in East Fork Tolkat Tributary, Hogan, Moose Creek, Tattler Creek, Sanctuary River.

3.3 Discussion

The main environmental factors driving variation in the persistence and the compositional stability of the macroinvertebrate community over the 22 year period were the local climatic variables air temperature, spring rainfall and winter snow. Total winter snowfall had no effect on the persistence and compositional stability of the macroinvertebrate community. Higher spring precipitation caused a decrease in the persistence and compositional stability of macroinvertebrates. Streams in northern latitudes are susceptible to spring rainfall variations or snowfall variability such as higher winter snow and spring precipitation producing spring floods (Beria et. al., 2018). Hence, impacts in aquatic habitats during spring and winter might be caused by changes in the amount of precipitation, its frequency and intensity (Behrangi et. al. 2016).

3.3.1 Macroinvertebrate community dynamics

Persistence and compositional stability of the macroinvertebrate community in each stream fluctuated over time and showed similar trends across all streams. Thus, Savage and Sanctuary rivers with unstable channels and turbid water especially during summer due to the input of some glacial water (Milner et. al., 2003) showed the highest variability in the macroinvertebrate structure, causing constant taxa fluctuations in the persistence and community stability through time. In contrast, those streams with stable channels and a close riparian border, such as Tattler and Hogan Creeks (Milner et. al., 2003) are aquatic habitats with less variability in conditions ensuring constancy and compositional stability over time. But also, after a disturbance event affecting the community, population recovery might be faster due to high resilience of different taxa.

Tattler Creek and Sanctuary River had the highest observed persistence values. Igloo Creek and East Fork Tolkat Tributary which are smaller streams showing channel stability as well as less variation in discharge and well-developed riparian vegetation (alder and willow trees) (Milner et. al., 2003). Milner et. al. (2006) showed that macroinvertebrate persistence in Denali streams was influenced by the relative lower macroinvertebrate diversity and their strong colonizing abilities to recover rapidly from disturbed conditions like high spring flows.

3.3.2 Environmental variables influencing benthic community

Climatic events have a major influence on macroinvertebrate community. In this study, most streams showed lower inter-annual persistence during 2006-2007 and 2007-2008.

This was a period in which two large-scale atmospheric pattern variables showed an opposite phase with respect the other. Thus, PDO was in a cool phase, however, a positive phase of PNA maintained warm air temperatures especially during spring in interior Alaska (Climatenexus. 2018; Farukh and Hayasaka. 2012), which would enhance melting of the snowpack. The registered amount of snowfall during 2006-2007 was < 100 cm and during 2007-2008 < 50cm. Thus, the observed inter-annual changes in the macroinvertebrate community during 2006-2007 in most of the streams might be caused high spring discharge due to warm air temperature increasing glacial and snow melt at higher elevations (Stewart et. al. 2013).

The local climatic environmental variable showing the largest influence on persistence and compositional stability in the macroinvertebrate community in the ten streams of DNP was spring precipitation. The macroinvertebrate community reflected their resilient ability to resist the impact rainfall precipitation variability (Behrangi et. al. 2016, Collier. 2007, Milner et. al. 2006), showing the highest resilience to spring precipitation events in East Fork Tolkat Tributary, L. Stoney Creek, Sanctuary River, Moose Creek and Hogan Creek. Most of these streams are typically less stable according to the official stream classification of the National Park Service (2016) (see Chapter 2). In addition, air temperature and humidity (snow and rainfall) are important environmental variables influencing the interannual variability of persistence and composition in macroinvertebrate community (Collier 2007). Abiotic disturbances, such as increases in runoff, droughts or erosion differ in frequency and severity have great physical impact on streams with marked effects in macroinvertebrate communities through time (Jackson and Füreder, 2006; Lake, 2000: Woodward et. al. 2016).

In this study, variations in the macroinvertebrate community might be a consequence of changes in the hydrological regime due to warmer (above normal) climatic conditions, caused by shifts in the phases of large-scale atmospheric patterns (positive to negative or negative to positive) such as PDO, PNA, ONI, affecting air temperature and hydrological regime (Climatenexus, 2018; National Oceanic and Atmospheric Administration, 2018). The relationship between large-scale atmospheric patterns and the macroinvertebrate community through time is explained in more detail in Chapter 4.

3.3.3 Conclusion

Taxonomic diversity in subarctic communities varies according to the type of stream and its location (i.e. proximity to anthropogenic areas) and climatic conditions, among other factors. Therefore, studies are required to understand the natural mechanisms forcing population changes in benthos communities. Aquatic habitats in DNP are expected to change with climate warming, increasing the growing season and precipitation events, and altering the seasonality, which might cause changes in spring melt and freeze-up (Douglas et. al. 2014, Jackson and Füreder. 2006). Hence, understanding the interannual variation of macroinvertebrate communities in freshwater systems is important to provide key insights into the response by the macroinvertebrate community to environmental variables, which might generate diversity patterns at different scales (Milner et. al. 2006). Furthermore, information obtained from long-term studies can be used in conservation and restoration actions of streams to preserve healthy aquatic ecosystems. However, an integrated approach is important in conservation and restoration work, because different processes taking place within streams are influenced not only by natural factors, but also by anthropogenic activities like tourism, mining, etc. (Albano et. al. 2013, Brabets & Ourso. 2013).

4 Temporal change in macroinvertebrate community structure

4.0 Introduction

Aquatic ecosystems in northern latitudes have been affected by climate changes that alter, amongst other things, water temperature, discharge, and turbidity (Hodkings, 2009; Bradley & Ormerod, 2001; Mol et al., 2000). Climate change also alters different aspects of the hydrological regime, such as the frequency and duration of droughts and floods, and the magnitude of low and high flow pulses (Bradley & Ormerod, 2001), both of which can have a major impact on aquatic habitats and their associated biotic communities (Puckridge et al., 2000; Bradley & Ormerod, 2001). Warmer air temperatures in the Arctic are causing areas covered with ice and snow to melt fast. It has also been suggested that the decrease of Arctic sea ice cover enhances evaporation in autumn which increases atmospheric moisture, leading to an increase in autumn snow fall (Vihma, 2014).

Anomalies in atmospheric circulation patterns caused by differences in the amount of heat distributed between areas of high and low pressure in the atmosphere are altering multiple climatic factors in the North Atlantic region, including temperature, rain, and cloudiness (MetOffice, 2018). Atmospheric circulation pattern anomalies have a greater impact in Interior Alaska, causing warmer temperatures during the winter season (Hodgkins, 2009; Shulski et al., 2010). The increased in mean winter temperature (3.3° C) has had indirect effects on precipitation, which now falls more as rain rather than snow; increasing the water filtered through the soil and enhancing the amount of groundwater (Hartmann & Wendler, 2005; Milner et al., 2009; Puckridge et al., 2000). The increase in water flow in the river basin leads to increased sediment removal from the highlands and then an increase in sediment deposition in low areas or pools, with negative implications (disruption of the normal functioning of gills, oxygen depletion, declines in periphyton food) for some macroinvertebrate taxa, such as Chironomidaes, Simuliidae, Baetis, Ephemerillidae (Harrsion et al., 2004; Hodgkins, 2009; Jones et al., 2011; Puckridge et al., 2000; Whitfield et al., 2010). However, winter rainfall in interior Alaska has increased at a slower rate compared with the rising amount of rainfall in coastal areas (Hodgkins, 2009; Whitfield et al., 2010).

The PDO and the El Niño/Southern Oscillation (ENSO) (see Chapter 2) directly affect biotic riverine systems (Mantua et al., 1997; see also Mol et al., 2000; Papineau, 2001). A PDO cold phase covered the period 1952-1977, whilst between 1977 and 2006, a warm phase was evident (Hodkings, 2009; Whitfield et al., 2010). As Papineau (2001) suggests, in interior Alaska when El Niño occurs during a PDO negative phase, winter is typically cooler and lasts longer than in a positive phase. In contrast, a positive PDO phase is associated with warmer air temperature, and an increase in the amount of precipitation falling as rainfall instead of snow, especially during winter (Bieniek & Walsh, 2014). In addition, when the PDO shifts from a cold to a warm phase the temperature increases in freshwater streams and rivers in Alaska, where those streams fed by glaciers exhibit increases in stream flow and sediment deposition. The ice and snow storage during the cold phase are melted due to the warmer temperatures of a positive PDO phase, increasing stream water flow. In contrast, rivers which do not receive discharge from glaciers (in the summer season) exhibit decreases in stream annual flow during warm PDO phases, because their water discharge depends on precipitation events (Hodkings, 2009). Overall, fluctuations in large-scale atmospheric patterns have an impact on the local weather conditions in interior Alaska, affecting the air temperature and causing shifts in the hydrological regime. However, despite this knowledge, there are no studies testing exactly how large-scale atmospheric patterns drive variations in stream discharge and water temperature in Alaska, and how these changes in hydrological conditions in turn affect freshwater macroinvertebrate community structure.

In recent years, the use of aquatic biota to assess water quality has increased considerably; as it has become increasingly recognised that fish and macroinvertebrate assemblages are effective bioindicators of aquatic degradation (Fierro et al., 2017). The effectiveness of aquatic macroinvertebrates as biological indicators is because they are often sensitive organisms, and their presence/absence and abundance shift with environmental conditions in streams and rivers, such as variations in water temperature, discharge, and nutrient inputs (Kenney et al., 2009; Holt & Miller, 2010; Milner et al., 2016). The macroinvertebrate orders useful for biomonitoring include Diptera, Annelida, Hemiptera, Odonata, Plecoptera, and Ephemerotera (Alavaisha et al., 2019). The core macroinvertebrate taxonomic groups that have been used to measure water quality are Ephemeroptera, Plecoptera and Trichoptera (EPT) (Stoyanova et al., 2014). EPT abundance, composition and distribution in aquatic habitats can be used as an indicator of whether the water is clean and well oxygenated (Stoyanova et al., 2014). In this manner, the presence/absence of certain key species as well as the richness and composition of the macroinvertebrate assemblage as a whole can be used to provide a measure of the overall water conditions (Fierro et al., 2017).

The aims of this chapter are: (i) to examine patterns in the macroinvertebrate community composition from 1994 to 2016 in 10 streams to see if years group together and major shifts in community trajectory, and (ii) to identify the key environmental variables driving these changes in macroinvertebrate community composition over time.

4.1 Methods

4.1.1 Macroinvertebrate

Prior to this analysis, all taxa with 3 or fewer individuals were removed to reduce the effect of very rare and/or transient species on the results. This left 125 021 insects from 40 taxa, which were used in this study to analyse their stability and abundance (Poos & Jackson, 2012).

A dataset was produced for each stream, and an all streams dataset was then constructed by pooling the data from all ten rivers; the abundance of taxa present in multiple rivers was summed.

4.1.2 Environmental data

A selection of relevant environmental variables were used for analysis. Air temperature, precipitation and snowfall variables for DNP were obtained from the National Oceanic Atmospheric Administration (NOAA) (National Oceanic and Atmospheric Administration, 2017). In addition, PDO, ONI, EP, NP and PNA variables (see Appendix 4.2 for further details) were obtained from the NOAA's website. The El Niño Southern Oscillation (ENSO) is known to influence air pressure in the Gulf of Alaska (National Oceanic and Atmospheric Administration, 2017), and for this project the ONI variable (the presence / absence of ENSO conditions) was used as a metric of ENSO, because ONI index shows historical ENSO events (see Appendix 4.2).

The subsequent data analyses were undertaken using 12 environmental variables. The broad scale variables PDO, EP-NP, PNA and ONI (see Appendix 4.2), which were calculated as a yearly average from the preceding September to August of each year. Four local-scale environmental variables (from Mckinley station) were calculated as yearly averages (from the preceding September to August of each year) using the monthly climate data: Mtemp (mean air temperature), SDtemp (air temperature standard deviation), Mprec (mean rainfall), SDprec (rainfall standard deviation), Msnow (mean snowfall) and SDsnow (snowfall standard deviation). WintSnow (depth of winter snowfall) for each year was calculated using monthly data from the preceding September to April (see Appendix 4.2). SpringTemp (spring temperature) and SpringPrec (spring precipitation) were calculated as averages using the monthly data from April and May of each year. Finally, SpringFlood was calculated as the number of events with three or more days of heavier than average rain during the period of April to July of each year.

4.2 Data analysis

To examine the relationships between the aforementioned environmental variables and changes in macroinvertebrate community composition through time at each of the ten rivers, a selection of three ordination techniques were used. A variety of methods were used to allow the examination of different types of data (i.e. abundance and presence-absence data) and to draw on the benefits of different ordination techniques (i.e. redundancy analysis and non-metric multidimensional scaling (NMDS)). First, for each site, the sample data were formatted into a taxa-year matrix (in which each taxon was a column and each row was a year). Thus, there were ten taxa-year matrices in total. The environmental variables were also formatted into a variable-year matrix.

Redundancy Analysis (RDA) was undertaken for each of the ten sites separately (and the global dataset, described below) using the procedure outlined in Borcard et al. (2011). RDA is an ordination method that combines linear regression with principal component analysis. Prior to running the RDA, the species data (i.e. the response matrix) were Hellinger transformed to avoid the influence of double zeros in the ordination analysis (Borcard et al., 2011). For each RDA analysis, all environmental variables (i.e. the matrix of explanatory variables) were included initially and a backwards-selection procedure was then used to produce a final model with only significant variables (alpha level of 0.05; Borcard et al., 2011) (see Appendix 4.4). The R^2 and adjusted R^2 of the full and final models were calculated using the approach of Peres-Neto et al., (2006). The RDA was undertaken using the vegan package (Oksanen et al., 2017) and the R programming language (R Core Team, 2017).

NMDS ordination was then undertaken using PrimerE (Clarke, 1993; Clarke & Gorley, 2015). NMDS works by arranging the data such that the rank order correlation between the real distances of the species over the years are maximised. Thus, the first and second highest distance between objects was preserved to represent macroinvertebrate community structure in the ordination diagram. The input data were square root transformed to reduce the weight of dominant species. A distance matrix was then calculated based on the selected similarity coefficient (Clarke, 1993). Bray-Curtis (abundance data) distance was the coefficient used to generate the dissimilarity results among the macroinvertebrate taxa from 1994 to 2016. In the NMDS ordination, the environmental vectors are simply projected on top of the ordination plot in order to maximise the correlation (see Appendix 4.4).

4.3 Results

NMDS ordination plots (Figs. 4.1, 4.4, 4.5, 4.8, 4.8 and Appendix 4.4) indicated that for Tattler Creek, Moose Creek, Igloo Creek and Highway Pass Creek the macroinvertebrate community formed two distinct groups of years, generally corresponding to the years pre- 2003 and post- 2005, and strong relationships with selected local (mean temperature, temperature standard deviation, spring precipitation, spring flood, snow standard deviation, PC1=less snow and PC3=more rainfall) and large-scale (NAO, EP-NP, PDO and ONI) environmental variables (Table 4.2). In the remaining streams, Savage River, Sanctuary, Little Stoney, Hogan and East Fork Tolkat Tributary, the NMDS showed strong dispersion of years, but there was no clear division of years into groups (Figs. 4.2, 4.3, 4.6, 4.8, 4.10 and Appendix 4.4).

The RDA backwards model selection indicated that a variety of different environmental variables (mean temperature, temperature standard deviation, spring precipitation, spring flood, snow standard deviation, PC1=less snow, PC3=more rainfall, NAO, EP-NP, PDO and ONI) explained variation in community composition between years (Table 4.2). For five of the ten sites, the best model generated through backwards-selection was significant (at the 0.05 level), (Table 4.2). The RDA biplot s(scaling 1) of the Hellinger-transformed macroinvertebrate data (pooled across all ten rivers) showing the locations of the objects (years) and the environmental variable(s) present in the best RDA model, selected using backwards selection, are provided in Appendix 4.4.

The results and plots of the global dataset analyses are provided at the end of the results section. The best model generated using the global dataset was significant at the 0.05 level.

In each plot, where possible circles have been drawn around groups of years.

Table 4.1 Summary statistics for the RDA models relating the environmental variables to variation in community composition between years, at each of the ten rivers. The best model was selected using a backwards-selection process.

Stream	Full Model			Best Model (Backwards)			Variables in the Best Model (Backwards Selection)
	R2	R2adj	P	R2	R2adj	P	
East Fork Tolkat Tributary	0.837	0.021	0.495	0.283	0.14	0.014	Mtemp+tempSD+PC1
Highway Creek	0.862	0.173	0.347	0.412	0.245	0.003	NAO+EP.NP+springPrec+SpringFlood
Hogan Creek	0.802	0.207	0.181	0.292	0.214	0.001	PDO+Mtemp
Igloo Creek	0.762	-0.43	0.887	0.106	0.054	0.073	springPrec
Little Stoney Creek	0.805	0.076	0.392	0.384	0.219	0.003	PDO+ONI+PC1+PC3
Moose Creek	0.874	-1.019	0.97	0.093	0.033	0.122	SpringFlood
N4	0.781	-0.041	0.598	0.156	0.057	0.128	ONI+PC3
Sanctuary River	0.693	-0.457	0.929	NA	NA	NA	NA
Savage River	0.789	-0.266	0.866	0.26	0.111	0.02	snowSD+SpringTemp+PC1
Tattler Creek	0.686	-0.256	0.93	0.085	0.036	0.073	NAO
Global				0.594	0.3	0.002	PDO+NAO+PNA+tempSD+SpringFlood+PC1+PC2+PC4

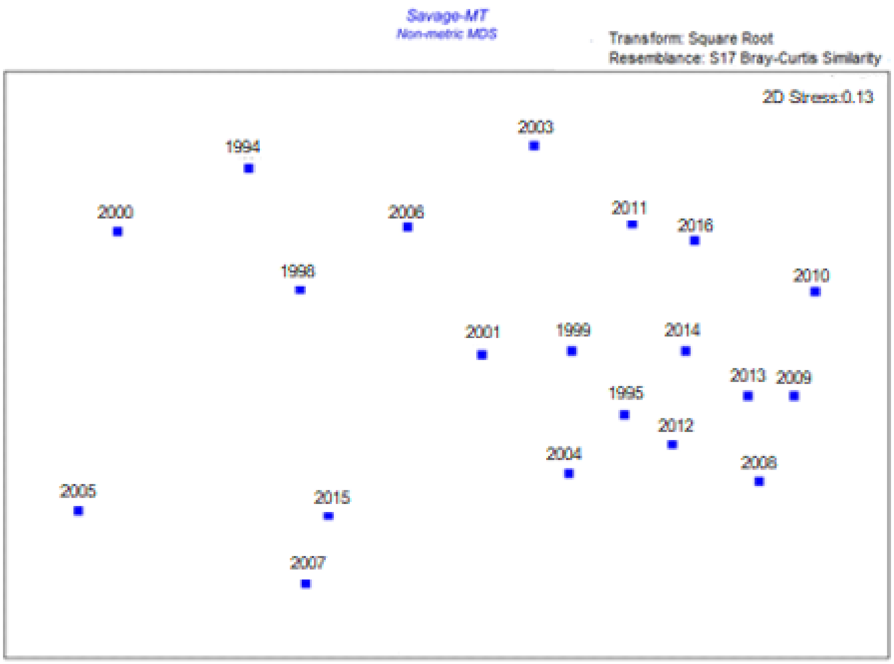


Figure 4.1 Savage River. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

Savage River

No distinct groups were evident between years, although 2005, 2007 and 2015 were clear outliers (Figure 4.1). The best RDA model indicated that snowSD, spring temperature and PC1(less snow) significantly influenced the macroinvertebrate community ($p < 0.05$).

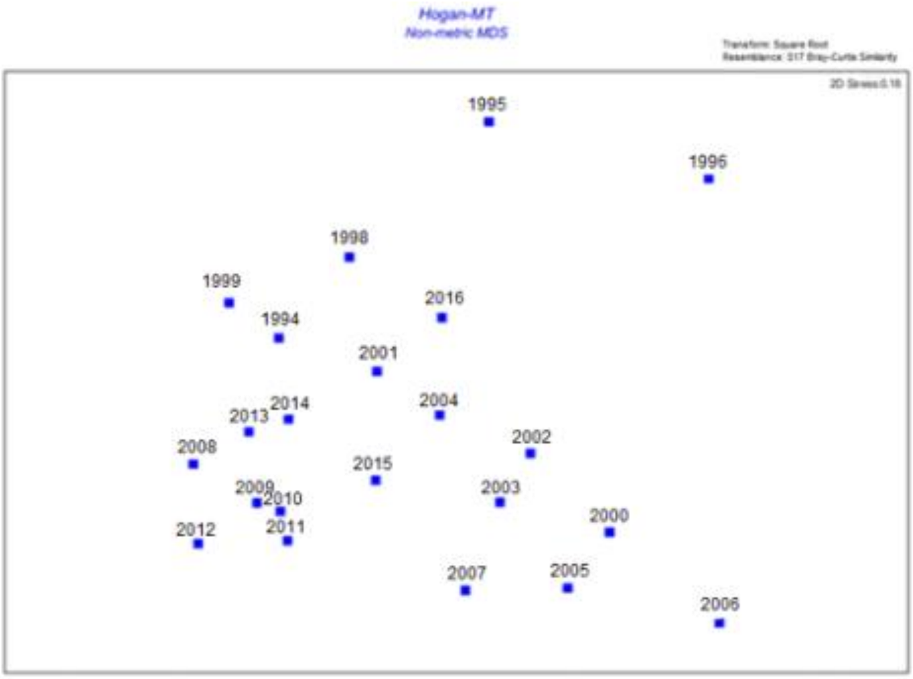


Figure 4.2 Hogan Creek. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

Hogan Creek

No clear groupings of years were evident in the NMDS plot (Bray-Curtis dissimilarity (Fig. 4.2), although two variables remained after the backwards selection process in the RDA analysis: PDO and Mtemp which were highly significant ($p<0.01$).

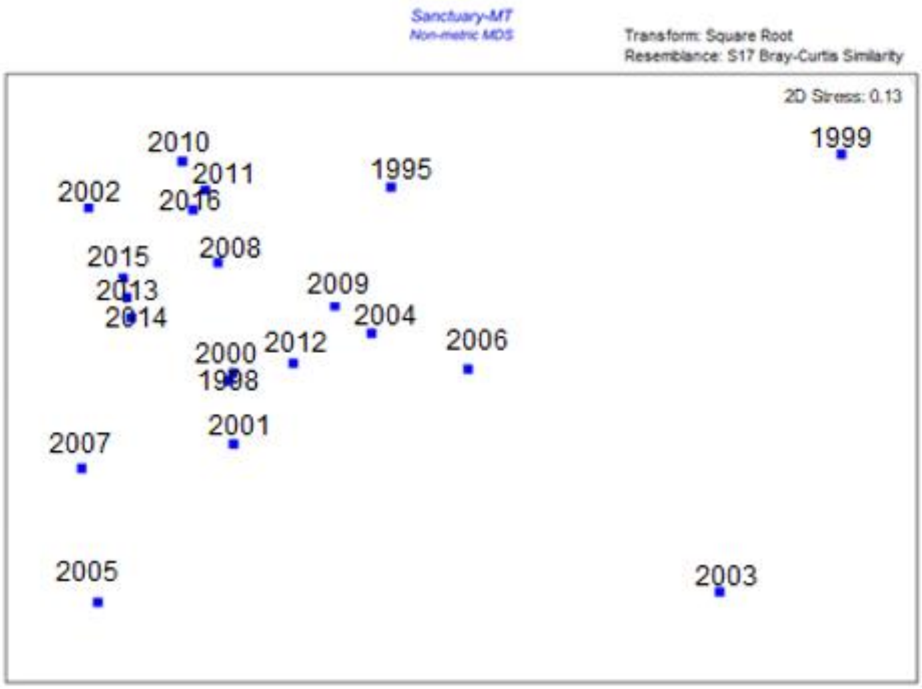


Figure 4.3 Sanctuary River. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

Sanctuary River

No clear groupings of years were evident and the best RDA model was not significant. The years 1999 and 2003 were clear outliers (Fig. 4.3).

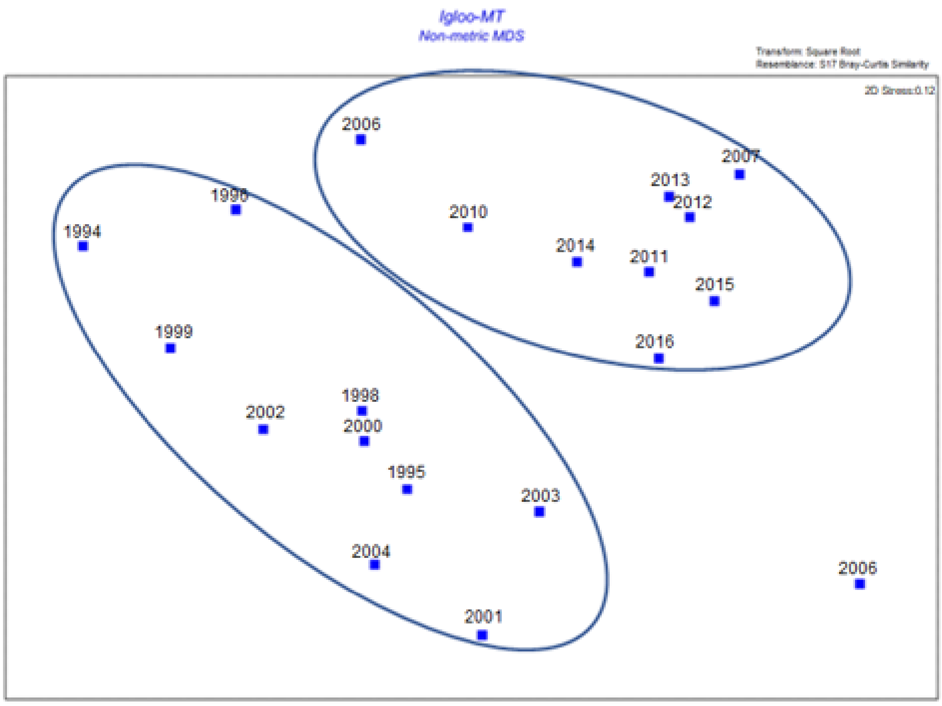


Figure 4.4 Igloo Creek. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

Igloo Creek

Two distinct groupings were evident corresponding to the years pre- and post- 2005 with 2006 as an outlier (Figure 4.4). The best RDA model indicated that SpringPrec was almost significant (p = 0.07).

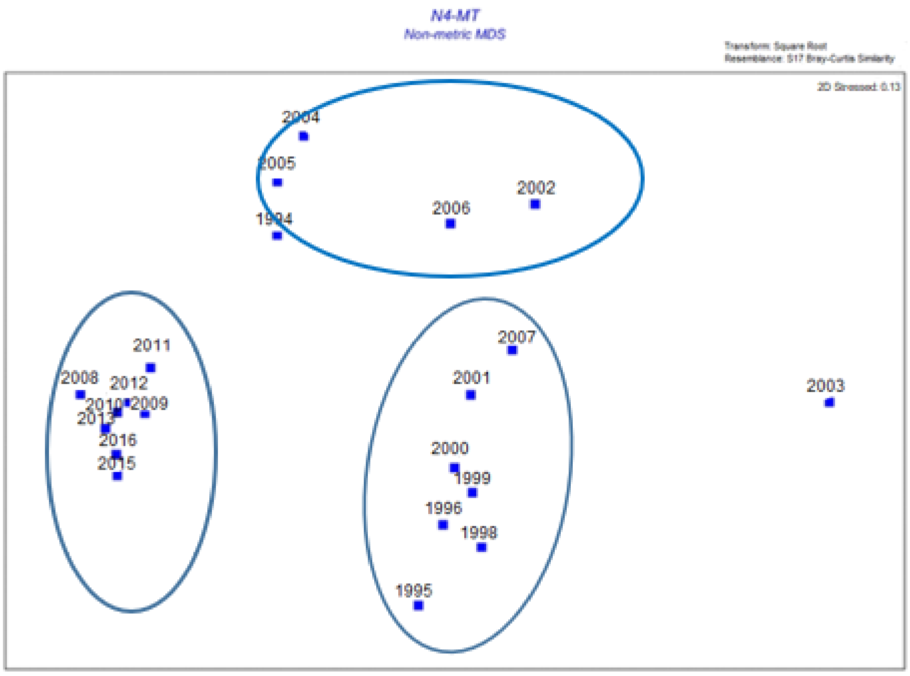


Figure 4.5 N4. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

N4

Three main groupings of years were evident, group 1: 1995-2001, and 2007, group 2: 1994 and 2002-2006, and group 3: 2008-2016 (Figure 4.5). The year 2003 was a clear outlier. The best RDA model shows that the two variables remaining at the end of the backwards selection were ONI and PC3 (more rainfall), although the best model was not significant.

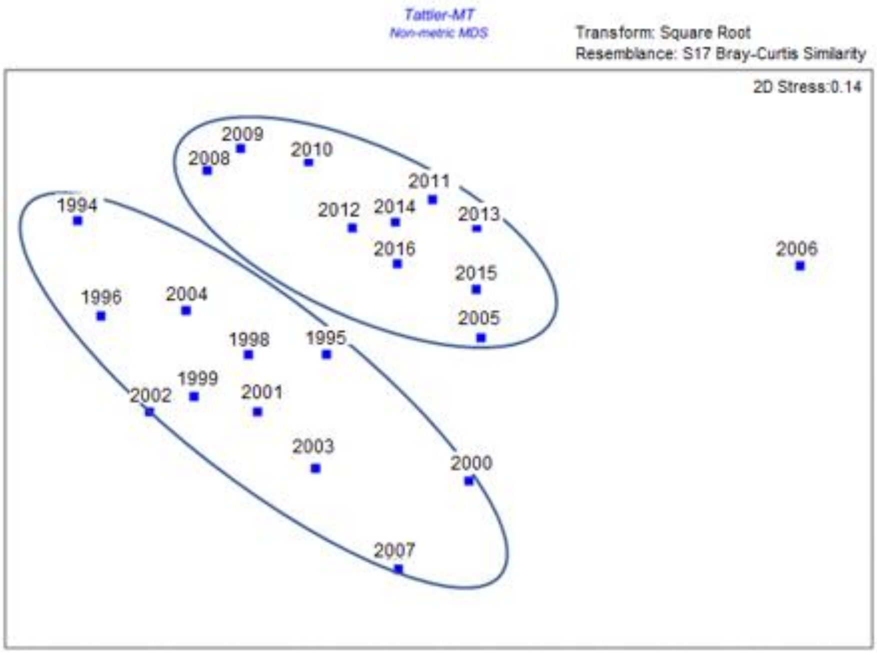


Figure 4.6 Tattler Creek. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

Tattler Creek

Two distinct groups of years were evident, corresponding to the years pre-2006 and post-2006 with 2006 a clear outlier (Figure 4.6). Although not significant, only NAO was retained in the best model describing the grouping.

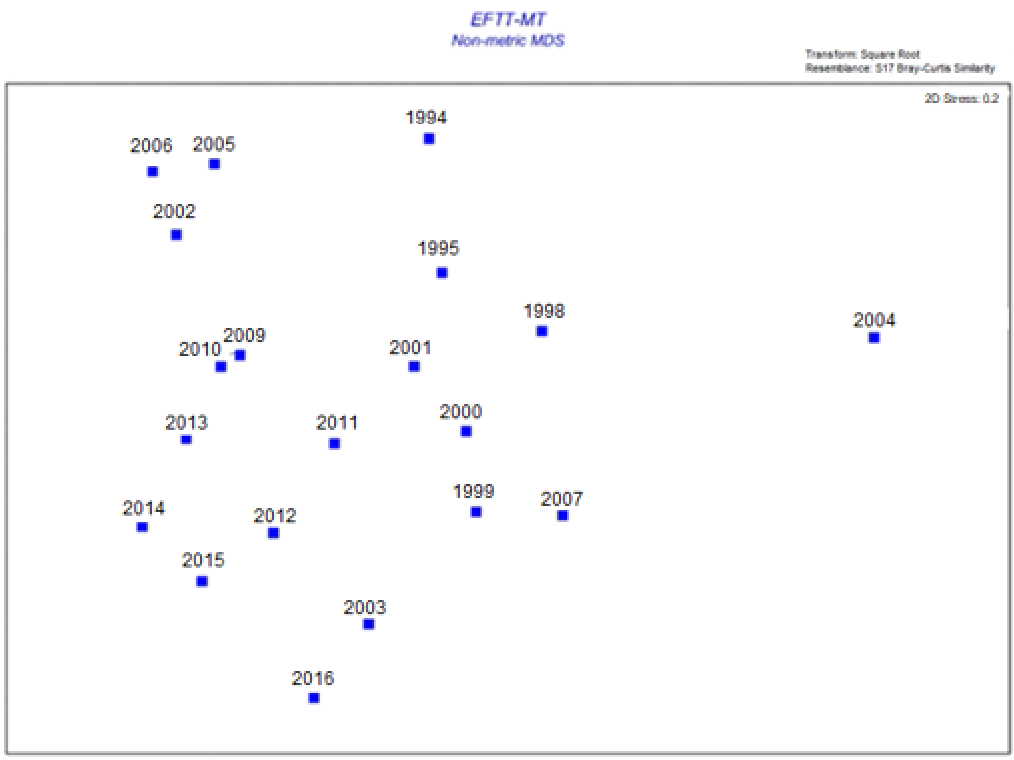


Figure 4.7 . East Fork Tolkat Tributary. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

East Fork Tolkat Tributary

The NMDS plot (Fig. 4.7) did not indicate any clear patterns between years, although 2004 was as a clear outlier. The RDA backwards selection identified three variables in the best model and was significant ($p < 0.01$): Mtemp, tempSD and PC1. The best model was significant.

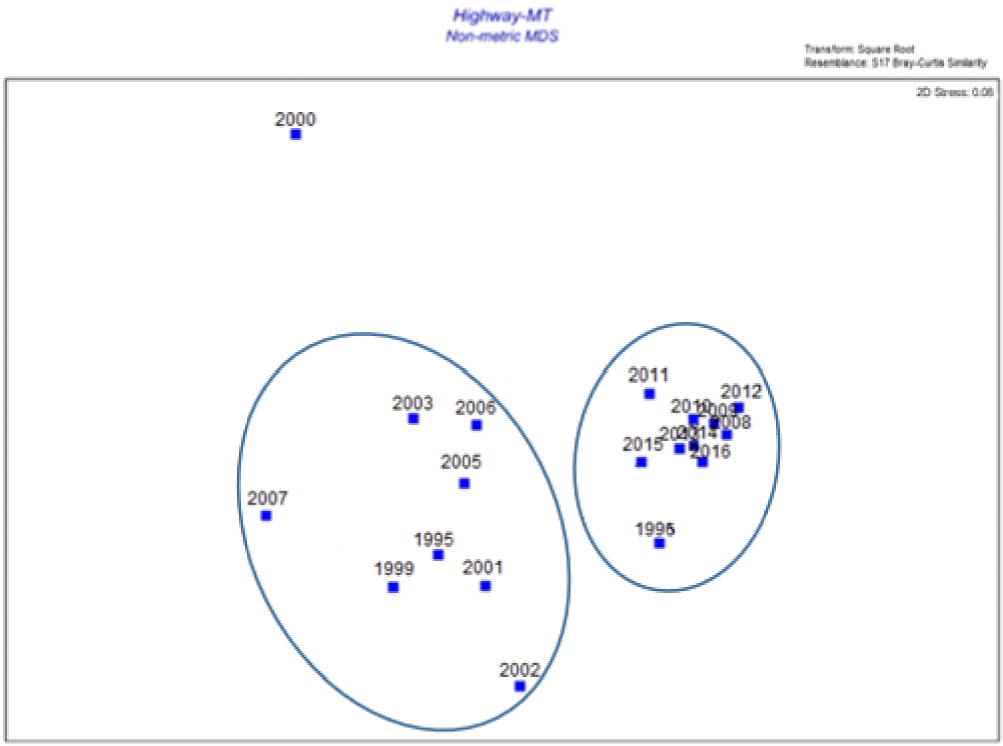


Figure 4.8 Highway Creek. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

Highway Creek

Two groups of years were clearly evident corresponding to the years pre- and post-2007 (Figure 4.8). The outlier year in the NMDS plots was 2000. The variables in the best RDA model were SpringFlood, NAO, springPrec and EP.NP, and the best model was significant ($p<0.01$).

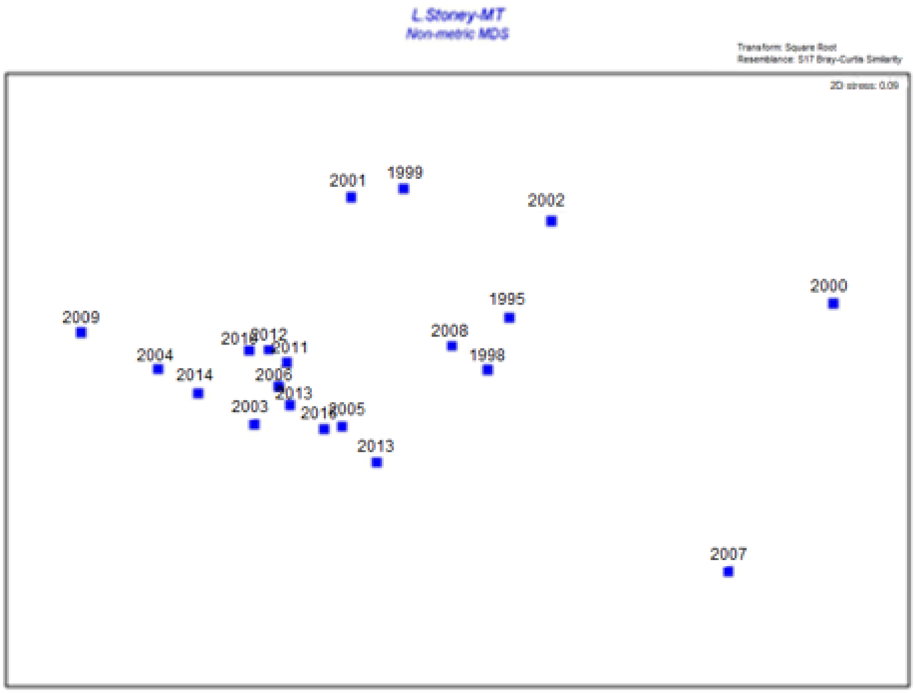


Figure 4.9 Little Stoney Creek. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

Little Stoney Creek

No clear groupings of years were evident in the NMDS biplot (Fig. 4.9), although four variables remained after the backwards selection process in the RDA analysis and the best model was significant: PDO, PC1 (less snow), PC3 (more rainfall) and ONI were the variables. The years 2000 and 2007 were outliers.

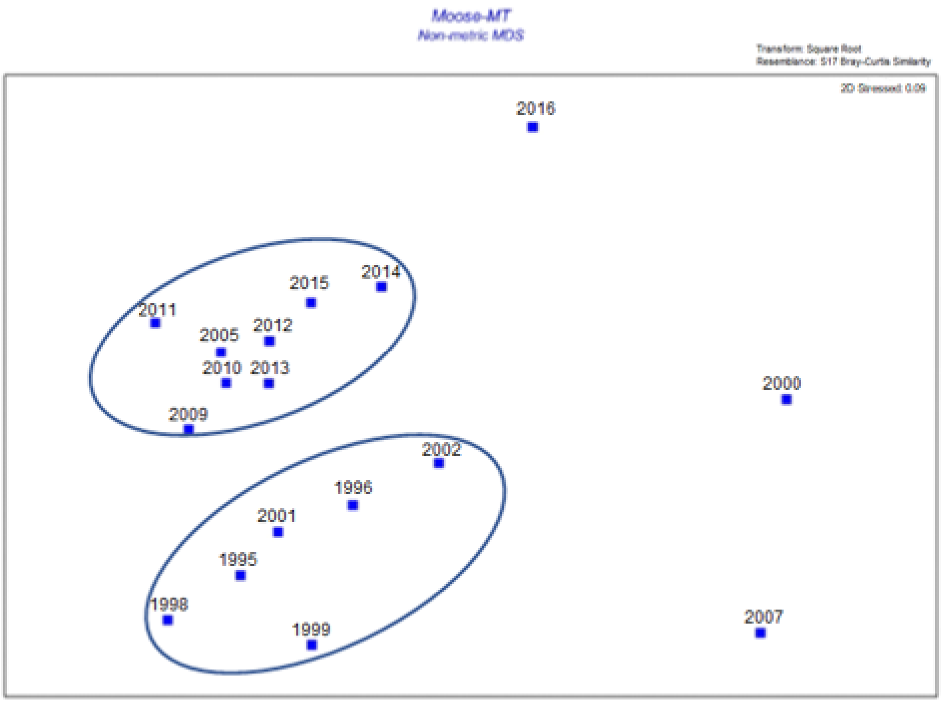


Figure 4.10 Moose Creek. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data.

Moose Creek

Clear groupings corresponding to the pre- and post-2003 years were found (Figure 4.10). The best RDA model contained SpringFlood, but was not significant. The years 200, 2007 and 2016 were outliers.

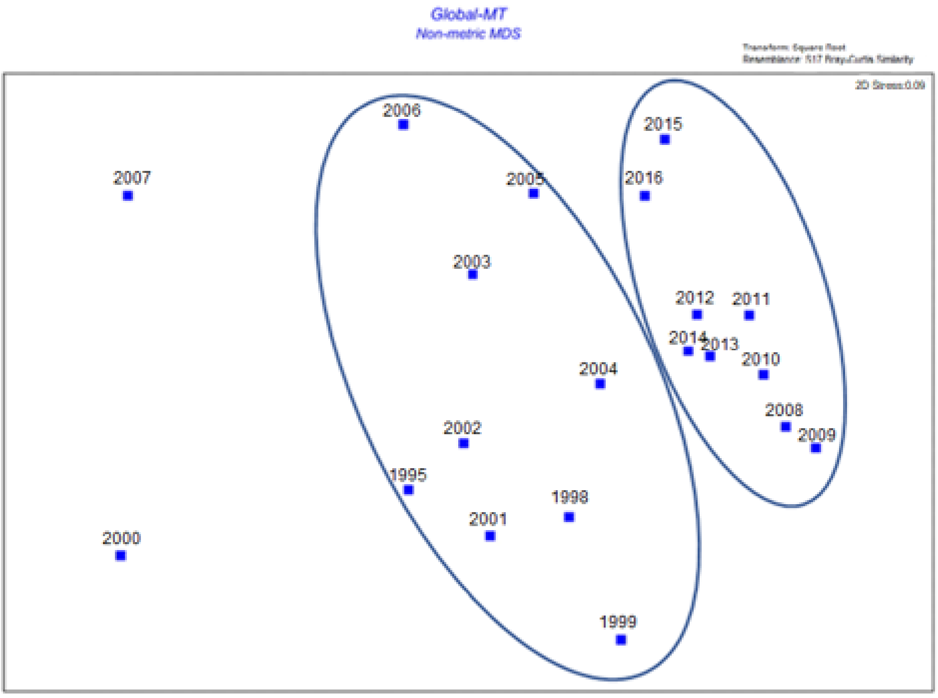


Figure 4.11 Global. NMDS biplot of a Bray-Curtis dissimilarity matrix of the macroinvertebrate abundance data (pooled across all ten rivers).

