Long-term Impacts of Marine Derived Nitrogen on Forest Productivity

and Carbon Balance in Central Idaho

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Abstract

Wild anadromous fish such as Pacific Chinook salmon (*Oncorynchus tshawytscha*) and steelhead (*Oncorhyncus mykiss*) were once abundant in Idaho, where their carcasses, rich in marine-derived nutrients (MDN) provided a nitrogen subsidy to otherwise nutrient-poor riparian soils. This nutrient subsidy ceased in the early 20th century primarily due to dams that blocked fish passage. This study investigated the long-term cumulative effect of absence versus presence of MDN on the carbon balance of riparian forests along historically salmon-bearing streams in the North Fork Boise River watershed in Idaho.

The ecosystem process model BIOME-BGC was used to simulate a representative forest ecosystem and predict the impact of decades of addition compared to continuing absence of MDN on riparian forest net primary productivity (NPP) and net ecosystem production (NEP). The model was parameterized using local ecophysiology and site data and 23 years of site-adjusted local climate data on riparian forests where salmon have been extricated since 1904. Simulations were run for historic conditions with no MDN since 1904, and MDN added at a rate of 5.3 kgN/ha/year based on historical estimates. The no-MDN simulation predicted present-day forest measures of LAI (a proxy for NPP) and soil moisture across six study sites. Simulated experimental addition of marine-derived nitrogen to match continual salmon occupancy, led to increases in productivity (NPP) by 7-8% annually, C sequestration (NEP) increased by up to 47% annually, and the standing site C pool increased by 3%, or 4.4 tons C per kilometer of stream. The magnitude of these effects varied substantially with environmental conditions. When other limiting factors were least restricting, MDN had its greatest effects, particularly when soil moisture is high and temperatures are high enough for carbon uptake. With nearly 20,000 km of historic salmon bearing streams on varied terrain within the Columbia Basin, these results suggest that salmon had a large, but heterogeneous, impact on the regional vegetative carbon balance.

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Biome-BGC version 4.2 was provided by Peter Thornton at the National Center for Atmospheric Research (NCAR), and by the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana. NCAR is sponsored by the National Science Foundation.

Dedication

Dedicated to my patient and supportive friends and family and health practitioners, without whom I could not have completed this work. Thanks especially to Eric Stuen for providing insight and support and love. Great thanks to my parents for believing in me, cheering me, and giving me thoughtful questions about the work. Many thanks to my many wonderful friends, who gave me cheerleading, academic perspective, mentoring, and moral support, which was so important to my being able to persevere.

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Introduction to the thesis:

Wild anadromous fish such as Pacific Chinook salmon (*Oncorynchus tshawytscha*) and steelhead (*Oncorhyncus mykiss*) were once abundant in Idaho, where they spawned, died and deposited their nutrient-rich carcasses in the tributaries of the Columbia River. However, since the early 20th century construction of dams has eliminated fish runs from many streams in which they once spawned, cutting off this nutrient source for decades to a century (Murray 1964, Webster 1978, NWPCC 2004). Anadromous fish are thought be an integral part of the nutrient cycling processes in the riparian forests along streams in which they spawn and deposit their carcasses, transporting nutrients acquired in the ocean to inland ecosystems (Helfield and Naiman 2001, Kohler et al 2007). Most of the research conducted on the effects of marine derived nitrogen (MDN) has taken place in Alaskan and coastal Pacific Northwest ecosystems. However, 55% of historic fall Chinook salmon and summer steelhead and 39% of spring Chinook salmon in the Columbia River Basin historically spawned in Idaho, a much more arid and nutrient-limited region than coastal and Alaskan systems. The goal of this research is to determine the change in forest productivity and carbon balance associated with a loss of marine derived nitrogen in streams in riparian forests in the unique habitat of central Idaho, in the Columbia River Basin, and illustrate how that response varies under a range of temporal and spatial scales and environmental factors. The focal area is composed of six tributaries in the North Fork Boise River watershed.

Marine derived nitrogen is deposited on shore through carcass deposition by stream flooding, carcass deposition and nutrient secretion by bears and other consumers, and by hyporheic flow of dissolved nutrients in the stream (Ben-David et al. 1998). Today, less than 8% of marine-derived nutrients historically deposited by spawning salmon reach streams in the Pacific Northwest (Gresh et al. 2000). In nutrient-poor Idaho Batholith soils, such as those found in the North Fork Boise River in central Idaho, marine-derived nitrogen carried by anadromous fish was likely to be an especially important nutrient source, as central Idaho streams are nitrogen limited relative to coastal riparian forests of the Pacific Northwest (Henderson et al. 1978). Marine nutrient input from salmon increases productivity throughout the stream food

web (Wipfli et al, 2004), and so we also expect increased productivity in the terrestrial environment where salmon carcasses are deposited.

Various nutrient loss mitigation efforts are currently being tested and used, such as placement of salmon carcasses, salmon carcass "analog" pellets, and inorganic fertilizers into streams and riparian areas. Nutrient effects of the carcass and analog on forest nutrient cycling appear to be similar (Wipfli and Hudson, 2004). Inorganic fertilizer, however, may have different effects in forest nutrient cycling, as it does in stream ecosystems (Wipfli et al, 2004). However, inorganic nitrogen fertilization alone increases forest productivity, and anadromous fish are known to be a source of inorganic N to forests surrounding spawning streams (Ben-David et al. 1998, Koyama et al. 2005).

Several studies have addressed the short-term impacts of salmon nutrients on stream and riparian ecosystems in coastal and Alaskan systems (Ben-David et al. 1998, Kohler at al. 2007, Wipfli et al. 2004). None of these studies, however, have substantially addressed the long-term impacts on forest productivity, with the exception of Quinn et al (2018), who showed an increase in forest growth after a 20-year enrichment experiment.

It is difficult to directly measure directly the impact of many decades of salmon-derived nutrients on net primary productivity (Koyama et al., 2005) and difficult and expensive to monitor long-term effects, as in Quinn et al (2018). Ecosystem modeling using a process-based biogeochemical model such as Biome-BGC provides an accessible avenue for assessing the effects of MDN on a landscape scale and over many decades. Biome-BGC simulates carbon, nitrogen and water cycles on a daily time step, and its major inputs are daily climate data and ecophysiology parameters (see methods).

It is important to study the long-term effects of marine-derived nutrients on inland forests because the semi-arid ecosystems of the Rocky Mountains have very different nutrient and climate characteristics than the more mesic coastal areas, where much of the research on MDN has been conducted. A long-term view is important to help guide managers in designing mitigation and monitoring efforts for this region. A 100 year projection based on modeling decades of nutrient addition and absence will aid in developing the desired future outcomes by providing a range of potential forest

responses to various nutrient-loss mitigation treatments in the context of a changing climate, and can reveal important information about the future health of the forests if salmon nutrients remain absent from the system. Understanding the carbon balance of these forests with respect to marine derived nutrients may also become important as forests play a larger role in the expanding climate change mitigation market.

There are opportunities for future research that could continue from the work presented in this thesis, including predicting effects and interactions of nutrient-loss mitigation in the context of a changing climate and the addition of other nutrients carried by anadromous fish, such as the input of organic carbon. The continuing availability of marine derived nitrogen, for example, may prove to be crucial to forest carbon uptake capacity and productivity in the environment of increasing atmospheric CO_2. Carbon dioxide enrichment experiments show that nitrogen availability to trees is a key factor in forests' ability to assimilate increased atmospheric carbon (Finzi et al 2006, Magnani et al 2007, Zak et al 2000, Zak et al 2003), and that nitrogen uptake by trees increases with increased atmospheric CO_2 concentrations (Finzi et al 2006). Modeling experiments by Vetter et al. (2005) show that high-altitude European forests increased their biomass accumulation in response to increased atmospheric CO_2, and that increase was amplified with nitrogen addition in N-limited sites. This process may make salmon nitrogen or mitigation efforts even more crucial to the ongoing health and carbon uptake ability of central Idaho's riparian forests.

Anadromous fish provide more to an ecosystem than nitrogen alone. Large amounts of organic carbon are supplied, in addition phosphorus and micronutrients (Kohler et al, 2007). The availability of additional organic carbon may be significant for forest growth and carbon uptake if the increase in nitrogen use by the system requires an increase in use of organic carbon. Kohler et al. (2007) discuss Larkin and Slaney's (1997) findings that trophic productivity in streams may be dependent on even small input of carbon, so it may be important to consider the carbon subsidy provided by anadromous fish as well. Evaluating the effects of carbon inputs from anadromous fish is beyond the scope of this thesis, but could be a productive avenue of future research.

Statement of Overall Purpose:

The purpose of this study is to estimate via modeling the long-term effects of anadromous fish loss on the carbon dynamics of riparian forests in central Idaho. The tributaries of the North Fork Boise River (and many others) have not experienced anadromous fish runs for over a century. Modeling a forest's net ecosystem production (NEP) and total site C accumulation over many decades can simulate the cumulative effects of this nutrient loss. Experimental simulated MDN addition can indicate whether that loss is causing deterioration in the forest's ability to assimilate carbon and maintain a positive carbon balance. Model output analysis can also shed light on some of the mechanisms behind any differences in the system with and without a marine nutrient subsidy.

In order to study the effects of nutrient loss and mitigation efforts on this ecosystem, we must first determine whether the model can adequately simulate the riparian forests of the North Fork Boise River tributaries. This involves parameterizing the model using site physical parameters and species ecophysiology parameters measured at the site and taken from the literature, and running simulations using these parameterizations and local climate data. Several model outputs will be compared to field measurements for evaluation. Once model performance is evaluated, predictions for forest carbon balance in the presence and absence of salmon nutrients can be analyzed. The project's objectives are 1) To determine whether the ecosystem process model BIOME-BGC can reasonably simulate riparian forests of central Idaho, and 2) To determine through process modeling how the loss of anadromous fish nitrogen has affected carbon dynamics (particularly net primary productivity (NPP) and net ecosystem production (NEP) of riparian forests in central Idaho).