Global Model of all streams

The best RDA model (chosen using backwards selection) contained eight variables, including SpringFlood and SDtemp, and a number of the large-scale ocean-atmosphere climate variability variable such as PDO. The model was significant and had an adjusted R2 value of 0.3. Due to the method of calculation, the adjusted R2 values of RDA models are generally lower relative to those observed when using standard linear models in ecological applications (Borcard et al., 2011).

The global NMDS plot (Fig. 4.11) indicated two main clusters of years, roughly corresponding to pre- and post-2003. The years 2000 and 2007 were outliers.

4.4 Discussion

In this study, the variability in macroinvertebrate community structure through time was analysed in 10 streams in DNP, Alaska, and the local and large atmospheric and environmental variables influencing macroinvertebrate community composition were identified. In five streams, there were two clear and distinct groups of years with a forcing factor(s) causing a distinct shift between these groups. Typically, these distinct groupings corresponded to the years pre- and post-2003/2005, and the significant variables driving change in the macroinvertebrate community composition were spring flood, spring precipitation, air temperature variation (i.e. the standard deviation of monthly average temperature) and total snowfall. According to the RDA and NMDS models, community structure in Sanctuary River was not influenced by local hydrological conditions or large-scale environmental variables. However, the RDA model showed that Savage River and Igloo Creek were affected by local hydrological conditions.

4.4.1 Environmental variables in all streams

In the global (all streams) dataset analysis, a clear division of years into two groups (pre- and post-2003) showed a range of important environmental variables, including SpringFlood, SDtemp, and some of the large-scale ocean-atmospheric variables (PDO, ONI and NAO), were the principal drivers of overall macroinvertebrate community structure in the ten streams over 22 years. It was significant that the global dataset showed a distinct grouping of years even though some of the individual streams did not.

In regard to the main variables driving changes in the global dataset analysis, an increased air temperature causes earlier snow melting, potentially resulting in floods during the spring season. Thus, depending on the seasonal rainfall, when the air temperature rises, the water temperature also increases, resulting in further variations in stream macroinvertebrate composition (Brittain & Milner, 2001). Aquatic macroinvertebrates are highly dependent on water temperature. As water temperature rises, cold-adapted species (Diamesinae, Orthoclaniidae, etc.) become vulnerable to local extirpation, while taxa with warmer climatic preferences will progressively colonize streams (Alba-Tercedor et al., 2017). For example, a study by Durance and Ormerod (2007) in Llyn Brianne (UK), where the climate is maritime and temperate, used a 25-year time-series dataset to show that macroinvertebrate assemblage composition changed significantly with increases in air temperature. Temperature increases were strongly connected with NAO, resulting in increased water flow in the river basin (Bradley and Ormerod, 2002).

4.4.2 Local climatic variables

The variables affecting the pre-2003 group and the years pre-2005 Hogan Creek mainly responded to, local-scale climatic variables, such as average rainfall, spring rainfall, and air temperature. The relationship between air temperature and hydrological annual or seasonal events (rainfall, snowfall, snow melt, etc) is reflected in the amount of water and sediments in the river basin (Jaeger et al. 2017; Lana-Renault, et al., 2011). A study conducted by Lana- Renault et al. (2011) in the Izas catchment (Central Spanish Pyrenees), showed that high-mountain environments are hydrologically sensitive to variability in air temperature and precipitation. In that study, the delivery mechanisms such as rainfall and snowmelt were the main drivers of suspended sediment occurrence in the Izas catchment.

Hydrological changes had an impact on the small streams (i.e.1-5m wide; Conn, 1998) with stable channels, such as Igloo Creek and Tattler Creek, as they are fed by snowmelt. These rivers do not have the capacity to contain large amounts of water, and thus increases in the water discharge destabilize the stream basin. Stable streams, such as Hogan Creek, fed by groundwater, and unstable streams like N4, were also affected by an increase in water discharge caused by rainfall events. In the four aforementioned streams, the registered high temperatures during the spring season in the years previous to 2005 caused unseasonable snow melt at higher elevations, resulting in floods, which were exacerbated by a damming effect of ice jams (U.S Department of Commerce, 2013).

The warming of air temperature is most evident during the late winter/spring season, causing increased rainfall instead of snow fall, and during spring snow starts to melt earlier (U.S. Fish & Wildlife Service, 2018). Therefore, physical disruptions in aquatic ecosystems due to warmer conditions may provide the conditions for new species adapted to warmer conditions to colonize habitats where taxa specialised in colder conditions were mainly previously found.

Air temperature in Alaska has been increasing (2.7°C) from 1979 to 2012 and the greatest loss of ice (~ 50 Gt/year) in the Alaska region occurred from 2003 to 2009 (Gardner et al., 2013; Moon et al., 2018; Vaughan et al., 2013, Wendler et al., 2014).

4.4.3 Large-scale atmospheric patterns

Interannual atmospheric variability plays an important role in aquatic habitat ecosystems in northern latitudes as these systems are strongly dependent on seasonal weather patterns, which are modified following changes from a positive to a negative phase (and *vice versa*) of ONI, PDO, PNA, NAO and EP.NP (Bradley &

Ormerod, 2001; Durance & Ormerod, 2007; Fleming et al., 2006; Mantua et al., 1997; Papipeau, 2001).

These shifts had considerable effects on community structure across different types of steams. For example, even though Little Stoney Creek and Hogan Creek have different physical features in comparison to N4, the shift in community structure observed in both streams around 2003 is considered to be linked to a PDO transition from a negative to a positive phase in 2003 (Hartmann & Wendler, 2005). This transition resulted in changes in temperature and precipitation in DNP, which in turn affected the amount of water in the stream basins at large geographical scales, leading to changes in the stream macroinvertebrate assemblages.

Post-2005 the large-scale atmospheric environmental variables had more substantial impacts in this stream. In contrast, Little Stoney Creek was mainly impacted by large-scale atmospheric environmental variables during the entire study period. Another example is the streams fed partially by glaciers: Savage River, Sanctuary River and Igloo Creek where the variations in air temperature and rainfall during spring across years may have been due, in part, to shifts from negative to positive phases of the large-scale atmospheric patterns, such as PDO.

Based on the different ordination plots, outlier years were evident in all streams; however, only some of them were seemingly related to anomalous air temperature variations during a positive PDO phase (i.e. 2000, 2003 and 2007) (see also Farukh & Hayasaka, 2012; Climatenexus, 2018).

In 2000 wetter conditions were experienced in interior and northern Alaska, while low air temperatures were registered in south of Alaska (NOAA, 2020). Thus, looking at the environmental variables in Chapter 2, the weather conditions in Alaska may explain the high snowfall during 2000.

During 2003, air temperature in the Northern Hemisphere increased by near 0.64°C (NOAA, 2020). Thus, annual mean air temperature variation can be seen as a key factor driving temporal variation in macroinvertebrate community structure across years (see also Milner et al., 2001; Woodward et al., 2017).

The outlier year 2007 repeatedly appeared as an outlier (in 7 streams), and which was characterised by above average warmer and drier conditions. According to NOAA (Climatenexus. 2018; National Oceanic and Atmospheric Administration, 2018), 2007 was ranked the 15th warmest in Alaska since 1918, with high temperatures registered all year, especially during the winter. In addition, during that year, the largest tundra fire above the polar circle occurred which, considering wind circulation patterns in the atmosphere, may have had an impact on the streams sampled in this study during 2007. The influence of wildfires on aquatic ecosystems is not well documented. However, it has been suggested that an increase in phosphorus and nitrogen after fires can influence physicochemical habitat in streams and the macroinvertebrates they support (Farukh & Hayasaka, 2012; Tecle & Neary, 2015).

4.4.4 Conclusion

Long term studies are important for examining changes in freshwater macroinvertebrate communities (which are important components of aquatic ecosystems) as a result of environmental change. Long-term term studies also allow for an examination of the role of different variables in driving temporal variation in community structure, which in turn enables a better understanding of the environmental processes underpinning macroinvertebrate community structure , and which might help to improve our ability to mitigate future similar impacts on aquatic ecosystems. To have a better understanding of freshwater ecosystems and their living communities, it is important to recognize that local climatic conditions and large-scale atmospheric patterns are part of a bigger system .Thus, interconnecting them with other different elements (i.e. topography, etc.) are responsible for variations in different physical, chemical and/or biological processes., that could have a strong impact on riverine systems in northern latitudes with resultant consequences on macroinvertebrate community stability. As this study has shown, the use of long data sets makes it possible to see the effects of a climatic event (e.g. a shift from a negative to a positive PDO or vice versa) in combination with those of climate change on macroinvertebrate community structure at a specific point in time and to analyse how these effects change through time.

5 Chironomidae community change in 4 Alaskan streams

5.0 Introduction

Sub-regions in the Arctic and Antarctic are characterized by extreme meteorological and hydrological conditions (Nilsson et al., 2015), short growing seasons, high habitat variability, extreme cold and limited food availability. These environmental characteristics have resulted in physical adaptations (tracheal gills, cutaneous breathers, mandibles with knife-like leading edge, dorsal-ventrally flattened body, etc.) in many taxa for survival and dispersal (Chapman et al., 2004; Cummins, 2018; Vinke et al., 2015).

The diversity of available substrate in-streams, varying in type (pebbles, leaves, wood etc.) and size (larger like pebbles or fine sediments like sand, is also an important consideration as it provides macroinvertebrates with refugia and food, and can enhance benthic community resilience (Khudhair et al., 2019; Pitt & Batzer, 2011; Sroczynska et al., 2019). In order to survive in harsh environments, such as the cold conditions characteristic of Alaska, macroinvertebrate taxa have multiple physiology adaptations. These include cocoon building to control oxygen supply, and protection against ice particles, etc. (Danks, 2007); the use of claws to cling to surfaces; gills in the body to increase water flow and oxygen uptake; rowing legs with stout hairs to increase the vertical force while swimming; and the production of cryoprotectants and 'antifreeze' to keep the temperature of body fluids lower than the freezing point of water (Hudson et al., 2012).

In streams across the subarctic region, aquatic Arthropoda species richness and diversity decrease with increasing latitude and altitude, due to the increasing harshness of the environmental conditions (Gíslason & Gardarsson, 2010; Lencioni, 2004; Leonard, 2010).

Due to natural and anthropogenic climate change, subarctic aquatic ecosystems are experiencing negative environmental impacts, such as permafrost disruption, loss of biodiversity and reduced habitat diversity (Anisimov, 2007; Bokhorst et al., 2008). The warmer winters and rise in air temperature have resulted in snow melt occurring earlier in the spring, involving reductions in snow cover (Bokhorst et al., 2008; Bradley & Ormerod, 2001; Callaghan et al., 2005; Rawlins et al., 2016). Fluctuations in seasonal hydrological regimes have an effect on aquatic habitats due to changes in the amount of water and suspended sediments, as well as increases in water temperature in streams, which in turn influence the distribution and diversity of aquatic insects (Nyman et al., 2005).

Fresh water ecosystems are also typically dominated by the family Chironomidae, which are recognized as the most widespread macroinvertebrate group globally and are adapted to live in a wide range of different types of running water ecosystems, including glacial and spring-fed streams (Ferrington, 2008; Francis, 2004; Rossaro et al., 2006; Tarrats et al., 2016). Chironomids are the most abundant and diverse taxon in aquatic ecosystems, representing 25% of aquatic insects and approximately 15,000 species (Cure, 1985; Cranston, 1995; Tarrats et al., 1995; Francis, 2004; Lencioni, 2004). Chironomids are considered biological indicators of water quality as they track changes in the environment and are sensitive to various environmental conditions (Kranzfelder et al., 2015). Thus, they have frequently been used as indicators of the environmental status of rivers and streams (Lindegaard, 1995; Nyman, et al., 2005; Self et al., 2011; Tarrats et al., 2016), and as bioindicators of the impacts of climate change on freshwater ecosystems. (Heino & Paasivirta, 2008; Nicacio & Juen, 2015). The most common chironomid community metrics used to evaluate water quality are: species composition, the dominance of pollution tolerant species, and the occurrence of morphological abnormalities during a select period of time (Marques et al., 1999; Oh et al., 2014). Chironomids are affected by stream trophic, physical and chemical conditions (König & Santos, 2013), as well as climatic conditions (Lods-Crozet et al., 2001). For example, water temperature is a primary factor influencing chironomid distribution in aquatic environments, and chironomid species are known to vary in their tolerance to water temperature (Francis, 2004; Hannesdóttir et al., 2012).

In North America, particularly in Arctic and sub-Arctic areas Chironomidae are the dominant dipteran family in aquatic environments, where seven subfamilies regularly occur. Tanypodinae, Orthocladiinae and Chironomidae are the most common subfamilies encountered in freshwaters (Hudson et al., 1990; Epler, 2001). Insect taxa in Alaskan streams are mainly found in non-frozen areas; however, 90 % of the individuals found in streams that are chironomids and Empididae (Merritt & Cummins, 1996).

In this chapter, a long-term study of Chironomidae communities of four pristine streams in DNP (from the 10 study streams), Alaska sampled over the period 2008-2016 was used to obtain a better understanding of the linkages between environmental variables and chironomid diversity, and thus to better understand which climatic conditions force shifts in chironomid community composition through time.

The objectives of this study were to: (i) analyse variations in Chironomidae community composition from 2008 to 2016, and (ii) to determine the environmental variables that drive chironomid distributions, and how these relationships change across time.

5.1 Methods

East Fork Tolkat Tributary, Hogan, Igloo and Tattler were the four streams in DNP selected for the Chironomidae analysis.

5.1.1 Chironomid data

Chironomidae sampling was undertaken from 2008 to 2016 - covering nine consecutive years. The sampling was undertaken during summer and autumn because it is during this time that the streams are free of ice. In DNP, riffles are the dominant habitat in rivers and streams, and they are characterized by being well oxygenated areas, supporting a high diversity of living organisms (Cook & Sullivan, 2018). In each of the four streams, six Surber samples per 10 m were collected from each riffle.

The chironomid sampling method was standardized. The equipment used to collect chironomid individuals in the streams was a Surber standard 0.093m^2 with a mesh size of 335 µm. The collected specimens were preserved in IMS solution (80 % ethanol) and labelled in a Whirlpack™ bag (Conn, 1998) in order to keep the chironomid individuals in good condition for further laboratory analysis.

Chironomid samples collected from 2008 to 2016 were identified to the lowest practical level (mainly genus) following the keys listed in Andersen et al. (1983).

5.1.2 Environmental data

The local and large-scale environmental variables used in this chapter are the same as those used in previous chapters, and are described in Chapter 2, section 2.2.3 (see Table 2.1).

5.2 Data analysis

The relationship between the environmental and climatic variables and changes in chironomid composition through time at the four rivers was examined using Redundancy Analysis (RDA). Prior to undertaking the RDA, the chironomid data were organized into a taxa-year matrix for each stream, whereby columns represented taxa and rows represented years; each element in the matrix was the abundance of a given taxon in a given year. The same formatting approaches were applied to the environmental variables (i.e. variable-year matrices were constructed). The RDA was undertaken using the procedure outlined in Borcard et al. (2011). The species data were Hellinger transformed (Borcard et al., 2011). At first, all environmental variables were included in each RDA analysis, and a backwards-selection procedure was used to generate a final model with only significant variables remaining (alpha level of 0.05; Borcard et al., 2011). The R^2 and adjusted R^2 values of the full and final models were calculated using the approach of Peres-Neto et al. (2006). Prior to this analysis, all chironomid taxa with fewer than three individuals were removed (Poos & Jackson, 2012). The RDA was undertaken using the vegan package (Oksanen et al., 2017) and the R programming language (R Core Team, 2017).

Replicate sample abundance of five common genera per stream were analysed using Excel in order to examine population persistence and stability. High abundance values denote high persistence and low standard deviation values indicate high stability. Data from each replicate sample were combined (i.e. the abundances were summed, as there were no clear differences between summer and autumn samples) to create one mean / standard deviation value per year per stream.

The above statistical analysis was then repeated to generate a global analysis showing total mean and standard deviation per stream.

5.3 Results

5.3.1 Assemblage dynamics

The four streams showed different patterns in the persistence and stability of their chironomid communities over time (Fig. 5.1a to 5.4b). In the all streams analyses (i.e. mean and standard Chironomidae population values per year per river; Table 5.1 and Appendix 5.1-5.2), Igloo Creek stream exhibited the highest community stability. Hogan exhibited the lowest stability, but had the highest chironomid mean persistence of the four streams.

Table 5.1 Mean Chironomidae total abundance (m2) and standard deviation per stream over the study.

	Igloo	Tattler	Hogan	EFTT
Mean	6.49	9.34	19.97	13.1
SD	3.28	8.2	12.54	10.46

Igloo Creek

The most common Chironomidae taxon in Igloo creek (Fig. 5.1 a,b) across all years was *Orthocladius s* type, which exhibited a maximum number of individuals in the years 2008 and 2014, with 25 individuals per m^2. This was followed by *Eukiefferiella gremhi type* (16 m^2 in 2008), which had a similar presence across all years. *Diamesa spp* had the largest number of individuals in 2014 (21 m^2). In contrast, the taxon with the lowest number during 2008 was *Limnophyes* (1 m^2) and during 2014 was *Corynoneura* (1 m^2). During 2010, the taxa with the highest numbers of individuals in

2012 was *Eukiefferiella gremhi type* with 5 individuals per m^2, whilst *Limnophyes* had only 1 individual per m^2. *Corynoneura* had the lowest numbers across all years, and was completely absent from the samples in 2012, 2015 and 2016.

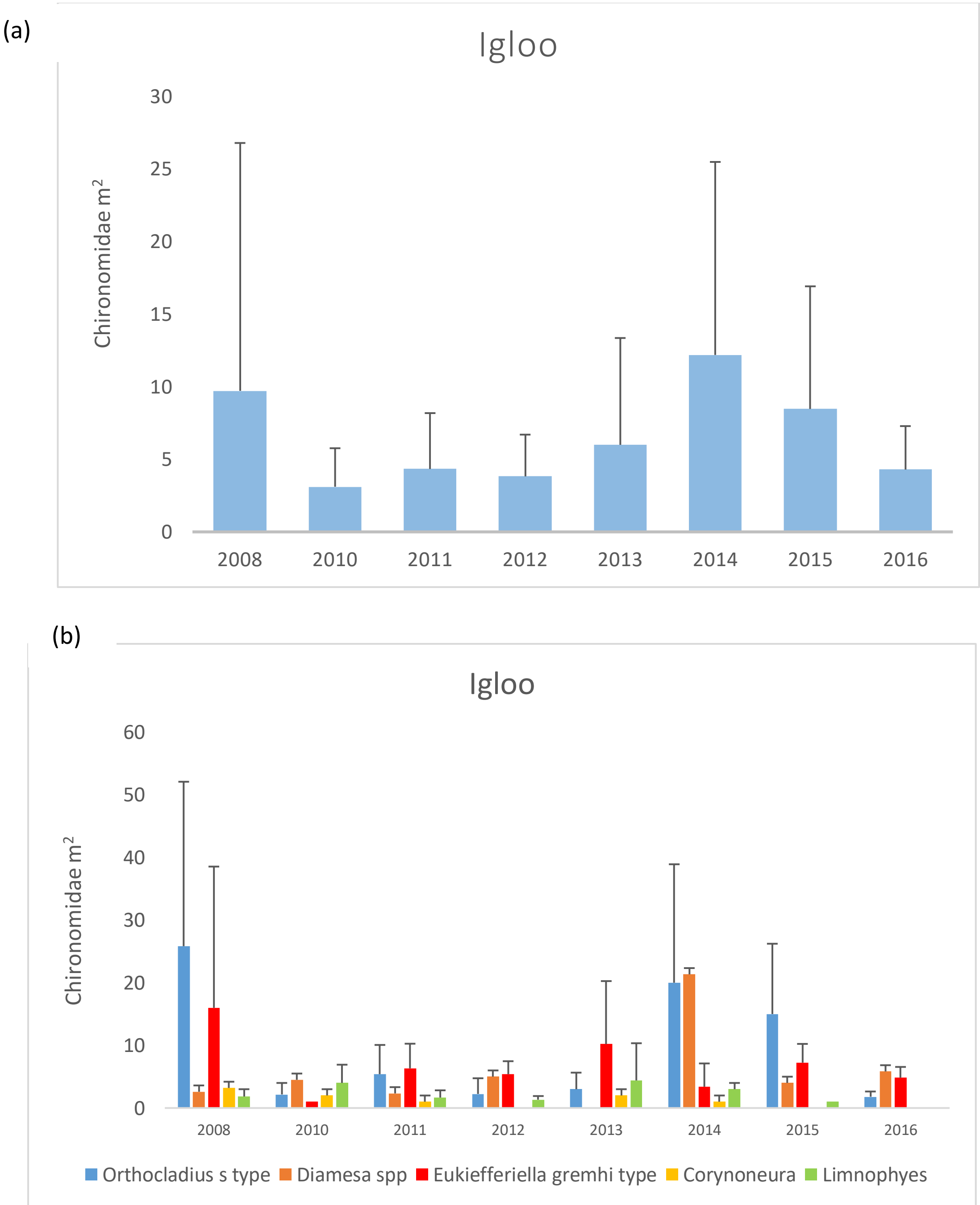
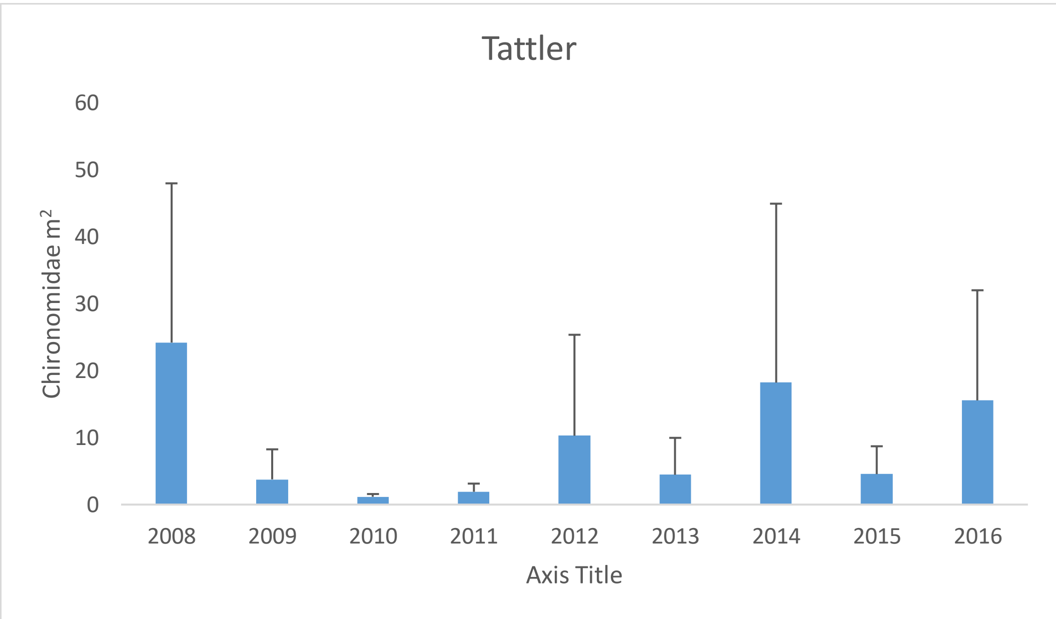


Figure 5.1 Igloo Creek. (a) Mean Chironomidae abundance +/- 1SD per year and (b) mean Chironomidae genus abundance and standard deviation per year.

Tattler Creek

Tattler Creek had the most diverse chironomid community during 2008 and 2014, with contrasting dominating genera. In 2008, *Orthocladius eurothocladius* (49 m^2), *Orthocladius s type* (31) and *Diamesa spp* (24 m^2) showed the highest number of individuals per m^2, and *Eukiefferiella undiff.* had the lowest number of individuals with 3 per m^2. Indeed *Diamesa spp* (36 m^2) dominated the Chironomidae community in 2016 followed by *Eukiefferiella gremhi type* (14 m^2) and *Eukiefferiella undiff*. (9 m^2). The years 2010 and 2011 showed major shifts in Diamesa abundance, the lowest numbers in each taxon, where *Orthocladius Eurothocladius* and *Eukiefferiella undiff* were absent in 2010 and *Orthocladius Eurothocladius* during 2011. In fact, *Orthocladius eurothocladius* was absent from 2010 to 2015, and then reappeared in 2016. In addition, although in 2011 there was a low persistence in the chironomid community, it exhibited temporal stability.

(a)



(b)

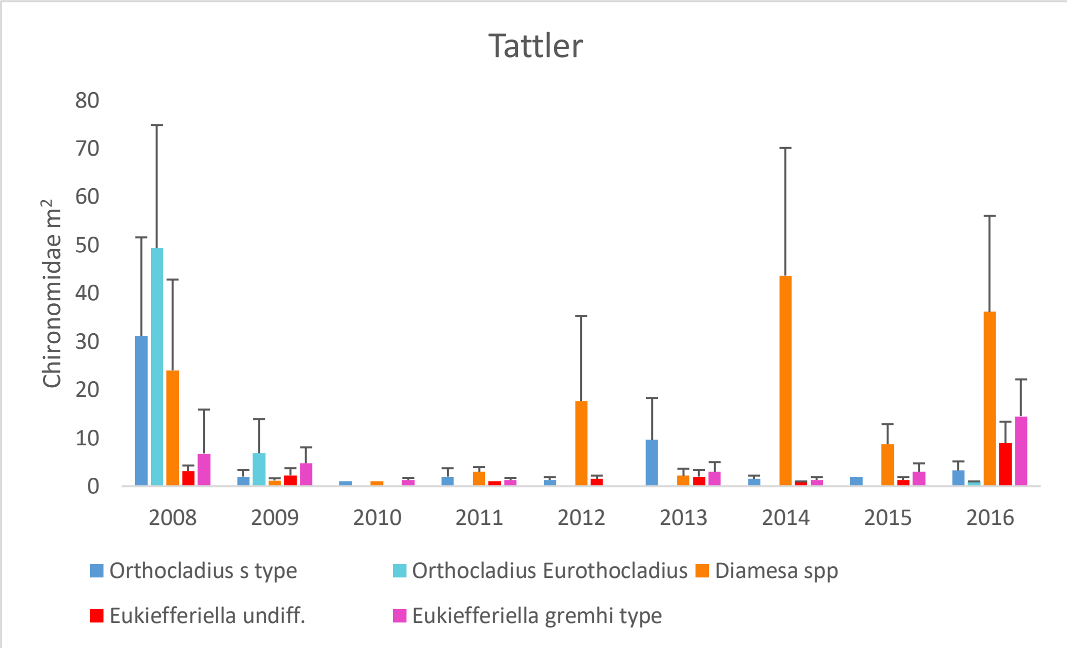
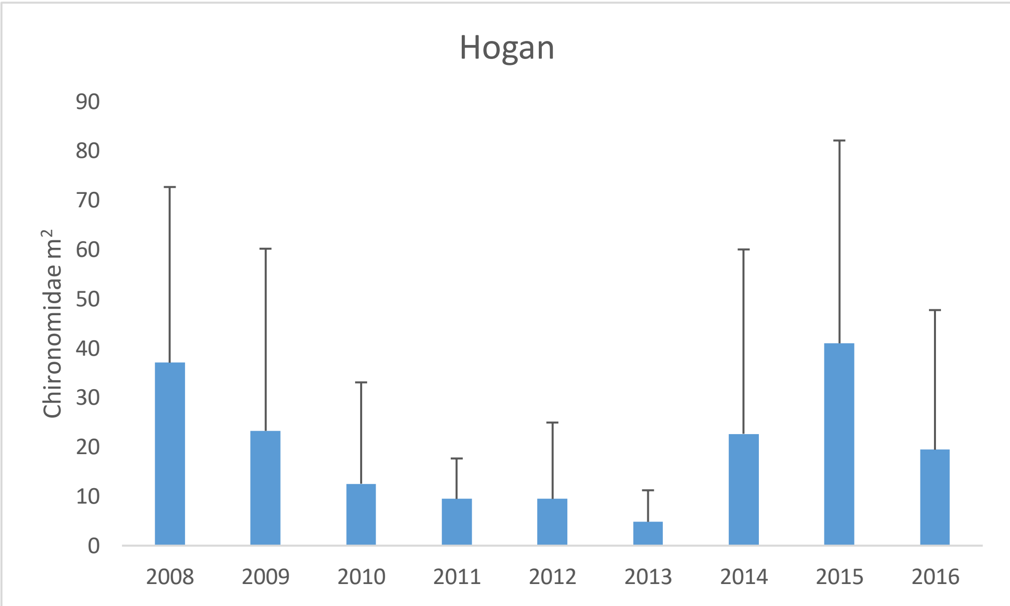


Figure 5.2 Tattler Creek. (a) Mean Chironomidae abundance and standard deviation per year and (b) mean Chironomidae genus abundance and standard deviation per year.

Hogan Creek

The years with the highest diversity of Chironomidae in Hogan Creek were 2008 and 2009. In 2008, *Pesudokiefferiella* (60 m^2) dominated the community, with 60 individuals per m^2, followed by *Diamesa spp* (42 m^2) and *Orthocladius s type* (33 m^2), while in 2009 *Pseudokiefferiella* (75 m^2) was the dominating genus in the community. In contrast, 2011 and 2013 had the lowest number of individuals per group. In 2011, *Pseudokiefferiella* had the highest presence with 16 per m^2 and, *Orthocladius s type* and *Hydrobaenus conformis type* were absent during that year, while during 2013, *Diamesa spp* (12 m^2) dominated the Chironomidae community and the absent genus was *Hydrobaenus conformis type*, which was absent in all of the following years. *Diamesa spp* was present in all years and had the largest number of individuals during three consecutive years (2014-2016).

(a)



(b)

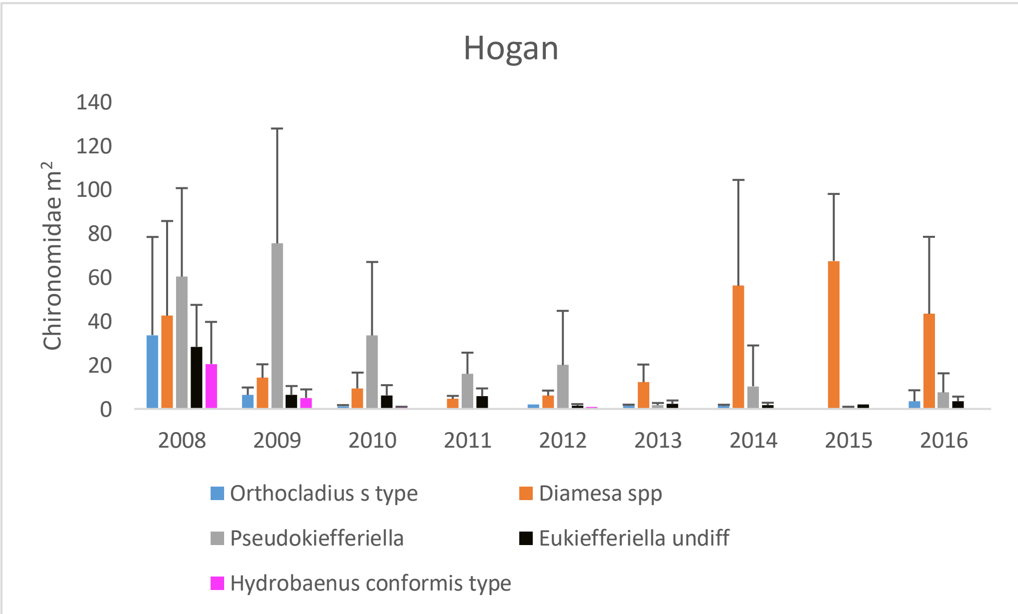
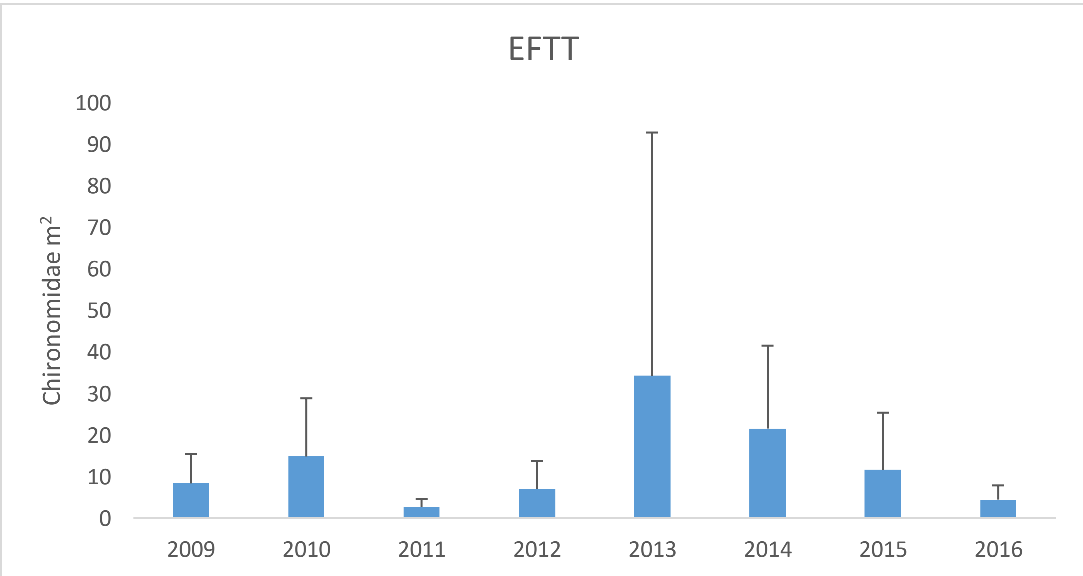


Figure 5.3 Hogan Creek. (a) Mean Chironomidae abundance and standard deviation per year and (b) mean Chironomidae genus abundance and standard deviation per year.

East Fork Tolkat Tributary

The population dynamics in East Fork Tolkat Tributary stream were characterized by high diversity during 2010 and 2013, where in both years *Orthocladius s type* had the most individuals with 26 m^2 and 96 m^2. There were 65 individuals per m^2 of *Orthocladius eurothocladius* sampled during 2013 but, in contrast, the same genus in 2010 registered just 1 m^2. The years with the lowest number of total abundance were 2011 and 2016. The diversity in 2011 showed homogeneity among the different genera, where *Orthocladius eurothocladius* and *Diamesa spp* registered 3 Chironomidae per m^2. In 2016, the dominant genus was Diamesa spp (6 m^2), followed by *Orthocladius s type* (3 m^2) *Orthocladius eurothocladius* was not present in the community during that year or in fact since 2014.

(a)



(b)

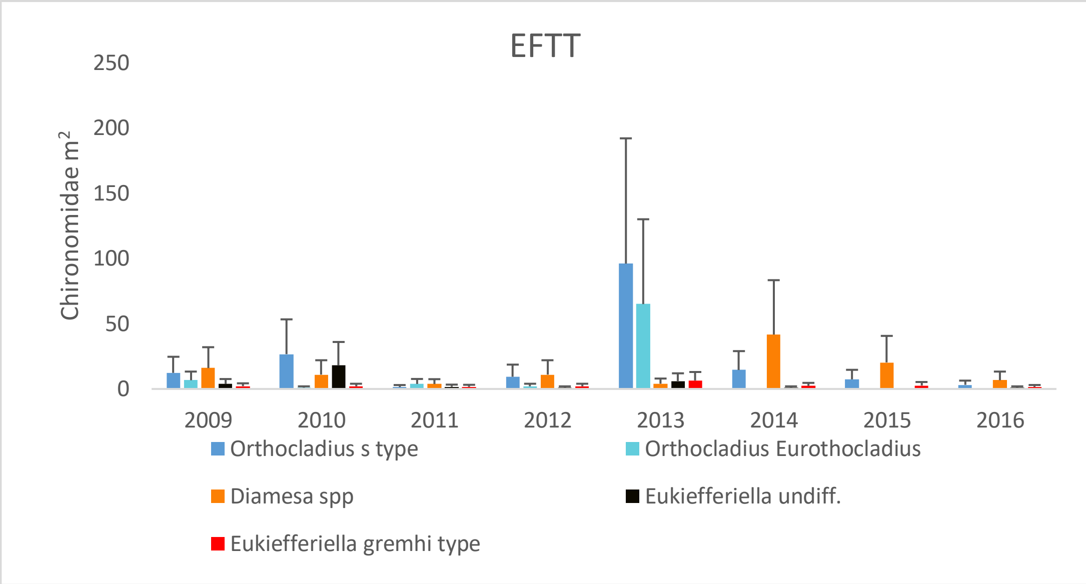


Figure 5.4 Figure 5.4 East Fork Tolkat Tributary. (a) Mean Chironomidae abundance and standard deviation per year and (b) mean Chironomidae genus abundance and standard deviation per year.

5.3.2 Environmental variables

The environmental variables in the best RDA model (selected using backwards selection) for each of the four streams are presented in Table 5.2. The adjusted R2 values of the best model were very high for three of the four streams, indicating that the models had relatively high explanatory power (Table 5.2). Whilst a range of different environmental variables were included in the best models, certain variables (e.g. Mtemp, SpringTemp and SpringFlood) were present in the best models for multiple streams. The RDA biplots of the best models are provided and discussed below for each individual stream, in turn.

Table 5.2 Summary statistics for the best RDA models for each of the four streams.

Stream	Best Model Statistics			Best Model Variables
	R2	R2adj	P	
East Fork Tolkat Tributary	0.995	0.965	0.001	NAO+EO.NP+Mtemp+Sdtemp+SpringTemp
Hogan Creek	0.726	0.562	0.003	PDO+Sdtemo+SpringTemp
Igloo Creek	0.857	0.5	0.059	EP-NP+Mtemp+SDsnow+SpringTemp+SpringFlood
Tattler Creek	0.305	0.206	0.024	SpringFlood

East Fork Tolkat Tributary

Fig 5.5 shows that the years 2012 and 2014-2016 form a group within the biplot and these years were mainly influenced by high Mtemp, a high EP.NP, high PC1(less snow) and high SpringTemp. The year 2013 was strongly influenced by variations in air temperature.

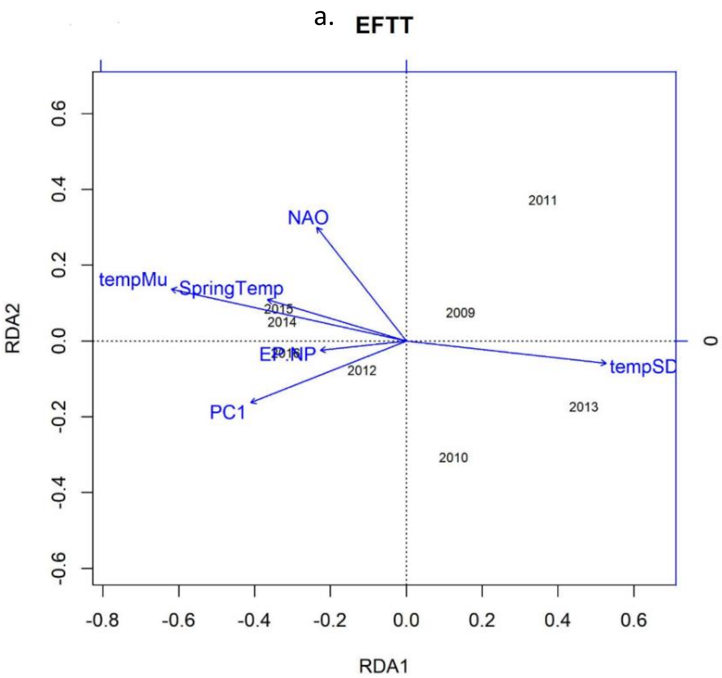


Figure 5.5 East Fork Tolkat Tributary. The RDA biplot (scaling 1) of the Hellinger-transformed Chironomidae data showing the locations of the objects (years) and the environmental variable(s) present in the best RDA model, selected using backwards selection.

Hogan Creek

Two main groups of years corresponding to pre- and post- 2013 are present in Fig. 5.6. The biplot shows the three variables in the best model: SDtemp, SpringTemp and PDO. The pre-2013 group was strongly affected by SDtemp (variations in air temperature), whilst the post-2013 group was related to high PDO and high average spring air temperature (SpringTemp). The year 2008 is an outlier in the biplot, showing no association with the environmental variables.

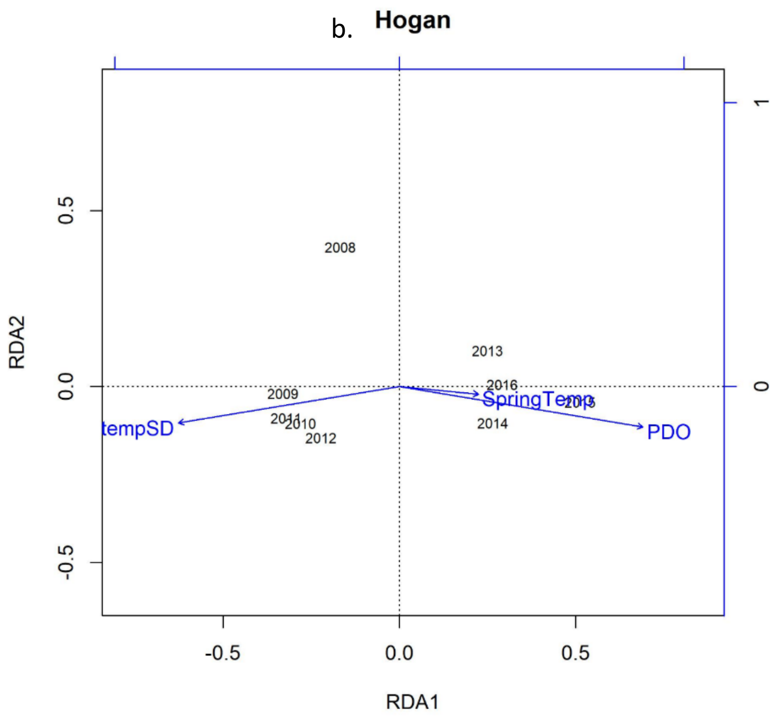


Figure 5.6 Hogan Creek. The RDA biplot (scaling 1) of the Hellinger-transformed Chironomidae data showing the locations of the objects (years) and the environmental variable(s) present in the best RDA model, selected using backwards selection.