Chapter 1: Long-term Impacts of Marine Derived Nitrogen on Forest Productivity
    and Carbon Balance in Central Idaho

Part 1: Introduction

Wild anadromous fish are an integral part of nutrient cycling processes in their native
habitats. These impacts are complex and interconnected, with studies showing direct
and indirect impacts on aquatic food-webs and terrestrial soil and vegetation over a
range of spatial and limited temporal scales. In their annual spawning runs, anadromous
fish transport nutrients acquired in the ocean to their inland natal streams, where they
are then transferred to the terrestrial ecosystem through carcass deposition and
nutrient secretion by brown and black bears and other consumers, stream flooding, and
by hyporheic flow of dissolved nutrients in the stream (Gende et al. 2007, Ben-David et
al. 1998, Ashkenas et al. 2004). As carcasses decay, marine derived nitrogen (MDN) and
other nutrients enter the soil, and through microbial action, become available for use by
trees and other plants (Koyama et al 2005, Wheeler et al. 2014, Wheeler and Kavanagh
2017). The nutrient flux from anadromous fish increases productivity throughout the
stream food web (Wipfli et al 2004., Collins et al. 2016, Marcarelli et al. 2014, Collins and
Baxter 2014), as well as in the terrestrial environment where their carcasses are
deposited (Wheeler and Kavanagh 2017, Bilby et al. 2003, Cederholm et al. 1999).

Although most studies have focused on coastal watersheds, the impacts of fish
life cycles (migration, spawning, decomposition) on inland riparian systems have
received increased attention in recent years (Wheeler and Kavanagh 2017, Collins et al
2016, Marcarelli et al. 2014, Collins and Baxter 2014). However, aside from a recent 20-
year Alaska study by Quinn et al (2018), neither the coastal nor inland research address
the long-term impact on forest productivity (Kohler et al. 2007, Wipfli et al. 2004, Bilby
et al. 2003, Ben-David et al. 1998). This knowledge gap is significant, given that more
than 80% of the historic range of anadromous fish in the Pacific Northwest is within
inland ecosystems, and coastal research may not readily transfer to semi-arid inland
ecosystems, which have very different climatic and nutrient dynamics (Wheeler et al
2014). Anadromous fish were historically likely to be an important source of nutrients

to otherwise oligotrophic riparian ecosystems such as much of the inland Columbia Basin (Cederholm, et al, 1999). In nutrient-poor Idaho Batholith soils, such as those found in the North Fork Boise River in central Idaho, marine-derived nitrogen (MDN) carried by anadromous fish was likely to be an especially important nutrient source, as central Idaho ecosystems are nitrogen limited relative to coastal forests of the Pacific Northwest (Henderson et al. 1978, Moore et al 1991).

Pacific Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss)* were abundant in pre-industrial Idaho; 55% of the fall Chinook and summer steelhead, and 39% of the spring Chinook in the Columbia River originated in Idaho (Mallet 1974). Koyama et al (2005) confirmed historic anadromous fish nitrogen uptake in central Idaho riparian forests through stable isotope analysis. Estimates of predevelopment Columbia River salmon runs range from 7 to 16 million fish per year resulting in annual deposition of an estimated 2302-3087 kg N in the Columbia River Basin (NRC 1996, NPPC 1986, PFMC 1978, Chapman 1986, Gresh, et al. 2000). Our calculated estimates of MDN deposition ranged from 1.6 to 5.3 kgN ha^{-1} yr^{-1} historically deposited in the 20m riparian zone on either side of spawning habitat streams. These nitrogen deposition levels are consistent with other estimates for the region (Wheeler and Kavanagh 2017), and higher than recovery goals set in the draft recovery plan (NMFS 1995), which Peery et al. (2003) suggest falls short of nutrient requirements in the Snake River watershed. This subsidy, over the lifetime of the trees, roughly equates to the amount of nitrogen fertilizer used in a single application in commercial forest operations (Gende et al. 2007, Thomas et al. 1999). However, since the early 20th century, construction of dams has eliminated anadromous fish runs from many streams in which they once spawned, cutting off this nutrient source for decades (Murray 1964, Webster 1978, NWPCC 2004). Today, less than 8% of marine-derived nutrients historically deposited by spawning salmon reach streams in the Pacific Northwest (Gresh et al. 2000). Because of habitat blockage by dams, other habitat loss, and the fact that more than 80% of fish returning to Idaho originate in and return to hatcheries (ISG 1999), Idaho now sees approximately 1% of estimated predevelopment abundance (NRC 1996) of wild spawning salmon and steelhead. Many streams, including

the Boise River and its tributaries, have been completely blocked to anadromous fish runs.

Recent studies have examined the ecological effects of the historic anadromous fish nutrient subsidy and its subsequent loss in semi-arid inland riparian ecosystems such as exist in central Idaho. This study expands on results of these related three-year experiments conducted in the same region, which showed numerous impacts of MDN in central Idaho ecosystems. In these experiments, salmon and steelhead carcasses and analog pellets were distributed in tributaries of the North Fork Boise River that historically had anadromous fish spawning runs. Following these additions, resident fish, insects and bears consumed carcass material (Collins 2014), and treated streams saw increases in biomass of aquatic invertebrates and in annual production of trout (Collins et al 2016). Stream biofilms showed short-term increases in biomass with salmon carcass addition (Marcarelli et al 2014). Terrestrial soil nitrogen saw a 480-fold increase, and soil microbial activity increased significantly following carcass deposition: these soil responses to MDN were much greater in central Idaho than reported in coastal ecosystems in the Pacific Northwest (Wheeler and Kavanagh 2017).

Mature tree growth responses are difficult to measure in field experiments with small additions into a large pool of N over short time frames of several years, as the lifespan of trees in the region can reach upwards of hundreds of years. Additionally, a host of other limiting factors (such as precipitation, landscape features, and temperature) may cause greater annual fluctuations in growth than marine nitrogen, obscuring any change attributable to MDN (Kirchoff 2003, Helfield and Naiman 2003), and efforts to monitor long-term effects are both difficult and expensive. These limitations mean that the shorter-term studies (3 years or less) of MDN effects will be of limited use in understanding multi-decade patterns and processes on stand productivity and carbon dynamics. Such information on long-term productivity is essential for understanding forest responses, and therefore forest management directions.

Experiments conducted using an ecosystem biogeochemical model such as BIOME-BGC (Thornton 1998), could provide insight into the long-term effects of MDN on forest productivity and carbon fluxes. A modeling approach allows us to assess the estimated magnitude of the effect over a broad temporal and spatial scale, and to

understand important environmental limiting factors that affect timing and magnitude of a forest carbon response to MDN (See Boisvenue and Running 2010 for discussion of limiting environmental factors over time).

The objectives of this study are to evaluate a robust simulation of the productivity and carbon exchange in central Idaho riparian coniferous forests, and to use model experiments on that ecosystem to estimate the long-term changes in forest productivity and carbon exchange associated with the historical loss of marine derived nutrients. Simulations are then used to better elucidate the factors that limit and affect ecosystem response to MDN across the landscape.

Part 2: Methods

2.1 Study Area

The study area focused on six tributaries of the North Fork Boise River, in the Boise National Forest in central Idaho (Figure 1.1). These tributaries were historically anadromous-fish bearing streams that have not had spawning runs since the early 1900s. They are located in a semi-arid region set in mixed conifer forest, and have relatively nutrient-poor Batholith-derived soils. Central Idaho forests are nitrogen-limited relative to coastal forests in the Pacific Northwest (Henderson et al. 1978, Moore et al. 1991). Along each stream, a riparian zone surrounding a 500-meter reach along each tributary was selected. Reaches were selected to meet the requirements of the concurrent field studies on MDN ecological effects (Collins and Baxter 2014, Collins et al. 2016, Marcarelli et al. 2014, Wheeler and Kavanagh 2017), with consideration of presence of riparian forest, batholith geology, presence of bull trout , and historic salmon presence. Half of the stream reaches were at an elevation of approximately 1400m above sea level: Trail Creek, Hunter Creek and Beaver creek. The other three were at an elevation of approximately 1650m above sea level: Little Beaver Creek, Pike's Fork, and Banner Creek. Study area is described in detail in Marcarelli et al. (2014) and Wheeler and Kavanagh (2017).

The study area is characterized by a mixed conifer forest, with dominant species including Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*) (19%), ponderosa pine (*Pinus ponderosa*) (32%), and subalpine fir (*Abies lasiocarpa*). Conifer species distribution varies widely among the six sites (Table 3.2). Non-conifer trees are rare, although willow shrubs (*Salix* species) and alder (*Alnus sinuata*) occur in patches. Ground cover at the upper sites is 26% shrub, 55% grasses and forbs, and 19% bare ground or water. At the lower elevation sites, ground cover is 31% shrub, 55% grasses and forbs, and 19% bare ground or water.
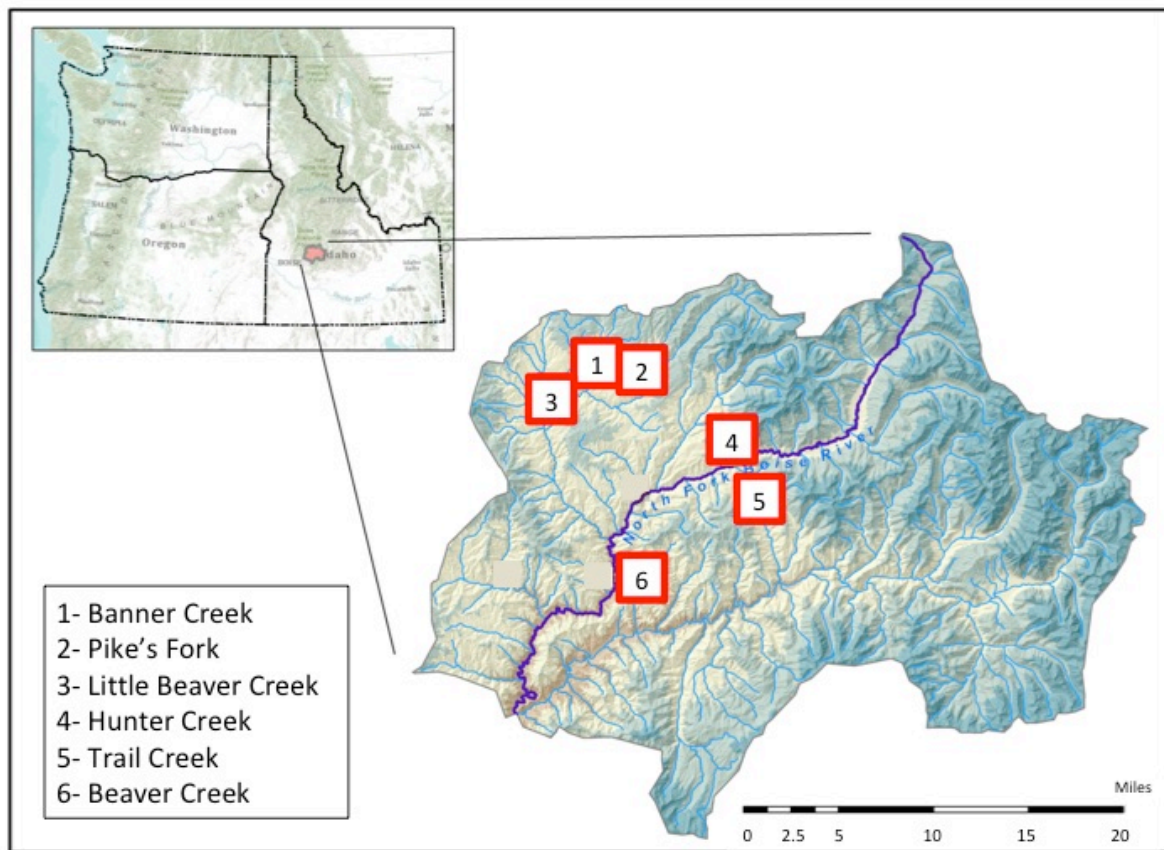
Figure 1.1 Map of the study area- North Fork Boise River watershed with six study stream locations highlighted in red.