Igloo Creek

Fig. 5.7 shows one group of years roughly corresponding to the post-2010 years. High Mtemp, high Spring Temp, high snowSD and low EP.NP were important variables for this group. The correlation between Mtemp and Springtemp was high. During 2008, the main driver was seemingly high SpringFlood. The plot indicates that 2013 was an outlier year.

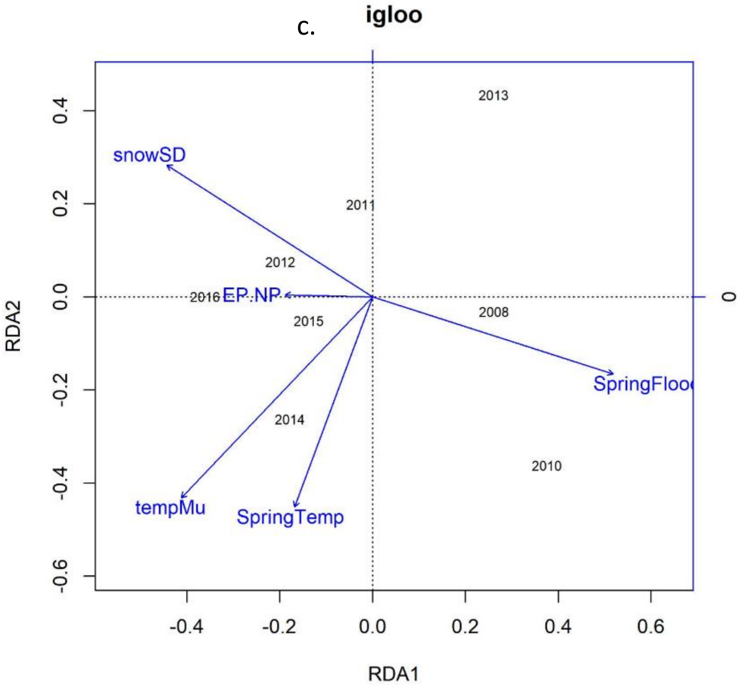


Figure 5.7 Igloo Creek. The RDA biplot (scaling 1) of the Hellinger-transformed Chironomidae data showing the locations of the objects (years) and the environmental variable(s) present in the best RDA model, selected using backwards selection.

Tattler Creek

The RDA model (Fig 5.8) did not show any groupings of years; however, the selection process produced a single significant variable: SpringFlood. However, the effect of SpringFlood does not appear to have been that strong, based on the biplot.

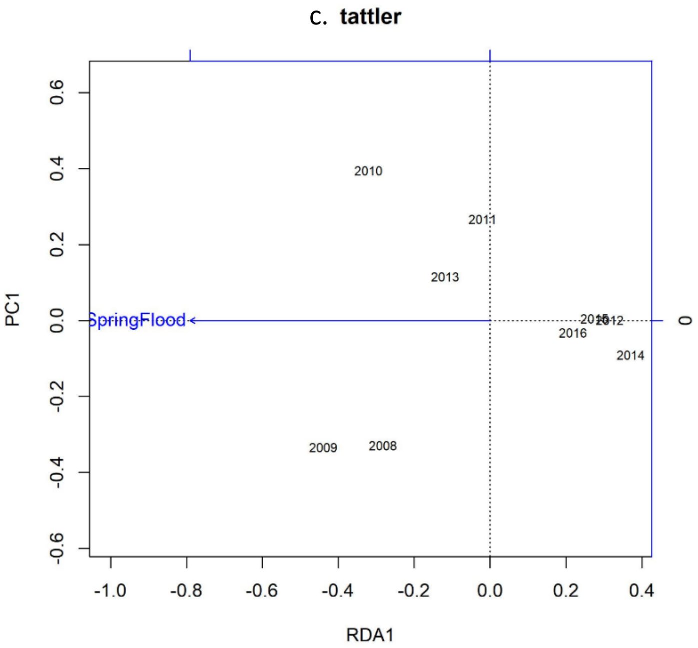


Figure 5.8 Tattler Creek. The RDA biplot (scaling 1) of the Hellinger-transformed Chironomidae data showing the locations of the objects (years) and the environmental variable(s) present in the best RDA model, selected using backwards selection.

5.4 Discussion

In this study, the effect of different environmental variables on chironomid community composition, and the persistence and stability of Chironomidae through time, was analyzed in four pristine glacier-fed streams in DNP. Across the four streams, the most important environmental variables were mean air temperature, spring floods, EP.NP and PDO (see Table 5.2).

5.4.1 Igloo Creek

Igloo Creek had high Chironomidae population. It is thus likely local low air temperatures reduce rainfall events during summer and consequently the runoff discharge (Milner et al., 2017). Hence, continual cold local environmental conditions preserved the habitat aquatic stability required to maintain Chironomidae community population stability. Furthermore, the influence of low air temperature in the aquatic habitat of Igloo Creek coincided with an increase in the number of individuals of the genus *Diamesa* that dominated streams with water temperature typically below 2°C (Milner et al., 2001).

5.4.2 Tattler Creek

Seasonal floods during spring were the major factor affecting the Chironomidae community in Tattler Creek. The rise of seasonal rainfall and snowmelt resulting from an increase in air temperature could increase runoff in Tattler Creek, destabilizing the stream channel and consequently producing variations in Chironomidae populations through time. Additionally, seasonal flow events caused destabilization and reducing Chironomidae *Diamesa* in this stream. Thus, it seems that Chironomidae communities in cold weather ecosystems comprise taxa that are highly sensitive to environmental habitat changes produced by hydrological variations due to shifts in air temperature (Schütz & Füreder, 2019).

5.4.3 Hogan Creek

The Chironomidae community in Hogan Creek displayed more variability and less stability through time in comparison to the other streams. Streams fed by groundwater like Hogan Creek exhibit local physicochemical variations according to the flowpath length, which regulates temperature and flow (Crossman et al., 2011). Thus, when the pathway length decreased, the water in the groundwater zone increases in temperature, which in turn has an impact on local ecosystem dynamics (Crossman et al., 2011; Hinzman et al., 2005). Variability in climatic conditions in interior Alaska likely had an impact on the local physiochemistry of Hogan Creek. This will then have affected the life cycle of various chironomid taxa, such as

Orthocladius s type, Hydrobaenus conformis type, Eukiefferiella undiff and *Pesudokiefferiella*, hindering their ability to sustain viable populations.

5.4.4 East Fork Tolkat Tributary

The chironomid community in East Fork Tolkat Tributary was mainly affected by warm air temperatures as a result of local and large-scale climatic conditions, highlighting that an above-average increase in air temperature was registered during the winter season. The main driver increasing snowmelt and water discharge inside the basin was the rise in air temperatures (Hinzman et al., 2005), and the variables discharges were likely the cause of the low observed numbers of the five chironomid genera in the stream. Overall, the populations of all genera in EFTT diminished through time, possibly due to the increasingly warmer temperatures.

5.4.5 Taxa and environmental conditions

The genus *Diamesa* exhibited the same trend in all streams, showing the highest number of individuals during 2014 and the lowest number of individuals between 2010 to 2013. The change in *Diamesa* abundance was likely the result of the flow events causing destabilization and reducing other chironomids and thus less competition. The destabilization in the Chironomidae community during 2014 in the four streams might be caused by a positive EP.NP phase (Galloway et al., 2014; NOAA, 2018) in combination with the polar vortex dynamics which encircle the Northern Hemisphere alternating between warm and cold air waves in interior Alaska, increasing air temperature and consequently precipitation during the winter season (Galloway et al., 2014; Walsh, 2014).

5.4.6 Conclusion

Fresh water macroinvertebrate communities are extremely sensitive to changes in air temperature. This is particularly the case for specialized species living in northern latitudes under extreme cold climatic conditions, where low water temperature is the main driver influencing chironomid community composition (Francis, 2004; Gardarsson & Gíslason, 2010; Hannesdóttir et al., 2012; Lencioni, 2004; Leonard, 2010). In the study of European glacier-fed streams conducted by Milner et al. (2001), *Diamesa* dominates the community in glacier-fed streams where water temperature is below 2°C, and channel stability low. High flow conditions during the spring that reduces other chironomids allows *Diamesa* to dominate the chironomid community. *Diamesa* are typically poor competitors (Flory and Milner 2005). *Diamesa* have adaptations for surviving in fast flowing conditions with strong tarsal claws and pro-legs. Other chironomid taxa, such as *Orthocladiinae*, together with *Baetidae* and *Simuliidae*, also increased in number when channel stability and water temperature increase. Thus, the variables driving shifts in Chironomidae abundance in these rivers appear to be maximum water temperature, high flow variability and channel stability.

In summary, Chironomidae are an important component of the invertebrate community in the streams of Denali and show high variability in their abundance and diversity. Where *Diamesa* dominates in certain years it indicates that spring flows may have been high removing other chironomid taxa and this may be an indication of more extreme events associated with climate change

6 Synthesis

6.0 Synthesis and main findings

The main aim of the research was to identify the variations in macroinvertebrate community structure from year to year in 10 different streams in DNP in Alaska, and to elucidate the principal environmental variables driving these changes. Most of the research to examine variations in macroinvertebrate communities has been short-term studies (using data sets from 1 to 4 consecutive years). in Mississippi, USA, Maul et. al. (2004) used macroinvertebrates samples collected from 17 streams, between 1999-2000. The results showed that degraded streams caused temporal variations in the macroinvertebrate community. Henriques-Oliveira & Nessimian (2010) in Southeastern Brazil, used macroinvertebrate samples collected in rivers with low altitude during August 2001 and August 2004. The results displayed that composition and abundance variations in macroinvertebrate community were affected by altitudinal distribution gradients. Zhang et. al. (2014) showed that macroinvertebrate composition from Qinjiang River (an undisturbed river), in Guangxi, China, was mainly influenced by local environmental variables in 2010. On the other hand, Bae et. al. (2016) revealed that the variability between the macroinvertebrate samples collected from 2009 to 2011 was different between seasons and sites, as a result of local processes like natural variability of physical habitats and seasonal changes. However, a long-term study examining aquatic macroinvertebrate responses to multiple climatic environmental variables has previously not been studied in detail as in this study. These variables included fluctuations in air temperature, and hydrological annual and seasonal regimes due to large-scale atmospheric patterns.

Local climatic conditions in DNP, Alaska were strongly influenced by large-scale atmospheric patterns (Fig. 1.1) with direct effects on air temperature and precipitation in terms of rainfall and snowfall (Hodgkins, 2009; Whitfield et.al., 2010). The anomalous weather conditions were mainly observed during spring and winter, where warmer air temperatures were recorded (Hodgkins, 2009; Shulski et. al., 2010). The relationship between sea surface air temperature and atmospheric air temperature produced shifts in PDO, PNA, ONI and EN-NP phases, changing from positive to negative and from negative to positive (Climatenexus, 2018; National Oceanic and Atmospheric Administration, 2018). NAO and ONI were the main large-scale atmospheric patterns impacting air temperature and hydrology regimes (annual and seasonal) in streams of DNP. Seasonal weather patterns such as rainfall during spring and anomalous high air temperatures during winter are mainly affected by the positive phase of NAO and/or ONI, which is characterized by warmer temperature (Behrangi et. al., 2016; Hartmann & Wendler, 2005; Jackson & Füreder, 2006; Keen 2008; Mantua et. al., 1997; U.S. Fish & Wildlife Service, 2009). A positive phase of NAO increased the amount of annual rainfall. Furthermore, when ONI experienced the same phase (positive or negative), the effects on air temperature and precipitation (rainfall and/or snowfall) during spring were strengthened due to anomalous extreme high or low air temperature (Bradley & Ormerod, 2001; Climatenexus, 2018; National Oceanic and Atmospheric Administration, 2018).

As all streams in this study were fed by snowmelt, groundwater and/or spring water (Conn, 1998), this makes them more vulnerable to influence by seasonal air temperature and hydrological regimes (Wrona et. al., 2016). The principal variables affecting the instream physicochemical characteristics, included fluctuations in water temperature, increased sediment transport through the stream channel and floods caused by the increment of water discharges due to snowfall and snowmelt (Bradt et. al., 1999; Brown et. al., 2005; Jackson & Füreder, 2006; Khaliq & Gachon, 2010;

Whitfield et.al., 2010; Jacobsen & Dangles, 2011; Pace et. al., 2013; Vinke et. al., 2015; Worthington et. al., 2015). Thus, the environmental disturbances affecting freshwater habitats consequently have an impact on the macroinvertebrate assemblages (Jackson & Füreder, 2006; Pace et. al., 2013; Vinke et. al., 2015).

Aquatic macroinvertebrate communities in DNP, Alaska were characterized by cold-adapted taxa living under harsh environmental conditions, where Chironomidae (e.g. *Diamesa, Orthocladius, Eukiefferiella spp* and *Hydrobaenus conformis typ*e) dominated the community due to their preferences for colder water temperature <2°C or to high flow and unstable channel conditions, such as *Diamesa* genus (Milner, et. al., 2001; Milner et. al., 2006). Taxa from Ephemeroptera, Plecoptera and Trichoptera families were also common in the streams of DNP due to their preferences for well oxygenated habitats, such as riffles (Milner et. al., 2006; Vilenica et.al., 2016). Across the years Ephemeroptera (e.g. *Baetis, Capniia, Ostrocerca*) and Plecoptera (e.g. *Epeorus and Doddsia*) orders were the most abundant in all streams, showing higher persistence, and the capacity to recover from environmental disturbances affecting the instream physical characteristics, such as changes in water discharge or water temperature (Jackson & Füreder, 2006; Pace et. al., 2013; Vinke et. al., 2015). It was also observed that genera like *Diamesa,* with no presence in some years, reappeared when water temperature decreased in the stream or after high flow disturbance events. The data suggests that macroinvertebrate communities vary markedly over long time periods and are dominated by some taxa depending on the environmental conditions that each stream shows seasonally or annually (Milner, et. al., 2001).

Across the years, climatic conditions caused fluctuations in macroinvertebrate community persistence and compositional stability in all streams. It is important to highlight that the lowest persistence and compositional stability occurred from 2006 to 2008 when there was a clear tipping point in the community structure for most streams (Tattler Creek, N4, Moose Creek, Little Stoney Creek, Igloo Creek, Hogan Creek and Highway Creek) and the community changed to a different state. These shifts were mainly caused by marked differences in air temperature compared to other years, (both spring and winter) being above normal. The warmer spring air temperatures caused higher snowmelt and linked to higher spring rainfall led to spring floods, with a marked impact and major shift in community structure. This was clearly a regional effect, affecting a large number of streams.

The order of Diptera was the most diverse group showing different genera (i.e. *Dicranota, Rhabdomastix*, etc.) as indicator taxa with high presence facing the influence of weather conditions. Moreover, in the overall results of this study, Ephemeroptera, Plecoptera and Trichoptera orders also showed distinctive genera (i.e. *Ephemerella, Ostrocerca, Plumiperla, Ecclisomyia,* etc) as indicator taxa, where the plecopteran *Doddsia* showed the highest presence (found in six streams) during the study period.

The large-scale atmospheric patterns PDO, ONI, EP-NP and PNA did not show a great impact on the local climatic conditions in DNP, Alaska. However, the main environmental variables that greatly influenced the macroinvertebrate community were changes in air temperature, and precipitation events during spring (i.e. rainfall, floods) and winter (i.e. rainfall) might caused by PDO, ONI and PNA. Whereas, mean air temperature, spring floods, PDO and EP-NP were the main environmental variables affecting the chironomidae community. The macroinvertebrate community, particularly the Chironomidae, were markedly influenced by hydrological seasonal variations.

Variations in weather conditions have a great impact on macroinvertebrate populations. However, the macroinvertebrate community with the highest persistence to resist natural disturbance events caused by hydrological seasonal variations over the study period was found in East Fork Tolkat Tributary, L. Stoney Creek, Moose Creek and Hogan Creek. According to National Park Service (2016), the aforementioned streams are considered stable systems due to low flow variation and their riparian vegetation. However, the results of this study show that variability in weather patterns has relevant implications in lotic water systems in northern altitudes, where has been observed the incremental rainfall events.

6.1 **Limitations**

Long-term studies done in challenging locations and requiring field campaigns at the same point of collection over several years have to face different issues in field and laboratory.

- Sampling completeness may vary between samples due to different researchers undertaking the sampling;
- Local environmental data does not correspond directly to the study site, but to the nearest weather station covering the years of the study period.
- The use of datasets with missing years in between.
- The use of an existent dataset (if there is any) with identified specimens by different people could cause errors in identification.
- The identification of Chironomidae requires the investment of a large amount of time.

6.2 Avenues for future research

It was found that large-scale atmospheric patterns influenced the air temperature and annual and the seasonal hydrological regime at the local-scale; together these variables drove temporal variation in macroinvertebrate community structure. Additional long-term studies examining changes in macroinvertebrate communities in response to changing climate are vital if we are to better understand i) the interacting mechanisms underpinning aquatic biodiversity across different spatial and temporal scale, and ii) how this biodiversity will shift in response to future global environmental change.

Denali National Park, Alaska, offers a great opportunity to continue doing ecological long-term scientific investigations in aquatic ecosystems. Efforts should focus on other taxa such as diatoms or fish and at trophic interactions, i.e. looking at whole food webs and how these change through time in response to the different environmental variables. Understanding the changing patterns between the environmental stressors should improve the ability to predict the consequences of climate change for freshwater biodiversity.

7 Appendices

7.0 Chapter 2

7.0.1 Appendix 2.1: Local weather data obtained from McKinley Station (NOAA, 2017)

Year	Environmental variable	Unit	Month											
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dic
1994	Temperature	°F	4.3	-0.4	10.5	28.9	45.6	52.2	57.7	54.8	40.7	20.6	6	3.1
		°C	-15.39	-18.00	-11.94	-1.72	7.56	11.22	14.28	12.67	4.83	-6.33	-14.44	-16.06
	Precipitation	Inn	0.17	0.28	0.98	0.41	0.21	5.68	0.76	1.29	0.40	0.60	1.41	1.29
		cm	0.43	0.71	2.49	1.04	0.53	14.43	1.93	3.28	1.02	1.52	3.58	3.28
		mm	4.32	7.11	24.89	10.41	5.33	144.27	19.30	32.77	10.16	15.24	35.81	32.77
	Snow	Inn	3.00	5.90	17.50	8.40						10.60	24.00	19.00
		cm	7.62	14.99	44.45	21.34	0.00	0.00	0.00	0.00	0.00	26.92	60.96	48.26
		mm	76.20	149.86	444.50	213.36	0.00	0.00	0.00	0.00	0.00	269.24	609.60	482.60
1995	Temperature	°F	8.00	8.70	6.00	34.80	47.60	52.20	56.30	49.70	48.20	26.80	4.10	5.60
		°C	-13.33	-12.94	-14.44	1.56	8.67	11.22	13.50	9.83	9.00	-2.89	-15.50	-14.67
	Precipitation	Inn	0.08	0.34	0.35	0.13	1.40	3.35	2.32	2.32	1.33	0.27	0.24	0.17
		cm	0.20	0.86	0.89	0.33	3.56	8.51	5.89	5.89	3.38	0.69	0.61	0.43
		mm	2.03	8.64	8.89	3.30	35.56	85.09	58.93	58.93	33.78	6.86	6.10	4.32
	Snow	Inn	1.40	6.00	5.90	0.80	2.00					5.20	3.80	3.70
		cm	3.56	15.24	14.99	2.03	5.08	0.00	0.00	0.00	0.00	13.21	9.65	9.40
		mm	35.56	152.40	149.86	20.32	50.80	0.00	0.00	0.00	0.00	132.08	96.52	93.98
1996	Temperature	°F	-7.40	3.20	17.00	28.20	42.60	53.00	55.60	47.50	36.60	9.80	7.00	-2.70
		°C	-21.89	-16.00	-8.33	-2.11	5.89	11.67	13.11	8.61	2.56	-12.33	-13.89	-19.28
	Precipitation	Inn	0.19	2.71	0.19	0.05		1.31	1.62	3.38	1.23	1.81	0.72	0.81
		cm	0.48	6.88	0.48	0.13	0.00	3.33	4.11	8.59	3.12	4.60	1.83	2.06
		mm	4.83	68.83	4.83	1.27	0.00	33.27	41.15	85.85	31.24	45.97	18.29	20.57
	Snow	Inn	3.60	45.20	3.60	0.10					13.00	26.30	9.10	13.20
		cm	9.14	114.81	9.14	0.25	0.00	0.00	0.00	0.00	33.02	66.80	23.11	33.53

		mm	91.44	1148.08	91.44	2.54	0.00	0.00	0.00	0.00	330.20	668.02	231.14	335.28
1998	Temperature	°F	-0.40	11.40	22.40	33.60	43.50	51.40	55.10	47.20	40.50	27.00	13.40	-1.80
		°C	-18.00	-11.44	-5.33	0.89	6.39	10.78	12.83	8.44	4.72	-2.78	-10.33	-18.78
	Precipitation	Inn	0.12	0.17		0.83	0.59	1.68	4.54	3.44	1.49	0.27	0.30	0.95
		cm	0.30	0.43	0.00	2.11	1.50	4.27	11.53	8.74	3.78	0.69	0.76	2.41
		mm	3.05	4.32	0.00	21.08	14.99	42.67	115.32	87.38	37.85	6.86	7.62	24.13
	Snow	Inn	2.00	2.50		11.00	4.40					1.40	4.40	14.90
		cm	5.08	6.35	0.00	27.94	11.18	0.00	0.00	0.00	0.00	3.56	11.18	37.85
		mm	50.80	63.50	0.00	279.40	111.76	0.00	0.00	0.00	0.00	35.56	111.76	378.46
1999	Temperature	°F	-4.60	-7.50	10.80	27.40	39.50	53.80	55.20	53.10	40.50	19.30	3.50	-3.70
		°C	-20.33	-21.94	-11.78	-2.56	4.17	12.11	12.89	11.72	4.72	-7.06	-15.83	-19.83
	Precipitation	Inn	0.53	0.20	0.23	0.08	1.67	1.45	3.51	1.50	2.86	0.65	0.44	3.12
		cm	1.35	0.51	0.58	0.20	4.24	3.68	8.92	3.81	7.26	1.65	1.12	7.92
		mm	13.46	5.08	5.84	2.03	42.42	36.83	89.15	38.10	72.64	16.51	11.18	79.25
	Snow	Inn	11.30	2.60	4.90	1.40	2.90				23.50	9.90	8.90	26.80
		cm	28.70	6.60	12.45	3.56	7.37	0.00	0.00	0.00	59.69	25.15	22.61	68.07
		mm	287.02	66.04	124.46	35.56	73.66	0.00	0.00	0.00	596.90	251.46	226.06	680.72
2000	Temperature	°F	-2.00	19.60	20.80	26.90	38.20	53.20	52.60	46.50	37.60	22.70	19.70	16.60
		°C	-18.89	-6.89	-6.22	-2.83	3.44	11.78	11.44	8.06	3.11	-5.17	-6.83	-8.56
	Precipitation	Inn	1.69	0.79	0.20	0.70	0.24	1.08	3.03	5.77	2.36	0.57	0.39	0.10
		cm	4.29	2.01	0.51	1.78	0.61	2.74	7.70	14.66	5.99	1.45	0.99	0.25
		mm	42.93	20.07	5.08	17.78	6.10	27.43	76.96	146.56	59.94	14.48	9.91	2.54
	Snow	Inn	21.60	9.60	5.40	11.00					7.50	7.80	6.80	1.70
		cm	54.86	24.38	13.72	27.94	0.00	0.00	0.00	0.00	19.05	19.81	17.27	4.32
		mm	548.64	243.84	137.16	279.40	0.00	0.00	0.00	0.00	190.50	198.12	172.72	43.18
2001	Temperature	°F	19.40	15.90	15.60	28.80	37.70	54.40	53.30	53.00	44.00	18.50	5.70	-1.70
		°C	-7.00	-8.94	-9.11	-1.78	3.17	12.44	11.83	11.67	6.67	-7.50	-14.61	-18.72
	Precipitation	Inn	0.25	0.44	0.37	0.21	1.09	1.03	4.02	2.22	0.60	0.97	0.13	0.19
		cm	0.64	1.12	0.94	0.53	2.77	2.62	10.21	5.64	1.52	2.46	0.33	0.48

		mm	6.35	11.18	9.40	5.33	27.69	26.16	102.11	56.39	15.24	24.64	3.30	4.83
	Snow	Inn	4.90	7.40	6.40	3.10	14.50					12.70	3.40	3.10
		cm	12.45	18.80	16.26	7.87	36.83	0.00	0.00	0.00	0.00	32.26	8.64	7.87
		mm	124.46	187.96	162.56	78.74	368.30	0.00	0.00	0.00	0.00	322.58	86.36	78.74
2002	Temperature	°F	13.40	13.10	13.40	21.50	44.70	51.70	54.50	49.40	43.40	33.70	27.70	
		°C	-10.33	-10.50	-10.33	-5.83	7.06	10.94	12.50	9.67	6.33	0.94	-2.39	
	Precipitation	Inn	0.39	0.22	0.18	2.75	0.80	3.86	4.59	5.39	0.81	1.13	0.19	
		cm	0.99	0.56	0.46	6.99	2.03	9.80	11.66	13.69	2.06	2.87	0.48	
		mm	9.91	5.59	4.57	69.85	20.32	98.04	116.59	136.91	20.57	28.70	4.83	
	Snow	Inn	6.80	3.20	3.60	26.10	3.90				0.50	10.10	1.00	
		cm	17.27	8.13	9.14	66.29	9.91	0.00	0.00	0.00	1.27	25.65	2.54	
		mm	172.72	81.28	91.44	662.94	99.06	0.00	0.00	0.00	12.70	256.54	25.40	
2003	Temperature	°F	10.80	19.10	12.20	29.30		52.40	56.00	51.30	36.80	21.10	10.00	4.90
		°C	-11.78	-7.17	-11.00	-1.50	-17.78	11.33	13.33	10.72	2.67	-6.06	-12.22	-15.06
	Precipitation	Inn	0.30	0.25	0.21		0.44	1.24	4.78	2.79	1.73	0.52	1.63	0.98
		cm	0.76	0.64	0.53	0.00	1.12	3.15	12.14	7.09	4.39	1.32	4.14	2.49
		mm	7.62	6.35	5.33	0.00	11.18	31.50	121.41	70.87	43.94	13.21	41.40	24.89
	Snow	Inn	5.20	0.20	4.10	0.30	0.50		0.10		0.60	0.80	28.70	13.10
		cm	13.21	0.51	10.41	0.76	1.27	0.00	0.25	0.00	1.52	2.03	72.90	33.27
		mm	132.08	5.08	104.14	7.62	12.70	0.00	2.54	0.00	15.24	20.32	728.98	332.74
2004	Temperature	°F	-5.00	16.90	8.90	31.80	47.90	58.90	59.00	58.00	34.50	29.10	17.80	9.00
		°C	-20.56	-8.39	-12.83	-0.11	8.83	14.94	15.00	14.44	1.39	-1.61	-7.89	-12.78
	Precipitation	Inn	0.31	0.51	0.53	0.22	2.20	1.25	2.86	1.19	1.10	0.35	1.00	1.55
		cm	0.79	1.30	1.35	0.56	5.59	3.18	7.26	3.02	2.79	0.89	2.54	3.94
		mm	7.87	12.95	13.46	5.59	55.88	31.75	72.64	30.23	27.94	8.89	25.40	39.37
	Snow	Inn	8.60	6.50	8.30	2.10					6.40	5.10	15.00	21.50
		cm	21.84	16.51	21.08	5.33	0.00	0.00	0.00	0.00	16.26	12.95	38.10	54.61
		mm	218.44	165.10	210.82	53.34	0.00	0.00	0.00	0.00	162.56	129.54	381.00	546.10
2005	Temperature	°F	5.40	10.90	21.60	29.20	48.00	54.80	56.70	54.70	42.80	26.10	-4.10	16.20

		°C	-14.78	-11.72	-5.78	-1.56	8.89	12.67	13.72	12.61	6.00	-3.28	-20.06	-8.78
	Precipitation	Inn	1.49	0.35	0.41	0.93			3.34	1.20	2.58	0.20	1.14	0.55
		cm	3.78	0.89	1.04	2.36	0.00	0.00	8.48	3.05	6.55	0.51	2.90	1.40
		mm	37.85	8.89	10.41	23.62	0.00	0.00	84.84	30.48	65.53	5.08	28.96	13.97
	Snow	Inn	16.90	3.70	8.70	17.40					2.30	3.10	19.70	2.00
		cm	42.93	9.40	22.10	44.20	0.00	0.00	0.00	0.00	5.84	7.87	50.04	5.08
		mm	429.26	93.98	220.98	441.96	0.00	0.00	0.00	0.00	58.42	78.74	500.38	50.80
2006	Temperature	°F	-9.30	15.20	9.30	25.40	44.00	51.70	54.80	49.60	45.60	30.20	-4.90	9.00
		°C	-22.94	-9.33	-12.61	-3.67	6.67	10.94	12.67	9.78	7.56	-1.00	-20.50	-12.78
	Precipitation	Inn	0.60	0.81	0.19	0.49	0.28	2.77	3.64	3.01	1.44	1.74	0.12	0.93
		cm	1.52	2.06	0.48	1.24	0.71	7.04	9.25	7.65	3.66	4.42	0.30	2.36
		mm	15.24	20.57	4.83	12.45	7.11	70.36	92.46	76.45	36.58	44.20	3.05	23.62
	Snow	Inn	9.00	11.80	1.20	9.20						3.00	2.80	8.70
		cm	22.86	29.97	3.05	23.37	0.00	0.00	0.00	0.00	0.00	7.62	7.11	22.10
		mm	228.60	299.72	30.48	233.68	0.00	0.00	0.00	0.00	0.00	76.20	71.12	220.98
2007	Temperature	°F	4.50	5.20	-5.20	34.10	44.60	55.10	57.60	54.80	43.80	22.00		8.00
		°C	-15.28	-14.89	-20.67	1.17	7.00	12.83	14.22	12.67	6.56	-5.56	-17.78	-13.33
	Precipitation	Inn	0.48	0.37	0.24	0.31	1.12	1.50	1.57	4.18	2.02	0.37		0.33
		cm	1.22	0.94	0.61	0.79	2.84	3.81	3.99	10.62	5.13	0.94	0.00	0.84
		mm	12.19	9.40	6.10	7.87	28.45	38.10	39.88	106.17	51.31	9.40	0.00	8.38
	Snow	Inn	6.90	7.50	3.10	1.70	0.50				0.20	7.60		5.70
		cm	17.53	19.05	7.87	4.32	1.27	0.00	0.00	0.00	0.51	19.30	0.00	14.48
		mm	175.26	190.50	78.74	43.18	12.70	0.00	0.00	0.00	5.08	193.04	0.00	144.78
2008	Temperature	°F		2.90	15.20	25.30	41.30	50.20	51.70	48.60	41.10	13.80	6.60	0.20
		°C		-16.17	-9.33	-3.72	5.17	10.11	10.94	9.22	5.06	-10.11	-14.11	-17.67
	Precipitation	Inn	0.56	0.52	0.25	1.29	0.26	1.44	4.92	3.33	1.06	0.96	1.02	0.58
		cm	1.42	1.32	0.64	3.28	0.66	3.66	12.50	8.46	2.69	2.44	2.59	1.47
		mm	14.22	13.21	6.35	32.77	6.60	36.58	124.97	84.58	26.92	24.38	25.91	14.73
	Snow	Inn	6.90	8.40	5.90	10.90	1.30				3.00	13.40	11.40	12.90

		cm	17.53	21.34	14.99	27.69	3.30	0.00	0.00	0.00	7.62	34.04	28.96	32.77
		mm	175.26	213.36	149.86	276.86	33.02	0.00	0.00	0.00	76.20	340.36	289.56	327.66
2009	Temperature	°F	-2.80	5.50	6.10	26.80	44.30	51.60	59.10	48.70	41.50	3.60	4.50	12.10
		°C	-19.33	-14.72	-14.39	-2.89	6.83	10.89	15.06	9.28	5.28	-15.78	-15.28	-11.06
	Precipitation	Inn	1.19	0.35	0.43	0.09	0.76	1.34	1.28	3.75	0.93	0.18	0.56	0.67
		cm	3.02	0.89	1.09	0.23	1.93	3.40	3.25	9.53	2.36	0.46	1.42	1.70
		mm	30.23	8.89	10.92	2.29	19.30	34.04	32.51	95.25	23.62	4.57	14.22	17.02
	Snow	Inn	8.70	7.80	10.10	3.10						2.60	9.00	10.60
		cm	22.10	19.81	25.65	7.87	0.00	0.00	0.00	0.00	0.00	6.60	22.86	26.92
		mm	220.98	198.12	256.54	78.74	0.00	0.00	0.00	0.00	0.00	66.04	228.60	269.24
2010	Temperature	°F	-4.00	13.30	13.00	30.00	45.50	51.40	53.60	53.20	42.30	28.00	15.60	-10.80
		°C	-20.00	-10.39	-10.56	-1.11	7.50	10.78	12.00	11.78	5.72	-2.22	-9.11	-23.78
	Precipitation	Inn	0.33	0.20	0.38	0.16	0.14	0.69	0.40	0.49	0.15	0.10	0.18	0.22
		cm	0.84	0.51	0.97	0.41	0.36	1.75	1.02	1.24	0.38	0.25	0.46	0.56
		mm	8.38	5.08	9.65	4.06	3.56	17.53	10.16	12.45	3.81	2.54	4.57	5.59
	Snow	Inn	6.00	2.80	7.60	3.20						3.40	12.10	9.60
		cm	15.24	7.11	19.30	8.13	0.00	0.00	0.00	0.00	0.00	8.64	30.73	24.38
		mm	152.40	71.12	193.04	81.28	0.00	0.00	0.00	0.00	0.00	86.36	307.34	243.84
2011	Temperature	°F	5.50	3.10	9.20	26.10	43.10	53.00	53.50	49.50	43.60	27.70	-4.10	9.80
		°C	-14.72	-16.06	-12.67	-3.28	6.17	11.67	11.94	9.72	6.44	-2.39	-20.06	-12.33
	Precipitation	Inn	0.36	2.46	0.02	0.05	0.73	1.94	2.49	1.86	0.27	0.38	0.65	1.69
		cm	0.91	6.25	0.05	0.13	1.85	4.93	6.32	4.72	0.69	0.97	1.65	4.29
		mm	9.14	62.48	0.51	1.27	18.54	49.28	63.25	47.24	6.86	9.65	16.51	42.93
	Snow	Inn	8.10	43.90	0.30	0.50	3.00					5.50	12.20	18.10
		cm	20.57	111.51	0.76	1.27	7.62	0.00	0.00	0.00	0.00	13.97	30.99	45.97
		mm	205.74	1115.06	7.62	12.70	76.20	0.00	0.00	0.00	0.00	139.70	309.88	459.74
2012	Temperature	°F	-18.60	16.60	3.00	33.20	10.40	52.80	53.90	50.30	41.40	20.00	-5.10	-3.10
		°C	-28.11	-8.56	-16.11	0.67	-12.00	11.56	12.17	10.17	5.22	-6.67	-20.61	-19.50
	Precipitation	Inn	1.01	0.74	0.30	0.11	0.60	4.77	0.79	1.78	2.41	1.06	0.50	0.41

		cm	2.57	1.88	0.76	0.28	1.52	12.12	2.01	4.52	6.12	2.69	1.27	1.04
		mm	25.65	18.80	7.62	2.79	15.24	121.16	20.07	45.21	61.21	26.92	12.70	10.41
	Snow	Inn	14.00	10.30	5.10	0.60	1.30					10.20	9.50	8.00
		cm	35.56	26.16	12.95	1.52	3.30	0.00	0.00	0.00	0.00	25.91	24.13	20.32
		mm	355.60	261.62	129.54	15.24	33.02	0.00	0.00	0.00	0.00	259.08	241.30	203.20
2013	Temperature	°F	9.80	11.80	11.10	13.60	36.00	57.80	56.20		38.40	34.70	10.30	1.00
		°C	-12.33	-11.22	-11.61	-10.22	2.22	14.33	13.44	-17.78	3.56	1.50	-12.06	-17.22
	Precipitation	Inn	0.60	0.35	0.97	0.82	0.33	0.79	1.91		2.15	1.80	2.03	0.42
		cm	1.52	0.89	2.46	2.08	0.84	2.01	4.85	0.00	5.46	4.57	5.16	1.07
		mm	15.24	8.89	24.64	20.83	8.38	20.07	48.51	0.00	54.61	45.72	51.56	10.67
	Snow	Inn	9.90	7.10	15.10	16.10	3.60				3.20	1.10	21.60	7.20
		cm	25.15	18.03	38.35	40.89	9.14	0.00	0.00	0.00	8.13	2.79	54.86	18.29
		mm	251.46	180.34	383.54	408.94	91.44	0.00	0.00	0.00	81.28	27.94	548.64	182.88
2014	Temperature	°F	22.90	1.30	15.20	28.90	45.10	49.10	53.20	51.80	41.40	19.50	18.90	16.20
		°C	-5.06	-17.06	-9.33	-1.72	7.28	9.50	11.78	11.00	5.22	-6.94	-7.28	-8.78
	Precipitation	Inn	0.90	0.41	0.27	0.01	0.48	3.67	4.61	2.32	2.25	0.45	0.06	0.29
		cm	2.29	1.04	0.69	0.03	1.22	9.32	11.71	5.89	5.72	1.14	0.15	0.74
		mm	22.86	10.41	6.86	0.25	12.19	93.22	117.09	58.93	57.15	11.43	1.52	7.37
	Snow	Inn	11.70	5.90	2.50		1.00					7.30	1.90	6.80
		cm	29.72	14.99	6.35	0.00	2.54	0.00	0.00	0.00	0.00	18.54	4.83	17.27
		mm	297.18	149.86	63.50	0.00	25.40	0.00	0.00	0.00	0.00	185.42	48.26	172.72
2015	Temperature	°F	5.20	9.80	17.00	31.40	47.80	54.00	54.40	49.20	36.90	30.70	12.40	5.10
		°C	-14.89	-12.33	-8.33	-0.33	8.78	12.22	12.44	9.56	2.72	-0.72	-10.89	-14.94
	Precipitation	Inn	0.75	0.08	0.25	0.52	0.42	2.47	6.18	5.17	3.91	0.76	2.06	0.24
		cm	1.91	0.20	0.64	1.32	1.07	6.27	15.70	13.13	9.93	1.93	5.23	0.61
		mm	19.05	2.03	6.35	13.21	10.67	62.74	156.97	131.32	99.31	19.30	52.32	6.10
	Snow	Inn	14.80	0.90	4.30	6.30				0.30	23.30	8.40	32.60	2.90
		cm	37.59	2.29	10.92	16.00	0.00	0.00	0.00	0.76	59.18	21.34	82.80	7.37
		mm	375.92	22.86	109.22	160.02	0.00	0.00	0.00	7.62	591.82	213.36	828.04	73.66

2016	Temperature	°F	14.80	19.90	20.40	37.30	45.10	53.70	56.20	53.90	42.00	27.00	10.50	1.10
		°C	-9.56	-6.72	-6.44	2.94	7.28	12.06	13.44	12.17	5.56	-2.78	-11.94	-17.17
	Precipitation	Inn	0.13	0.13	0.78	0.01	1.51	2.56	5.83	1.78	2.25	0.43	0.30	1.49
		cm	0.33	0.33	1.98	0.03	3.84	6.50	14.81	4.52	5.72	1.09	0.76	3.78
		mm	3.30	3.30	19.81	0.25	38.35	65.02	148.08	45.21	57.15	10.92	7.62	37.85
	Snow	Inn	0.70	2.70	12.40		0.10					2.60	4.80	23.00
		cm	1.78	6.86	31.50	0.00	0.25	0.00	0.00	0.00	0.00	6.60	12.19	58.42
		mm	17.78	68.58	314.96	0.00	2.54	0.00	0.00	0.00	0.00	66.04	121.92	584.20

7.0.2 Appendix 2.2: Local environmental variables

Mean and Standard Deviation values for Temperature, Precipitation and Snow (a), Mean values for Spring season (b); Spring flood mean values (c) and, Mean winter snowfall and Mean total snowfall data (d).

a)

Mean Total / Standard Deviation			
Year	Unit	Mean	SD
1994-1995	Temp	-2.329	11.682
	Prec	1.641	1.308
	Snow	14.753	20.577
1995-1996	Temp	-2.755	12.353
	Prec	1.766	2.577
	Snow	13.801	32.219
1996-1998	Temp	10.801	51.100
	Prec	3.374	3.521
	Snow	17.251	20.476
1998-1999	Temp	-3.574	12.947
	Prec	2.578	2.513
	Snow	9.271	12.164
1999-2000	Temp	-3.176	11.251
	Prec	4.354	4.262
	Snow	24.702	24.479
2000-2001	Temp	-0.431	8.582
	Prec	4.858	7.099
	Snow	12.721	10.960
2001-2002	Temp	-2.583	11.126
	Prec	4.248	4.918
	Snow	13.293	19.064
2002-2003	Temp	-0.813	10.440
	Prec	2.803	3.692
	Snow	4.847	7.840
2003-2004	Temp	-1.102	12.653
	Prec	2.949	2.082
	Snow	14.542	21.559
2004-2005	Temp	-0.569	10.464
	Prec	2.481	2.330
	Snow	20.045	20.038
2005-2006	Temp	-2.884	12.182
	Prec	3.442	3.215
	Snow	12.340	15.882

Mean Total / Standard Deviation			
Year	Unit	Mean	SD
2006-2007	Temp	-3.861	13.310
	Prec	2.963	2.825
	Snow	7.239	8.093
2007-2008	Temp	-2.172	11.009
	Prec	3.236	3.798
	Snow	10.958	15.812
2008-2009	Temp	-3.726	12.447
	Prec	2.711	2.367
	Snow	14.901	13.701
2009-2010	Temp	-1.819	11.362
	Prec	2.345	2.595
	Snow	8.848	9.878
2010-2011	Temp	-3.051	12.178
	Prec	2.523	2.356
	Snow	17.124	31.640
2011-2012	Temp	-3.491	13.435
	Prec	2.771	3.230
	Snow	14.203	16.455
2012-2013	Temp	-6.227	12.196
	Prec	2.076	1.798
	Snow	16.828	14.933
2013-2014	Temp	-1.486	10.616
	Prec	4.036	3.692
	Snow	11.472	16.497
2014-2015	Temp	-0.889	10.054
	Prec	3.998	5.290
	Snow	9.017	11.615
2015-2016	Temp	0.111	9.833
	Prec	4.172	4.498
	Snow	17.590	27.300

b)

Spring Mean																						
Year	1994		1995		1996		1998		1999		2000		2001		2002		2003		2004		2005	
Unit	T	P	T	P	T	P	T	P	T	P	T	P	T	P	T	P	T	P	T	P	T	P
Mean	2.92	0.79	5.11	0.77	1.89	0.06	87.64	1.80	0.81	2.22	0.31	1.19	0.69	1.65	0.61	4.51	-9.64	0.56	4.36	3.07	3.67	1.18

Year	2006		2007		2008		2009		2010		2011		2012		2013		2014		2015		2016	
Unit	T	P	T	P	T	P	T	P	T	P	T	P	T	P	T	P	T	P	T	P	T	P
Mean	1.50	0.98	4.08	1.82	0.72	1.97	1.97	1.08	3.19	0.38	1.44	0.99	2.67	0.90	-4.00	1.46	2.78	0.62	4.22	1.19	5.11	1.93

c)

Spring Flood																						
Year	1994	1995	1996	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Flood	87.1	97.5	58.4	99.1	95.5	67.1	72.1	161.5	81.8	81.3	121.7	96.3	49.5	93.0	50.8	76.2	56.6	99.1	55.7	137.7	103.4	93.7

d)

Winter snowfall		
Year	Mean winter snowfall	Mean total snowfall
1994-1995	21.495	171.958
1995-1996	20.701	165.608
1996-1998	24.479	162.814
1998-1999	12.986	103.886
1999-2000	37.052	212.344
2000-2001	14.478	96.774
2001-2002	18.701	149.606
2002-2003	6.795	53.086
2003-2004	21.812	172.974
2004-2005	30.067	224.282
2005-2006	18.510	142.240
2006-2007	10.700	85.598
2007-2008	16.024	127.686
2008-2009	22.352	171.196
2009-2010	13.272	106.172
2010-2011	24.733	197.866
2011-2012	20.892	204.470
2012-2013	24.098	192.786
2013-2014	16.891	127.000
2014-2015	13.430	107.442
2015-2016	26.353	151.638

7.0.3 **Appendix 2.3: Large scale environmental variables**

PDO NOAA												
Year	January	Feb	March	April	May	June	July	August	Sep	Oct	Nov	Dic
1994	0.86	0.4	0.27	0.52	0.46	-0.08	-1	-0.98	-1.54	-1.1	-2.04	-2.16
1995	-0.87	0.09	0.36	0.41	0.69	0.85	0.8	-0.35	1.02	0.46	0	0.38
1996	0.94	0.92	0.93	1.33	1.93	0.91	0.48	-0.72	0.03	0.3	0.36	0.01
1998	1.12	1.51	1.33	0.05	-0.8	-0.7	-1.2	-0.83	-1.54	-2.23	-1.04	-1.05
1999	-0.64	-0.94	-1.09	-1.76	-2.2	-2.34	-1.9	-1.84	-2.23	-2.49	-2.15	-1.77
2000	-2.13	-1.22	-0.65	-0.64	-0.86	-0.66	-1.5	-1.74	-1.55	-1.67	1.06	0.06
2001	0.64	0.05	-0.3	-1.23	-1.1	-1.28	-2.3	-1.86	-2.13	-1.87	-1.17	-0.99
2002	-0.34	-1.29	-1.13	-1.23	-1.57	-1.27	-1	-0.15	-0.38	0.25	1.04	1.63
2003	1.58	1.32	1.08	0.32	0.06	-0.51	0.11	0.4	-0.46	0.54	-0.19	-0.41
2004	-0.42	-0.11	-0.13	-0.2	0.23	-0.49	-0.2	0.02	-0.17	-0.76	-1.24	-0.74
2005	-0.13	0.17	0.69	0.21	1.06	0.56	-0.2	-0.61	-1.11	-2.05	-1.84	-0.1
2006	0.54	0.38	-0.72	-0.55	-0.45	-0.04	0.12	-1.13	-1.75	-0.6	-0.83	-0.54
2007	-0.63	-0.63	-1.05	-0.56	0.53	-0.37	0.16	-0.15	-1.04	-2.24	-1.38	-0.92
2008	-1.47	-1.33	-1.26	-2	-1.93	-2.11	-2.2	-2	-2.02	-1.8	-1.57	-1.31
2009	-1.7	-1.76	-2.03	-2.28	-1.45	-0.85	-0.9	-0.5	0.19	-0.23	-1.01	-0.51
2010	0.06	0.16	-0.21	-0.28	-0.36	-0.94	-2.2	-2.44	-2.44	-1.6	-1.58	-1.99
2011	-1.73	-1.45	-1.29	-1.26	-0.97	-1.32	-2.5	-2.59	-2.63	-1.95	-2.96	-2.32
2012	-1.72	-1.27	-1.62	-0.94	-2.01	-1.43	-2.3	-2.51	-3.05	-1.22	-0.59	-1.25
2013	-0.94	-1.32	-1.19	-0.63	-0.42	-1.26	-1.8	-1.79	-1.1	-1.9	-1.18	-1.15
2014	-0.6	0.42	0.29	0.41	1.07	-0.33	0.13	-0.06	0.54	1.33	1.34	1.93
2015	1.69	1.74	1.48	0.89	0.29	0.63	1.2	0.68	0.82	0.74	0.13	0.52
2016	0.81	1.25	1.55	1.62	1.44	0.79	0.16	-0.87	-1.06	-0.68	0.84	0.55

b)

ONI NOAA												
Year	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON	OND	NDJ
1994	0.1	0.1	0.2	0.3	0.4	0.4	0.4	0.4	0.6	0.7	1	1.1
1995	1	0.7	0.5	0.3	0.1	0	-0.2	-0.5	-1	-1	-1	-1
1996	-0.9	-0.8	-1	-0.4	-0.3	-0	-0.3	-0.3	-0	-0.4	-0.4	-1
1998	2.2	1.9	1.4	1	0.5	-0	-0.8	-1.1	-1	-1.4	-1.5	-2
1999	-1.5	-1.3	-1	-1	-1	-1	-1.1	-1.1	-1	-1.3	-1.5	-2
2000	-1.7	-1.4	-1	-0.8	-0.7	-1	-0.6	-0.5	-1	-0.6	-0.7	-1
2001	-0.7	-0.5	-0	-0.3	-0.3	-0	-0.1	-0.1	-0	-0.3	-0.3	-0
2002	-0.1	0	0.1	0.2	0.4	0.7	0.8	0.9	1	1.2	1.3	1.1
2003	0.9	0.6	0.4	0	-0.3	-0	0.1	0.2	0.3	0.3	0.4	0.4
2004	0.4	0.3	0.2	0.2	0.2	0.3	0.5	0.6	0.7	0.7	0.7	0.7
2005	0.6	0.6	0.4	0.4	0.3	0.1	-0.1	-0.1	-0	-0.3	-0.6	-1
2006	-0.8	-0.7	-1	-0.3	0	0	0.1	0.3	0.5	0.7	0.9	0.9
2007	0.7	0.3	0	-0.2	-0.3	-0	-0.5	-0.8	-1	-1.4	-1.5	-2
2008	-1.6	-1.4	-1	-0.9	-0.8	-1	-0.4	-0.3	-0	-0.4	-0.6	-1
2009	-0.8	-0.7	-1	-0.2	0.1	0.4	0.5	0.5	0.7	1	1.3	1.6
2010	1.5	1.3	0.9	0.4	-0.1	-1	-1	-1.4	-2	-1.7	-1.7	-2
2011	-1.4	-1.1	-1	-0.6	-0.5	-0	-0.5	-0.7	-1	-1.1	-1.1	-1
2012	-0.8	-0.6	-1	-0.4	-0.2	0.1	0.3	0.3	0.3	0.2	0	-0
2013	-0.4	-0.3	-0	-0.2	-0.3	-0	-0.4	-0.4	-0	-0.2	-0.2	-0
2014	-0.4	-0.4	-0	0.1	0.3	0.2	0.1	0	0.2	0.4	0.6	0.7
2015	0.6	0.6	0.6	0.8	1	1.2	1.5	1.8	2.1	2.4	2.5	2.6
2016	2.5	2.2	1.7	1	0.5	0	-0.3	-0.6	-1	-0.7	-0.7	-1

c)

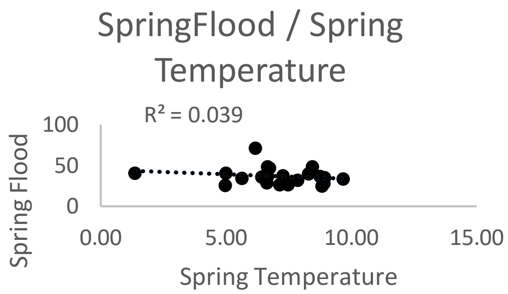
YEAR	1994											
NAO	1.36	0.08	0.92	1.1	-0.48	1.84	1.34	0.36	-1.14	-0.54	-0.54	1.78
EP/NP	-99.9	0.47	-1.06	0.98	-76	-0.14	0.9	0.83	0.24	-0.4	-2.04	-99.9
PNA	0.42	-1.27	0.23	-0.7	0.48	-1.36	-0.06	-1.38	-2.02	-0.09	-1.61	0.39
Expl. Var.	66	64	46.6	36.1	61.5	63.3	65.1	56.6	52	54.9	93.2	87.2
YEAR	1995											
NAO	0.57	0.85	0.91	-1.07	-1.33	0.44	-0.19	0.76	0.45	0.72	-1.59	-1.64
EP/NP	1.03	0.05	0.61	1.13	0.72	0.02	1.11	-0.92	1.9	-0.32	1.07	-99.9
PNA	0.2	0.68	0.03	0.04	0.09	0.9	-0.74	-0.33	1.22	0.11	-0.73	0.62
Expl. Var.	61.9	81.9	69.2	62.7	53	55.9	44.8	76.3	74.1	31.6	70.2	72
YEAR	1996											
NAO	-0.65	-0.52	-0.66	-0.33	-0.93	0.87	0.7	1.19	-0.69	0.15	-0.72	-1.4
EP/NP	0.26	0.27	2.41	0.07	1.15	-0.96	-0.17	0.92	-0.02	-0.54	1.61	-99.9
PNA	-0.68	-0.7	-0.75	0.51	0.37	-1.18	0.18	-0.93	-0.27	-0.67	-0.44	-1.53
Expl. Var.	59.7	56.6	57.9	76.4	68	44.5	51.3	68.1	52.8	43.2	52.6	70.3
YEAR	1998											
NAO	-0.05	-0.57	0.51	-0.88	-1.17	-2.44	-0.45	-0.15	-1.8	0.2	-0.43	0.72
EP/NP	0.62	-0.33	1.31	-0.49	-1.36	0.23	0.12	-1.67	-0.52	-1.27	-0.52	-108
PNA	0.3	0.89	0.69	0.85	-1.87	0.09	1.67	-0.6	0.42	0.77	0.7	-0.39
Expl. Var.	55.1	93.6	60.5	77.8	84.1	56.9	63.6	77.5	81.2	72.3	43.1	68.1
YEAR	1999											
NAO	0.39	-0.11	-0.16	-1.18	0.9	1.44	-0.87	0.38	0.5	0.73	0.55	1.4
EP/NP	-0.89	-1.12	-0.73	-0.57	-0.69	-1.44	0.34	0.32	-0.44	-0.24	-1.33	-99.9
PNA	-0.44	-0.46	0.38	0.05	-0.05	0.43	-0.92	1.95	0.33	0.62	0.45	-0.09
Expl. Var.	65	83.4	76.5	49.2	59.9	46.3	50.1	55.7	37.8	38.1	52	63.4
YEAR	2000											
NAO	0.19	1.48	0.4	-0.18	1.52	0.28	-1	-0.5	-0.06	1.51	-1.1	-0.63
EP/NP	-0.92	-0.55	-0.4	-0.08	-0.62	-0.24	-1.26	0.63	0.49	-0.72	0.2	-99.9
PNA	-1.7	1.2	0.95	-0.58	-0.16	-1.19	-2.55	-0.51	-1.21	0.44	0.7	0.92
Expl. Var.	46.6	61.3	61.9	45.7	71.1	61	61.5	32.9	53.7	68.3	67.8	72.2
YEAR	2001											
NAO	-0.22	0.07	-1.73	-0.15	0.03	0.11	-0.22	-0.22	-0.49	0.25	0.53	-0.86
EP/NP	-0.9	0.26	-1.16	0.06	-1.42	0.55	-1.3	-1.17	-0.46	-0.04	-0.33	-99.9
PNA	1.29	-0.51	0.39	-0.7	-0.01	-0.89	-0.36	-0.14	0.04	-0.08	1.03	0.26
Expl. Var.	60.7	67.2	69.2	50.7	52	27.1	29.6	62	66.1	70.7	55.4	65.3

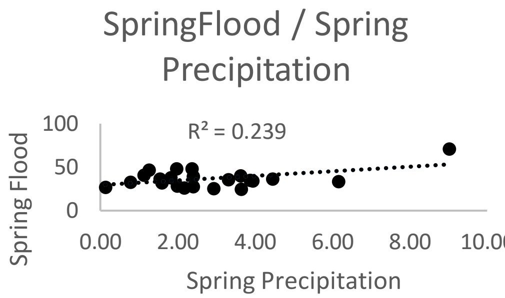
YEAR	2002											
NAO	0	0.8	0.32	1.14	-0.15	0.69	0.65	0.36	-0.54	-1.97	-0.32	-0.96
EP/NP	-0.11	-0.89	1.99	0.45	1.52	-0.2	-0.69	-0.07	-0.4	1.77	2.05	-99.9
PNA	-0.7	-0.11	-1.56	-2.4	-0.56	0.06	0.4	0.61	0.6	-0.55	1.46	1.28
Expl. Var.	78.9	81.1	39.4	62	48.9	62.9	49.2	37.4	59.1	71.7	70.2	82.7
YEAR	2003											
NAO	-0.32	0.26	-0.07	-0.34	0.06	0.24	0.16	-0.22	0.16	-0.86	0.77	0.5
EP/NP	2.07	0.94	0.56	0.34	-0.57	0.17	-0.14	-1.46	-0.7	0.85	-0.11	-99.9
PNA	1.01	0.68	-0.36	-0.1	-1.85	-0.53	0.73	-0.31	0.59	1.23	-1.65	0.56
Expl. Var.	73.5	66.6	55	49.4	49.1	66.5	43.2	51.2	29.8	54.2	74.6	66.9
YEAR	2004											
NAO	-0.85	-0.6	0.67	1.11	0.23	-0.59	1.16	-0.74	0.52	-0.69	0.63	1.03
EP/NP	0.66	-0.5	-1.28	1.23	1.92	3.36	1.19	0.07	-2.21	-0.71	-0.26	-99.9
PNA	-0.12	1.12	0	0.25	-1.46	-0.28	-0.33	1.52	-0.11	-1.37	0.29	-0.04
Expl. Var.	33.1	49.6	61	57.8	54	56.8	19.5	39.6	61.4	47.3	62.1	53.2
YEAR	2005											
NAO	1.26	-0.51	-2.32	-0.47	-1.11	0.26	-0.48	0.35	0.76	-0.55	-0.46	-0.5
EP/NP	0.73	-0.29	0.31	0.81	0.09	1.43	-1.11	-0.6	-1.98	-1.6	0.35	-99.9
PNA	-0.62	-0.11	0.56	1	1.62	0.42	-0.02	0.69	1.32	1.16	-0.74	1.07
Expl. Var.	53.2	53.3	73.3	57.7	59.4	44.1	57.2	47.2	70.6	56.5	42.3	60.8
YEAR	2006											
NAO	0.97	-1.02	-1.75	1.2	-1.01	1.15	0.93	-2.35	-1.43	-1.92	0.33	1.15
EP/NP	-1.07	0.57	0.2	-1.57	-0.31	-0.49	-0.46	0.13	0.47	0.97	-0.38	-99.9
PNA	-0.1	-0.44	-0.56	0.2	-1.03	-1.02	1.29	-1.45	0.31	-0.76	-1.34	1.55
Expl. Var.	73.8	77.9	47	24.5	32.4	46.2	81.7	52.6	55	71	55.3	82.8
YEAR	2007											
NAO	-0.25	-0.98	1.11	0.04	0.66	-1.01	-0.55	-0.31	0.85	1	0.48	0.23
EP/NP	-1.14	0.93	-1.27	-0.19	-0.67	0	0.49	-0.67	-1.29	-1.96	0.68	-99.9
PNA	0.27	-0.42	-0.12	0.97	0.03	-0.3	1.65	1.96	1.52	0.77	0.65	-0.16
Expl. Var.	82.2	50.8	56.7	76.1	48.8	25.8	46.6	41.4	56.2	41.2	59.9	50.3
YEAR	2008											
NAO	0.53	0.38	-0.32	-1.31	-1.55	-1.09	-1.24	-1.62	1.14	0.47	-0.47	-0.35
EP/NP	-1.25	-0.4	-1.62	-0.5	0.21	-1.13	-1.13	-0.36	-0.11	-1	0.65	-99.9
PNA	-1.06	0.37	-0.61	-1.18	1.25	-1.76	-0.51	0.89	0.89	1.11	1.05	-1.71
Expl. Var.	61.6	46.4	59.8	31.7	49.3	45.9	46.3	25.4	45.6	59.2	51.6	68.1

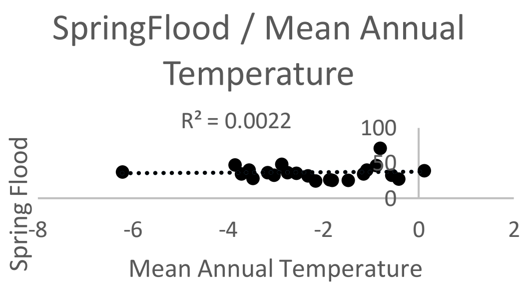
YEAR	2009											
NAO	-0.52	-0.38	0.19	-0.36	1.61	-0.91	-2.11	-0.37	1.62	-0.61	-0.16	-1.88
EP/NP	-0.18	0.32	-1.12	0.49	1.31	-0.39	1.65	-1.39	-1.02	-0.7	-1.62	-99.9
PNA	0.13	-1.57	-1.29	-0.04	-0.43	0.48	0.72	0.62	1.03	0.64	0.19	0.04
Expl. Var.	58.3	61.2	60.8	42.8	62.3	36.9	54.4	83.8	63.7	70.4	62.9	74.9
YEAR	2010											
NAO	-1.8	-2.69	-1.33	-0.93	-1.33	-0.52	-0.39	-1.69	-0.62	-0.5	-1.84	-1.8
EP/NP	-0.58	-0.51	-1.63	-1.21	-0.15	1.5	-0.22	-1.48	-0.34	-0.58	0.27	-99.9
PNA	0.96	0.48	1.68	1.26	-0.73	-0.1	0.89	1.07	1.07	2.15	-0.81	-2.08
Expl. Var.	58.2	82	73.1	61.5	54.1	71.5	69.5	50.8	47.9	54	55.2	84.7
YEAR	2011											
NAO	-1.53	0.35	0.24	2.55	-0.01	-0.98	-1.48	-1.85	0.67	0.94	1.3	2.25
EP/NP	-0.42	-0.12	-0.03	-0.63	-1.18	-0.48	-2.23	-0.67	-0.53	-0.81	-1.34	-99.9
PNA	1	-2.41	0.38	-1.78	0.25	0.35	-0.75	1.4	-0.39	0.86	-0.76	0.06
Expl. Var.	64.4	58.9	41.1	61	32.2	36.8	32.4	39.2	60.3	46.5	73.4	78.4
YEAR	2012											
NAO	0.86	0.03	0.93	0.37	-0.79	-2.25	-1.29	-1.39	-0.43	-1.73	-0.74	0.07
EP/NP	-1.92	-0.33	-2.59	0.31	-1.46	-0.95	-1.01	0.63	0.16	0.58	0.12	-99.9
PNA	0.13	0.7	-0.19	-0.09	-0.29	-0.42	-0.57	-0.2	-0.39	-1.13	-1.06	-1.31
Expl. Var.	74.6	62	60.5	27.8	39.9	51.2	33.1	51.4	41.3	57.3	44.7	60.7
YEAR	2013											
NAO	-0.11	-0.96	-2.09	0.6	0.58	0.83	0.7	1.12	0.38	-0.88	0.81	0.79
EP/NP	0.12	-0.88	0.7	1.24	-0.26	1.68	0.93	-1.94	-1.44	0.99	1.16	-108
PNA	0.05	0.3	-0.26	-1.76	-0.24	-0.35	-0.71	-0.06	0.41	-0.21	-1.14	-17
Expl. Var.	52.1	75.5	78.8	53	36.1	58.4	33.1	69.1	61	78.6	57.1	84.9
YEAR	2014											
NAO	-0.17	1.07	0.44	0.19	-0.8	-0.67	0.21	-2.28	1.72	-0.87	0.58	1.63
EP/NP	1.11	0.31	1.24	-0.05	0.77	-0.69	0.33	-1.03	0.2	-0.66	3.21	-99.9
PNA	0.59	-1.57	-0.5	0	-0.59	-1.44	0.5	1.35	0.78	1.14	0.64	0.37
Expl. Var.	70.5	74.9	54.6	67.1	36.1	38.1	49.5	55	67.6	49	76.1	48.4
YEAR	2015											
NAO	1.57	1.05	1.12	0.64	0.19	0.24	-3.14	-1.1	-0.49	0.99	1.7	1.99
EP/NP	1.27	1.18	1.13	-0.35	0.49	1.72	0.23	-0.28	-1.38	0.33	-0.94	-99.9
PNA	0.14	0.49	-0.52	-0.39	-0.05	-0.07	0.29	0.05	-0.8	2.12	0.2	0.47
Expl. Var.	61.7	68.5	57.2	63.8	61.7	45.9	64.7	45.8	50.2	71.4	70.2	83.1
YEAR	2016											
NAO	-0.37	1.35	0.37	0.26	-0.67	-0.13	-1.72	-2.24	0.74	0.96	-0.31	0.35
EP/NP	-0.35	0.23	0.24	1.47	0.14	1.26	-0.36	-0.42	-1.41	-0.84	-1.43	-99.9
PNA	1.94	1.68	0.41	0.6	-0.85	-0.64	0.53	-0.91	0.11	1.53	1.44	-0.65
Expl. Var.	56.8	71.6	56.9	47.8	55.3	61.8	62.4	61.7	73.5	60.9	51.1	86

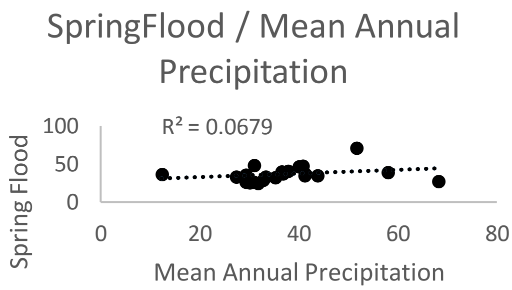
7.0.4 Appendix 2.4: Regression analysis local climatic variables

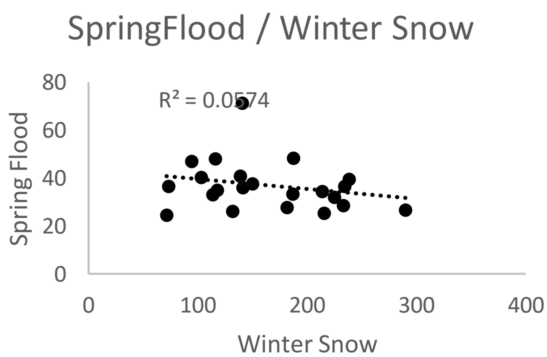
Relationship between local climatic variables: spring flood, spring temperature, spring precipitation, mean annual temperature, mean annual precipitation, winter snow, winter temperature.

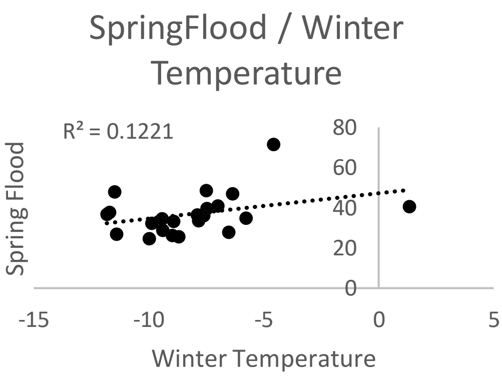


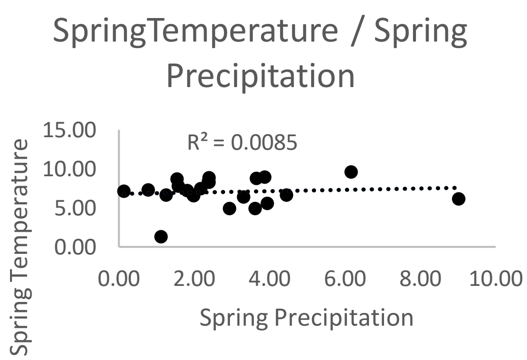


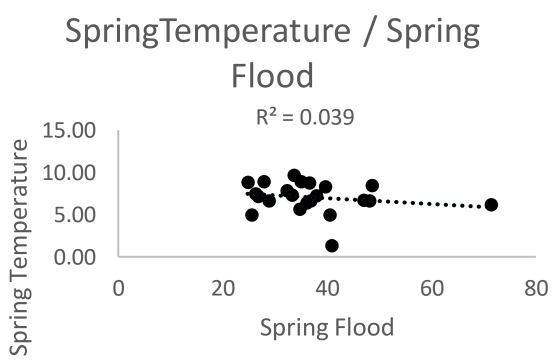


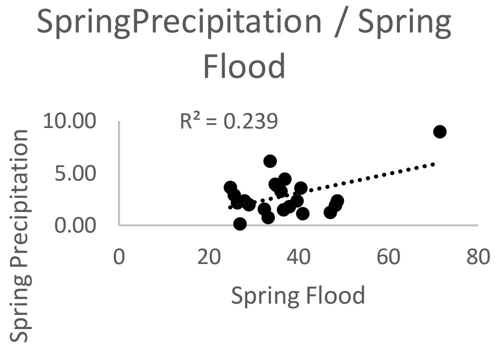


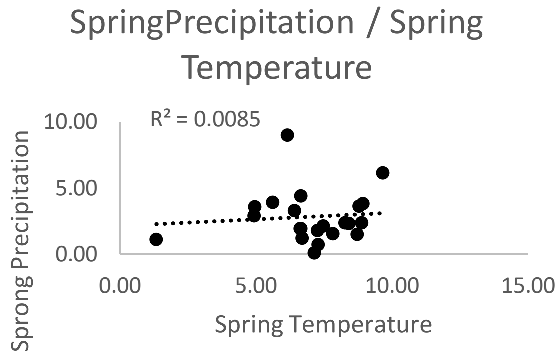


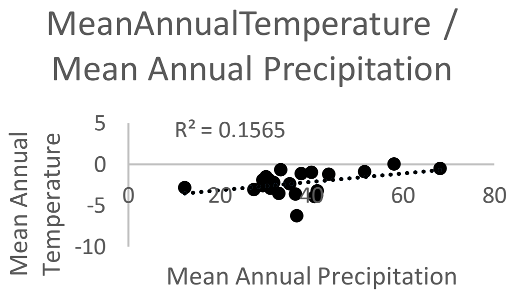


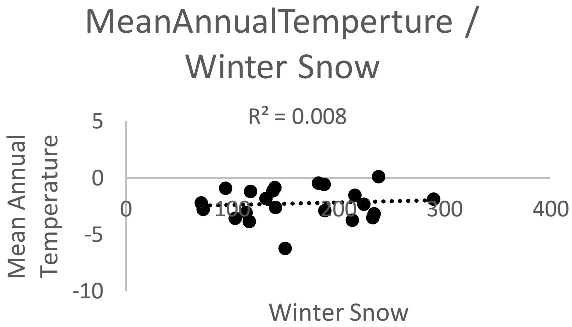


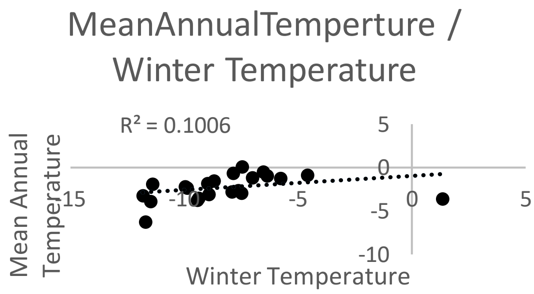


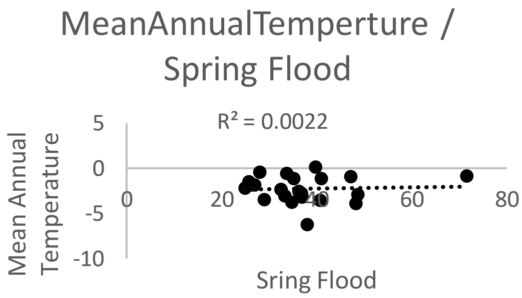

SpringPrecipitation / Spring Flood
R² = 0.239
Spring Precipitation
Spring Flood

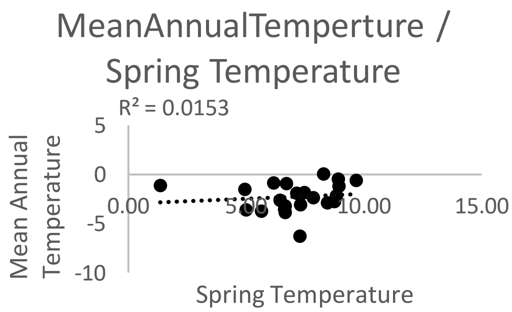

SpringPrecipitation / Spring Temperature
R² = 0.0085
Sprong Precipitation
Spring Temperature

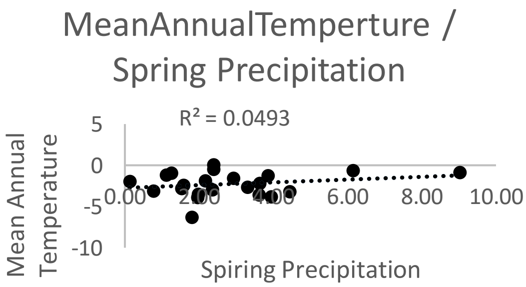

MeanAnnualTemperature / Mean Annual Precipitation
R² = 0.1565
Mean Annual Temperature
Mean Annual Precipitation

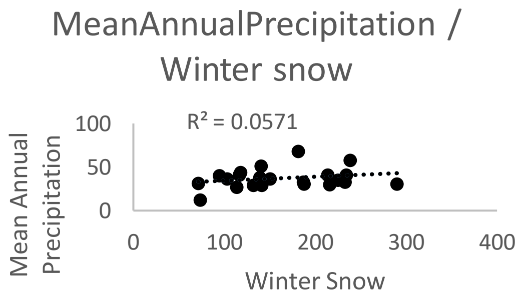

MeanAnnualTemperture / Winter Snow
R² = 0.008
Mean Annual Temperature
Winter Snow

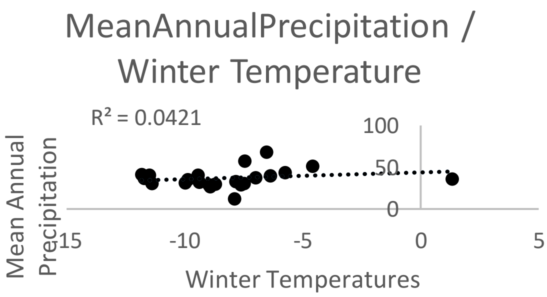

MeanAnnualTemperture / Winter Temperature
R² = 0.1006
Mean Annual Temperature
Winter Temperature

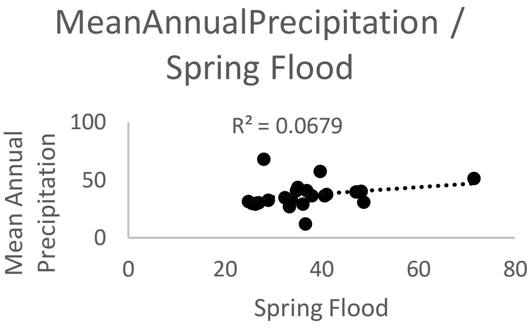

MeanAnnualTemperture / Spring Flood
R² = 0.0022
Mean Annual Temperature
Sring Flood

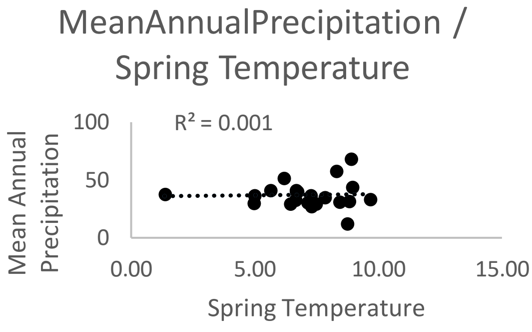

MeanAnnualTemperture / Spring Temperature
R² = 0.0153
Mean Annual Temperature
Spring Temperature

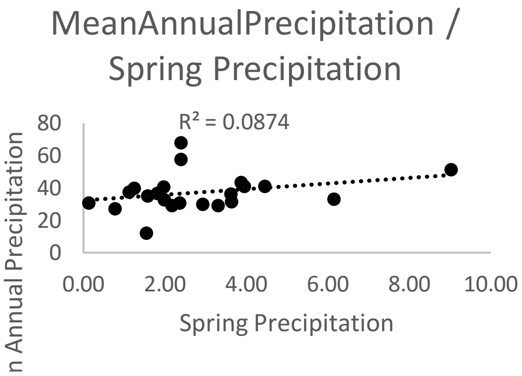

MeanAnnualTemperture / Spring Precipitation
R² = 0.0493
Mean Annual Temperature
Spiring Precipitation

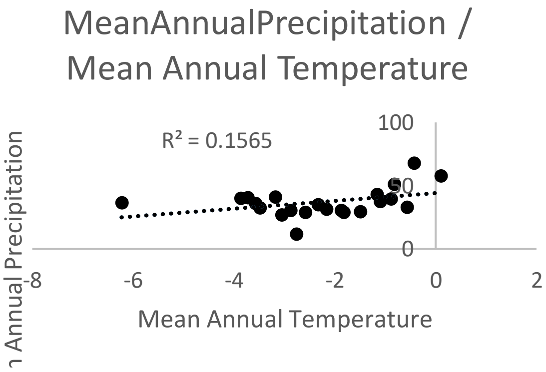

MeanAnnualPrecipitation / Winter snow
R² = 0.0571
Mean Annual Precipitation
Winter Snow

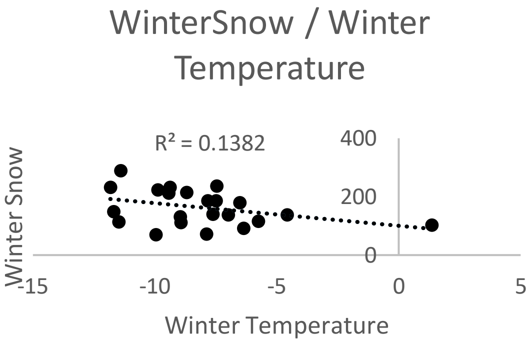

MeanAnnualPrecipitation / Winter Temperature
R² = 0.0421
Mean Annual Precipitation
Winter Temperatures

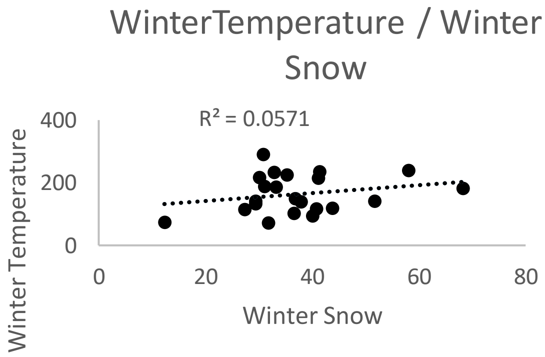

MeanAnnualPrecipitation / Spring Flood
Mean Annual Precipitation
Spring Flood
R² = 0.0679
100
50
0
0
20
40
60
80


MeanAnnualPrecipitation / Spring Temperature
Mean Annual Precipitation
Spring Temperature
R² = 0.001
100
50
0
0.00
5.00
10.00
15.00


MeanAnnualPrecipitation / Spring Precipitation
n Annual Precipitation
Spring Precipitation
R² = 0.0874
80
60
40
20
0
0.00
2.00
4.00
6.00
8.00
10.00


MeanAnnualPrecipitation / Mean Annual Temperature
n Annual Precipitation
Mean Annual Temperature
R² = 0.1565
100
50
0
-8
-6
-4
-2
0
2


WinterSnow / Winter Temperature
Winter Snow
Winter Temperature
R² = 0.1382
400
200
0
-15
-10
-5
0
5


WinterTemperature / Winter Snow
Winter Temperature
Winter Snow
R² = 0.0571
400
200
0
0
20
40
60
80

7.1 Chapter 3

7.1.1 Appendix 3.1: Environmental variables.

Glossary of acronyms and abbreviations used in the text.