2.2 Biome-BGC and simulations

Biome-BGC 4.2 (Thornton 2002, Running and Hunt 1993) is a well-tested ecosystem model (White et al. 2000) that incorporates knowledge of forest ecosystem processes and their responses to environmental differences and changes. The model simulates pools and fluxes of carbon, nitrogen, and water for a given biome (here, evergreen needle forest) over time, and partitions these components among living and nonliving, foliar and woody vegetation pools, litter and soil. Biome-BGC is driven by daily climate data and can be parameterized for each site with topography and ecophysiology (EPC) parameters that affect biological processes such as photosynthetic capacity (parameters such as leaf nitrogen, nitrogen in Rubsico), water use (maximum stomatal conductance,

canopy water interception), and carbon allocation (to new leaves vs. new roots, for example).

Each Biome-BGC simulation was comprised of two stages, the spinup stage in which a biome was "grown" to steady state conditions based on starting parameters and repetitions of the 23-year input climate record, and a second, simulation stage during which experiments can be conducted. In this study, the spinup stage represented preindustrial conditions when salmon were abundant, and included atmospheric deposition, biological N-fixation, and estimated levels of nitrogen from historic anadromous fish migrations. The pools of carbon, nitrogen and water developed in the spinup stage were the baseline for the two experimental simulations. We ran two simulations for each of the six sites to represent the century of tree growth following the eradication of fish migrations from the Boise River due to construction of dams, which began in 1906 with the construction of Barber dam. The first set of simulations ran each site to present-day with MDN removed, and serve as representations of recent historic and current forest conditions. The second set of simulations experimentally run each site to present day with MDN present at pre-development levels, to represent conditions that would have occurred without the eradication of anadromous fish nitrogen.

We evaluated model performance on these historical re-creation simulations by comparing model output from the locally parameterized Biome-BGC simulations with leaf area index (LAI) and soil volumetric water content (VWC) measured at each study site. We chose these parameters for assessment because LAI is a measurable proxy for productivity on which many model processes are based, and soil water is a major environmental control on productivity. We then compared daily and annual output from the historical and MDN scenarios to determine the magnitude of difference in net primary productivity (NPP) and net ecosystem production (NEP) between the two sets of simulations, and to describe the environmental patterns and driving factors behind those differences.

2.3 Data collection for Biome-BGC input and evaluation

2.3.1 Climate data

A twenty three year climate record was created for each of the six study sites. We contend that this record was long enough to capture inter-annual variation, because it included relatively dry and wet years (precipitation as low as 521mm and 767mm per year at lower and upper elevation sites, respectively, and as high as 1267mm and 1943mm per year at upper at lower elevation sites, respectively) as well as a range of temperature extremes Table 2.1). Two SNOTEL weather stations (NRCS) nearest the study sites provided baseline maximum daily temperature (T_{max}), minimum daily temperature (T_{min}), and precipitation values. Mores Creek Summit station provided baseline data for the higher elevation sites (Little Beaver Creek, Banner Creek, and Pike's Fork), and Graham Guard station for the lower sites (Trail Creek, Hunter Creek, and Beaver Creek). All study sites were located within 25 km of a SNOTEL station. At each of the six study reaches, we recorded over two years of T_{max}, T_{min}, and relative humidity (RH) data with Hobo Pro® relative humidity and temperature sensors (Onset Computer Corporation, Pocasset, MA), shielded from sunlight with vented PVC shelters. To reflect the seasonal temperature variations seen at each site in a longer climate record, measured site-specific T_{max} and T_{min} were regressed with lags against SNOTEL temperature records, and the relationships found in the regressions were applied to SNOTEL temperature data. This created six 23-year temperature records that better reflect seasonal patterns at each site (Table 2.1 and Appendix A, Figure A.2). Average daily temperature data are in Appendix A. Precipitation at the upper and lower study sites is assumed to be the same as precipitation measured at Mores Creek Summit and Graham Guard SNOTEL stations, respectively. All other weather data required by Biome-BGC (Vapor pressure deficit, incoming solar radiation, average daytime temperature, and day length) were simulated for each site based on the above climate data and site parameters such as horizon angles and aspect using the MTCLIM model (Running and Coughlan 1988, Kimball et al. 1997, Thornton and Running 1999).

We created a century of climate input data by repeating the 23-year site-adjusted SNOTEL records. Atmospheric carbon dioxide levels, however, increased to align with

the growth in global emissions, using the default levels included in Biome-BGC (default values run from 1930 through 2001, and the trend was extrapolated to create a complete record for our simulations.)

		T_{max}		T_{min}		Precipitation (mm)	
Upper sites	Little Beaver	14.4	(1.0)	-6.9	(0.9)		
	Banner	15.6	(1.0)	-6.9	(0.9)	1146	(239)
	Pike's Fork	15.0	(1.0)	-6.7	(0.9)		
Lower sites	Trail	14.9	(1.1)	-3.6	(1.2)		
	Hunter	13.8	(1.1)	-3.8	(1.2)	773	(172)
	Beaver	15.3	(1.2)	-2.8	(1.1)		

Table 2.1. Average daily maximum and minimum temperatures (T_{max} and T_{min}), and average total annual precipitation (mm) at upper elevation and lower elevation sites. Standard deviation among years in parentheses.

2.3.2 Stand data and site physical parameters

Biome-BGC simulates canopy processes on a leaf area basis; consequently, species distribution was calculated based on percentage of total leaf area index composed of each species. This species distribution was used to create a weighted average of each ecophysiology parameter for each site. Tree species distribution and leaf area were collected from 10-m radius circular plots located on alternating sides of the study stream every 75 m, centered 5 and 20 meters distance from stream center. Where potential plots were completely out of the riparian zone (i.e. on the steep adjacent hillslope), no plot was placed, resulting in 9 to 11 plots at each stream. Species, crown depth (distance from top to bottom of live crown), and total height were recorded for each tree (1,447 trees). A subsample of trees in each plot, consisting of each species and diameter class (± about 4 cm), were cored for age, sapwood depth, and bark thickness (Table A.1, Appendix A). These data yielded leaf area for each measured tree based on known allometric relationships using measured sapwood area (Waring and Running, 2007). Sapwood area values for cored trees were assigned to other trees of the same species that were within the same diameter class within each plot. For each plot, total leaf area was divided by ground area of the plot to compute LAI for each plot. Average LAI was calculated for each site, to be used in evaluating model performance.

We recorded slope and aspect of each study reach, and from the center of each reach we recorded the angles of east and west horizons. Site latitude, longitude and elevation were recorded by GPS.

2.3.3 Ecophysiology data

Ecophysiology parameters influence ecosystem response to nutrient levels and climate. We customized the ecophysiology parameters to best represent the species composition at each site, with each parameter weighted by the percent leaf area comprised of each species for each study reach (Table 3.2). Net primary productivity output from Biome-BGC is most sensitive to six of the 43 ecophysiology parameters required by the model (White, et al. 2000). However, of these six, only four were practical to measure (Table 2.2). Remaining parameters were derived from the literature. White et al. (2000) contains a large survey of literature reporting measured values for the ecophysiology parameters. We used the subset of values reported in White et al. (2000) reported for each of our sites' species when available. If no values were reported for a given species, we then used the average for the genus, and for all other values we used the evergreen needle forest (ENF) default values, which were also derived from White et al. (2000). If species-specific data included multiple sources across a variety of landscapes, we chose the values from systems most like our study sites, and removed studies focusing only on seedlings in a greenhouse setting.

Parameter	Units	Source	Effect
$C:N_{leaf}$	kg C kg N^{-1}	Measured	Limits photosynthesis; increased $C:N_{leaf}$ decreases NPP
PLNR		Literature	Limits maximum rate of carboxylation; increasing PLNR increases NPP
$C:N_{fr}$	kg C kg N^{-1}	Measured	Increasing $C:N_{fr}$ makes more N available to leaves; increasing NPP
FRC:LC	kg C kg C^{-1}	Literature	Increasing FRC:LC decreases NPP
SLA	m^2 kg C^{-1}	Measured	Increasing SLA increases LAI without increasing photosynthetic capacity, thus increasing water stress and decreasing NPP
g_{smax}	m s^{-1}	Measured	Increasing g_{smax} increases water stress, thus reducing NPP

Table 2.2. Important BIOME-BGC parameters based on sensitivity analysis by White, et al (2000). $C:N_{leaf}$ is leaf carbon to nitrogen ratio; PLNR is percent leaf nitrogen in Rubisco; $C:N_{fr}$ is fine root carbon to nitrogen ratio; FRC:LC is new fine root carbon to new leaf carbon allocation; SLA is specific leaf area; and g_{smax} is maximum stomatal conductance.