Variable	**Acronym**	**Time**
Mean temperature	Mtemp	September to August following year
Mean precipitation	Mprecip	September to August following year
Winter snowfall	WintSnow	September to April following year
Spring mean temperature	SpringTemp	April and May
Spring mean Precipitation	SpringPrecip	April and May
Spring flood	SpringFlood	number of events with three or more days of heavier than average rain during spring or summer covering April to July

7.1.2 Appendix 3.2: Jaccard, Bray Curtis and 1– Bray Curtis values

Global				Savage				N4			
Pair Year	Jaccard	BC	1 - Bray-Curtis	Pair Year	Jaccard	BC	1 - Bray-Curtis	Pair Year	Jaccard	BC	1 - Bray-Curtis
95-98	0.789474	0.167	0.833	94-95	0.384615	0.375	0.625	94-95	0.545455	0.294	0.706
98-99	0.75	0.143	0.857	95-98	0.375	0.25	0.75	95-96	0.545455	0.294	0.706
99-00	0.6875	0.185	0.815	98-99	0.5	0.125	0.875	96-98	0.555556	0.286	0.714
00-01	0.733333	0.185	0.815	99-00	0.375	0.286	0.714	98-99	0.625	0.231	0.769
00-02	0.65	0.235	0.765	00-01	0.4	0.385	0.615	99-00	0.555556	0.286	0.714
02-03	0.48	0.351	0.649	01-03	0.545455	0.368	0.632	00-01	0.25	0.6	0.4
03-04	0.727273	0.179	0.821	03-04	0.545455	0.455	0.545	00-02	0.25	0.6	0.4
04-05	0.551724	0.289	0.711	04-05	0.2	0.692	0.308	02-03	0.5	0.333	0.667
05-06	0.730769	0.156	0.844	05-06	0.166667	0.636	0.364	03-04	0.25	0.6	0.4
06-07	0.391304	0.438	0.562	06-07	0.333333	0.5	0.5	04-05	0.8	0.111	0.889
07-08	0.416667	0.412	0.588	07-08	0.3	0.714	0.286	05-06	0.8	0.111	0.889
08-09	0.689655	0.184	0.816	08-09	0.5	0.308	0.692	06-07	0.5	0.333	0.667
09-10	0.928571	0.037	0.963	09-10	0.52381	0.185	0.815	07-08	0.285714	0.556	0.444
10-11	1	0	1	10-11	0.5625	0.217	0.783	08-09	0.777778	0.125	0.875
11-12	0.928571	0.037	0.963	11-12	0.545455	0.368	0.632	09-10	1	0	1
12-13	0.928571	0.037	0.963	12-13	0.6	0.455	0.545	10-11	0.8	0.111	0.889
13-14	0.925926	0.038	0.962	13-14	0.818182	0.28	0.72	11-12	0.818182	0.1	0.9
14-15	0.785714	0.12	0.88	14-15	0.5	0.556	0.444	12-13	0.769231	0.13	0.87
15-16	0.88	0.064	0.936	15-16	0.538462	0.364	0.636	13-15	0.666667	0.2	0.8
Mean	0.735529	0.171421	0.828579	Mean	0.458628	0.395737	0.604263	15-16	0.636364	0.222	0.778
								Mean	0.596548	0.27615	0.72385

Little Stoney				Hogan				EFTT			
Pair Year	Jaccard	BC	1 - Bray-Curtis	Pair Year	Jaccard	BC	1 - Bray-Curtis	Pair Year	Jaccard	BC	1 - Bray-Curtis
95-98	0.416667	0.412	0.588	94-95	0.636364	0.2	0.8	94-95	0.888889	0.059	0.941
98-99	0.545455	0.294	0.706	95-96	0.545455	0.263	0.737	95-98	0.727273	0.158	0.842
99-00	0.555556	0.286	0.714	96-98	0.5	0.333	0.667	98-99	0.818182	0.1	0.9
00-01	0.5	0.333	0.667	98-99	0.909091	0.048	0.952	99-00	0.7	0.176	0.824
00-02	0.363636	0.467	0.533	99-00	0.454545	0.375	0.625	00-01	0.5	0.333	0.667
02-03	0.214286	0.647	0.353	00-01	0.555556	0.286	0.714	01-02	0.4	0.429	0.571
03-04	0.642857	0.217	0.783	00-02	0.5	0.333	0.667	02-03	0.363636	0.467	0.533
04-05	0.75	0.143	0.857	02-03	0.571429	0.273	0.727	03-04	0.4	0.429	0.571
05-06	0.75	0.143	0.857	03-04	0.4	0.429	0.571	04-05	0.625	0.286	0.714
06-07	0.272727	0.571	0.429	04-05	0.384615	0.474	0.526	05-06	1	0	1
07-08	0.5	0.333	0.667	05-06	0.6	0.25	0.75	06-07	0.444444	0.385	0.615
08-09	0.5	0.333	0.667	06-07	0.428571	0.4	0.6	07-09	0.333333	0.529	0.471
09-10	0.8	0.111	0.889	07-08	0.3	0.538	0.462	09-10	0.857143	0.077	0.923
10-11	0.75	0.143	0.857	08-09	0.7	0.176	0.824	10-11	0.8125	0.103	0.897
11-12	0.923077	0.04	0.96	09-10	0.7	0.176	0.824	11-12	0.8125	0.103	0.897
12-13	0.642857	0.217	0.783	10-11	0.818182	0.1	0.9	12-13	0.875	0.067	0.933
13-14	0.642857	0.2	0.8	11-12	0.714286	0.167	0.833	13-14	0.5625	0.28	0.72
14-15	0.764706	0.133	0.867	12-13	0.928571	0.037	0.963	14-15	0.583333	0.263	0.737
15-16	0.8125	0.103	0.897	13-14	0.933333	0.034	0.966	15-16	0.75	0.143	0.857
Mean	0.59722	0.269789	0.730211	14-15	0.705882	0.172	0.828	Mean	0.65546	0.230895	0.769105
				15-16	0.875	0.067	0.933				
				Mean	0.626709	0.244333	0.755667				

Tattler				Sanctuary				Moose			
Pair Year	Jaccard	BC	1 - Bray-Curtis	Pair Year	Jaccard	BC	1 - Bray-Curtis	Pair Year	Jaccard	BC	1 - Bray-Curtis
94-95	0.73	0.158	0.842	96-98	0.625	0.231	0.769	95-96	0.588235	0.259	0.741
95-96	0.55	0.333	0.667	98-99	0.222222	0.636	0.364	96-98	0.705882	0.172	0.828
96-98	0.50	0.333	0.667	99-00	0.222222	0.636	0.364	98-99	0.611111	0.241	0.759
98-99	0.70	0.176	0.824	00-01	0.5	0.333	0.667	99-00	0.384615	0.444	0.556
99-00	0.89	0.059	0.941	01-02	0.375	0.455	0.545	00-01	0.357143	0.474	0.526
00-01	0.80	0.111	0.889	02-03	0.285714	0.556	0.444	00-02	0.5625	0.28	0.72
01-02	0.64	0.222	0.778	03-04	0.285714	0.556	0.444	02-05	0.409091	0.419	0.581
02-03	0.64	0.222	0.778	04-05	0.142857	0.75	0.25	05-07	0.181818	0.75	0.25
03-04	0.90	0.053	0.947	05-06	0.142857	0.714	0.286	07-09	0.142857	0.75	0.25
04-05	0.43	0.4	0.6	06-07	0.285714	0.556	0.444	09-10	0.772727	0.128	0.872
05-06	0.45	0.375	0.625	07-08	0.222222	0.636	0.364	10-11	0.95	0.026	0.974
06-07	0.33	0.5	0.5	08-09	0.666667	0.2	0.8	11-12	0.863636	0.073	0.927
07-08	0.27	0.579	0.421	09-10	0.777778	0.125	0.875	12-13	0.818182	0.073	0.927
08-09	0.67	0.231	0.769	10-11	0.818182	0.1	0.9	13-14	0.761905	0.135	0.865
09-10	0.86	0.077	0.923	11-12	0.636364	0.222	0.778	14-15	0.85	0.081	0.919
10-11	0.77	0.13	0.87	12-13	0.666667	0.2	0.8	15-16	0.590909	0.257	0.743
11-12	0.79	0.12	0.88	13-14	0.75	0.143	0.857	Mean	0.596913	0.285125	0.714875
12-13	0.93	0.037	0.963	14-15	0.666667	0.2	0.8				
13-14	0.79	0.12	0.88	15-16	0.727273	0.158	0.842				
14-15	0.77	0.13	0.87	Mean	0.474691	0.389842	0.610158				
15-16	0.67	0.2	0.8								
Mean	0.67	0.217429	0.782571								

Igloo			
Pair Year	Jaccard	BC	1 - Bray-Curtis
94-95	0.909091	0.048	0.952
95-96	0.727273	0.158	0.842
96-98	0.727273	0.158	0.842
98-99	0.909091	0.048	0.952
99-00	0.818182	0.1	0.9
00-01	0.5	0.333	0.667
00-02	0.5	0.333	0.667
02-03	0.636364	0.222	0.778
03-04	0.9	0.053	0.947
04-06	0.5	0.333	0.667
06-07	0.555556	0.286	0.714
07-08	0.6	0.25	0.75
08-10	0.692308	0.182	0.818
10-11	0.916667	0.043	0.957
11-12	0.75	0.143	0.857
12-13	0.583333	0.263	0.737
13-14	0.75	0.143	0.857
14-15	0.75	0.182	0.818
15-16	0.909091	0.048	0.952
Mean	0.717591	0.175053	0.824947

Highway			
Pair Year	Jaccard	BC	1 - Bray-Curtis
95-96	0.6	0.25	0.75
96-99	0.5	0.333	0.667
99-00	0.375	0.455	0.545
00-01	0.285714	0.566	0.434
00-02	0.8	0.111	0.889
02-03	0.625	0.455	0.545
03-05	0.363636	0.467	0.533
05-06	0.454545	0.375	0.625
06-07	0.857143	0.75	0.25
07-08	0.9	0.818	0.182
08-09	0.642857	0.217	0.783
09-10	0.846154	0.083	0.917
10-11	0.714286	0.167	0.833
11-12	1	0	1
12-13	0.846154	0.083	0.917
13-14	0.846154	0.083	0.917
14-15	0.538462	0.273	0.727
15-16	0.538462	0.3	0.7
Mean	0.651865	0.321444	0.678556

Mean Stream		
Stream	Jaccard	1 - Bray-Curtis
Tattler Creek	0.67	0.78
Savage River	0.46	0.60
Sanctuary River	0.47	0.61
N4	0.60	0.72
Moose River	0.60	0.73
Little Stoney Creek	0.60	0.73
Igloo Creek	0.72	0.82
Hogan Creek	0.63	0.76
Highway Creek	0.65	0.68
East Fork Tolkat Tributary	0.66	0.77
Global	0.74	0.83

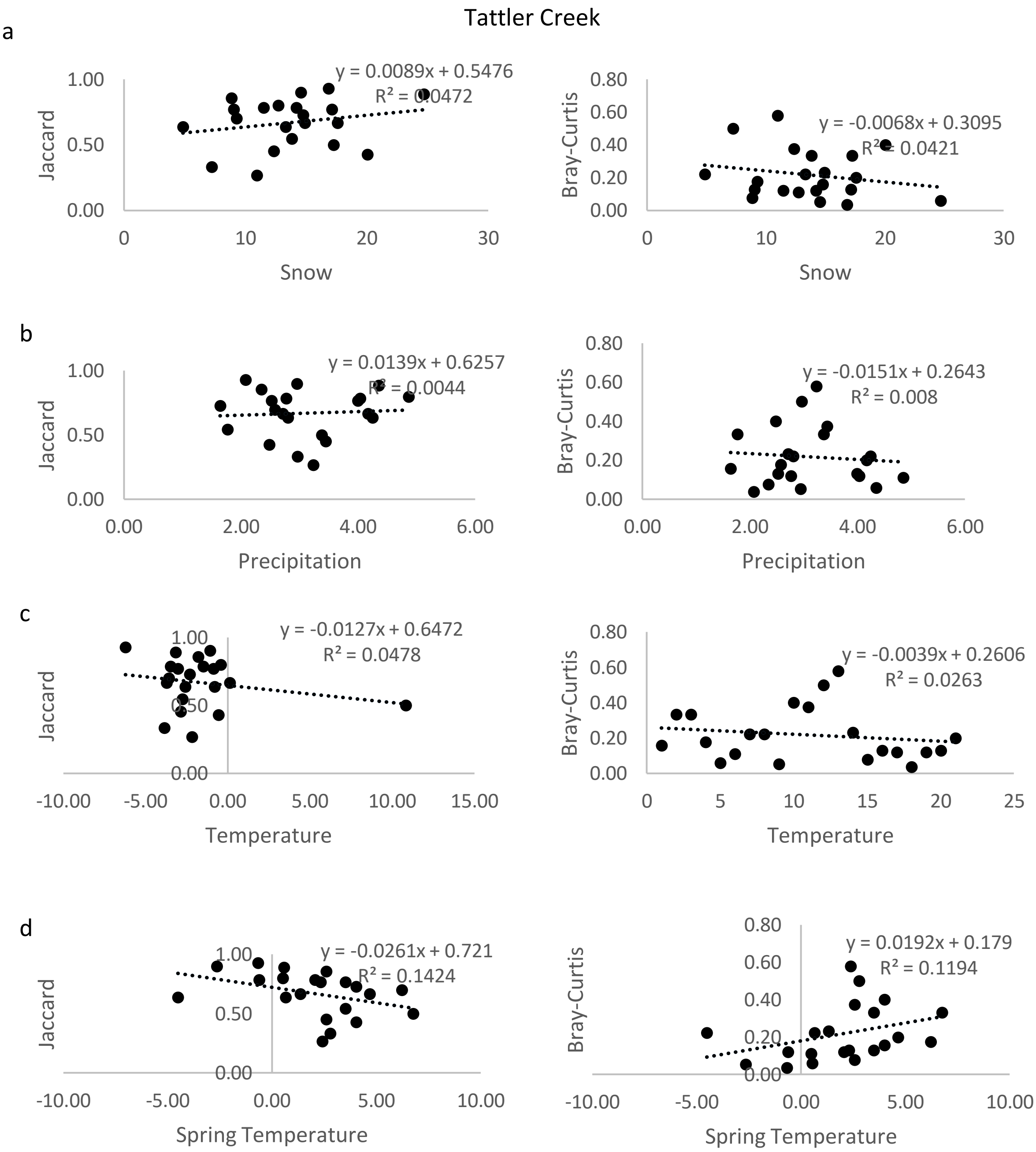
7.1.3 Appendix 3.3 Regression Coefficients

Jaccard similarity (community persistence) / Bray-Curtis distance (compositional stability) coefficient values.

Stream	Index	Snow	Precipitation	Temperature	Spring Temperature	Spring Precipitation	Winter Snow
Tattler	J	0.047	0.004	0.048	0.142	0.032	0.035
	BC	0.042	0.008	0.026	0.119	0.024	0.030
Savage	J	0.008	0.001	0.027	0.182	0.129	0.008
	BC	0.005	0.011	0.014	0.025	0.072	0.009
Sanctuary	J	0.001	0.003	0.015	0.007	0.389	0.003
	BC	0.004	0.001	0.018	0.003	0.361	0.007
N4	J	0.003	0.156	0.004	0.089	0.241	0.036
	BC	0.004	0.163	0.001	0.113	0.249	0.045
Moose	J	0.019	0.021	0.000	0.082	0.297	0.022
	BC	0.038	0.010	0.001	0.093	0.264	0.039
Little Stoney	J	0.111	0.005	0.028	0.066	0.372	0.210
	BC	0.145	0.001	0.025	0.074	0.371	0.240
Igloo	J	0.224	0.072	0.056	0.033	0.085	0.099
	BC	0.248	0.090	0.061	0.028	0.091	0.107
Hogan	J	0.004	0.008	0.058	0.007	0.110	0.005
	BC	0.008	0.012	0.052	0.007	0.150	0.009
Highway	J	0.156	0.143	0.127	0.009	0.000	0.122
	BC	0.025	0.046	0.042	0.003	0.037	0.031
EFTT	J	0.059	0.117	0.090	0.143	0.357	0.017
	BC	0.054	0.084	0.075	0.134	0.379	0.105
All streams	J	0.057	0.004	0.000	0.015	0.394	0.048
	BC	0.079	0.079	0.001	0.012	0.367	0.073

7.1.4 Appendix 3.4 Regression Analysis Plots

Relationship between Jaccard similarity coefficients (community persistence) / Bray-Curtis distance (compositional stability) and (a) mean annual snow, (b) mean annual precipitation, (c) mean annual temperature, (d) spring temperature, (e) spring precipitation and (f) winter snow between year pairs across.



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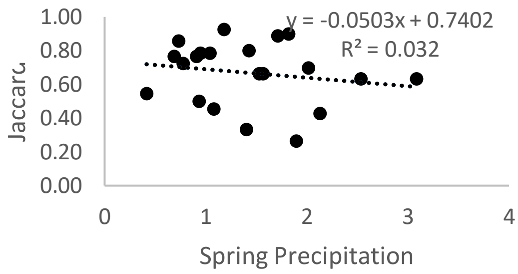

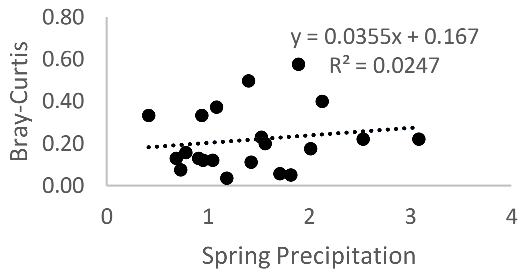

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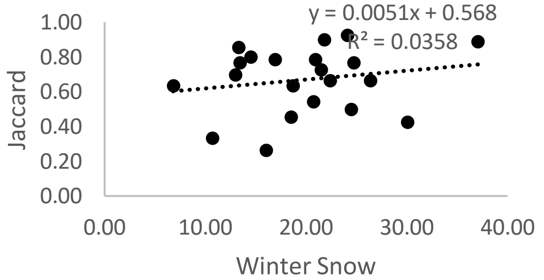
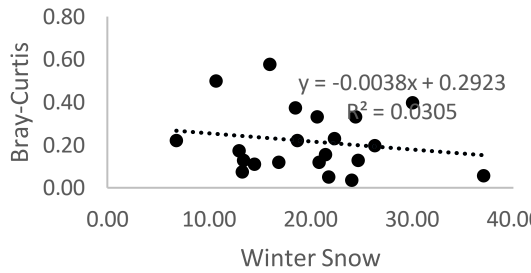
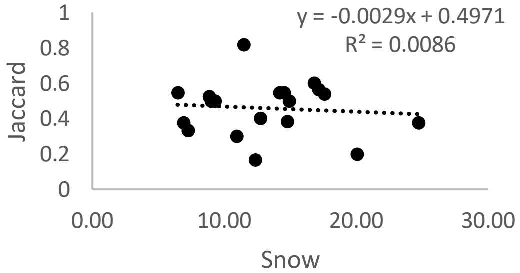
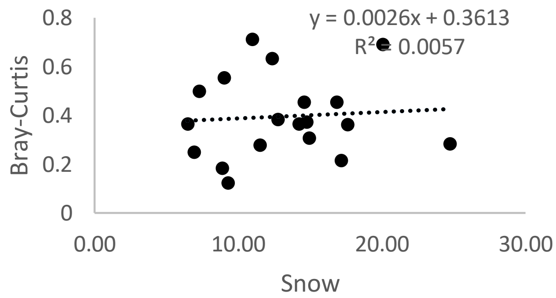




Savage River

a





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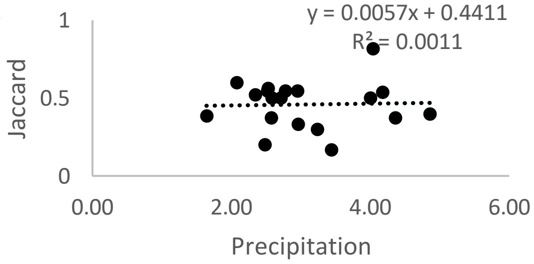
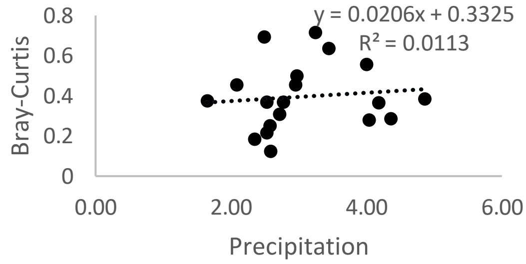
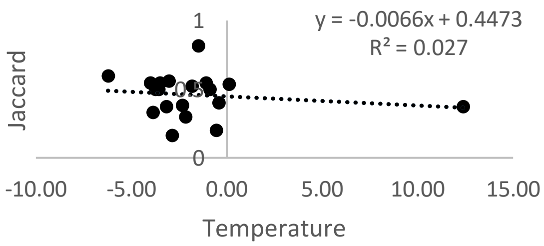
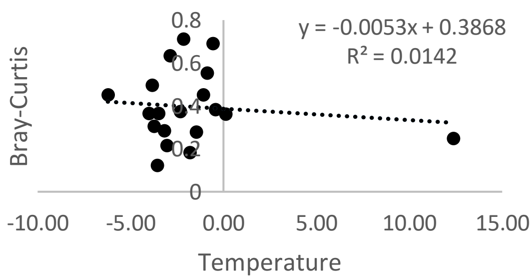
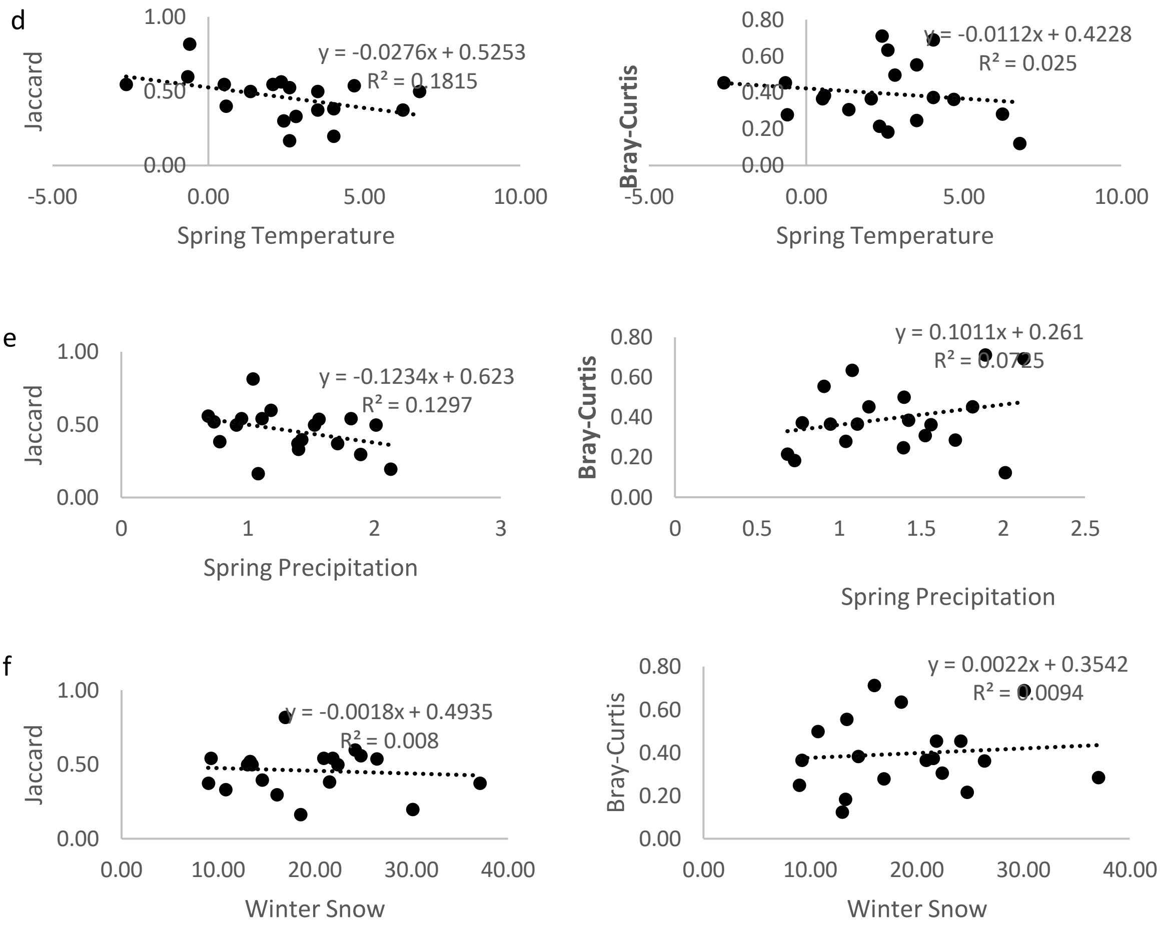




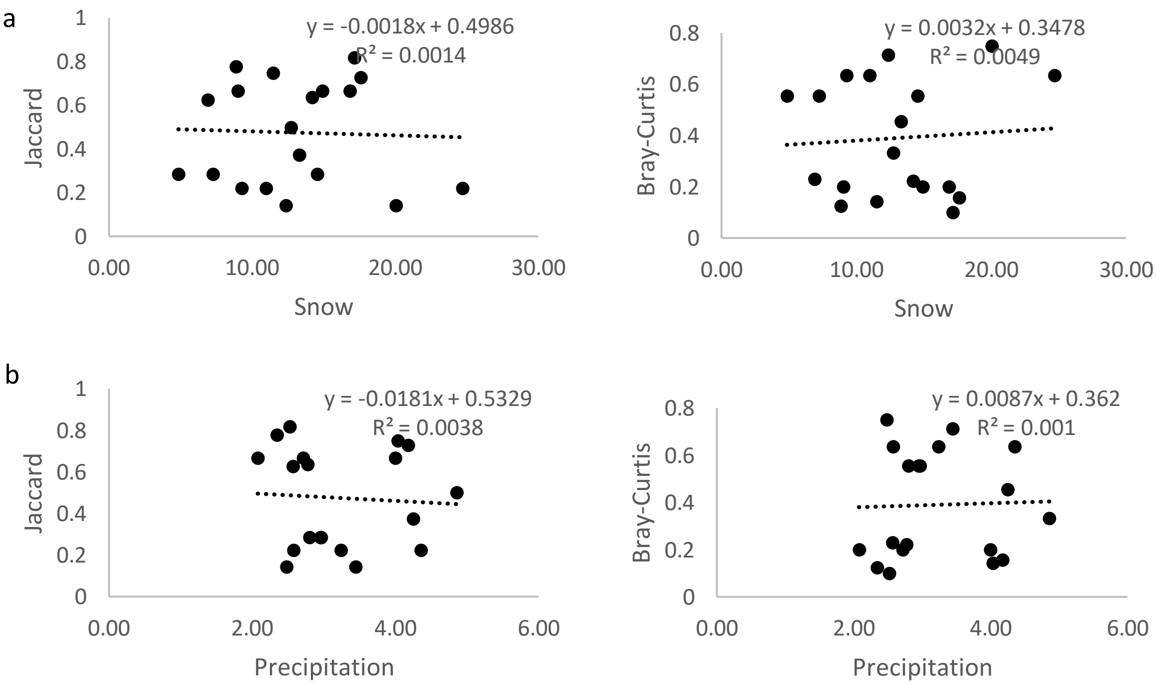
c



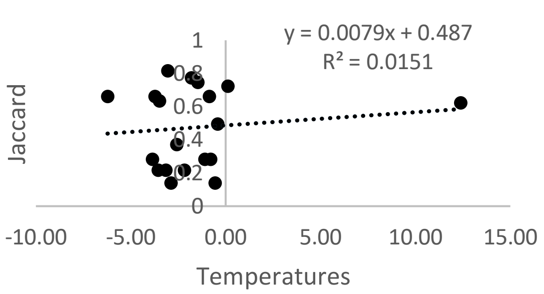


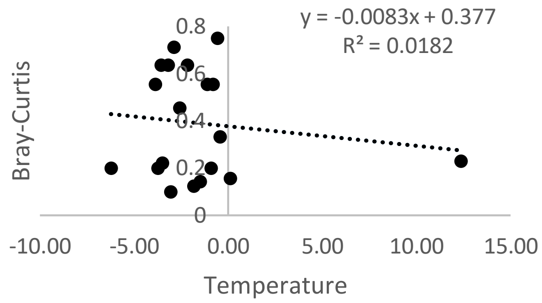


Sanctuary River



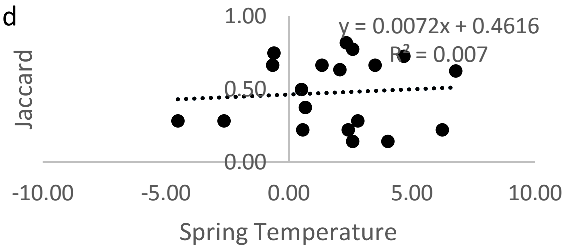
c

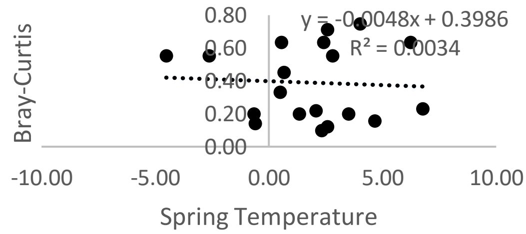

y = 0.0079x + 0.487
R^2 = 0.0151
Jaccard
Temperatures


y = -0.0083x + 0.377
R^2 = 0.0182
Bray-Curtis
Temperature

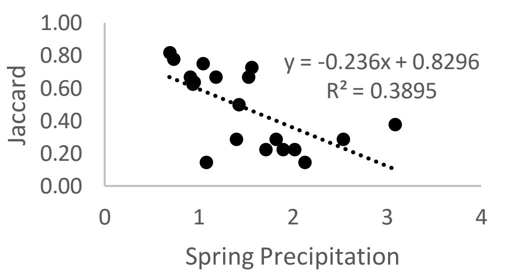
.

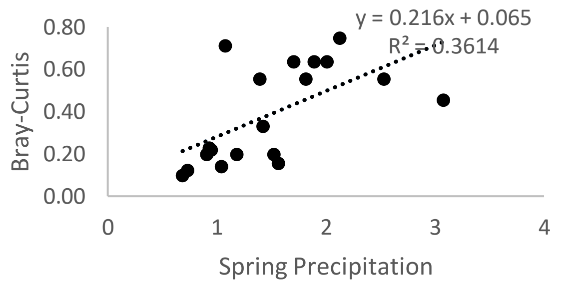
d


y = 0.0072x + 0.4616
R^2 = 0.007
Jaccard
Spring Temperature

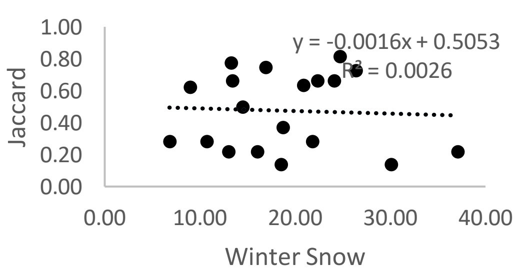

y = -0.0048x + 0.3986
R^2 = 0.0034
Bray-Curtis
Spring Temperature

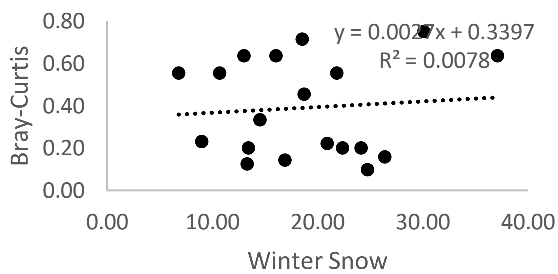
e


y = -0.236x + 0.8296
R^2 = 0.3895
Jaccard
Spring Precipitation


y = 0.216x + 0.065
R^2 = 0.3614
Bray-Curtis
Spring Precipitation

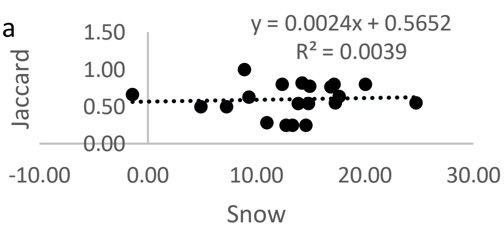
f

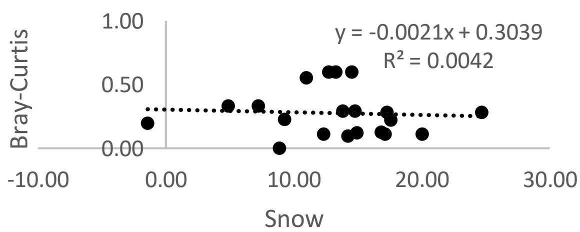

y = -0.0016x + 0.5053
R^2 = 0.0026
Jaccard
Winter Snow

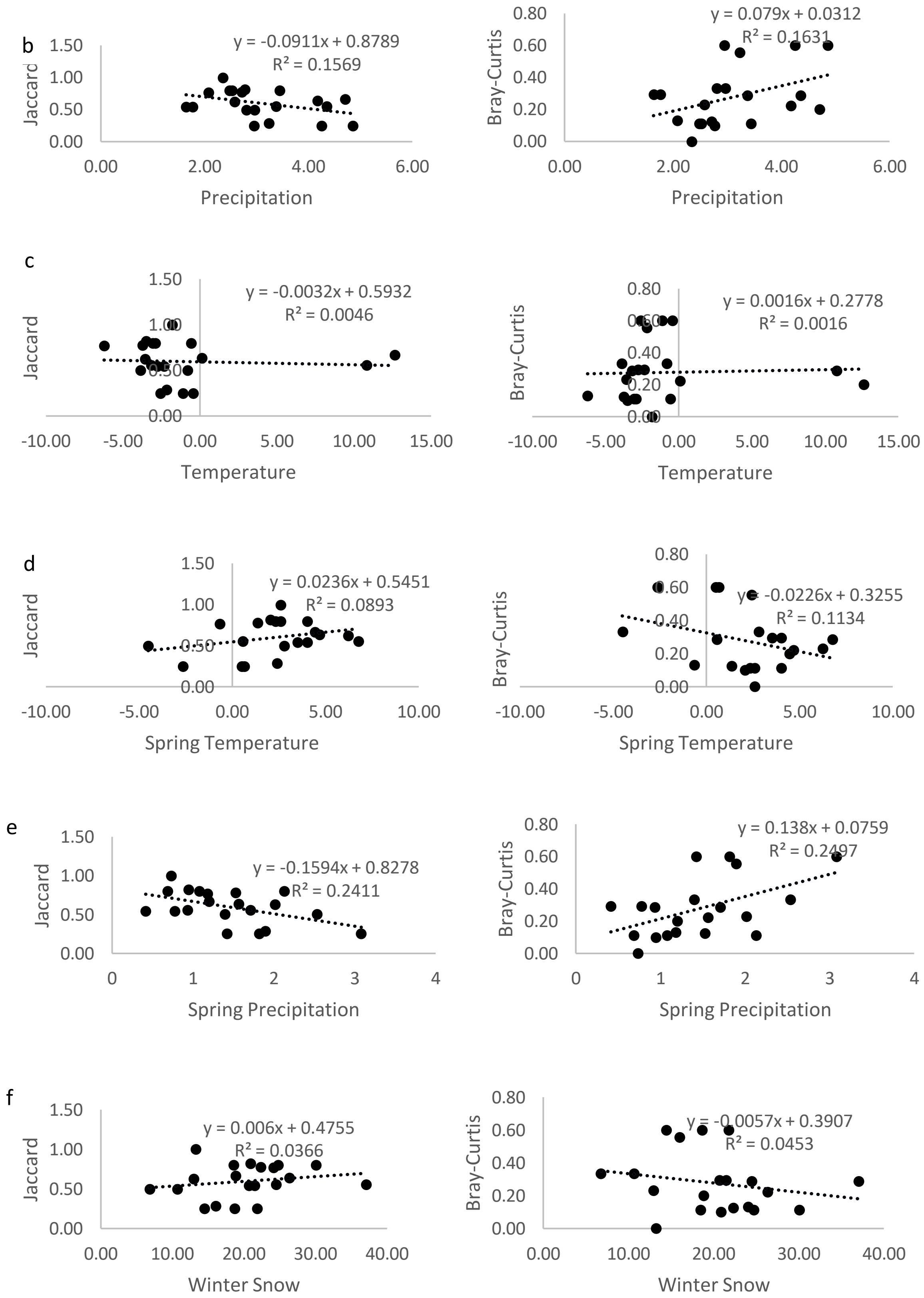

R^2 = 0.0078
Bray-Curtis
Winter Snow

N4

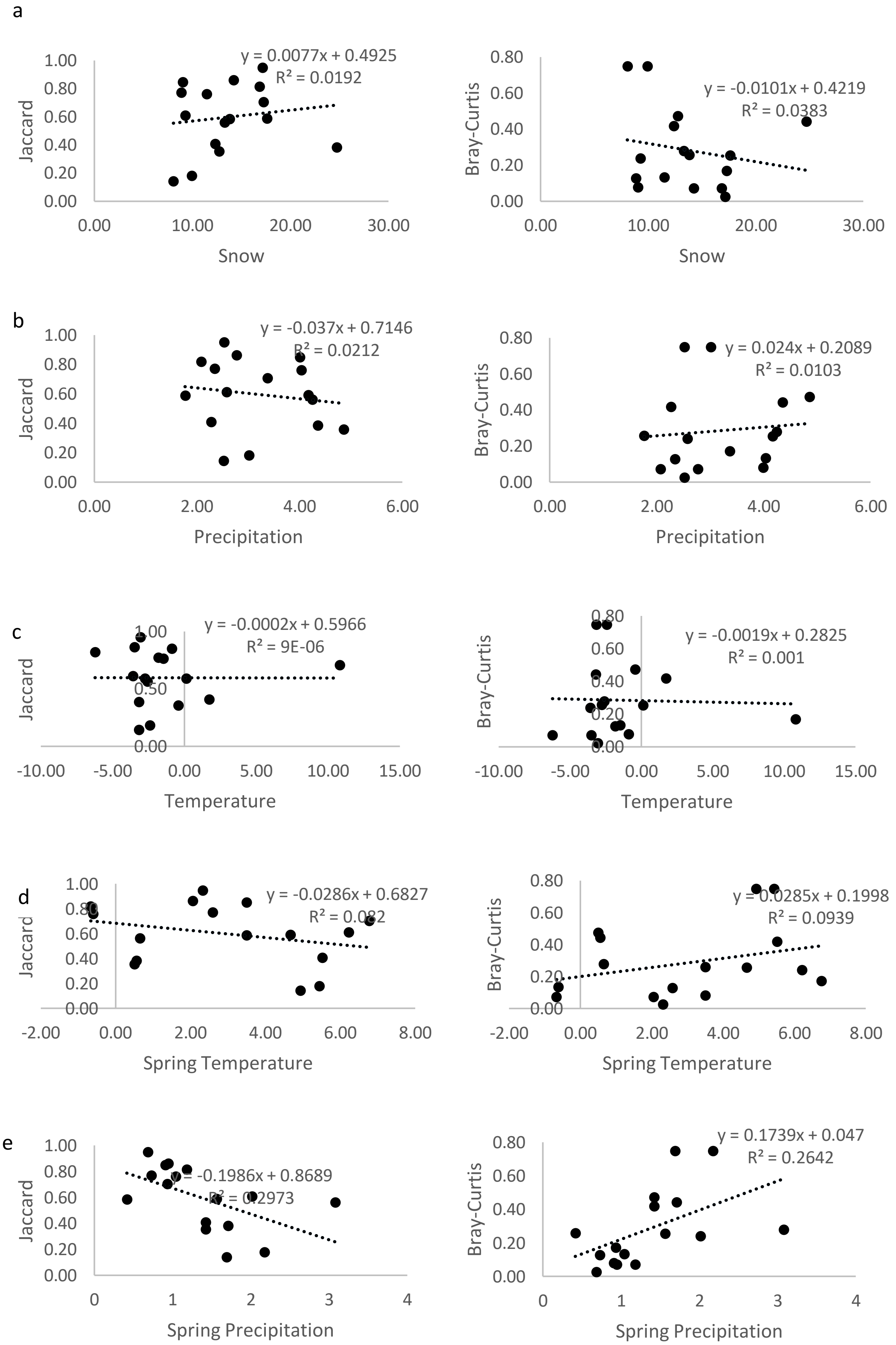
a


y = 0.0024x + 0.5652
R^2 = 0.0039
Jaccard
Snow


y = -0.0021x + 0.3039
R^2 = 0.0042
Bray-Curtis
Snow

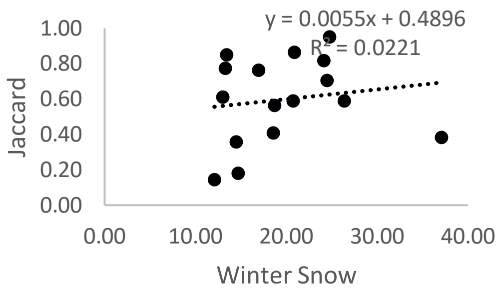

b
Jaccard
y = -0.0911x + 0.8789
R² = 0.1569
Precipitation
Bray-Curtis
y = 0.079x + 0.0312
R² = 0.1631
Precipitation
c
Jaccard
y = -0.0032x + 0.5932
R² = 0.0046
Temperature
Bray-Curtis
y = 0.0016x + 0.2778
R² = 0.0016
Temperature
d
Jaccard
y = 0.0236x + 0.5451
R² = 0.0893
Spring Temperature
Bray-Curtis
y = -0.0226x + 0.3255
R² = 0.1134
Spring Temperature
e
Jaccard
y = -0.1594x + 0.8278
R² = 0.2411
Spring Precipitation
Bray-Curtis
y = 0.138x + 0.0759
R² = 0.2497
Spring Precipitation
f
Jaccard
y = 0.006x + 0.4755
R² = 0.0366
Winter Snow
Bray-Curtis
y = -0.0057x + 0.3907
R² = 0.0453
Winter Snow

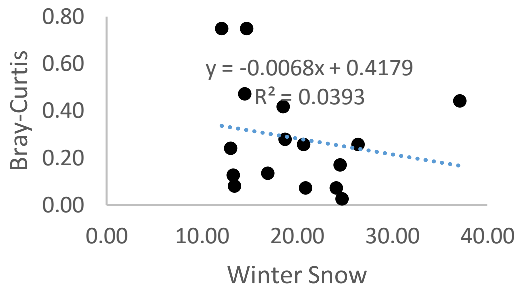
Moose Creek



a
Jaccard
y = 0.0077x + 0.4925
R² = 0.0192
Snow
Bray-Curtis
y = -0.0101x + 0.4219
R² = 0.0383
Snow
b
Jaccard
y = -0.037x + 0.7146
R² = 0.0212
Precipitation
Bray-Curtis
y = 0.024x + 0.2089
R² = 0.0103
Precipitation
c
Jaccard
y = -0.0002x + 0.5966
R² = 9E-06
Temperature
Bray-Curtis
y = -0.0019x + 0.2825
R² = 0.001
Temperature
d
Jaccard
y = -0.0286x + 0.6827
R² = 0.082
Spring Temperature
Bray-Curtis
y = 0.0285x + 0.1998
R² = 0.0939
Spring Temperature
e
Jaccard
y = -0.1986x + 0.8689
R² = 0.2973
Spring Precipitation
Bray-Curtis
y = 0.1739x + 0.047
R² = 0.2642
Spring Precipitation

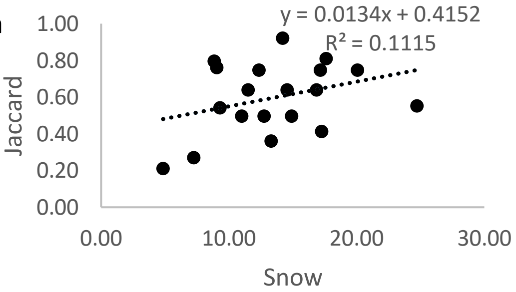
f

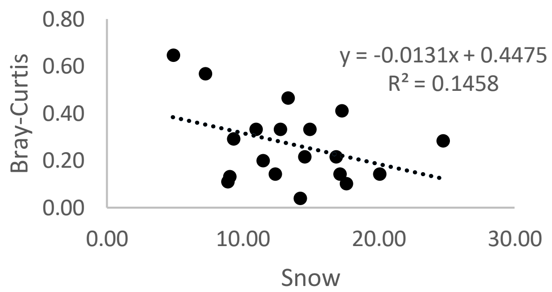




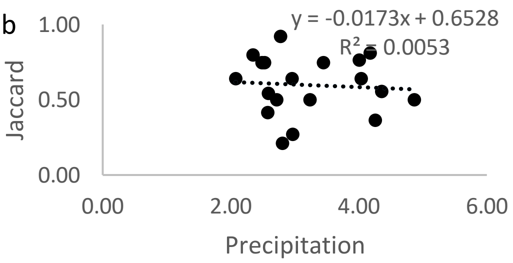
Little Stoney Creek

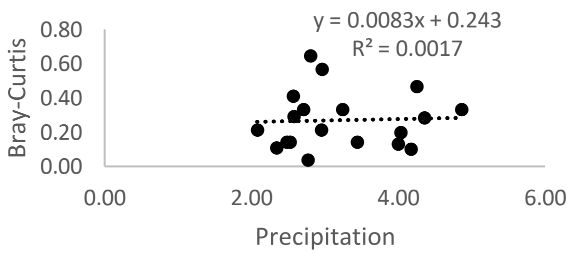
a





b





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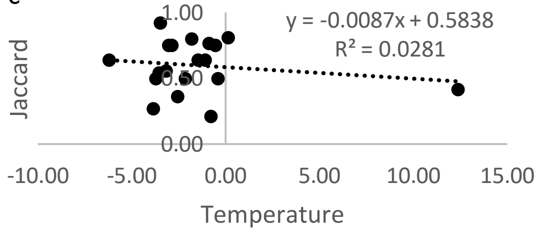
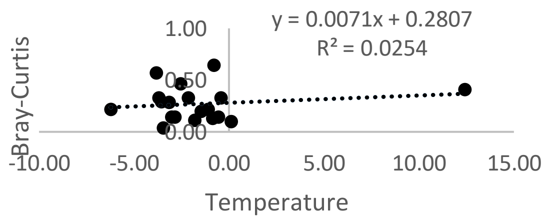
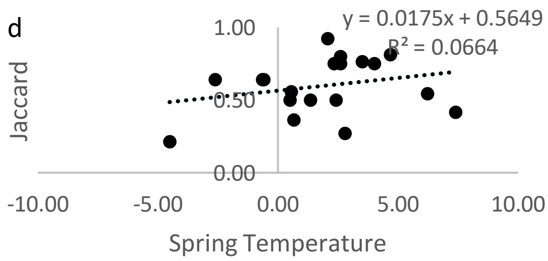
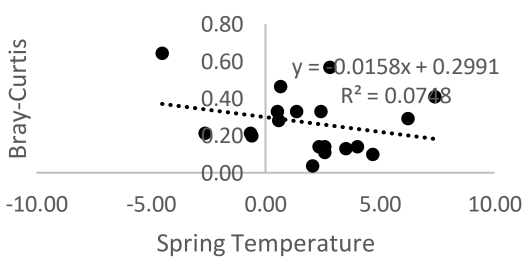


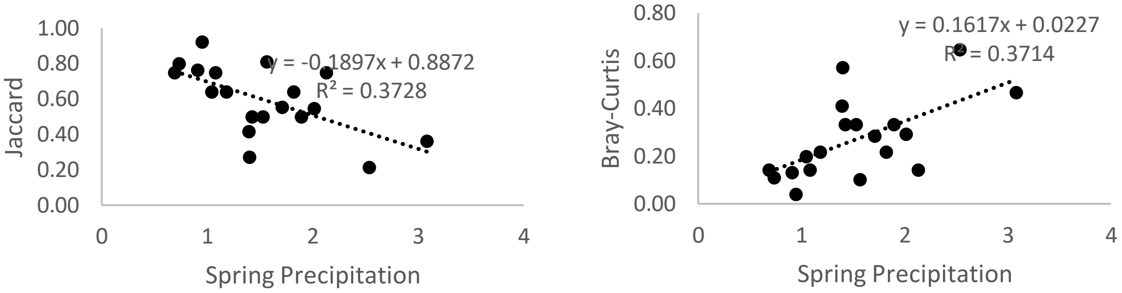


d

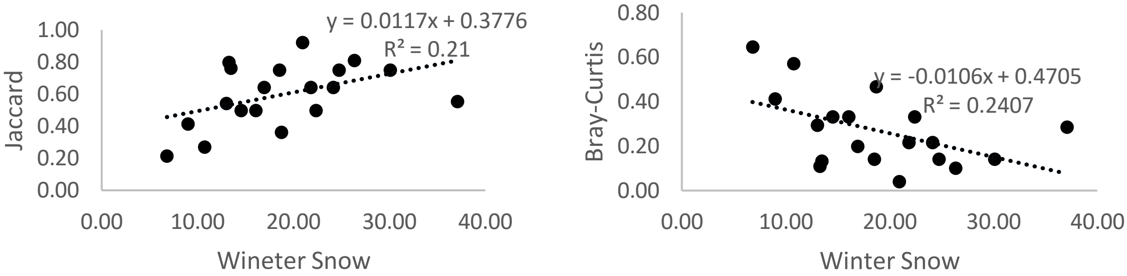




e

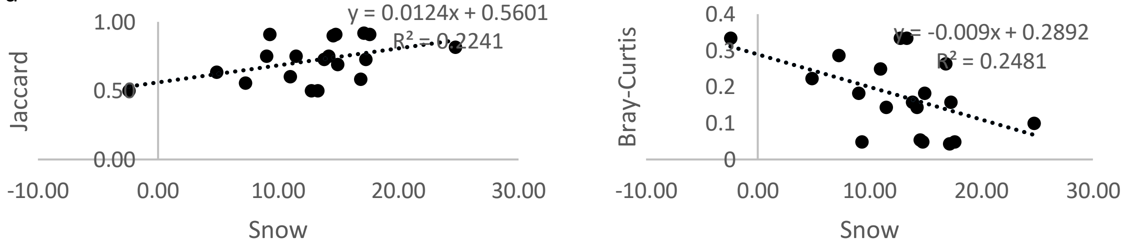


f



Igloo Creek

a



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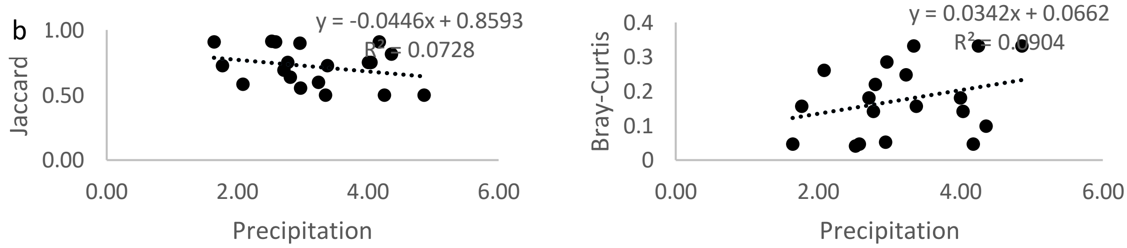

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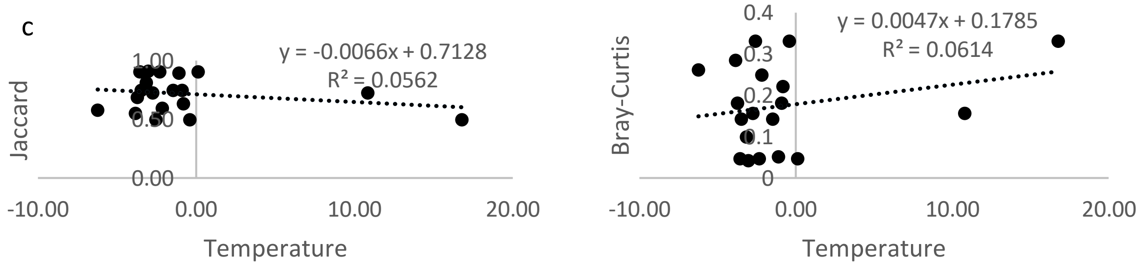

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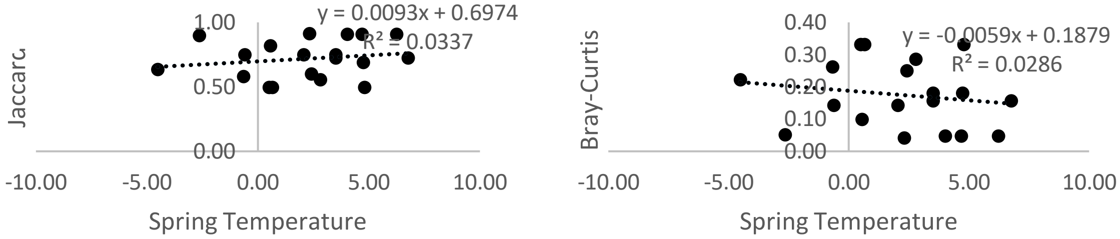
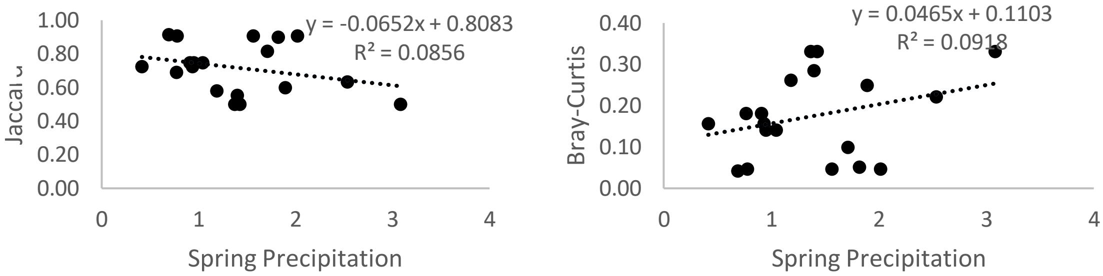
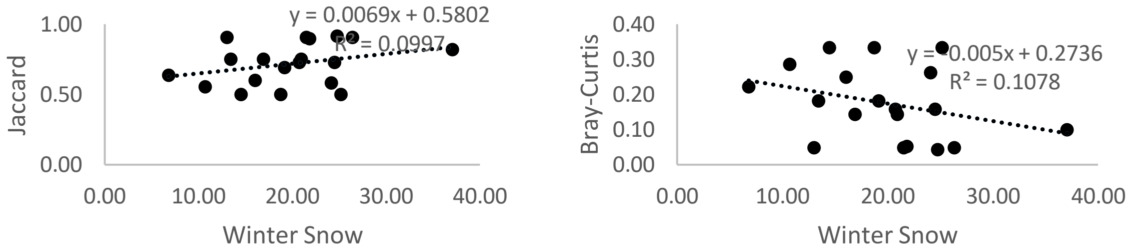


e

c

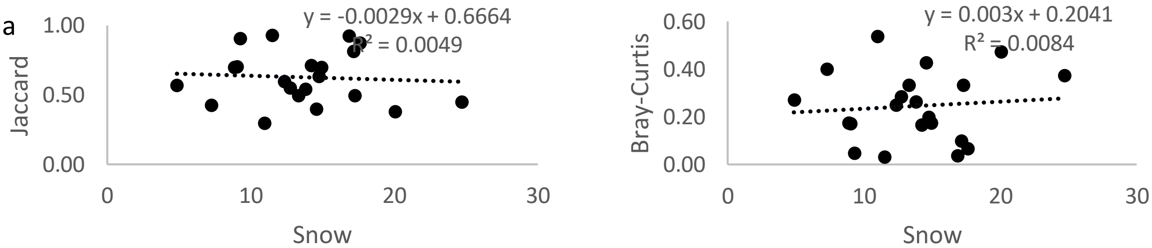


f



Hogan Creek

a



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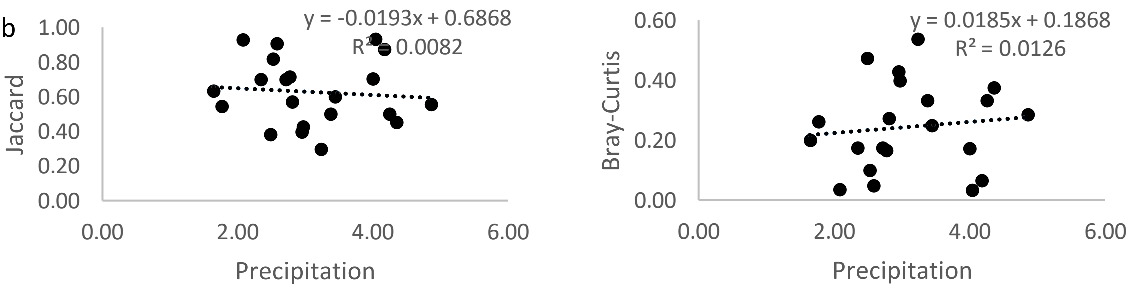
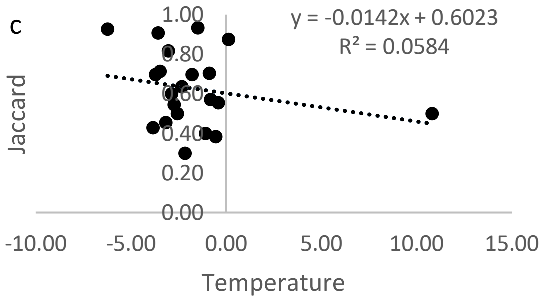
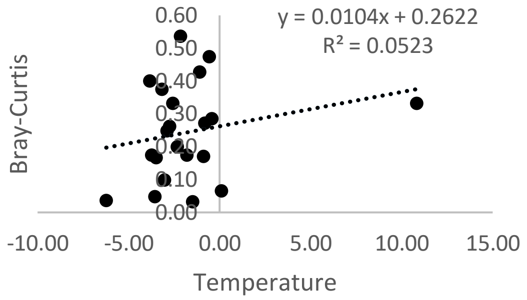
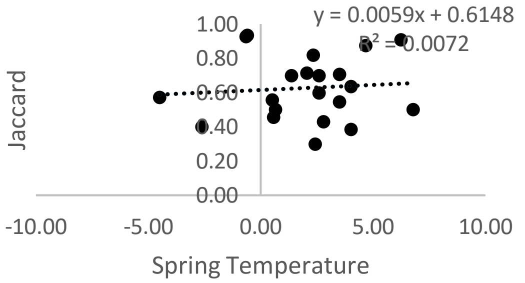
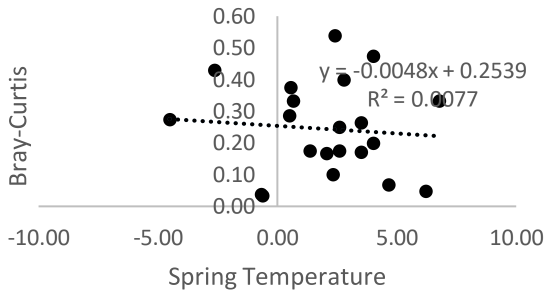


c



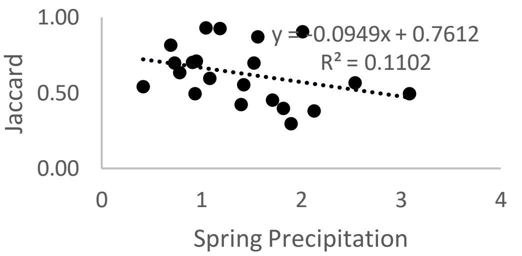


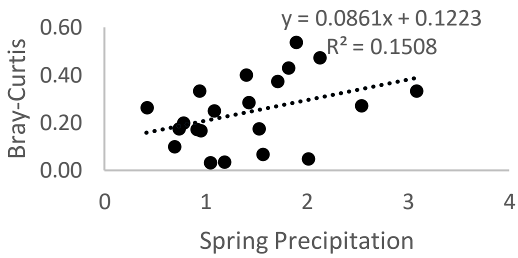




d

e





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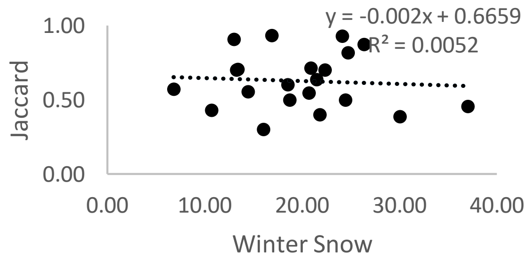
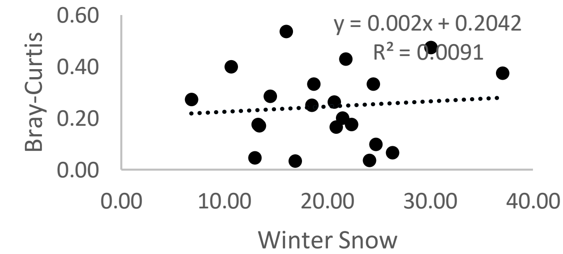
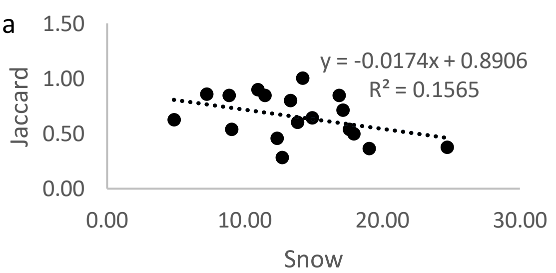
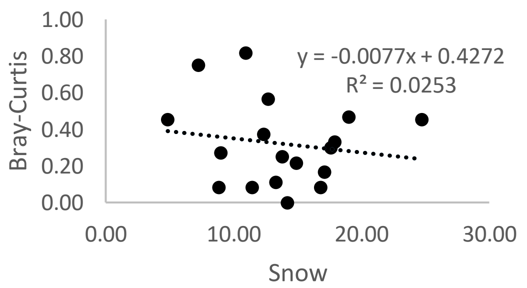


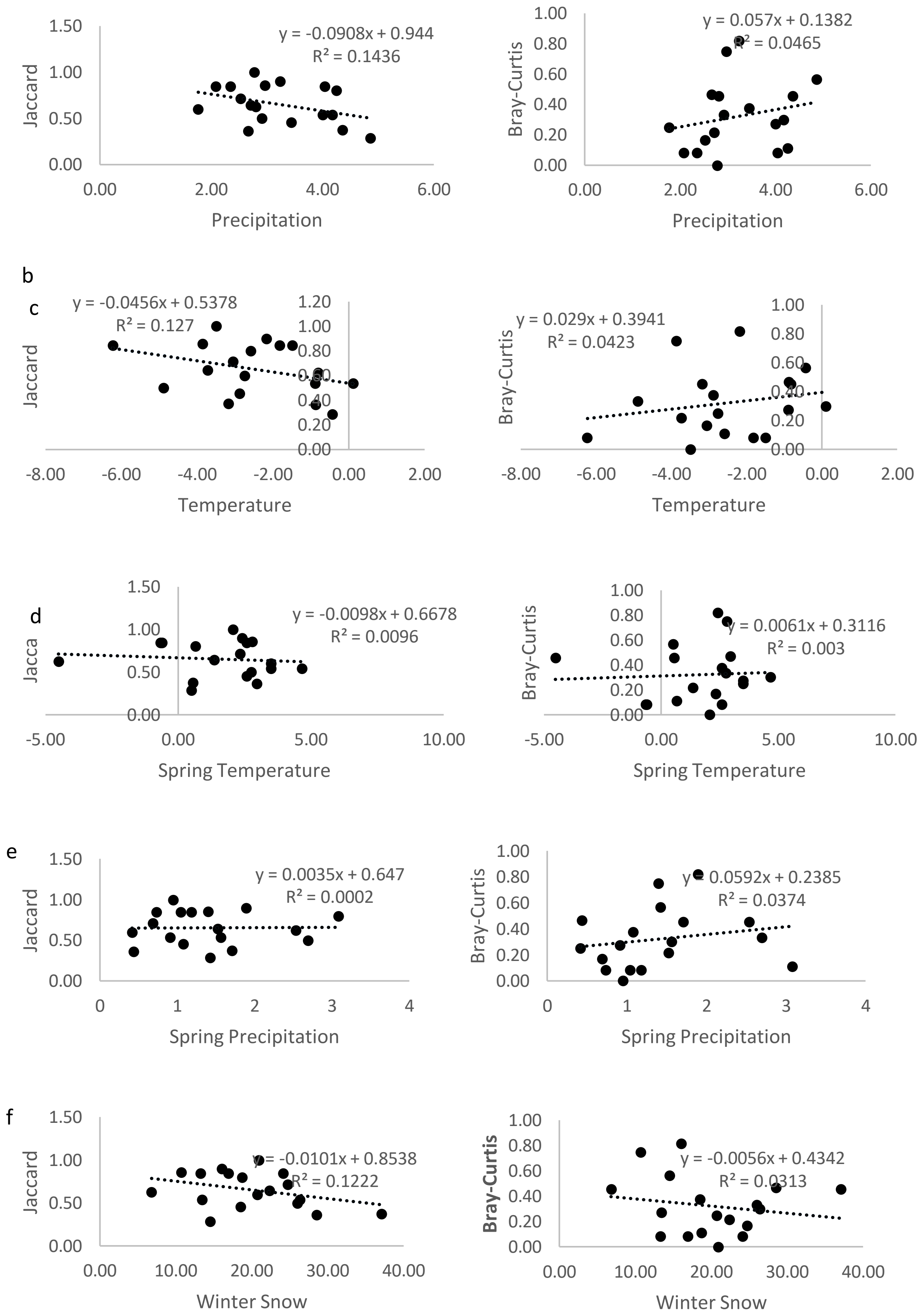


Highway Creek

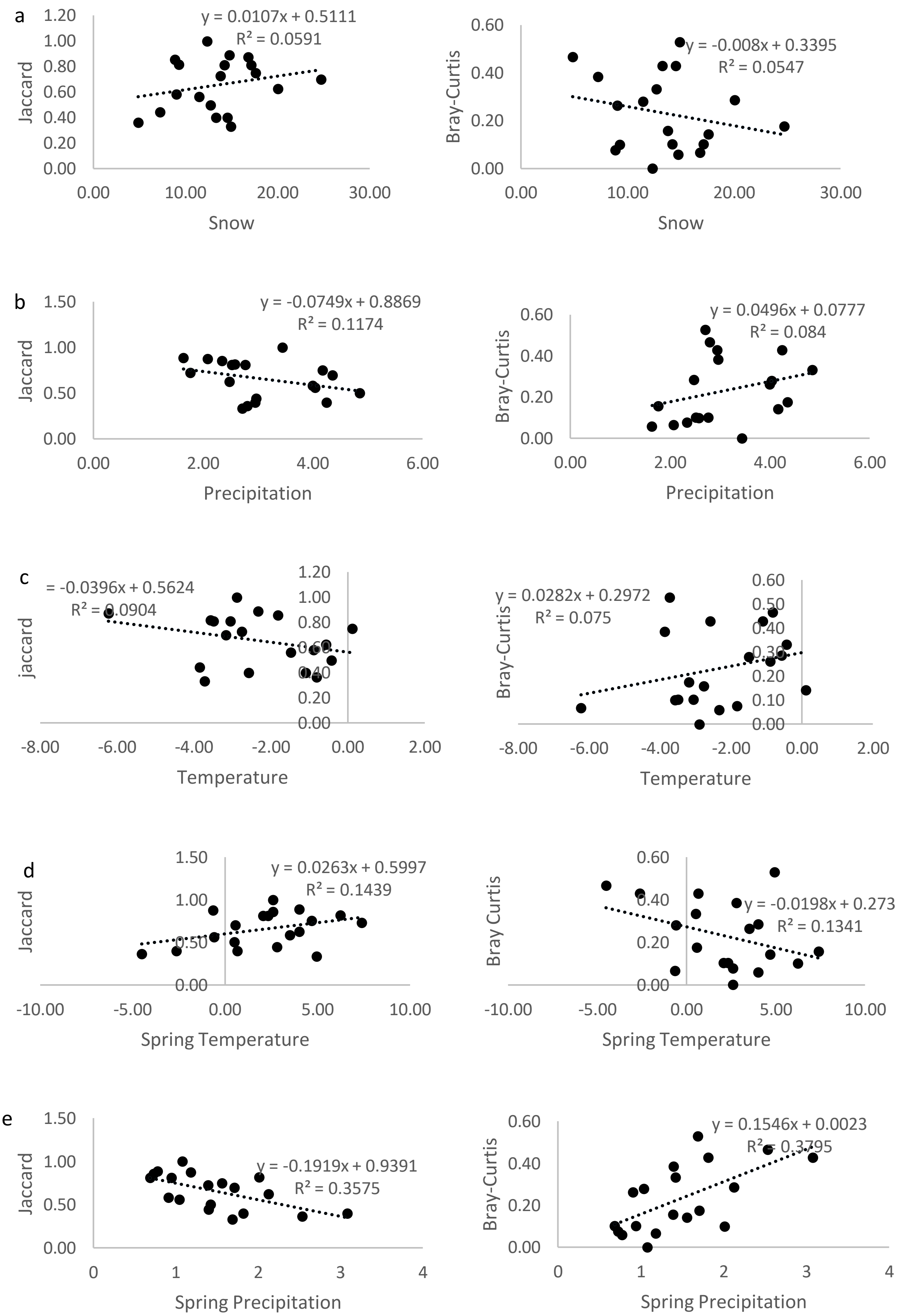
a



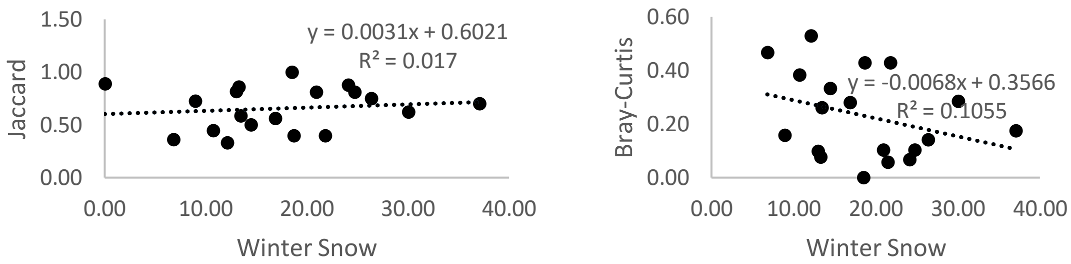



y = -0.0908x + 0.944
R² = 0.1436
Jaccard
Precipitation
y = 0.057x + 0.1382
R² = 0.0465
Bray-Curtis
Precipitation
b
c
y = -0.0456x + 0.5378
R² = 0.127
Jaccard
Temperature
y = 0.029x + 0.3941
R² = 0.0423
Bray-Curtis
Temperature
d
y = -0.0098x + 0.6678
R² = 0.0096
Jacca
Spring Temperature
y = 0.0061x + 0.3116
R² = 0.003
Bray-Curtis
Spring Temperature
e
y = 0.0035x + 0.647
R² = 0.0002
Jaccard
Spring Precipitation
y = 0.0592x + 0.2385
R² = 0.0374
Bray-Curtis
Spring Precipitation
f
y = -0.0101x + 0.8538
R² = 0.1222
Jaccard
Winter Snow
y = -0.0056x + 0.4342
R² = 0.0313
Bray-Curtis
Winter Snow

East Fork Tolkat Tributary

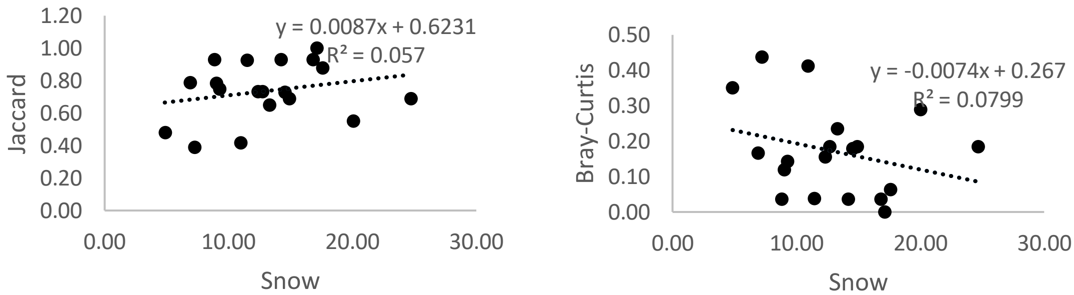


f

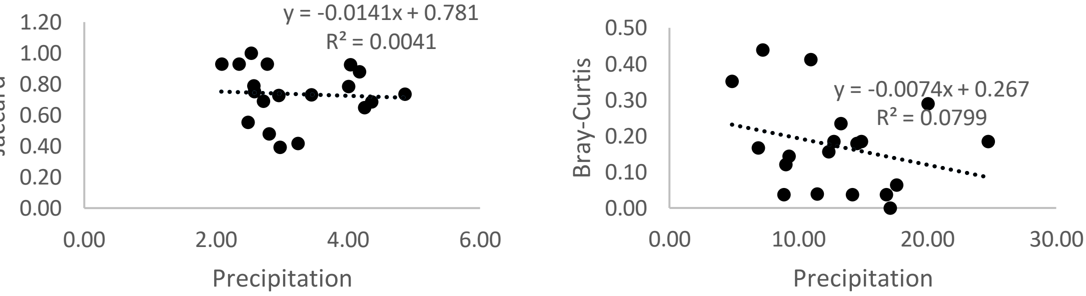


Global

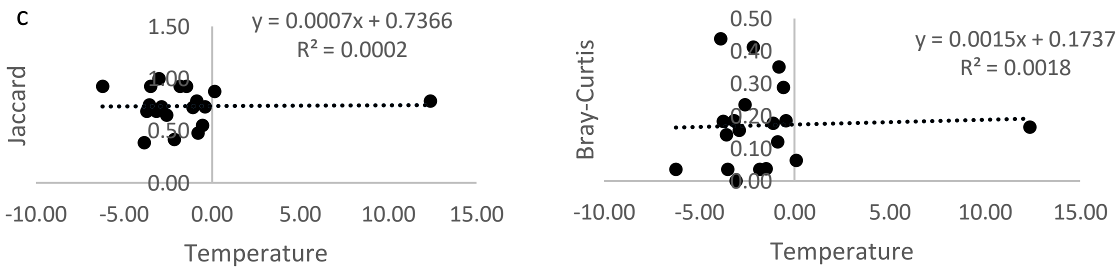
a



b

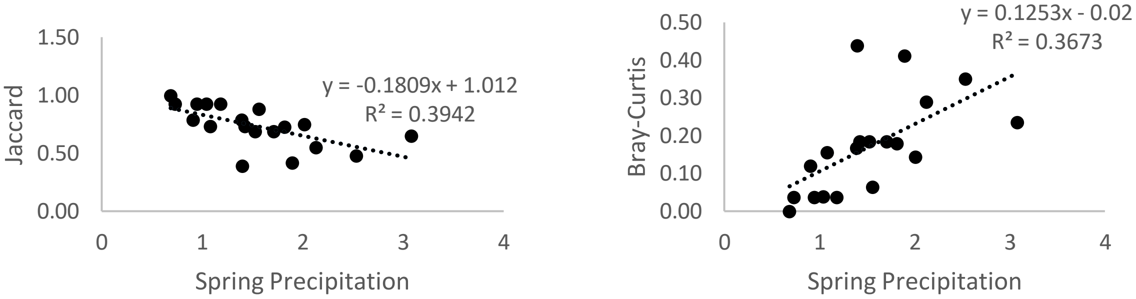


c



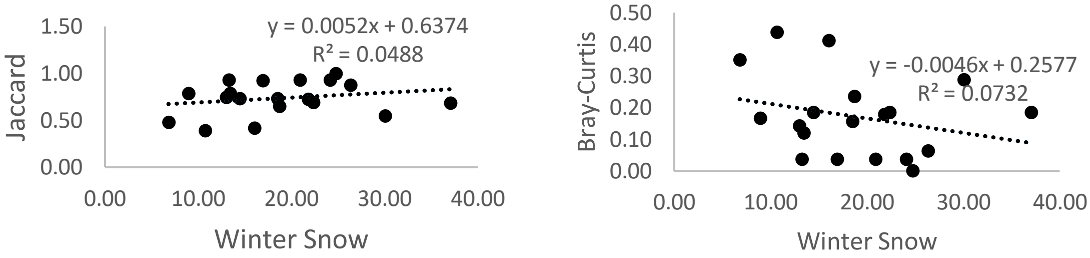
d

e



1.50
1.00
0.50
0.00
Jaccard
0
1
2
3
4
Spring Precipitation
y = -0.1809x + 1.012
R² = 0.3942
0.50
0.40
0.30
0.20
0.10
0.00
Bray-Curtis
Spring Precipitation
y = 0.1253x - 0.02
R² = 0.3673

f

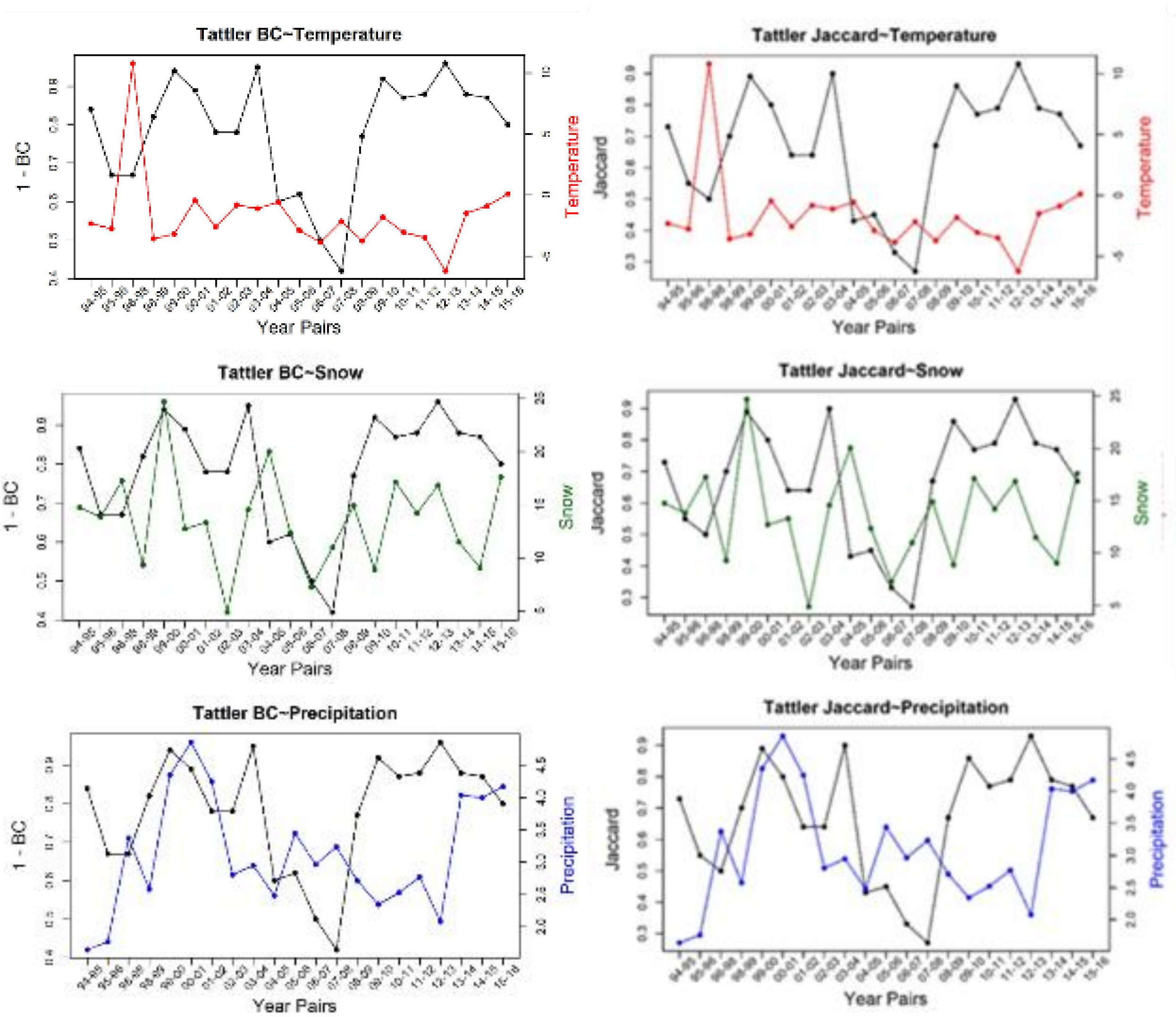


1.50
1.00
0.50
0.00
Jaccard
0.00
10.00
20.00
30.00
40.00
Winter Snow
y = 0.0052x + 0.6374
R² = 0.0488
0.50
0.40
0.30
0.20
0.10
0.00
Bray-Curtis
Winter Snow
y = -0.0046x + 0.2577
R² = 0.0732

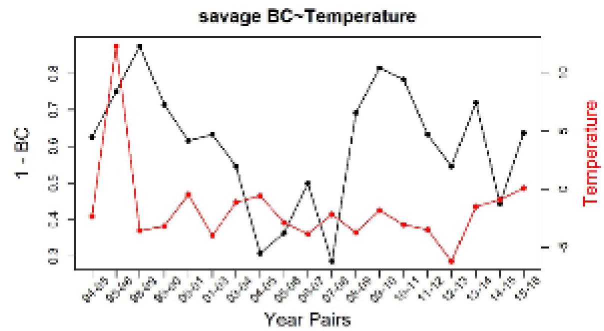
7.1.5 Appendix 3.5 Time series linear regression

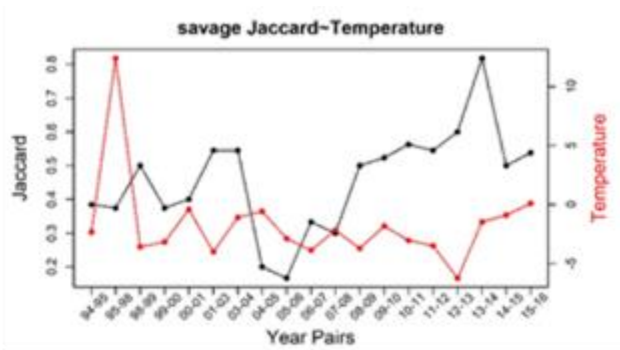
The results of time-series linear regression, using Jaccard (persistence) and BD (compositional stability) as the response variable. Unlike standard R^2 values, adjusted R^2 values can be negative. Each model includes the coefficient for the trend parameter, which models the time-series component.

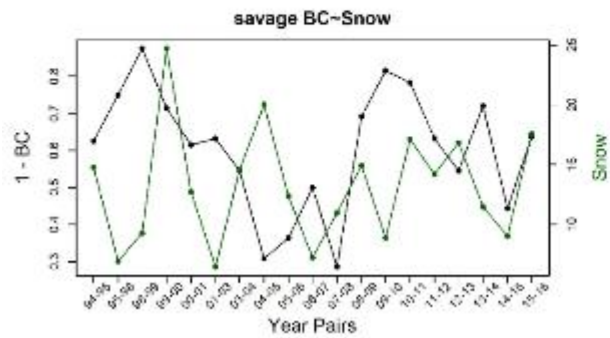
Tattler Creek

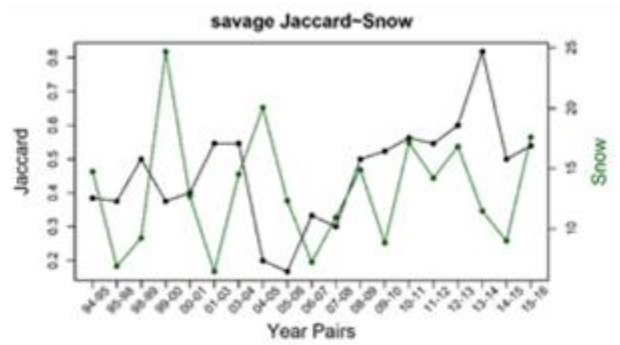


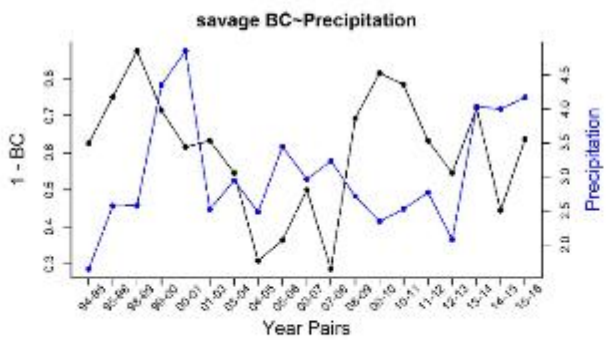
Savage River

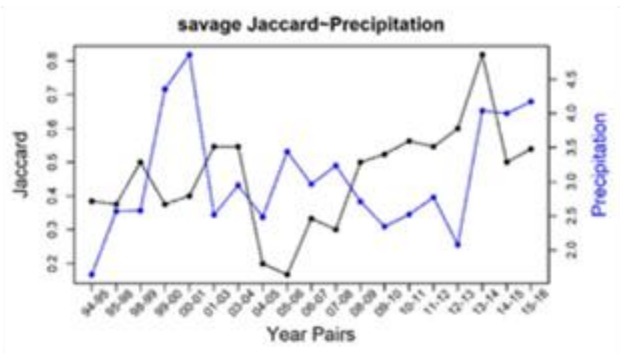




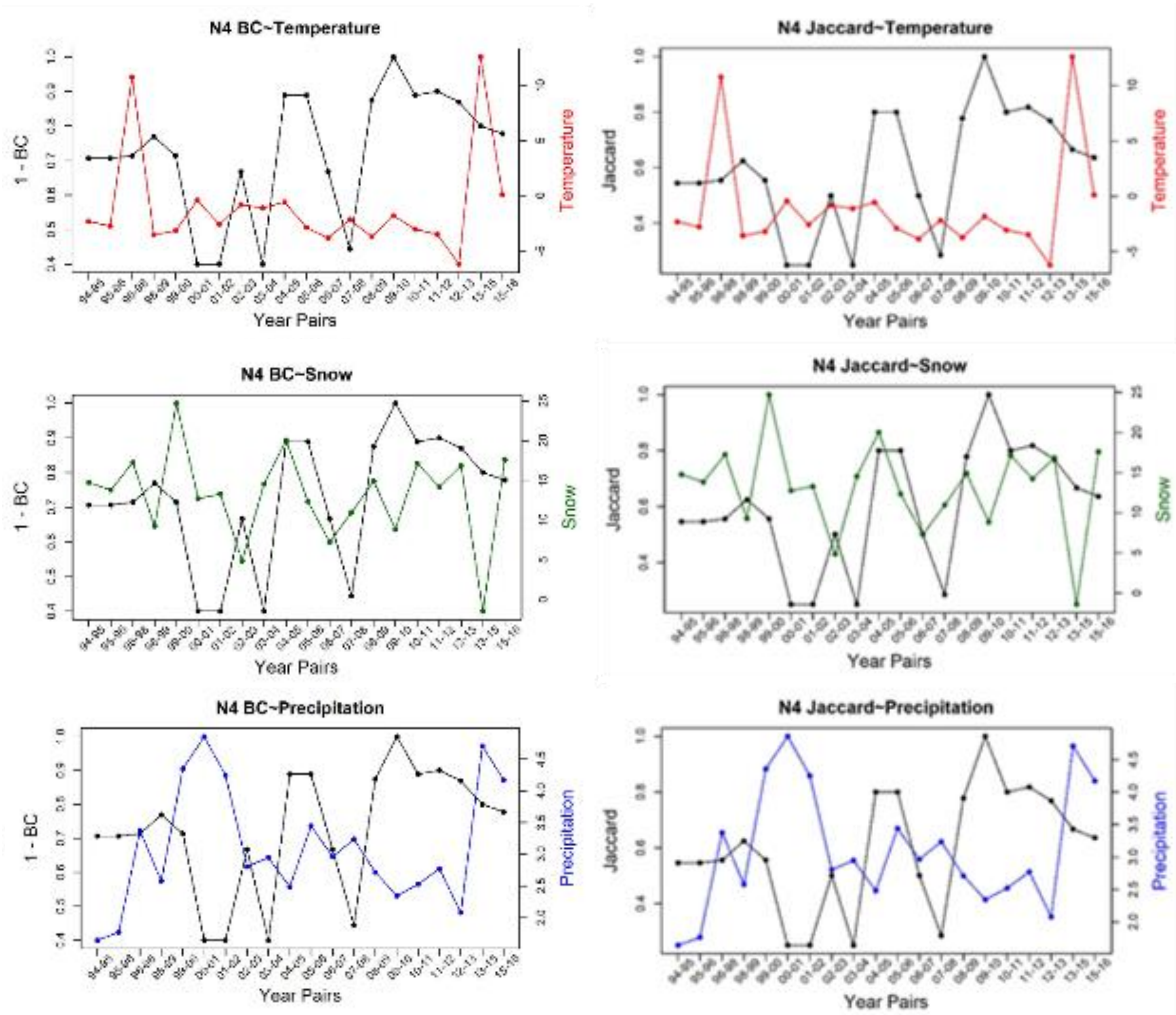




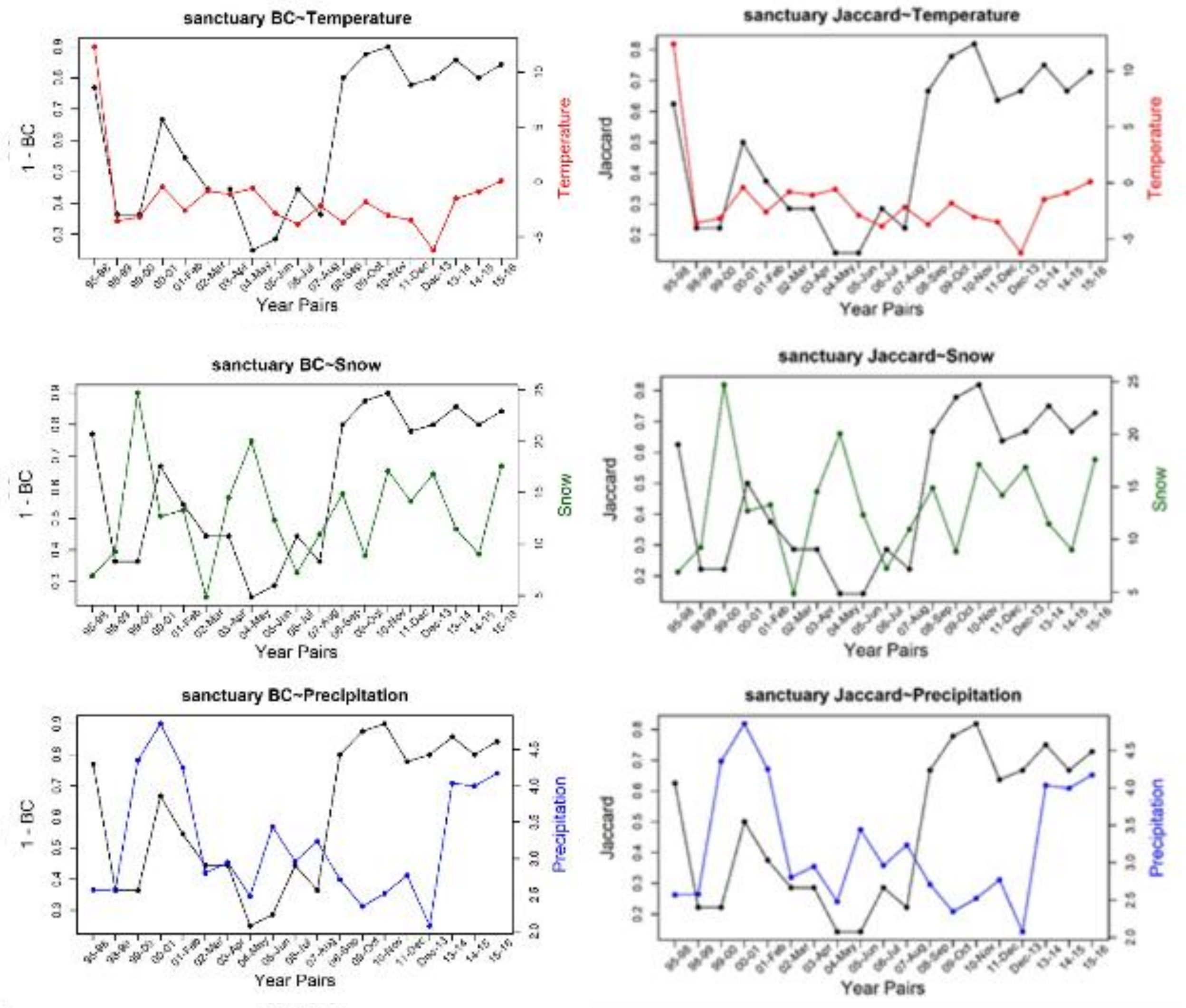




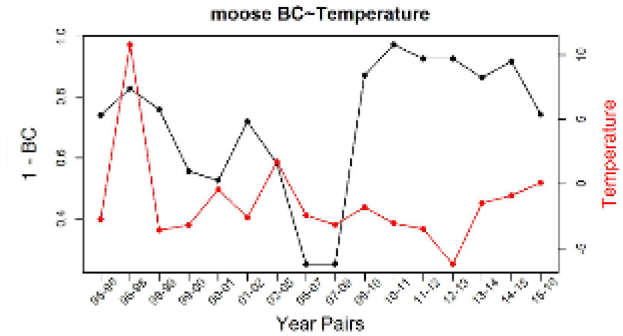
N4

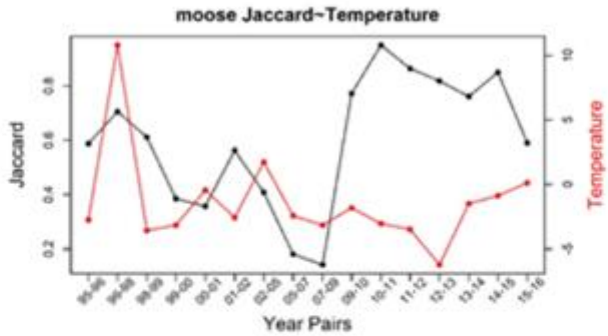

N4 BC~Temperature
1 - BC
Temperature
Year Pairs
N4 Jaccard~Temperature
Jaccard
Temperature
Year Pairs
N4 BC~Snow
1 - BC
Snow
Year Pairs
N4 Jaccard~Snow
Jaccard
Snow
Year Pairs
N4 BC~Precipitation
1 - BC
Precipitation
Year Pairs
N4 Jaccard~Precipitation
Jaccard
Precipitation
Year Pairs