Maximum stomatal conductance (g_{smax}) was calculated at one upper elevation site (Pike's) and one lower elevation site (Trail). Stomatal conductance was measured on cloudless days in late June of 2010, when environmental factors were least limiting (moist soil, peak solar radiation). Pre-dawn and midday leaf water potential measurements were made with a pressure chamber (PMS Instrument Company, Corvallis, OR) and adjusted for nocturnal conductance (Hubbart et al 2007, Kavanagh et al 2007). We selected eight and ten trees at Pike's and Trail, respectively, to include both elevation groups and all species, and collected foliage approximately hourly for each tree between the hours of 8:00 and 11:00 am. Leaf-level stomatal conductance (g_s) and transpiration were measured with a Li-Cor LI-1600 immediately after collection by pole-pruner. Average g_{smax} was calculated for each species.

Predawn leaf water potentials were measured using a pressure chamber at Pike's Fork, representing the upper sites, and Trail Creek, representing the lower sites, on five dates between June and November of 2010, and adjusted by height of sample to estimate soil water potential. However, for the evaluation of Biome-BGC simulations, this data was not included, as Biome-BGC more accurately simulates VWC than psi. See Appendix A for soil water potential results.

Foliage and fine root parameters

Foliage (52 trees) and fine root (49 trees) samples were collected across all sites, and processed to measure C:Nleaf, C:Nroot, and specific leaf area (SLA). Foliage on branchlets was sampled by pole pruner and shotgun, and fine roots (those with a diameter of less than 3mm, McLaugherty et al. 1982 and Stump and Binkley 1993) were dug by hand from the top 30 cm of soil after following a root from the bole so we could be sure to match roots to individual trees. Foliage was sampled from midway through the canopy depth to best represent average canopy parameter values, (Duursma 2005). Samples were placed in plastic zip bags and stored on ice, and analyzed or frozen within 3 days of collection.

Biome-BGC requires SLA on a basis of leaf area per mass of carbon ($m^2\ kg\ C^{-1}$): therefore, SLA was calculated by dividing projected leaf area (PLA) by the mass of carbon in the measured leaf (White et al 2000). PLA for Douglas-fir, subalpine fir and

Engelmann spruce was measured with a desktop scanner and analyzed using ImageJ version 1.47 (National Institutes of Health, USA). PLA for lodgepole pine and ponderosa pine were measured using digital calipers. Foliage samples were then dried at 60-70°C for 48 hours and dry mass weighed on a microbalance. Mass of carbon of the PLA samples was determined using dry weight of leaves and percent carbon measured with a Finnegan MAT Delta Plus isotope ratio mass spectrometer (Finnegan MAT Gmbh, Germany) at the Idaho Stable Isotopes Laboratory, Moscow, ID. $C:N_{leaf}$ and $C:N_{fr}$ were calculated from dry mass and carbon and nitrogen percentages of leaves and fine roots analyzed.

Soil parameters

We dug a soil pit at each site to measure soil depth (depth to water table or rock) and collect samples to measure percent sand, silt and clay. At each site, a soil sample was collected across the full depth of the soil pit and we estimated percent sand, silt and clay by mixing each sample with water, measuring settled layers, and calculating volume of each component. Biome-BGC calls for effective soil depth, with rock fraction removed. Starting soil depth was measured to water table or rock at each study site. Photographs were taken of the vertical profile at each soil pit with a measuring tape, and large rock fraction was estimated using ImageJ software. Soil samples from the entire vertical profile were collected and sieved with a 2mm screen. Small rock fraction (>2mm) was estimated as a portion of the collected sample, and added to the visible large rock fraction. Remaining soil <2mm comprised the effective rooting portion of soil, and measured depth was reduced to the same percentage to develop effective soil depth for each site.

Soil volumetric water content was measured at each stream at depths of 1, 3, 8, and averaged over 10-30 cm, using Decagon em5b loggers with EC-10 and EC-20 soil moisture sensors. Sensors were calibrated in the lab using site soil samples (Wheeler 2014 and direct communication).

Stomatal closure response to nighttime temperature minimums

Biome-BGC's model structure includes several controls on the start and completion of stomatal closure in response to environmental conditions, including stomatal closure response to the minimum daily temperature the night before a given day's photosynthesis. Default values for the start and completion of reduction in stomatal conductance are 0°C and -8°C, respectively. In preliminary simulations, some of the upper elevation sites failed to spinup to steady state conditions, indicating ecosystem failure due to some limiting factor, likely the fact that these sites saw, on average, only 67 days a year (s.d. 17) with T_{min} above 0°C. Smith et al (1984) reported that among six subalpine conifers (three of which were also present at our study sites) complete stomatal closure occurred at a T_{min} as low as -20°C. Because -20°C was the extreme case, we averaged this value with the default in Biome-BGC for complete closure, resulting in a new T_{min} for complete reduction at -14°C, with start of conductance reduction at -2°C. These changes were made in the canopy evapotranspiration module of Biome-BGC. Zheng et al (2002) similarly changed the lower threshold for stomatal closure with T_{min} in a process-based model. The number of days at the upper sites with T_{min} above -14°C was 312 days (s.d. 15).

2.4 Estimate of historical MDN deposition and other N sources

Estimates of MDN deposited in pre-development history rely on a variety of historical estimates, including historical habitat area, numbers of fish in annual spawning runs, and amount of nitrogen in each carcass (Table 2.3). To see the clearest signal from MDN in our simulations, we chose the upper end of range estimates for several components of our estimation of MDN influx (spawning run sizes and fraction of run transported on shore by bears). However, this estimate may still be somewhat conservative because it does not include all pathways for MDN to reach the terrestrial environment (e.g. consumption by invertebrates that move nutrients ashore, and nutrients moved by water though hyporheic flow and flooding).

Estimates of MDN deposition per-area of riparian zone are calculated as follows,

$$MDN \ Deposition = \frac{Run * Transport * Nitrogen}{Stream * 2 * Riparian \ width}$$

where Run is the average annual population of spawning run fish, Transport is the fraction of the run transported on shore by bears, Nitrogen is average nitrogen content per carcass, Stream is length of historic stream habitat available to anadromous fish, and Riparian width is the estimated width of riparian zone from stream edge to upslope transition (Table 2.3). Values and sources are listed in Table 2.3 and described below.

The smallest geographical region for which we found estimates of historical length of spawning stream and estimates of historical run size was the area above the Hells Canyon Dam on the Snake River (Chandler 2001). The North Fork Boise River is a tributary of the Snake, which then feeds into the Columbia River, and into the Pacific Ocean. Chandler's estimates are based on peak catch, estimated harvest rates, freshwater habitat for the Columbia River, and estimates of the Snake River component of Columbia basin. Our run size estimates included Chandler's upper end estimate of spring and summer Chinook and steelhead, which spawn in higher order tributaries, and excluded primarily main-stem spawning fall Chinook (NRC 1996). The study streams are within historical spawning habitat area (Chandler 2001).

The width of riparian zone for terrestrial MDN deposition was defined as 20m from the stream on either side, because this distance is well within the reported range that captures the majority of salmon derived N, as determined in observational and stable isotope studies (Ben-David et al. 1998, Gende et al. 2007, Quinn et al. 2009, Helfield and Naiman 2001, Koyama et al. 2005), and it captures most of the riparian area/floodplain of our study streams. When siting plots on lines perpendicular to the stream at 5 and 20 m from the stream, 59 out of 72 possible plot centers (82%) were located within the floodplain/riparian zone, which was clearly defined from the surrounding terrain that sloped abruptly and had much less ground cover vegetation.

Percentage of the run transferred to shore is typically measured by bear activity. We chose the upper end of the range (38% of carcasses transferred to shore by bears) presented in Quinn et al 2009, though up to 63% of an entire run has been reported transferred to terrestrial riparian area by 3-8 black bears (*Ursus americanus*) in a British

Columbia stream (Reimchen 1994). We did not account for N movement from the stream to the terrestrial environment through mechanisms including flooding, hyporheic flow, and emergence of invertebrates that fed on carcass material. However, Collins (2014) describes the effects of salmon carcasses on increasing insect emergence (primarily raising numbers of flies near carcasses and across the landscape), and Ashkenas (2004) quantifies some of the additional pathways of nutrient transfer.

Average nitrogen content of spawned Chinook salmon and steelhead carcasses was measured at 164 gN per carcass (Wheeler and Kavanagh 2017). We assumed all N from carcasses removed from the stream transfers into the riparian ecosystem, which created a high end estimate of amount of N reaching the riparian environment. Realistically, some N is lost to volatilization and other processes during decomposition, as well as leave the riparian area via consumers, but much of the nitrogen removed from the immediate vicinity of the carcass, such as a significant portion by fly larva consuming carcass material (Collins 2014, Wheeler et al. 2014) and migrating away from the carcass, will remain in the ecosystem.

We estimate up to 5.3 kg MDN ha-1 yr-1 was historically deposited in the riparian areas of our study streams, and chose to use this upper end of estimated deposition to most clearly isolate effects of MDN.

Nitrogen was also added to the modeled ecosystem through atmospheric deposition and biological nitrogen fixation. Biological N fixation was assumed the same in modern and pre-development times at 2 kg N ha^{-1} yr^{-1} (default Biome-BGC values). Preindustrial atmospheric wet and dry atmospheric deposition was estimated at 1 kg N ha^{-1} yr^{-1} (model default) and modern atmospheric deposition was estimated at 2 kg N ha^{-1} yr^{-1} (USDA 2012, NADP 2014, Galloway 2008, Jurgenson et al 1990). Values for all mechanisms of N deposition used in Biome-BGC simulations are summarized in Table 2.4.