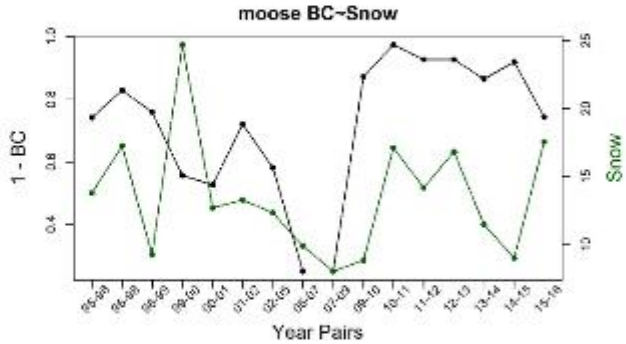
Sanctuary Creek

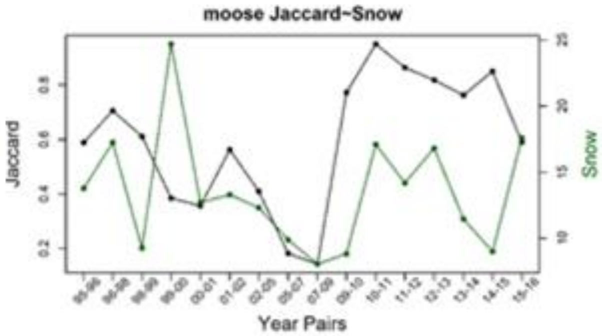


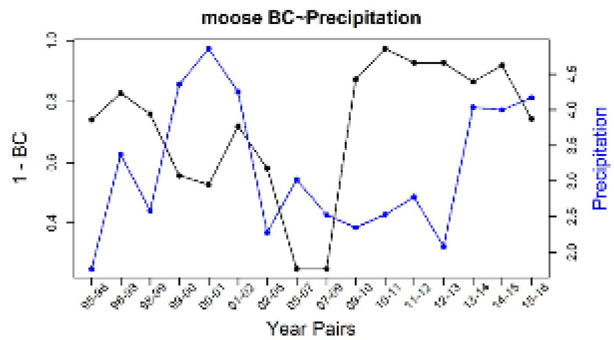
Moose

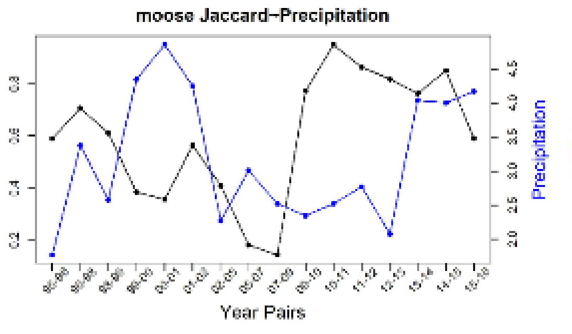

moose BC~Temperature
1 - BC
Temperature
Year Pairs


moose Jaccard~Temperature
Jaccard
Temperature
Year Pairs

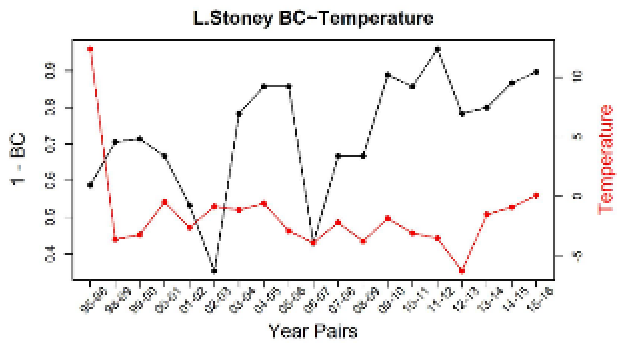

moose BC~Snow
1 - BC
Snow
Year Pairs

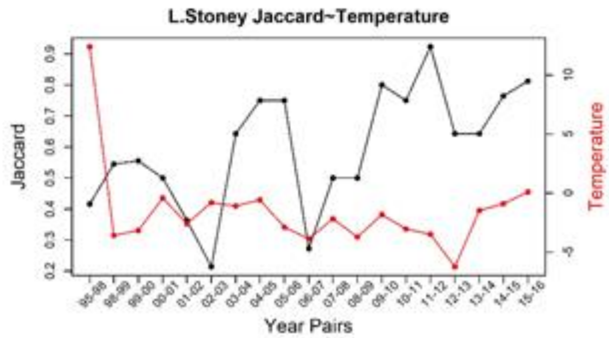

moose Jaccard~Snow
Jaccard
Snow
Year Pairs

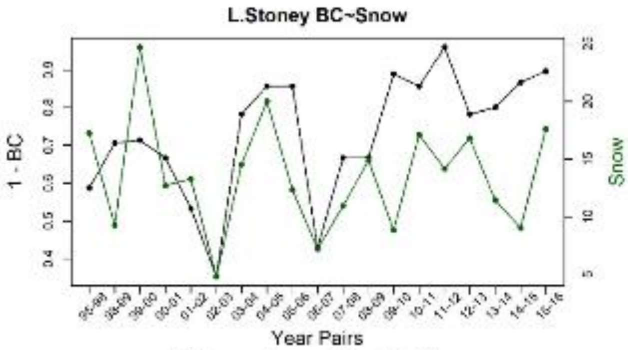

moose BC~Precipitation
1 - BC
Precipitation
Year Pairs

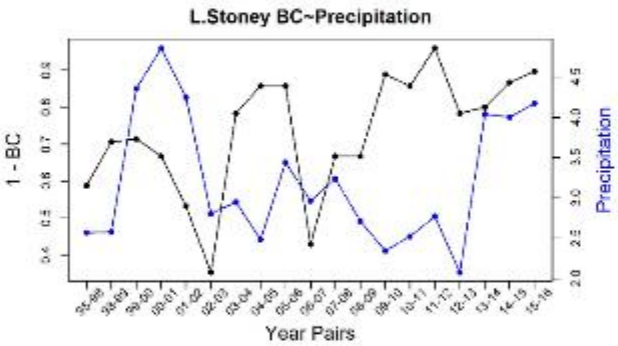

moose Jaccard~Precipitation
Jaccard
Precipitation
Year Pairs

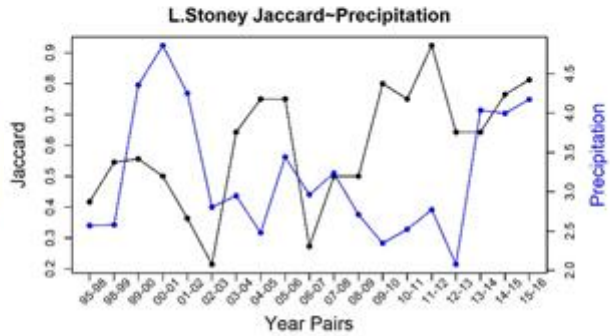
Little Stoney Creek



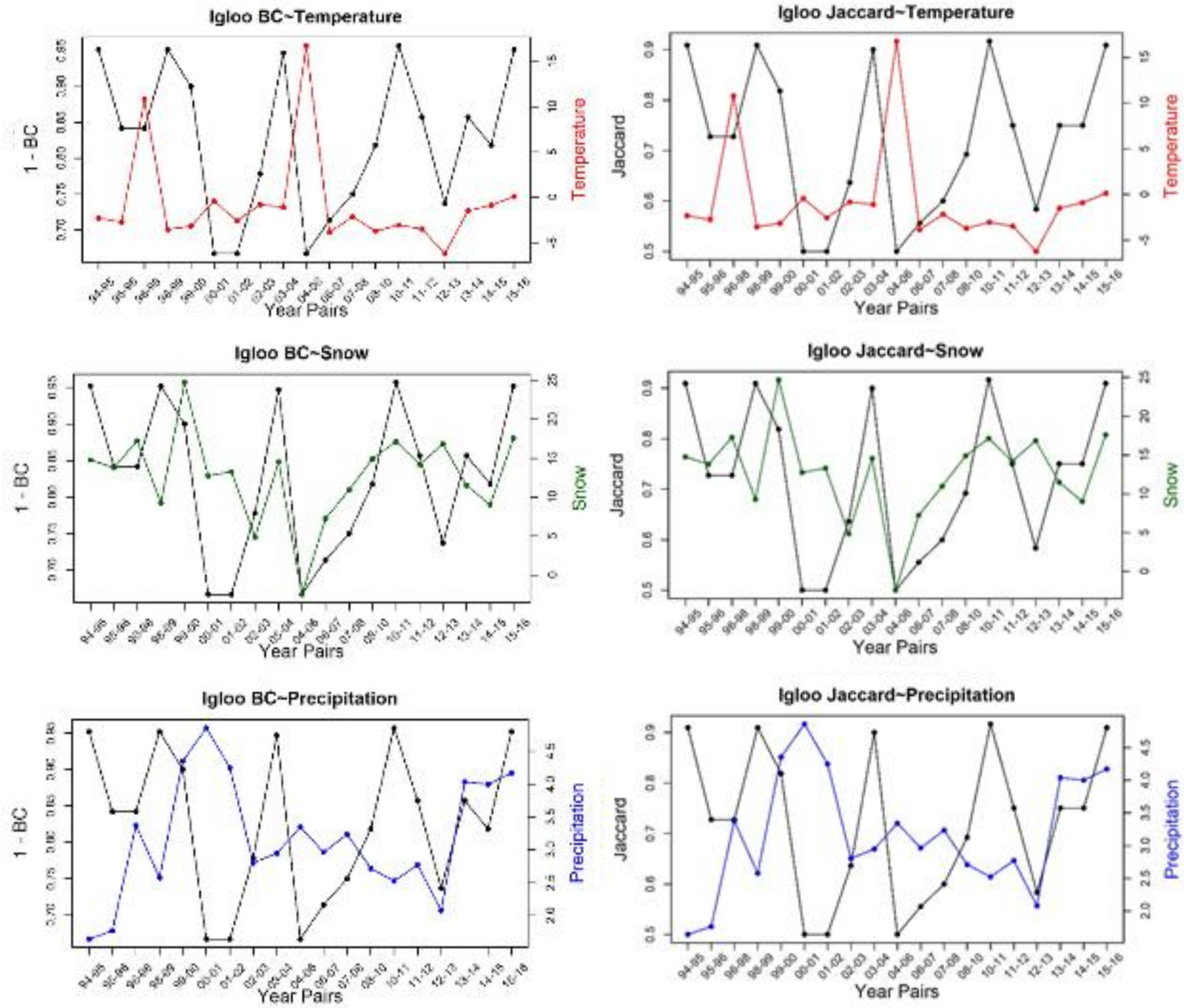




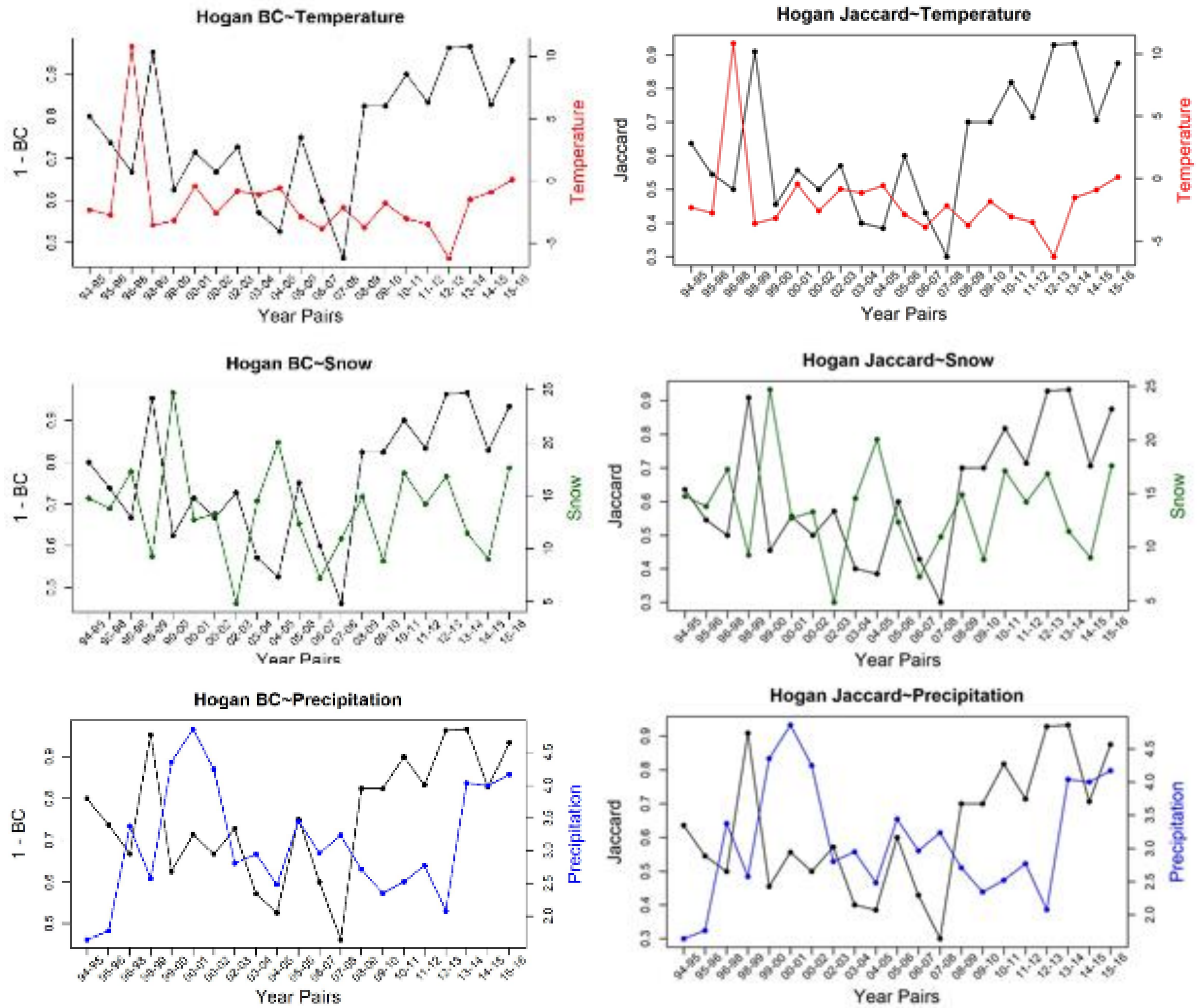




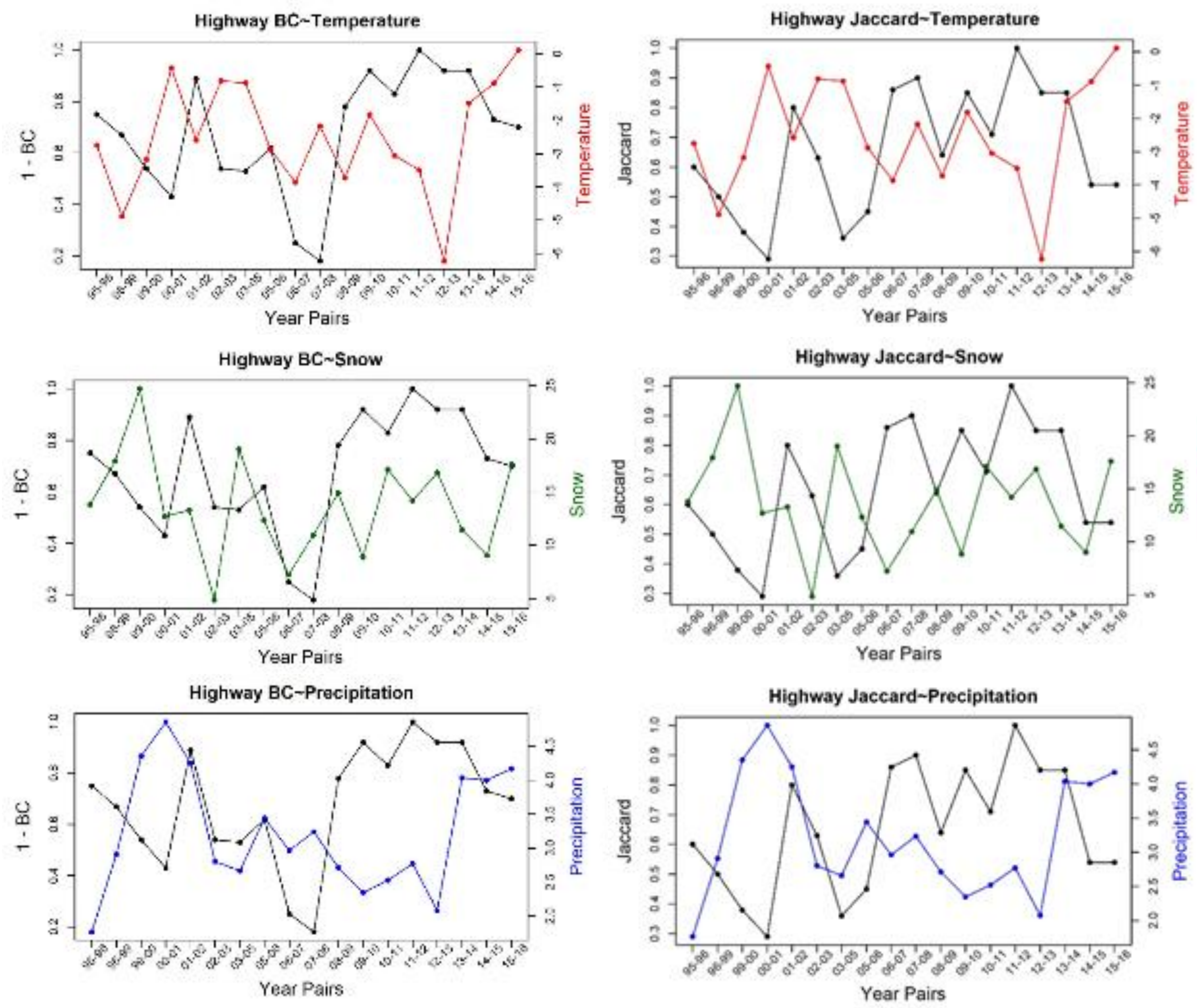
Igloo Creek


Igloo BC~Temperature
1 - BC
Temperature
Year Pairs
Igloo Jaccard~Temperature
Jaccard
Temperature
Year Pairs
Igloo BC~Snow
1 - BC
Snow
Year Pairs
Igloo Jaccard~Snow
Jaccard
Snow
Year Pairs
Igloo BC~Precipitation
1 - BC
Precipitation
Year Pairs
Igloo Jaccard~Precipitation
Jaccard
Precipitation
Year Pairs

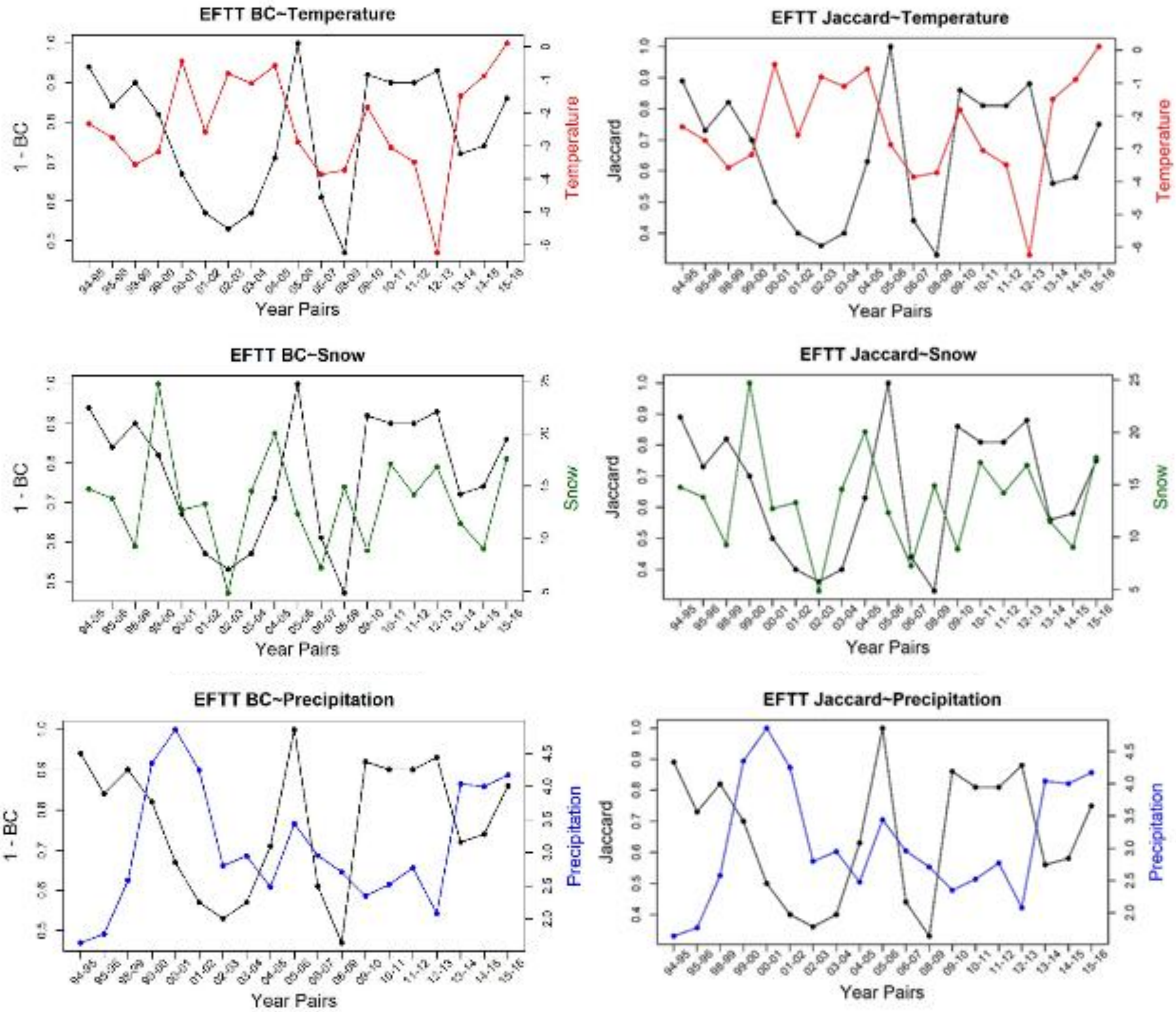
Hogan Creek


Hogan BC~Temperature
1 - BC
Temperature
Year Pairs
Hogan Jaccard~Temperature
Jaccard
Temperature
Year Pairs
Hogan BC~Snow
1 - BC
Snow
Year Pairs
Hogan Jaccard~Snow
Jaccard
Snow
Year Pairs
Hogan BC~Precipitation
1 - BC
Precipitation
Year Pairs
Hogan Jaccard~Precipitation
Jaccard
Precipitation
Year Pairs

Highway Creek



East Fork Tolkat Tributary



7.1.6 Appendix 3.6 Regression coefficients, P values and R^2 values

The regression coefficients, P-values and adjusted R^2 values) for the three local climate variables: temperature, snow and precipitation.

BRAY CURTIS					JACCARD				
Variable	Coef.	P	Adjusted_R2	site	Variable	Coef.	P	Adjusted_R2	site
(Intercept)	0.73	0	-0.05	EFTT	(Intercept)	0.64	0.03	0.01	EFTT
trend	0	0.57	-0.05	EFTT	trend	0.01	0.58	0.01	EFTT
temp	-0.01	0.65	-0.05	EFTT	temp	-0.02	0.63	0.01	EFTT
snow	0.01	0.33	-0.05	EFTT	snow	0.01	0.28	0.01	EFTT
prec	-0.05	0.33	-0.05	EFTT	prec	-0.07	0.22	0.01	EFTT
(Intercept)	0.83	0	0.26	global	(Intercept)	0.73	0	0.25	global
trend	0.01	0.02	0.26	global	trend	0.02	0.02	0.25	global
temp	0.02	0.32	0.26	global	temp	0.02	0.38	0.25	global
snow	0.01	0.16	0.26	global	snow	0.01	0.16	0.25	global
prec	-0.06	0.06	0.26	global	prec	-0.09	0.07	0.25	global
(Intercept)	0.48	0.17	0.03	Highway	(Intercept)	0.69	0.01	0.46	Highway
trend	0.02	0.1	0.03	Highway	trend	0.02	0.03	0.46	Highway
temp	-0.02	0.72	0.03	Highway	temp	-0.06	0.05	0.46	Highway
snow	0.01	0.42	0.03	Highway	snow	-0.02	0.04	0.46	Highway
prec	-0.05	0.51	0.03	Highway	prec	-0.03	0.62	0.46	Highway
(Intercept)	0.73	0	0.02	Hogan	(Intercept)	0.56	0.01	0.08	Hogan
trend	0.01	0.1	0.02	Hogan	trend	0.01	0.05	0.08	Hogan
temp	0	0.75	0.02	Hogan	temp	0	0.74	0.08	Hogan
snow	0	0.91	0.02	Hogan	snow	0	0.99	0.08	Hogan
prec	-0.03	0.5	0.02	Hogan	prec	-0.03	0.51	0.08	Hogan
(Intercept)	0.81	0	0.2	Igloo	(Intercept)	0.69	0	0.14	Igloo
trend	0	0.62	0.2	Igloo	trend	0	0.61	0.14	Igloo
temp	0	0.65	0.2	Igloo	temp	0	0.68	0.14	Igloo
snow	0.01	0.03	0.2	Igloo	snow	0.01	0.05	0.14	Igloo
prec	-0.04	0.11	0.2	Igloo	prec	-0.06	0.16	0.14	Igloo
(Intercept)5	0.39	0.03	0.36	L.Stoney	(Intercept)	0.24	0.23	0.36	L.Stoney
trend5	0.02	0.01	0.36	L.Stoney	trend	0.02	0.01	0.36	L.Stoney
temp5	0	0.99	0.36	L.Stoney	temp	0	0.99	0.36	L.Stoney
snow5	0.02	0.04	0.36	L.Stoney	snow	0.02	0.06	0.36	L.Stoney
prec5	-0.01	0.76	0.36	L.Stoney	prec	-0.02	0.65	0.36	L.Stoney
(Intercept)	0.54	0.07	-0.04	moose	(Intercept)	0.44	0.15	0.03	moose
trend	0.02	0.14	-0.04	moose	trend	0.03	0.08	0.03	moose
temp	0.01	0.53	-0.04	moose	temp	0.01	0.52	0.03	moose
snow	0.02	0.3	-0.04	moose	snow	0.01	0.34	0.03	moose
prec	-0.06	0.36	-0.04	moose	prec	-0.08	0.28	0.03	moose
(Intercept)	0.83	0	0.33	N4	(Intercept)	0.69	0	0.35	N4
trend	0.02	0.01	0.33	N4	trend	0.02	0.01	0.35	N4
temp	0.01	0.22	0.33	N4	temp	0.01	0.28	0.35	N4

snow	0.01	0.32	0.33	N4	snow	0.01	0.33	0.35	N4
prec	-0.12	0.01	0.33	N4	prec	-0.13	0.02	0.35	N4
(Intercept)	0.37	0.11	0.35	sanctuary	(Intercept)	0.22	0.33	0.39	sanctuary
trend	0.03	0	0.35	sanctuary	trend	0.03	0	0.39	sanctuary
temp	0.02	0.09	0.35	sanctuary	temp	0.03	0.07	0.39	sanctuary
snow	0	0.92	0.35	sanctuary	snow	0	0.92	0.39	sanctuary
prec	0	0.98	0.35	sanctuary	prec	-0.01	0.82	0.39	sanctuary
(Intercept)	0.7	0	-0.24	savage	(Intercept)	0.4	0.02	0.04	savage
trend	0	0.77	-0.24	savage	trend	0.01	0.07	0.04	savage
temp	0	0.75	-0.24	savage	temp	0	0.83	0.04	savage
snow	0	0.91	-0.24	savage	snow	0	0.6	0.04	savage
prec	-0.02	0.75	-0.24	savage	prec	-0.01	0.85	0.04	savage
(Intercept)	0.58	0	-0.12	Tattler	(Intercept)	0.41	0.07	-0.08	Tattler
trend	0	0.65	-0.12	Tattler	trend	0	0.61	-0.08	Tattler
temp	-0.01	0.49	-0.12	Tattler	temp	-0.01	0.37	-0.08	Tattler
snow	0.01	0.35	-0.12	Tattler	snow	0.01	0.31	-0.08	Tattler
prec	0.02	0.71	-0.12	Tattler	prec	0.02	0.76	-0.08	Tattler

7.2 Chapter 4

7.2.1 Appendix 4.1: Stream Classification

Stream grouping according physico-chemical properties of the study streams in Denali National Park during 1995 (adapted from Conn, 1998).

Group	Creek	Latitude	Longitude	Order	Elevation	Stability	Water Source	Invertebrate Productivity
1. Small stable streams	Tattler Creek	63.34.04	-149.38.27	1	1053	High	Snowmelt and rain runoff	High
	East Fork Tolkat Tributary	63.33.50	-149.47.40	2	945	Low	Snowmelt and rain runoff	High
2. Spring-fed streams	Little Stoney	63.27.14	-150.14.17	3	1130	High	Springs (Groundwater)	Very High
	Hogan Creek	63.43.41	-149.24.39	2	789	High	Springs (Groundwater)	Very High
3. Streams of the Kantishna area	Moose Creek	63.32.03	-150.58.45	3	628	High	Variable	Very High
4. Large river systems partially fed by glacier-melt water	Savage	63.35.50	-149.47.40	4	808	Moderate	Snowpack	Moderate
	Sanctuary	63.44.22	-149.17.39	3	807	Moderate	Snowpack	Moderate
	Igloo River	63.35.08	-149.37.10	2	864	High	Snowpack	Moderate
5. Small, unstable snowmelt fed creeks	N4	63.34.42	-149.37.28	1	975	Low	Snowmelt and rain runoff	Only specialist taxa
	Highway Creek	63.28.13	-150.09.47	2	985	Low	Snowmelt and rain runoff	Low

7.2.2 Appendix 4.2: Environmental variables

Glossary of acronyms and abbreviations used in the text.

Variable	**Acronym**	**Time**
Pacific Decadal Oscillation	PDO	Positive/Negative phase 20 to 30 years
East Pacific / North Pacific Pattern	EP.PA	Spring-Summer-Fall pattern
Pacific/North American Pattern	PNA	Autumn, winter and spring
North Atlantic Oscillation	NAO	Difference of atmospheric pressure fluctuation between Icelandic low and Azores High
Oceanic Niño Index	ONI	El Niño en La Niña events in the tropical Pacific
Temperature standard deviation	tempSD	September to August following year
Mean temperature	Mtemp	September to August following year
Mean total precipitation	Mprecip	September to August following year
Snow standard deviation	snowSD	September to August following year
Mean total snowfall	Msnow	September to August following year
Winter snowfall	WintSnow	September to April following year
Spring mean temperature	SpringTemp	April and May
Spring mean Precipitation	SpringPrecip	April and May
Spring flood	SpringFlood	number of events with three or more days of heavier than average rain during spring or summer covering April to July

7.2.3 Appendix 4.3: Correlations between four axes of a PCA analysis

Correlations between the four axes of a PCA analysis and the four variables used in the PCA: winter snow, mean monthly snow, mean monthly precipitation and precipitation standard deviation.

	PC1	PC2	PC3	PC4
WinterSnow	-0.95	0.32	0.03	0
Msnow	-0.96	-0.29	-0.03	0
Mprec	-9	-0.28	0.92	-0.27
SDprec	0.1	-0.18	0.97	0.14

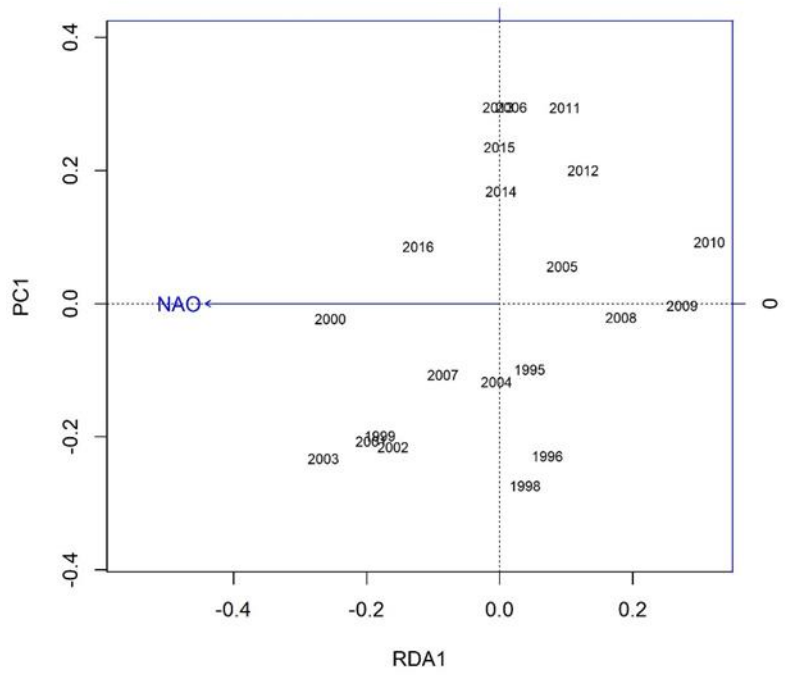
7.2.4 Appendix 4.4: RDA and NMDS plots

The full set of environmental vectors have been projected onto the ordination space. (a) RDA biplot (scaling 1) of the Hellinger-transformed macroinvertebrate data (pooled across all ten rivers) showing the locations of the objects (years) and the environmental variable(s) present in the best RDA model, selected using backwards selection. (b) NMDS biplot of a Jaccard dissimilarity matrix of the macroinvertebrate presence-absence data (pooled across rivers).