Component	Value	Sources
Length of historic stream habitat	6714 km	Chandler 2001
Width of riparian MDN deposition area each side of stream	20 m	Typical riparian zone width in NFBR watershed, consistent with literature for width seeing majority of salmon deposition, primarily by bears (Koyama et al 2005, Ben-David et al 1998, Gende et al 2007, Helfield and Naiman 2001)
Run size of tributary spawning fish (# of fish)	1146350	Chandler 2001, excluding species that spawn primarily in main stem, upper end of range
Fraction of salmon transported ashore by bears	0.38	Quinn et al 2009, upper end of range
Total N per fish carcass	164 g	Wheeler and Kavanagh 2017
Riparian MDN deposition Estimate $(kgN/m^2/yr)$	0.00053	Calculated
Riparian MDN deposition Estimate $(kgN/ha/yr)$	5.3	Calculated

Table 2.3. Estimation of marine derived nitrogen (MDN) deposited in riparian areas by tributary spawning anadromous fish (spring and summer Chinook salmon and steelhead) in habitat above Hells Canyon Dam on the Snake River in Idaho.

	Spinup/Preindustrial simulation	1906-2011 No MDN simulations	1906-2011 MDN simulations
MDN	0.5	0	0.5
Atmospheric N deposition	0.1	0.2	0.2
Biological N fixation	0.2	0.2	0.2

Table 2.4. Nitrogen deposition $(gN/m^2/yr)$ by simulation type for riparian areas in tributaries of the North Fork Boise River

2.5 Analysis

Model representations of study forest stands were evaluated against measured values for leaf area index (LAI) and soil volumetric water content (VWC) collected at the study sites. We chose these parameters for assessment because LAI is a measurable proxy for productivity on which many model processes are based, and soil water is a major environmental control on productivity.

Given that the 106 year simulated output record was created with repeated climate data (not including atmospheric CO_2) for 1989-2011, we present in the analysis primarily data from the only the final repetition of these 23 years at the end of the 106 year simulation without MDN. This allows an analysis of conditions closest to the

present state with a cumulative effect of the 106 years with or without MDN, while still including enough years to capture climate variability.

To illustrate underlying environmental limiting factors and patterns in annual and daily NPP and NEP, we compared modeled carbon outputs with environmental factors in the no-MDN scenario and the MDN scenario. We compared yearly and daily patterns in productivity and environmental conditions to better understand the environmental conditions under which MDN has the greatest impact. To illustrate differences among years, we also report model output divided into high productivity years and low productivity years, grouping the 10 most and least productive years from the 23 year period for which we have actual climate data. Comparing high and low productivity years allows an assessment of which patterns in environmental factors most affect productivity. Averaging ten years each of high and low productivity years ensures that the influential environmental patterns are not outliers. We additionally broke down results by average growing season (days 89-301) and non-growing season (days 301-88), as this illustrates important temporal differences in productivity and limiting factors. Growing season was calculated based on consecutive days with positive NPP using the technique used by Boisvenue and Running 2010, modified to extend through the fall positive NPP period. Comparisons of multi-decade simulations can predict the overall effects of MDN on a long time scale.

Part 3: Results

3.1 Site Description

During the 23 year climate record, Graham Guard SNOTEL (adjacent to lower sites) reported an average daily T_{max} of 14.4°C and average daily T_{min} of -5.1°C, and Mores Creek Summit SNOTEL (adjacent to upper sites) reported an average daily T_{max} of 11.8°C and average daily T_{min} -0.7°C. The upper elevation sites experienced, on average, 22 more days per year in which T_{min} caused complete stomatal closure. The average annual precipitation was 77cm at the lower elevation sites and 117 cm at the upper sites, with periodic precipitation events punctuating a summer drought period.

3.2 Model input Parameters

Table 3.1 shows the range of ecophysiology input parameters by species used in Biome-BGC simulations, along with Biome-BGC's default evergreen needle forest (ENF) values for comparison. Default values were used for all additional ecophysiology parameters (not shown) for which we did not find species or genus data. All values are average values of available data for each species or genus, with the exception of new fine root to new leaf carbon allocation, which used median values as recommended in White et al. (2000).

Of the parameters we measured, values were similar to those reported in the literature, with some variation. Leaf carbon to nitrogen ratios (C:N_{leaf})were higher for all species than the default ENF value in Biome-BGC. C:N_{leaf} was within the range reported for Engelmann spruce, lodgepole pine and ponderosa pine, though all were in the upper end of their ranges (White et al 2000). Douglas-fir C:N_{leaf} was slightly higher than reported values, and no comparison was found for subalpine fir. Measured fine root carbon to nitrogen ratios were also somewhat higher than values reported in the literature. Measured specific leaf area was slightly lower than literature values for all species except ponderosa pine, which was notably higher, but all were lower than the ENF value. Measured maximum stomatal conductance was somewhat lower than the

estimate used in White, et al. (2000), except in lodgepole pine, which fit within reported values.

| Parameter | Species | | | | | | Source |
	DF	ES	LP	PP	SAF	ENF Default	
Leaf and fine root turnover (1 yr^{-1})	0.20	0.26	0.39	0.42	0.23	0.25	White et al. (2000)
New fine root C to new leaf C allocation (kg C kg C^{-1}, median)	1.4	0.7	3.2	1.1	5.5	1	White et al. (2000)
New stem C to new leaf C allocation (kg C kg C^{-1})	2.6	2.1	2.0	0.9	1.4	2.2	White et al. (2000)
New live wood C to new total wood C allocation (kg C kg C^{-1})	0.06	0.06	0.08	0.08	0.06	0.1	White et al. (2000)
Coarse root C to stem C allocation (kg C kg C^{-1})	0.30	0.19	0.28	0.28	0.35	0.30	White et al. (2000)
Leaf carbon to nitrogen ratio (kg C kg N^{-1})	**60.7**	**61.7**	**51.1**	**47.0**	**56.4**	**42**	**Measured**
Litter carbon to nitrogen ratio (kg C kg N^{-1})	70.3	90.8	111.4	77.1	94.7	93	White et al. (2000)
Fine root carbon to nitrogen ratio (kg C kg N^{-1})	**98.2**	**90.6**	**100.4**	**93.2**	**99.4**	**42.0**	**Measured**
Dead wood carbon to nitrogen ratio (kg C kg N^{-1})	883	411	1030	867	629	729	White et al. (2000)
Litter labile proportion	0.31	0.49	0.24	0.20	0.54	0.32	White et al. (2000)
Litter cellulose proportion	0.24	0.49	0.37	0.45	0.46	0.44	White et al. (2000)
Litter lignin proportion	0.24	0.20	0.31	0.29	0.21	0.24	White et al. (2000)
Dead wood cellulose proportion	0.73	0.71	0.71	0.71	0.70	0.76	White et al. (2000)
Dead wood lignin proportion	0.27	0.29	0.29	0.29	0.30	0.24	White et al. (2000)
Shaded to sunlit leaf area ratio (SLA SLA^{-1})	2.6	2.6	2.6	2.4	2.6	2.6	White et al. (2000)
Specific leaf area, carbon basis (m^2 kg C^{-1})	**7.5**	**5.1**	**6.6**	**7.4**	**7.1**	**12**	**Measured**
Fraction of leaf nitrogen in Rubisco	0.028	0.009	0.046	0.046	0.245	0.040	*
Maximum stomatal conductance (m s^{-1})	**0.002**	**0.005**	**0.006**	**0.004**	**0.003**	**0.003**	**Measured**
Leaf water potential at initial reduction to stomatal conductance (MPa)	-0.6	-0.6	-0.5	-0.7	-0.6	-0.6	White et al. (2000)
Leaf water potential at complete reduction to stomatal conductance (MPa)	-1.7	-1.7	-1.4	-1.9	-1.7	-2.3	White et al. (2000)
Vapor pressure deficit at initial reduction to stomatal conductance (MPa)	700	500	700	700	500	930	White et al. (2000)
Vapor pressure deficit at complete reduction to stomatal conductance (MPa)	3500	2500	3150	3150	2000	4100	White et al. (2000)

Table 3.1. Ecophysiology constants (EPC) used for Biome-BGC simulations, by species present at six tributaries of the North Fork Boise River, Idaho. Bolded parameters are those measured in this paper at six study sites in the North Fork Boise River watershed. ENF values are the default evergreen needle forest values in Biome-BGC. Values from White et al (2000) presented here were species- or genus-specific, when species values were not available. Species are Douglas-fir (DF, *Pseudotsuga menziesii*), Engelmann spruce (ES, *Picea engelmanii*), lodgepole pine (LP, *Pinus contorta*), ponderosa pine (PP, *Pinus ponderosa*), and subalpine fir (SAF, *Abies lasiocarpa*). *Sources: White et al. (2000), Thornton et al. (2002), Turner et al. (2003), Ueyama et al (2010), Hikosaka and Shigeno (2009), Ripullone (2003), Arain (2006), Thurnbull et al. (1998), Nagano et al. (2009), Pietsch et al (2005), Wullschleger et al. (1993).

3.2a Species composition

Species composition by percentage of LAI composed of each species at each study site is reported in Table 3.2. The lower elevations were composed primarily of Douglas-fir and ponderosa pine, except Trail Creek, which had a high percentage of subalpine fir. The upper elevation sites were dominated by lodegpole pine, except Pike's, which had a high percentage of Engelmann spruce. Pike's high spruce component may be exaggerated by the presence of one very large spruce in one of the plots.

Table A.1 in Appendix A provides data by site and species on measurements made in the forest plots, including tree diameter, height, age, and sapwood area used to calculate leaf area.

	Lower elevation sites			Upper elevation sites		
Species	Trail	Hunter	Beaver	Little Beaver	Pike's	Banner
DF	45.8	39.6	33.4	4.8	8.5	2.1
ES	2.9	0.0	0.0	0.0	64.8	0.0
LP	5.0	10.0	0.0	80.5	16.8	97.3
PP	6.9	42.2	66.6	0.0	0.1	0.0
SAF	39.4	8.2	0.0	14.7	9.8	0.7
Site LAI	1.9 (0.46)	0.8 (0.27)	1.1 (0.36)	0.8 (0.09)	0.8 (0.40)	0.9 (0.21)

Table 3.2. Species composition of each site by percent of total LAI and site average LAI (standard error in parentheses). DF is Douglas-fir (*Pseudotsuga menziesii*); ES is Engelmann spruce (*Picea engelmanii); LP is lodgepole pine (Pinus contorta*); PP is ponderosa pine (*Pinus ponderosa), and SAF is subalpine fir (Abies lasiocarpa). Standard error in parentheses.*

3.2b Soil depth and texture

Soils were observed to be very sandy at all sites (73-96% of sieved soil), most notably at the lower elevation sites (Table 3.3). Soil depth measured at soil pits, to rock or water table, ranged from 0.7m to 1.1m among the six sites. Effective soil depth varied more widely, ranging from 0.34m to 0.96m between sites (Table 3.3).

Site	Effective soil depth (m)	% Sand	% Silt	% Clay
Trail	0.61	93	5	2
Hunter	0.34	96	2	2
Beaver	0.55	94	4	2
Little Beaver	0.62	86	12	2
Pike's	0.96	90	6	4
Banner	0.69	73	6	21

Table 3.3. Soil parameters at six tributaries of the North Fork Boise River in central Idaho.

3.3 Evaluation of Model Performance

Two key simulated variables controlling forest productivity (maximum LAI and seasonal soil water content.) were within the range of values measured at the study sites. Specifically, measured average LAI across study sites was 1.12 ±1.29 SD, which is broadly typical for inland mixed conifer forests (Figure 3.1). Average LAI of the upper elevation sites was 0.8 ±0.1 SD and 1.2 ±0.1 SD, measured and modeled, respectively. Average at the lower elevation sites was 1.3 ±0.3 SD and 1.7 ±0.2 SD, measured and modeled, respectively.

Simulated soil volumetric water content (VWC) generally followed the trends and magnitude of measured VWC for the three years of measurement at Beaver Creek (Figure 3.2), the only site with a complete measured VWC record. Linear regression of modeled and observed soil VWC at this site also showed a good relationship ($r^2 = 0.73$).
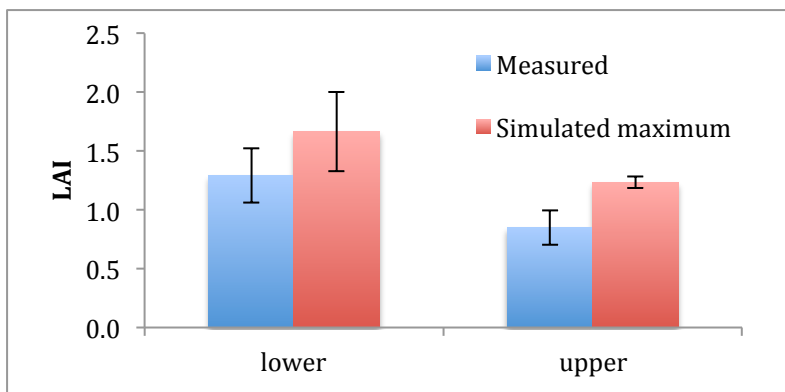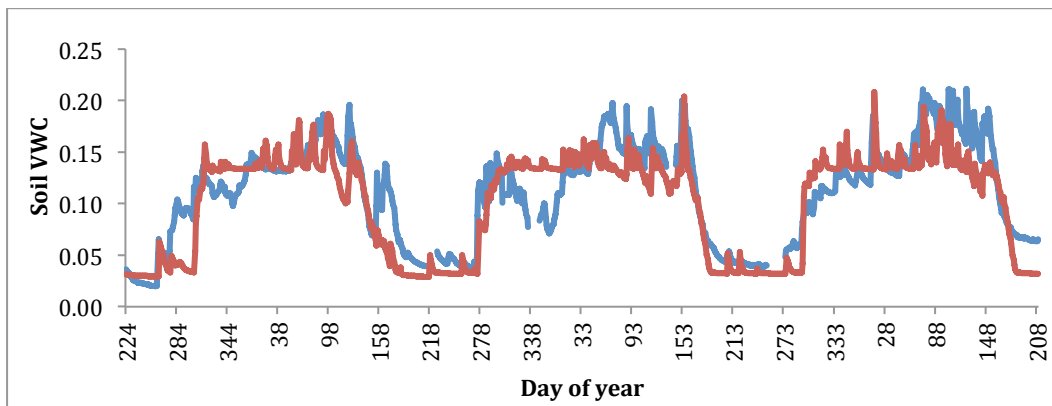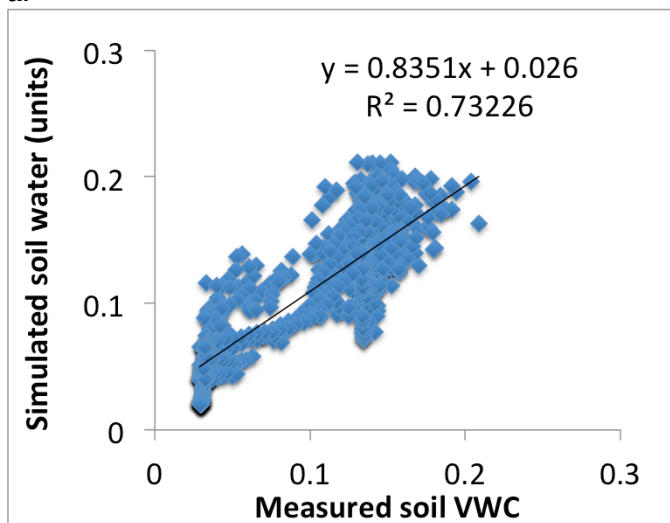

Figure 3.1. Measured and simulated LAI for three higher elevation sites (upper) and three lower elevation sites (lower) in the North Fork Boise River watershed.. Simulated LAI is a potential maximum LAI for the site; measured is actual LAI. Error bars represent standard error among sites.

a.

b.

Fig 3.2. Comparison of simulated and measured soil volumetric water content (VWC) at Beaver Creek for August 2008 through July 2011. Seasonal course (a): blue line is measured VWC for 0-30cm soil depth; red line is modeled SWC for measured soil depth of 0-55cm effective soil depth (110cm with rock fraction included). (b) Scatterplot between observed and modeled soil VWC.

3.4 One hundred and six years of simulations without MDN: Limiting factors on productivity (NPP) and carbon balance (NEP) vary by elevation and among years.

Model output for the 23-year period at the end of the 106 year simulation coinciding with the years of actual climate record (1989-2011) revealed patterns of productivity due to environmental limitations by elevation, within years and among years. Overall, upper elevation sites were 14% more productive than lower sites 0.370 kg C/m^2/yr ± 0.019 SE and 0.326 kg C/m^2/yr ±0.027 SE, respectively). However, NEP was similar between elevation groups 0.032 kg C m^{-2} yr^{-1} ±0.016 SE and 0.030 kg C m^{-2} yr^{-1} ±0.023 SE at upper and lower elevation sites, respectively). Variation in NPP and NEP was much greater among years, however, with both elevations showing high NPP 0.409 kg C/m^2/yr ±0.019 SE and 0.402 kg C/m^2/yr ±0.018 SE at upper and lower sites, respectively) in the ten highest productivity years, and dropping in the ten lowest productivity years by 18% and 39%, to 0.334 kg C/m^2/yr ±0.012 SE and 0.246 kg C/m^2/yr ±0.012 SE at upper and lower sites, respectively. NEP varied even more among years, with the ten highest productivity years seeing 97% and 137% higher NEP in high productivity years, at upper and lower elevation groups, respectively (Table 3.4).

Within years, NPP and NEP were highest in spring and early summer (approximately days 70 to 200), when water, temperature, and solar radiation were not limiting (Figure 3.3). Figure 3.3 shows differences by elevation in patterns of NPP and related environmental limiting factors. The more productive upper elevation sites had substantially higher soil water throughout the season, associated with 50% greater precipitation at those sites, 61-70% of which fell in winter (Table 3.4). The upper sites, on average, maintained positive NPP throughout the year, while lower elevation sites saw negative NPP during late summer, when soil moisture was low and VPD was high. Even though the upper elevation sites had a shorter growing season than the lower sites by 21 days, they retained higher NPP throughout the summer drought period, associated with higher soil moisture and lower VPD (Figure 3.3).

NPP and NEP varied more widely among years than by elevation, and these differences were also largely driven by water. The ten highest productivity years had 18% and 39% greater NPP than the ten lowest productivity years at upper and lower

elevations, respectively. NPP values at upper and lower elevation sites were similar in the highest productivity years (2% greater at upper elevation sites) despite very different annual precipitation (50% greater at upper elevation sites). This pattern suggests that total annual precipitation was not limiting, and that other factors constrained productivity. Notably, in the high productivity years, precipitation during the growing season was 31 and 33% higher at upper and lower elevation groups, respectively, while winter precipitation was actually lower in the high-productivity years (by 12 and 8% at upper and lower elevations, respectively), suggesting that summer precipitation was a more important driver of overall modeled productivity than even annual precipitation. Linear relationships of NPP vs seasonal precipitation support this result: r^2 values for NPP and growing season precipitation (that which fell on days 89-301) were 0.2 and 0.5 at upper and lower elevation sites, respectively, and r^2 values for NPP and precipitation falling the rest of the year were 0.04 and 0.01 (Figure A.3 in Appendix A). Other environmental factors were implicated, however. High productivity years had longer growing seasons (14% and 6% longer at upper and lower sites, respectively), associated with fewer nights where T_{min} reached below -14 °C (6 and 4 fewer days at upper and lower sites).