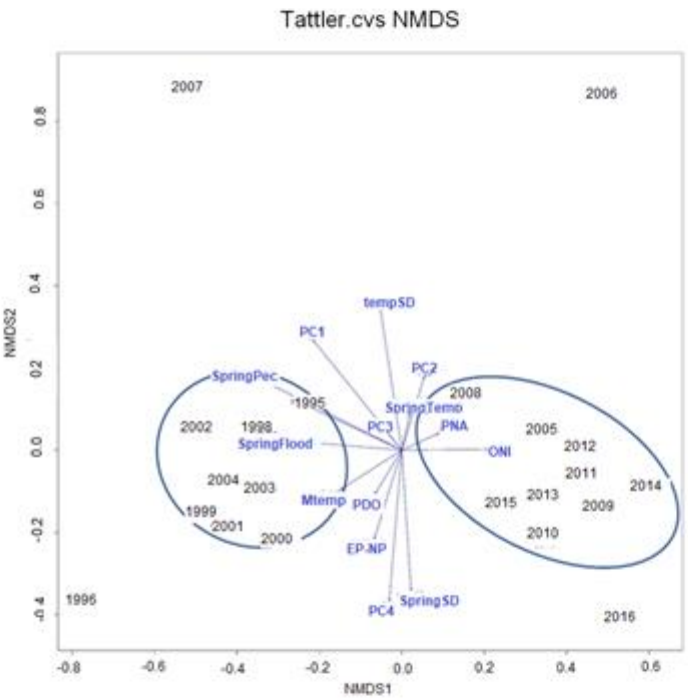
Tattler

(a)

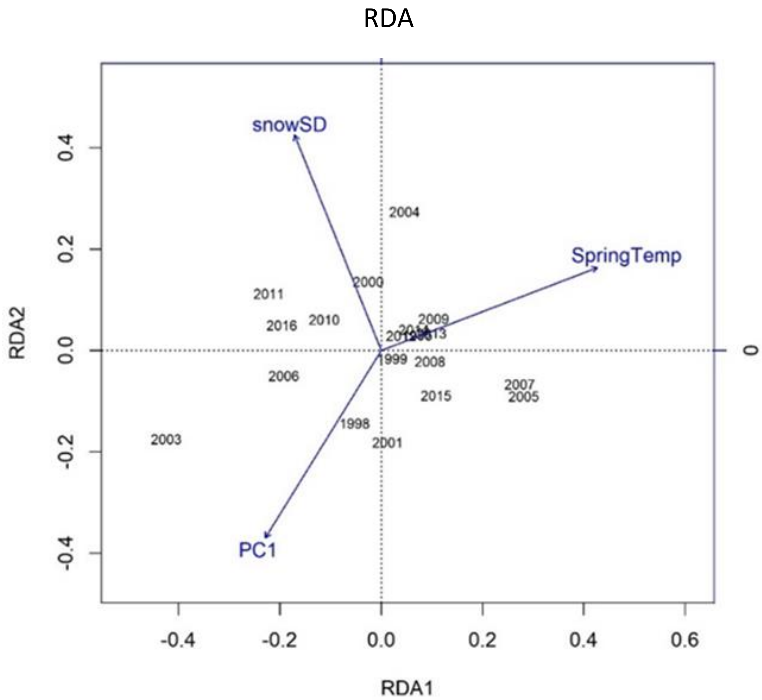
RDA



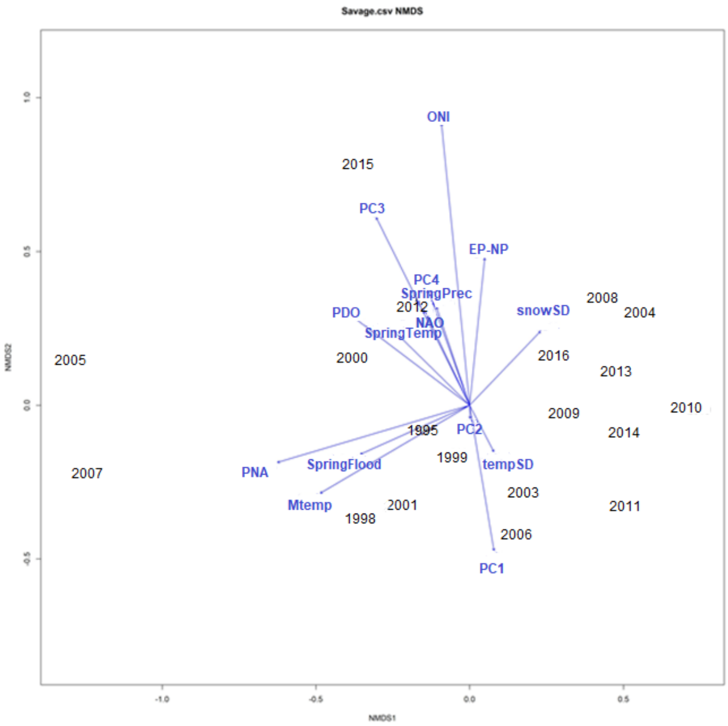
(b)


Tattler.cvs NMDS
NMDS2
NMDS1
2007
2006
1996
2016
tempSD
PC1
PC2
SpringPec
1995
2008
SpringTemp
PC3
PNA
2002
1998
2005
SpringFlood
2012
ONI
2011
2004
2003
2014
Mtemp
PDO
2015
2013
2009
1999
2001
2000
2010
EP-NP
SpringSD
PC4

Savage


RDA
(a)
snowSD
2004
SpringTemp
2000
2011
2010
2016
2009
1999
2008
2006
2007
2005
2015
1998
2003
2001
PC1
0
RDA2
RDA1

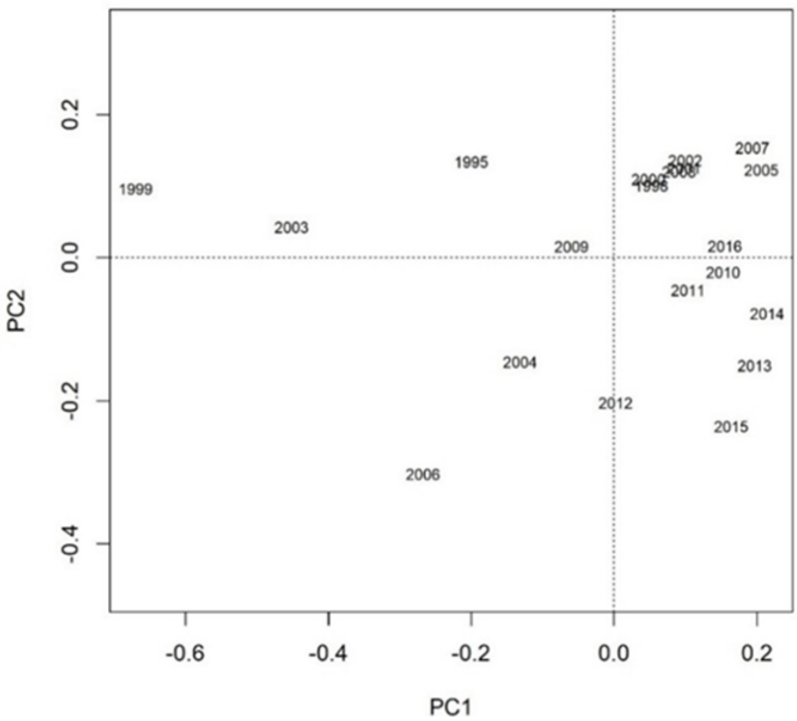
(b)



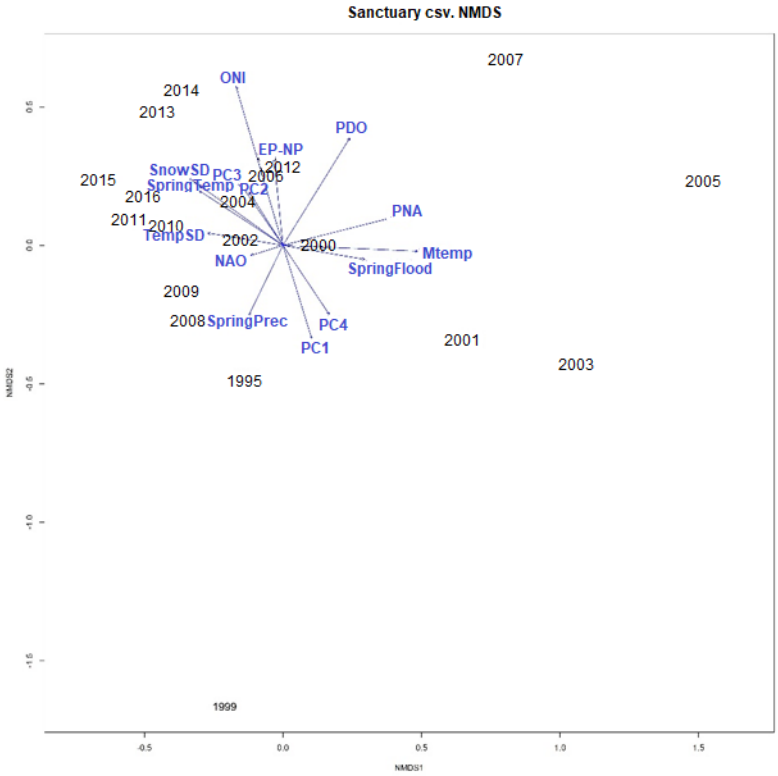
Sanctuary

RDA

(a)

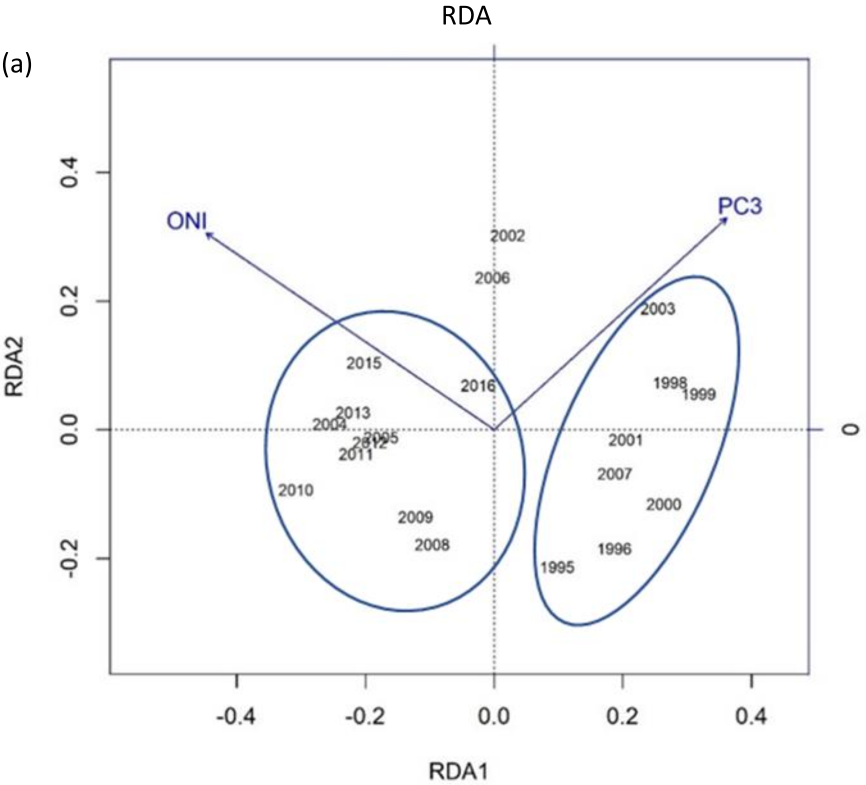


(b)

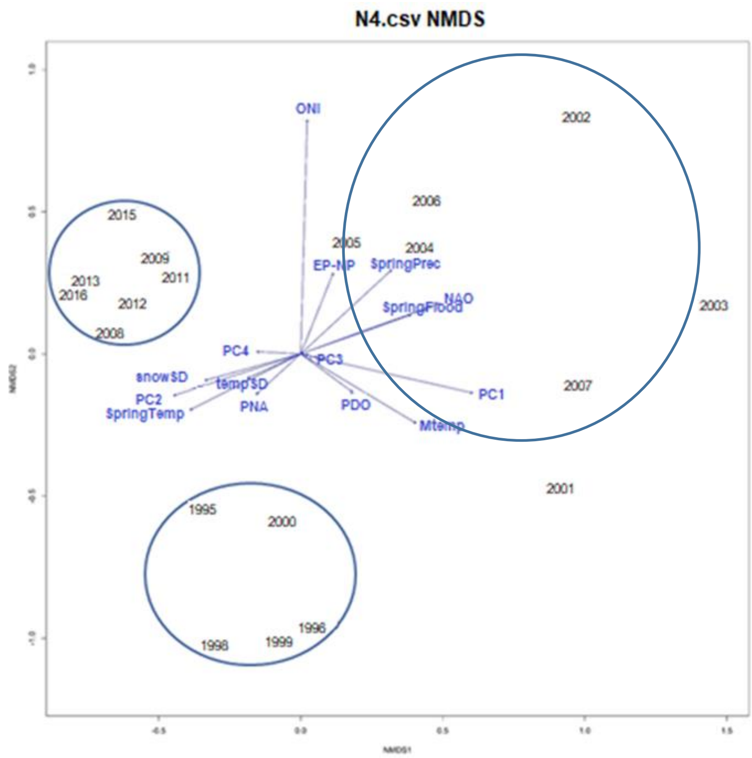

Sanctuary csv. NMDS
2007
ONI
2014
2013
PDO
EP-NP
2012
2015
SnowSD
PC3
2006
SpringTemp
PC2
2005
2016
2004
PNA
2011
2010
TempSD
2002
2000
Mtemp
NAO
SpringFlood
2009
2008
SpringPrec
PC4
PC1
2001
2003
1995
1999
NMDS1
NMDS2

N4

(a)


RDA
ONI
PC3
2002
2006
2003
2015
2016
1998
1999
2013
2004
2005
2012
2011
2001
2007
2010
2000
2009
2008
1996
1995
0
RDA1
RDA2

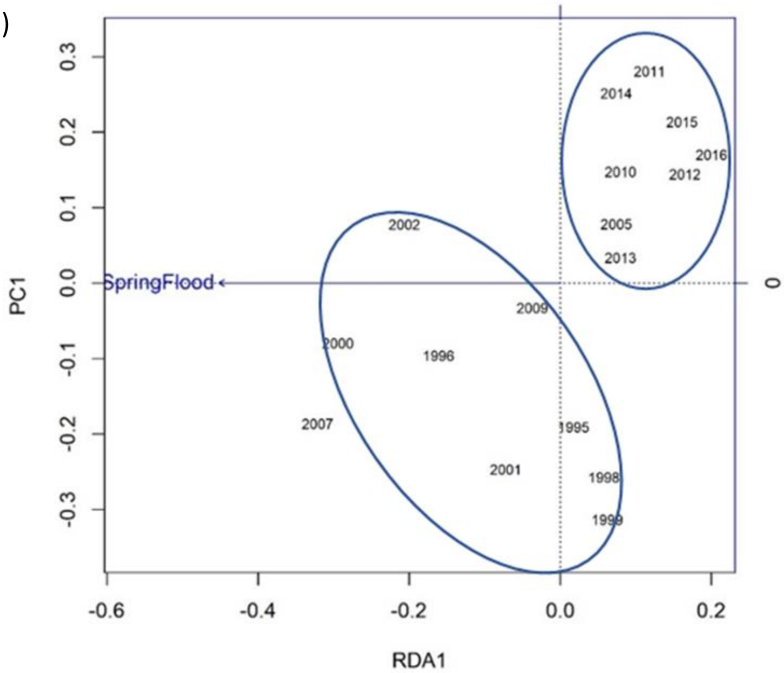
(b)


N4.csv NMDS
ONI
2002
2006
2005
2004
EP-NP
SpringPrec
NAO
SpringFlood
2003
2015
2009
2011
2013
2016
2012
2008
PC4
PC3
snowSD
tempSD
PC2
SpringTemp
PNA
PDO
PC1
Mtemp
2007
2001
1995
2000
1996
1998
1999

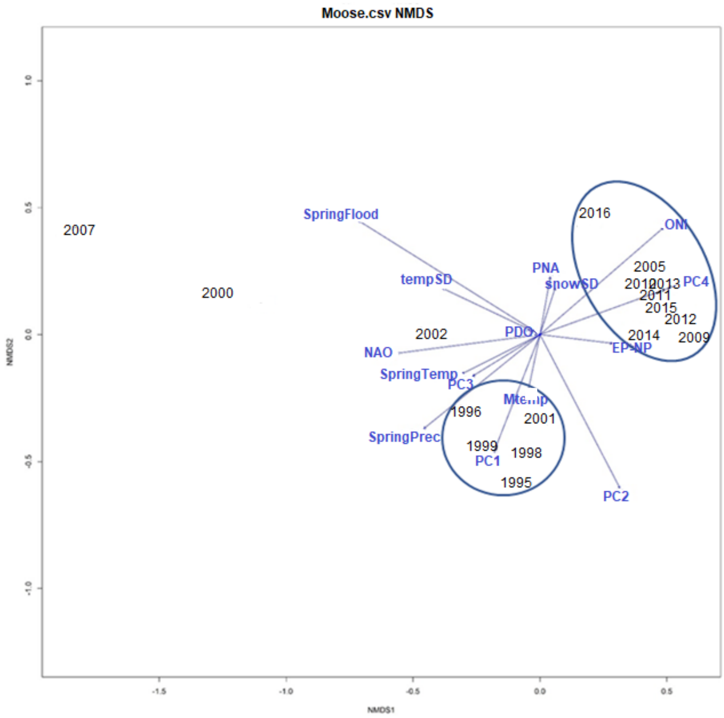
Moose

RDA

(a)


2011
2014
2015
2016
2010
2012
2005
2013
2002
SpringFlood
2009
2000
1996
2007
1995
2001
1998
1999
PC1
RDA1
0

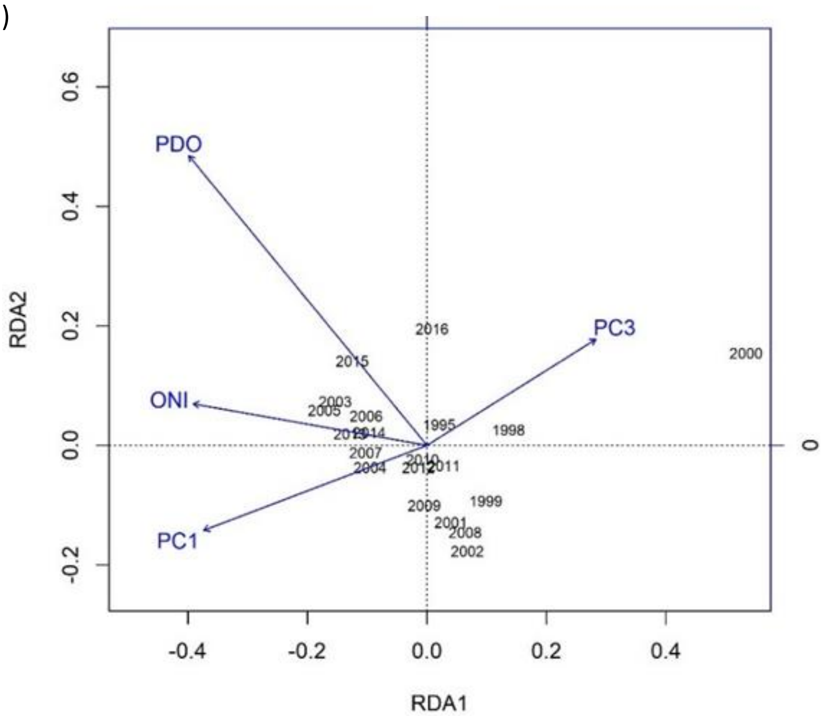
(b)



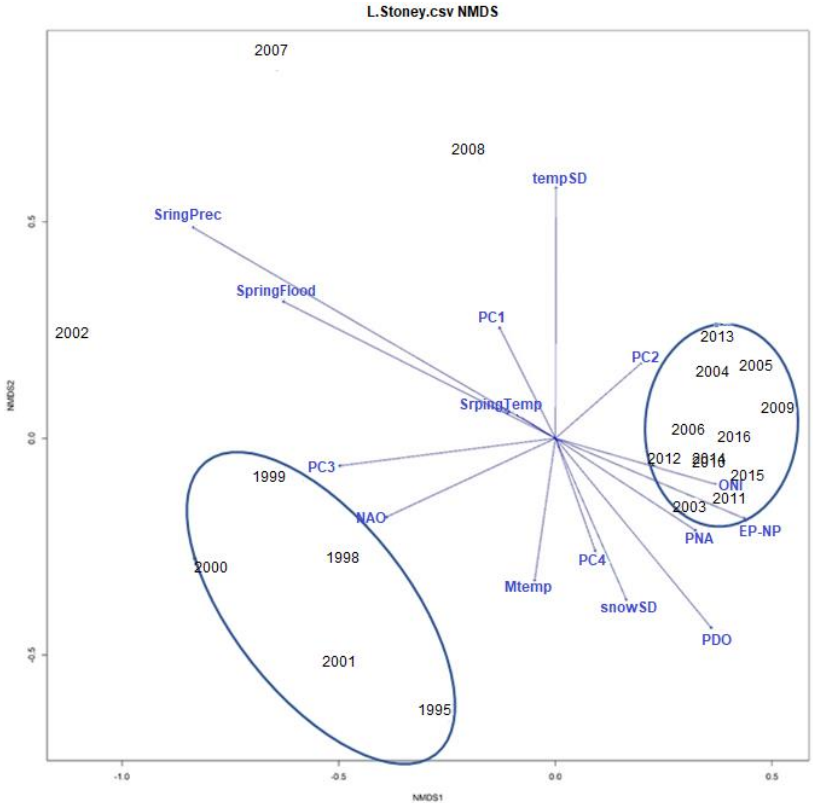
Little Stoney Creek

RDA

(a)



(b)

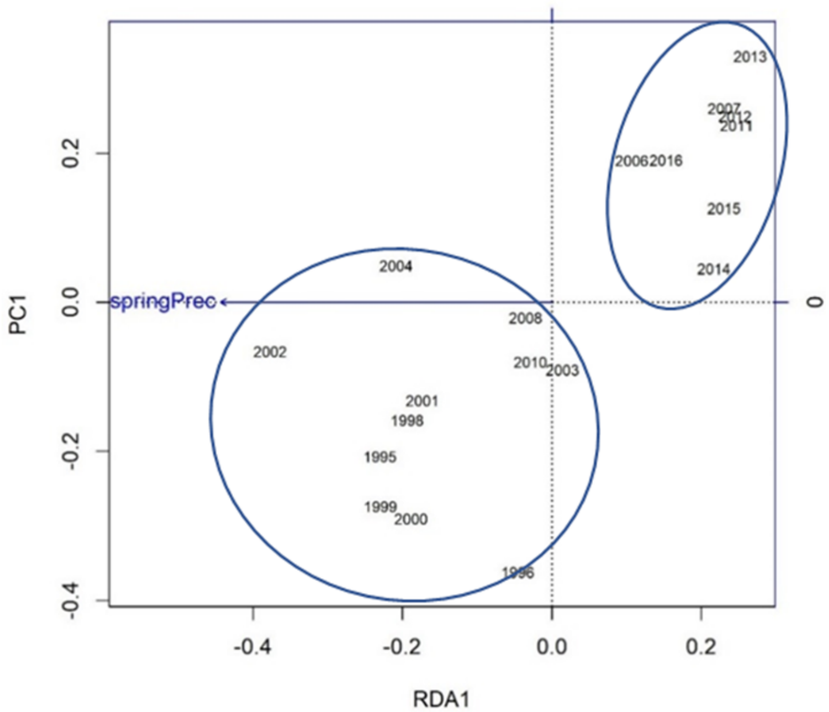


L.Stoney.csv NMDS
2007
2008
tempSD
SringPrec
SpringFlood
PC1
2002
PC2
2013
2004
2005
SrpingTemp
2009
2006
2016
2012
2015
PC3
ONI
1999
2011
NAO
2003
EP-NP
PNA
1998
PC4
2000
Mtemp
snowSD
PDO
2001
1995
NMDS1
NMDS2

Igloo

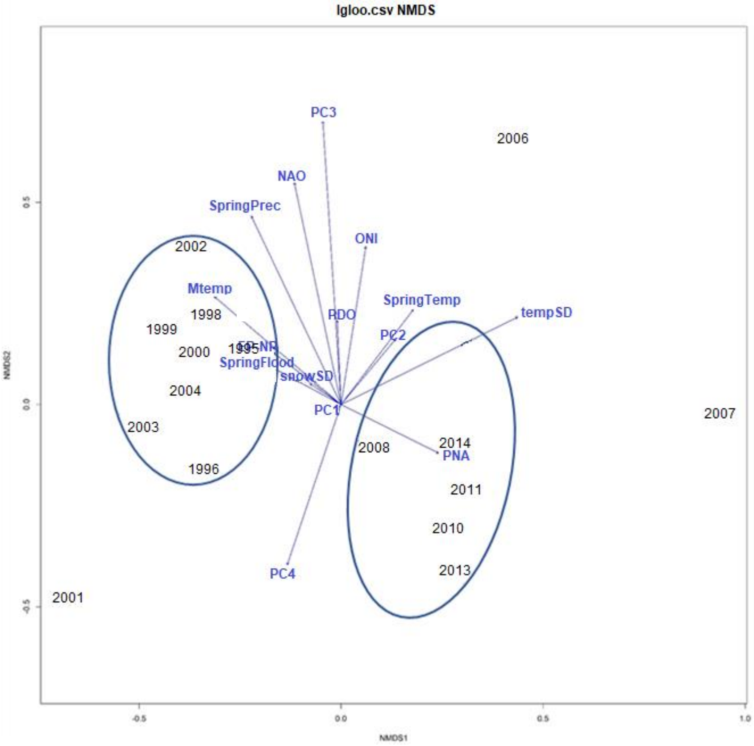
RDA

(a)



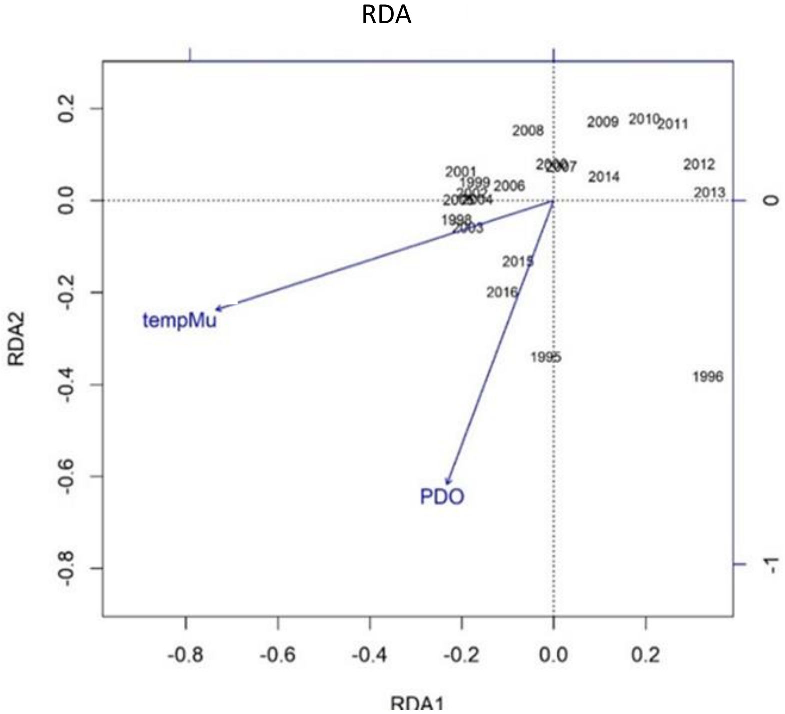
2013
2007
2012
2011
0.2
20062016
2015
2004
2014
0.0
springPrec
0
PC1
2008
2002
2010
2003
2001
1998
-0.2
1995
1999
2000
-0.4
-0.4
-0.2
0.0
0.2
RDA1

(b)

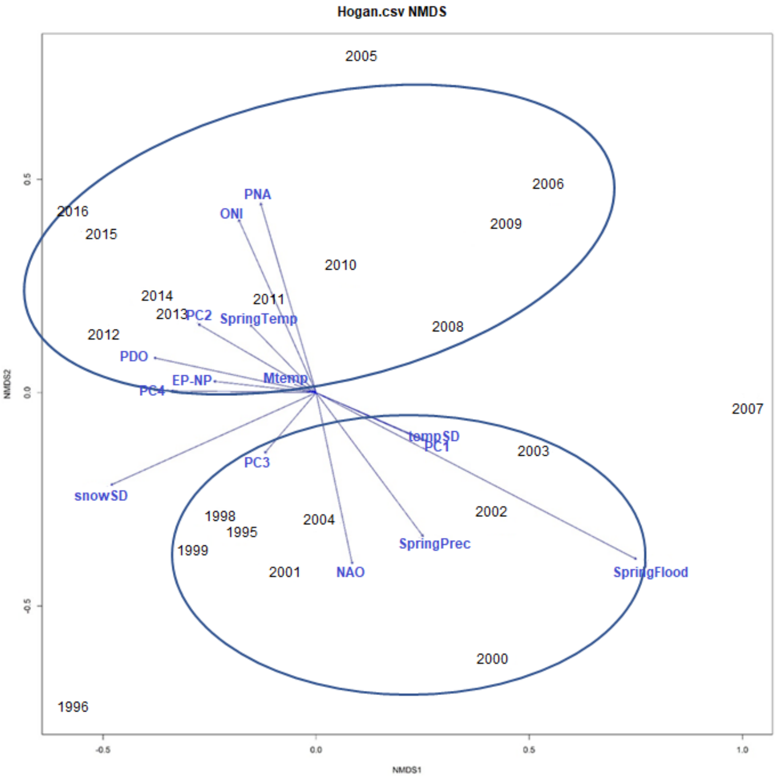

Igloo.csv NMDS
NMDS1
NMDS2
PC3
NAO
SpringPrec
ONI
Mtemp
RDO
SpringTemp
tempSD
PC2
SpringFlood
snowSD
PC1
PNA
PC4
2006
2002
1998
1999
2000
2004
2003
1996
2007
2014
2008
2011
2010
2013
2001

Hogan

(a)


RDA
RDA1
RDA2
tempMu
PDO
2008
2009
2010
2011
2012
2013
2014
2007
2001
1999
2006
2004
2003
2015
2016
1995
1996

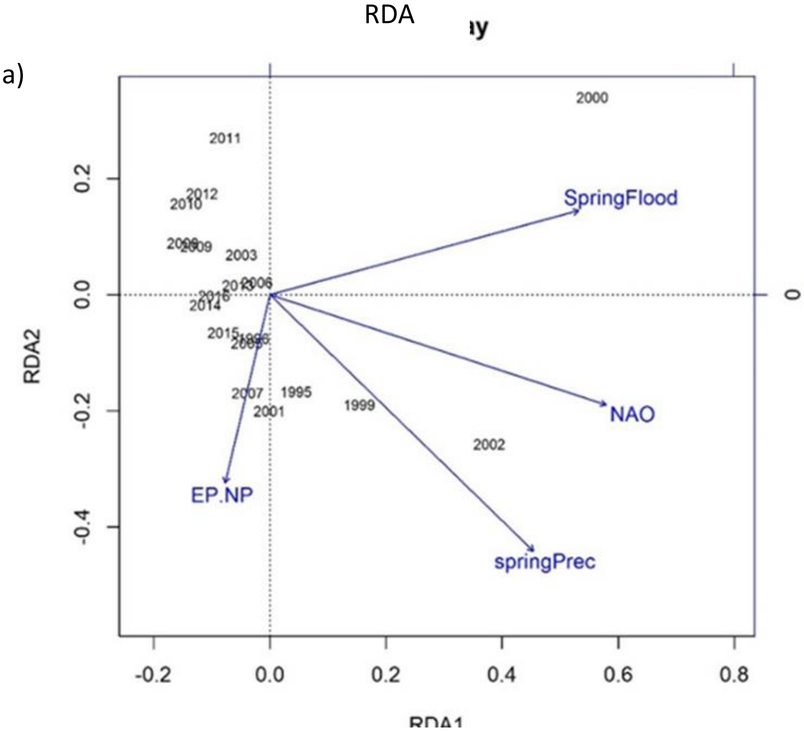
(b)



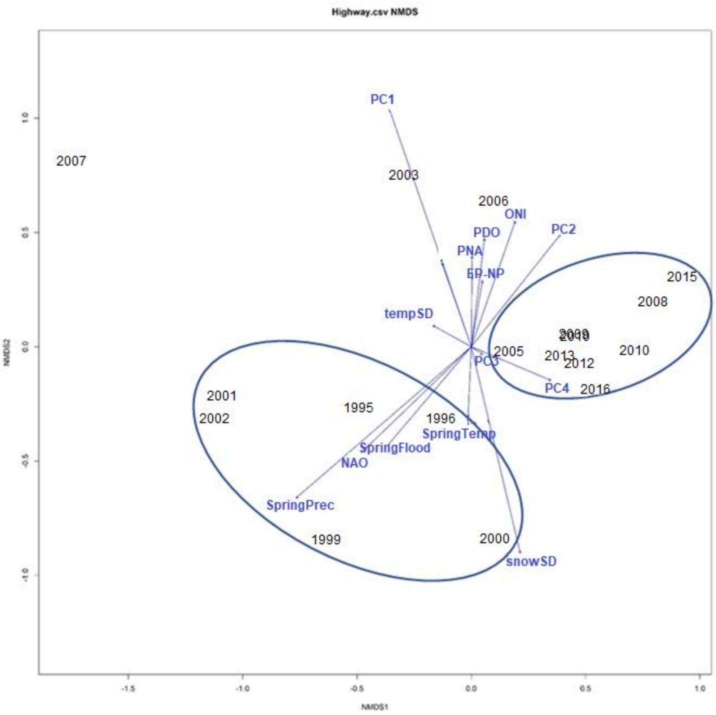
Highway

RDA

(a)



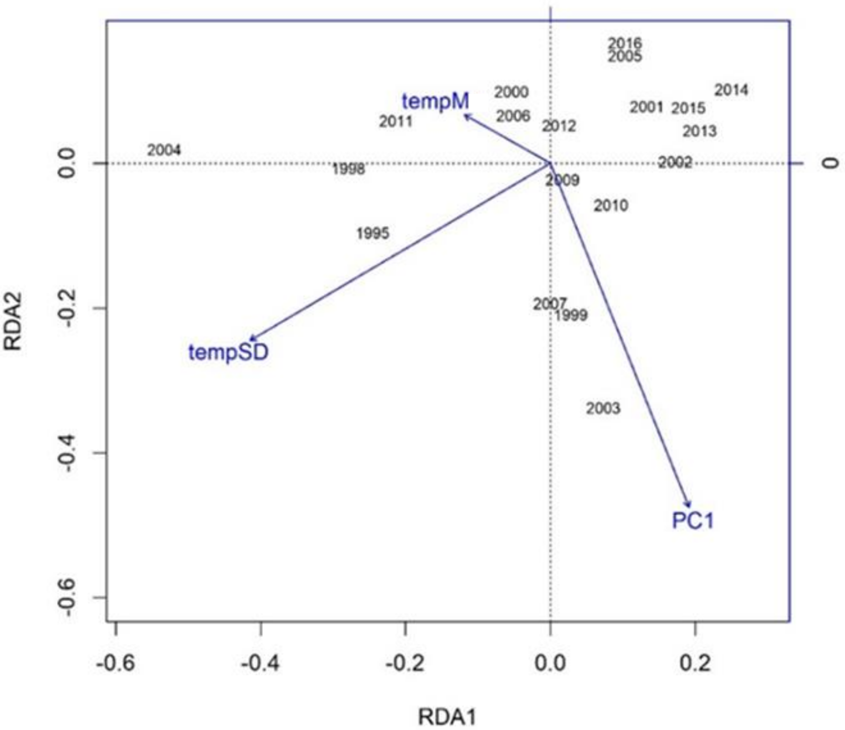
(b)



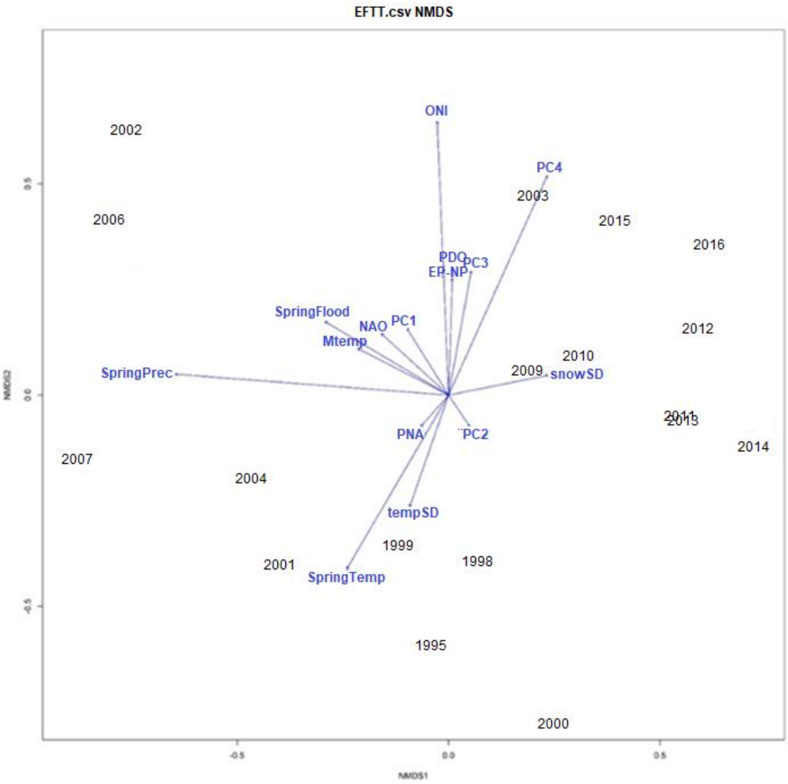
East Fork Tolkat Tributary

RDA

(a)



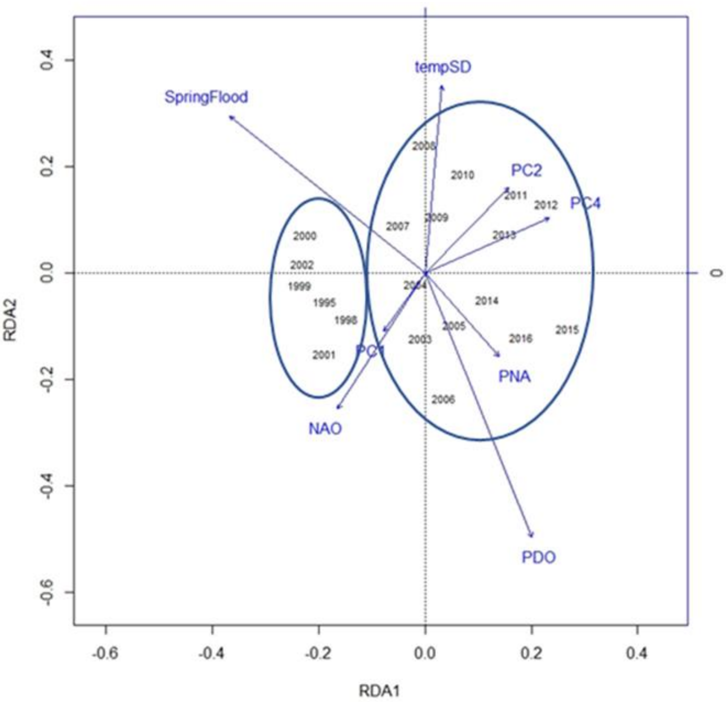
(b)



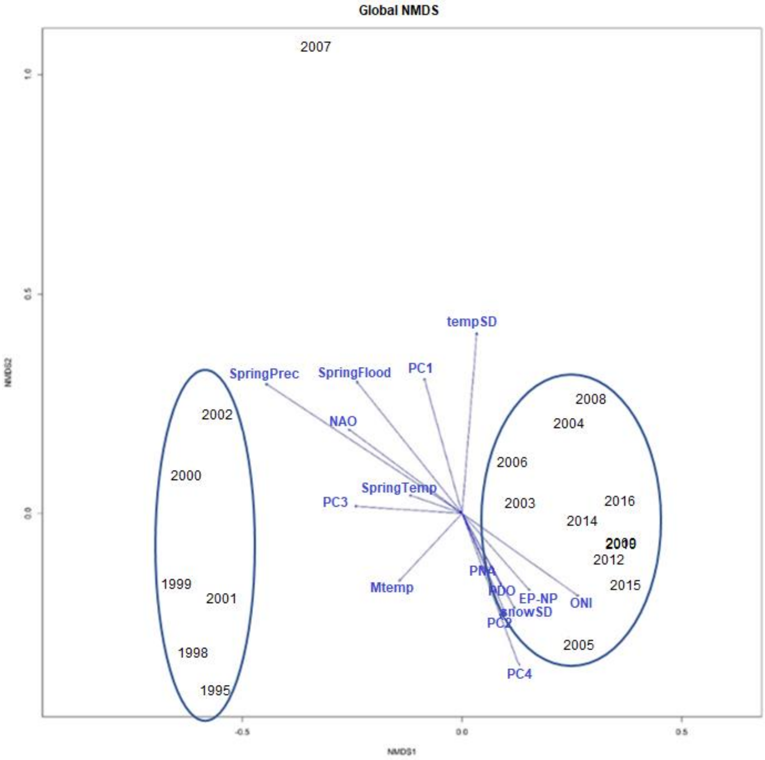
Global model of all streams

RDA

(a)



(b)


Global NMDS
2007
tempSD
SpringPrec
SpringFlood
PC1
NAO
SpringTemp
PC3
Mtemp
PNA
PDO
EP-NP
ONI
snowSD
PC2
PC4
2002
2000
1999
2001
1998
1995
2008
2004
2006
2003
2016
2014
2012
2015
2005
NMDS1
NMDS2
-0.5
0.0
0.5
1.0

7.3 Chapter 5

7.3.1 Apoendix 5.1: Annual mean and standard deviation per year.

Igloo	2008	2010	2011	2012	2013	2014	2015	2016
Mean	9.72	3.11	4.33	3.82	6.00	12.19	8.47	4.29
SD	17.1	2.65	3.85	2.88	7.36	13.3	8.449	3

Tatler	2008	2009	2010	2011	2012	2013	2014	2015	2016
Mean	24.18	3.76	1.17	1.91	10.27	4.44	18.20	4.55	15.54
SD	23.76	4.48	0.41	1.22	15.07	5.51	26.70	4.16	16.44

Hogan	2008	2009	2010	2011	2012	2013	2014	2015	2016
Mean	37.07	23.26	12.54	9.47	9.47	4.82	22.67	41.00	19.44
SD	35.61	36.91	20.54	8.20	15.48	6.40	37.36	41.10	28.30

EFTT	2009	2010	2011	2012	2013	2014	2015	2016
Mean	8.34	14.83	2.7	7.06	34.25	21.56	11.6	4.46
SD	7	14.01	1.89	6.70	58.59	19.96	13.79	3.41

7.3.2 Appendix 5.2: Annual mean and standard deviation per specie and year

	2008		2010		2011		2012		2013		2014		2015		2016	
Igloo	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Orthocladius s type	25.83	26.25	2.17	1.83	5.40	4.67	2.25	2.50	3.00	2.65	20.00	18.91	15.00	11.22	1.80	0.84
Diamesa spp	2.60	0.89	4.50	3.79	2.33	2.31	5.00	3.46			21.33	8.41	4.00	3.10	5.83	3.97
Eukiefferiella gremhi type	16.00	22.54	1.00		6.33	3.93	5.40	2.07	10.20	10.06	3.40	3.71	7.25	2.99	4.83	1.72
Corynoneura	3.20	1.64	2.00	1.41	1.00				2.00		1.00	0.00				
Limnophyes	1.83	1.17	4.00	2.92	1.67	1.15	1.33	0.58	4.40	5.94	3.00	1.00	1.00			

	2008		2009		2010		2011		2012		2013		2014		2015		2016	
Tatler	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Orthocladius s type	31.17	20.41	2.00	1.41	1.00		2.00	1.73	1.33	0.58	9.60	8.68	1.50	0.71	2.00		3.25	1.89
Orthocladius Eurothocladius	49.33	25.48	6.83	7.08													1.00	0.00
Diamesa spp	24.00	18.84	1.20	0.45	1.00		3.00	1.00	17.67	17.59	2.17	1.47	43.67	26.43	8.75	4.11	36.17	19.87
Eukiefferiella undiff.	3.20	1.10	2.25	1.50			1.00		1.50	0.71	2.00	1.41	1.00	0.00	1.33	0.58	9.00	4.38
Eukiefferiella gremhi type	6.80	9.09	4.75	3.30	1.25	0.50	1.25	0.50			3.00	2.00	1.33	0.58	3.00	1.73	14.50	7.64

	2008		2009		2010		2011		2012		2013		2014		2015		2016	
Hogan	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Orthocladius s type	33.67	44.76	6.33	3.44	1.25	0.50			2.00		1.40	0.55	1.33	0.58			3.50	5.00
Diamesa spp	42.50	43.21	14.17	6.18	9.33	7.23	4.60	1.34	6.00	2.37	12.20	8.04	56.17	48.28	67.50	30.55	43.33	35.17
Pseudokiefferiella	60.33	40.37	75.50	52.39	33.50	33.52	16.00	9.65	20.00	24.73	1.75	0.96	10.33	18.61	1.00	0.00	7.50	8.74
Eukiefferiella undiff	28.33	19.12	6.40	4.04	6.17	4.67	5.75	3.59	1.50	0.71	2.33	1.53	1.67	1.15	2.00		3.50	2.12
Hydrobaenus conformis type	20.50	19.20	5.00	3.92	1.00	0.00			1.00									

	2009		2010		2011		2012		2013		2014		2015		2016	
EFTT	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Orthocladius s type	12.33	6.53	26.67	17.41	1.50	0.71	9.33	7.20	96.00	32.27	14.50	7.82	7.33	8.52	3.20	1.30
Orthocladius Eurothocladius	6.67	4.50	1.00	0.00	3.83	2.71	2.00		65.00							
Diamesa spp	16.00	6.93	11.00	5.59	3.75	0.96	11.00	6.36	4.00	3.32	41.67	16.80	20.33	17.25	6.67	3.78
Eukiefferiella undiff.	3.80	3.11	18.00	12.28	1.67	0.58	1.00	0.00	6.00	6.69	1.00				1.00	0.00
Eukiefferiella gremhi type	2.17	2.40	2.00	0.00	1.60	0.89	2.00	1.41	6.50	2.65	2.33	1.53	2.67	1.53	1.53	

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