In our simulations, the upper sites were net carbon sinks in 83% of years, and lower sites were sinks in 57% of years (Figure 3.6). In high productivity years, NEP was much higher than average at both elevations (0.068 kg C m^{-2} yr^{-1} and 0.098 kg C m^{-2} yr^{-1} at upper and lower sites, respectively). In low productivity years, NEP was near zero at the upper sites and became negative, or a net carbon source to the atmosphere at the lower sites (0.002 kg C m^2 yr^{-1} and -0.036 kg C m^2 yr^{-1} at upper and lower sites, respectively). This pattern, where NEP fluctuated more widely at the lower elevation sites, occurred because HR remained relatively stable from high to low productivity years, while NPP dropped considerably more at the lower sites than the upper sites when conditions were drier (Table 3.4).
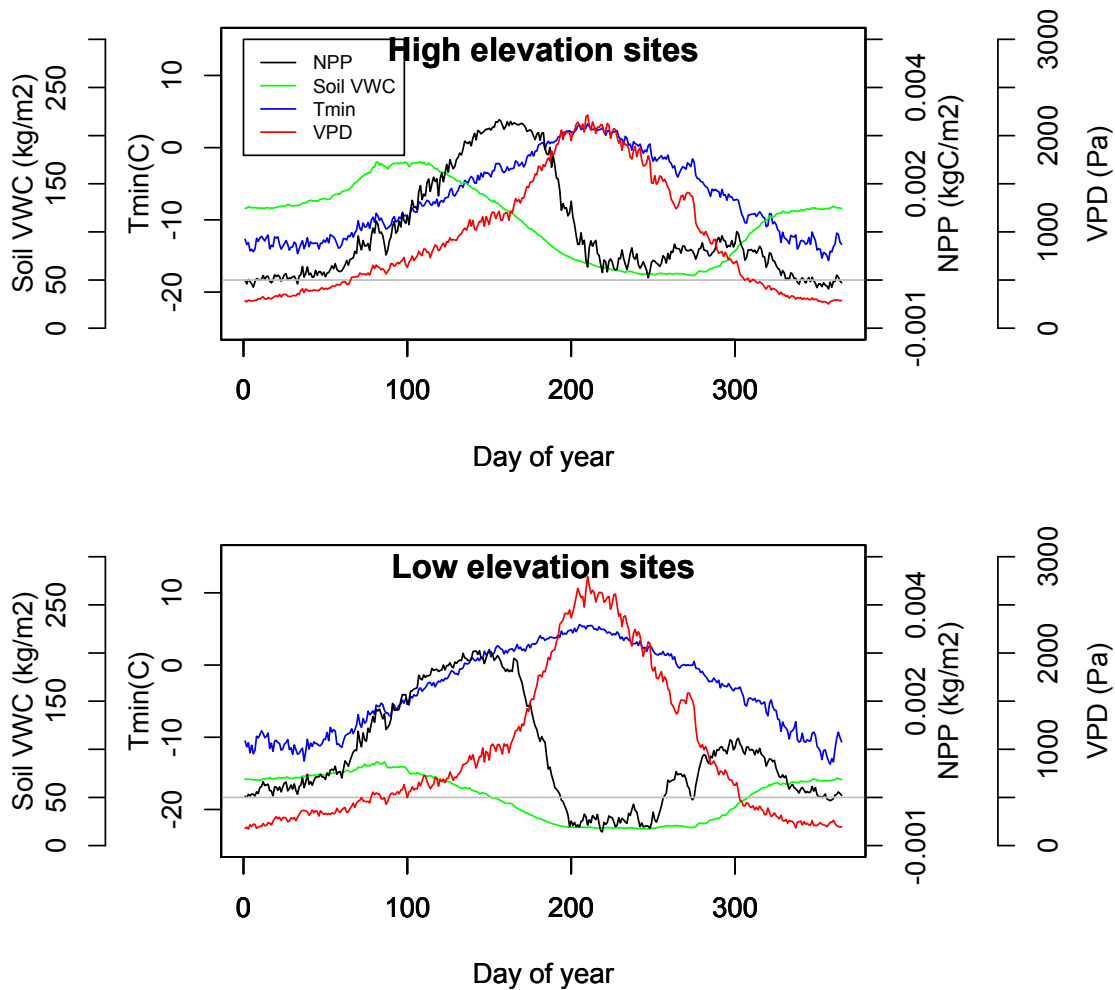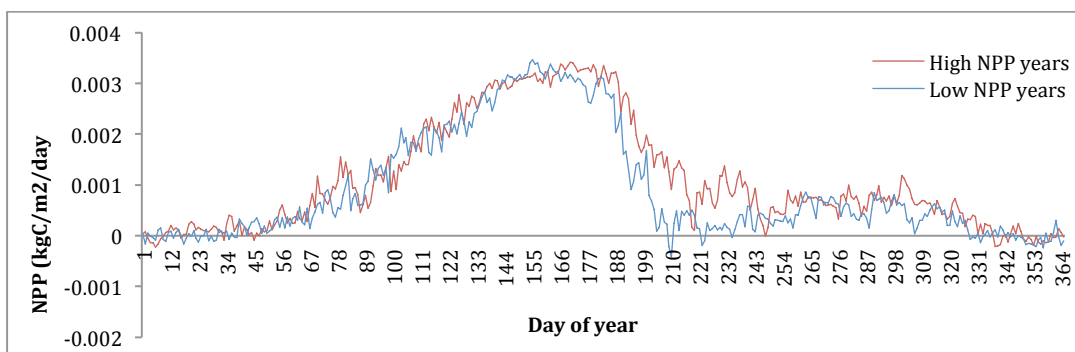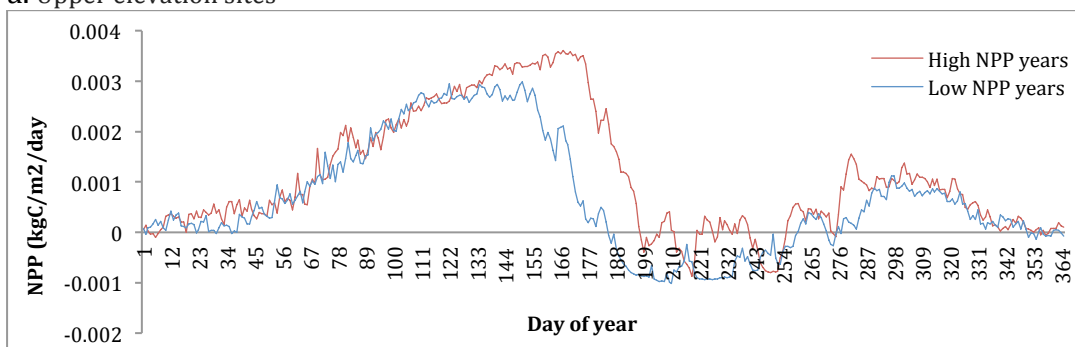
Figure 3.3. Daily modeled net primary productivity (NPP), measured daily minimum temperature (T_min), and modeled soil volumetric water content (Soil VWC), and calculated daily vapor pressure deficit (VPD), averaged across 1989-2011 for upper and lower elevation sites. Grey line indicates NPP = 0 kgC m⁻².

	Upper sites				Lower sites			
	High NPP years		Low NPP years		High NPP years		Low NPP years	
Annual precipitation (mm)	1182	(191)	1154	(311)	811	(143)	739	(212)
Summer (Day 89-301) precipitation (mm)	400	(91)	277	(91)	338	(63)	228	(61)
Winter (Day 301-88) precipitation (mm)	782	(165)	876	(254)	472	(135)	511	(156)
Growing season (days)	210	(55)	184	(42)	225	(40)	213	(28)
Nights below -14 C	50	(18)	56	(12)	29	(16)	33	(9)
Annual NPP (kg/m²/yr)	0.409	(0.019)	0.334	(0.012)	0.402	(0.018)	0.246	(0.012)
Annual NEP (kg/m²/yr)	0.068	(0.018)	0.002	(0.007)	0.098	(0.015)	-0.036	(0.008)
Annual HR (kg/m²/yr)	0.341	(0.009)	0.332	(0.008)	0.304	(0.007)	0.282	(0.005)

Table 3.4. Comparison of average climate variables and simulated net primary production (NPP), net ecosystem production (NEP), and heterotrophic respiration (HR) in no MDN scenarios for the ten highest and ten lowest productivity (NPP) years of the measured climate record (1989-2011), at upper and lower elevation sites. Standard deviation in parentheses, except for NPP, NEP and HR, which are standard error.

a. Upper elevation sites

b. Lower elevation sites

Figure 3.4. Daily average modeled net primary productivity (NPP) at upper (a) and lower (b) elevation sites for the 10 highest productivity years (red lines) and 10 lowest productivity years (blue lines) of simulations for years of actual climate record (1989-2011).

3.5 Simulations with continuous deposition of MDN

Net primary productivity at all sites responded positively to long term MDN addition: upper and lower sites saw average annual increases in NPP of 8% and 7%, respectively, with a similar percentage increase in NPP in high and low productivity years at both elevations (Table 3.6). The greatest increase was at the upper elevation sites, which saw a boost of 34 gC/m²/yr (Table 3.5). Lower elevation sites saw a boost of 27 gC/m²/yr. Low productivity years also saw an increase in NPP with MDN, just to a lesser extent (22 gC/m²/yr and 17 gC/m²/yr at upper and lower elevation groups, respectively). Heterotrophic respiration, though also stimulated by MDN, increased at a lower rate (3-4%) and amount than NPP, allowing NEP to increase along with NPP across all sites and years. In high productivity years, NEP increased by 20 gC/m²/yr and 17 gC/m²/yr at

upper and lower elevation sites respectively, and by 10 gC/m^2/yr and 7 gC/m^2/yr, respectively, in the low productivity years. Low elevation sites in low productivity years still had negative NEP, remaining a source of C to the atmosphere, but to a lesser extent than without MDN (Table 3.6). Figure 3.6 summarizes the effect of MDN on NEP at both elevation groups overall and by high and low productivity years; under all subsets, MDN resulted in an increase in NEP. With MDN, the percentage of years in which the riparian forest was a carbon sink increased by 4% at upper elevation sites and 9% at lower sites, to 85% and 65% of years, respectively (Figure 3.6).

All of these patterns were associated with differences in environmental factors varying among years, within years, and across locations. MDN led to the greatest increases in NPP and NEP when warm, wetter conditions already favored high NPP, primarily in spring and early summer. High NPP was strongly associated with high growing season precipitation (Figures 3.3 and 3.4), while it did not follow total annual precipitation. Within years, seasonal increases in NPP with MDN occurred almost entirely during spring and early summer, when soil moisture was high (Figures 3.5 and 3.3). Most of the growing season precipitation occurred in spring and early summer, prolonging the elevated soil moisture beyond the end of snowmelt, and thus extending the period in which water was not limiting and MDN can further lift the limitations on productivity (Figure 3.5). Figure 3.4 compares NPP in high and low productivity years (before MDN addition) and illustrates this elongated period of high productivity in the high NPP years. In the late summer drought period MDN made little difference, and in fact, under conditions with most extreme limiting factors (during the summer drought in low NPP years), NPP was lower with MDN than without (Figure 3.5). This temporary reversal in the positive effect of MDN on NPP is a result of greater simulated plant respiration costs imposed by increased growth combined with conditions under which productivity was greatly limited.

The increase in NEP followed similar trends as NPP, increasing more in years with greater growing season precipitation, longer growing season, and fewer nights below -14 °C. High productivity years saw 2.0 to 2.7 times larger increase in NEP than low productivity years, whereas by elevation, the differences were more modest (Table 3.6).

Increase with MDN	Upper sites	%	Lower sites	%
NPP (kgC/m²/yr)	0.029	8	0.022	7
HR (kgC/m²/yr)	0.013	4	0.011	4
NEP (kgC/m²/yr)	0.016	48	0.012	38

Table 3.5. Average increase in simulated NPP (net primary productivity), HR (heterotrophic respiration), and NEP (net ecosystem production) with the addition of MDN in simulations of six tributaries of the North Fork Boise River for the 23 years of climate record (2989-2011). % indicates percent increase from baseline no-MDN simulations.

		High NPP years				Low NPP years			
		Upper sites		Lower sites		Upper sites		Lower sites	
Environmental factors	Annual precipitation (mm)	1182	(191)	811	(143)	1154	(311)	739	(212)
	Growing season (Day 89-301) precipitation (mm)	400	(91)	338	(63)	277	(91)	228	(61)
	Winter (Day 301-88) precipitation	782	(165)	472	(135)	876	(254)	511	(156)
	Growing season length (days)	50	(18)	29	(16)	56	(12)	33	(9)
	Nights below -14°C	210	(55)	225	(40)	184	(42)	213	(28)
No MDN Simulations	Annual NPP (kgC/m²/yr)	0.409	(0.019)	0.402	(0.018)	0.334	(0.012)	0.246	(0.012)
	Annual NEP (kgC/m²/yr)	0.068	(0.018)	0.098	(0.015)	0.002	(0.007)	-0.036	(0.008)
	Annual HR (kgC/m²/yr)	0.341	(0.009)	0.304	(0.007)	0.332	(0.008)	0.282	(0.005)
MDN Simulations	Annual NPP (kgC/m²/yr)	0.443	(0.021)	0.430	(0.018)	0.356	(0.014)	0.263	(0.013)
	Annual NEP (kgC/m²/yr)	0.088	(0.020)	0.115	(0.015)	0.012	(0.009)	-0.029	(0.009)
	Annual HR (kgC/m²/yr)	0.355	(0.009)	0.315	(0.007)	0.344	(0.008)	0.293	(0.006)
Increase with MDN	NPP increase (kgC/m²/yr)	0.034		0.027		0.022		0.017	
	NEP increase (kgC/m²/yr)	0.020		0.017		0.010		0.007	
	HR increase (kgC/m²/yr)	0.014		0.011		0.012		0.010	

Table 3.6. Comparison of environmental data and simulated net primary production (NPP), net ecosystem production (NEP), and heterotrophic respiration (HR) for the ten highest and ten lowest productivity (NPP) years of the measured climate record (1989-2011), at upper and lower elevation sites. Data shown for simulations without marine derived nitrogen (MDN) simulations and simulations with MDN. Standard error in parentheses.
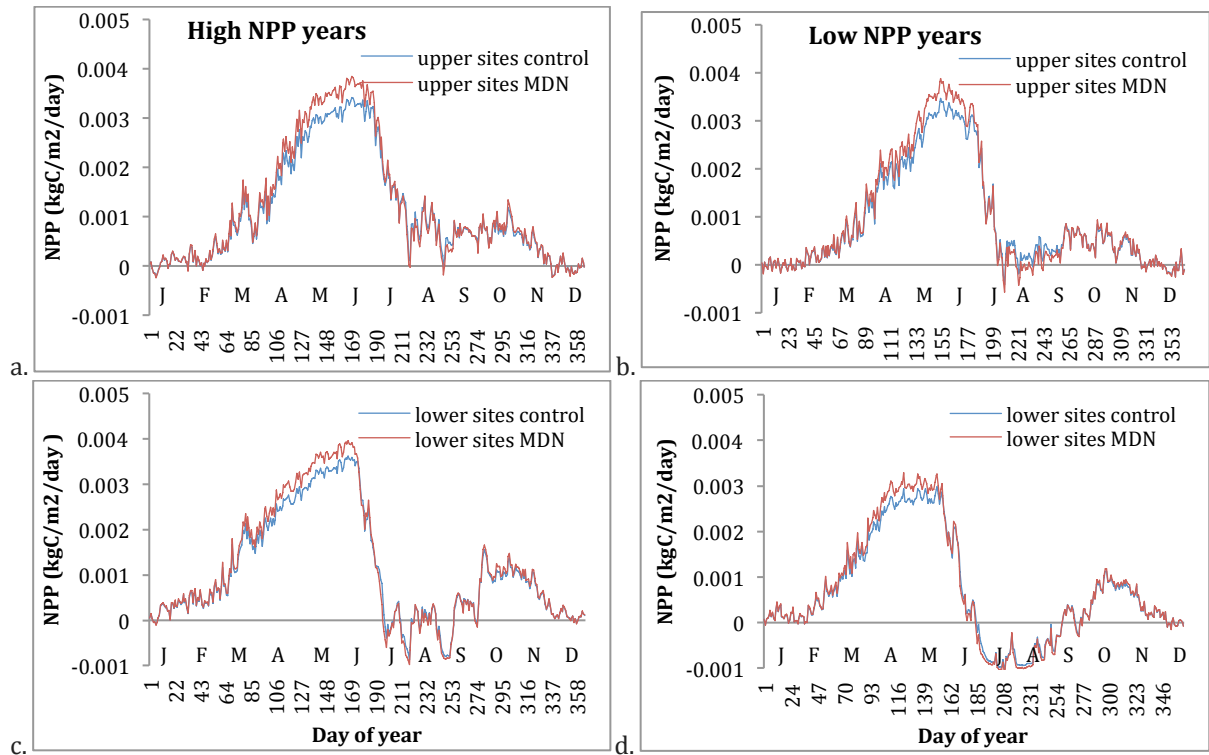
Figure 3.5. Average daily simulated net primary productivity (NPP, kgC m^{-2} day^{-1}) for control (blue lines) and MDN (marine derived nutrients, red lines) scenarios at a) upper elevation sites in the ten highest productivity years from the 1989-2011 climate record, b) upper elevation sites in the ten lowest productivity years, c) lower elevation sites in the ten highest productivity years, and d) lower elevation sites in the ten lowest productivity years.
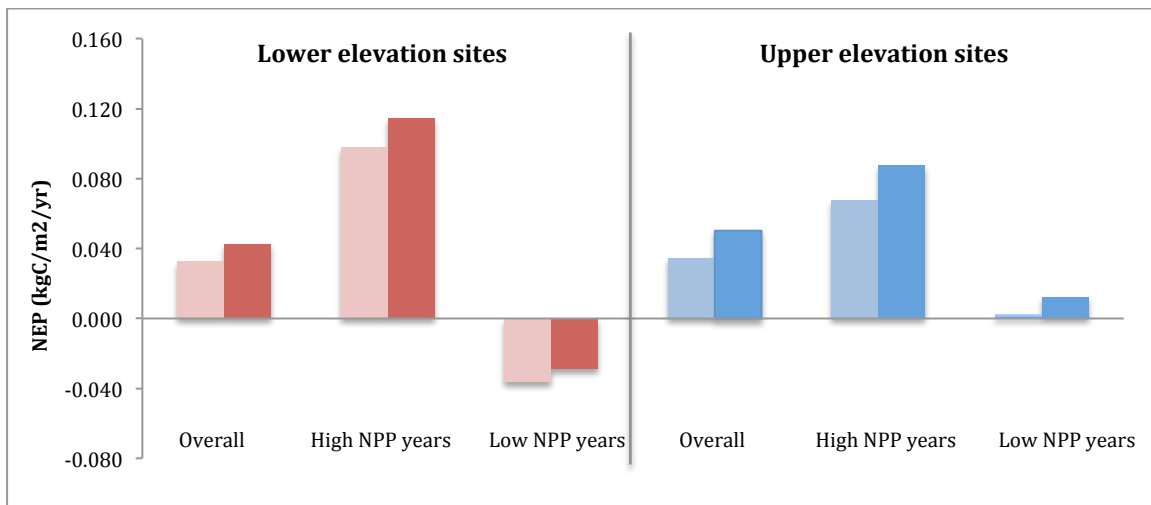

Figure 3.6. Average annual NEP at upper and lower elevation site groups. Overall includes all years of the climate record (1989-2011); High and low NPP years include the ten highest and lowest productivity years from that period.
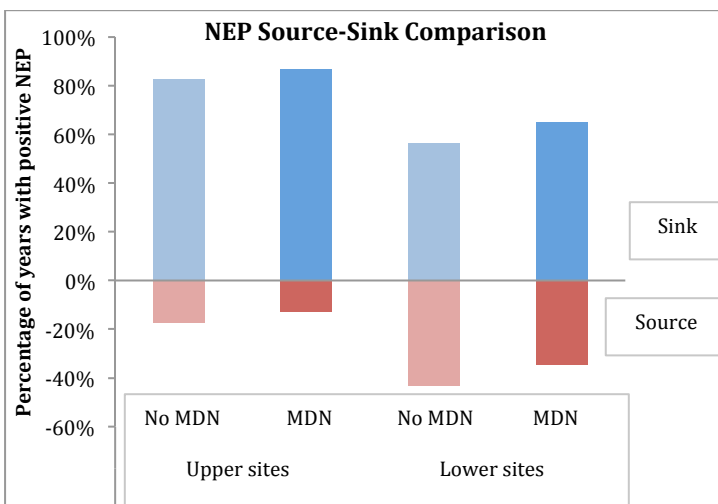
Figure 3.6. Carbon source/sink analysis of upper and lower elevation sites in the North Fork Boise River watershed during the period 1989-2011, without and with marine derived nitrogen (MDN), as simulated using Biome-BGC . Lighter colored columns indicate no-MDN scenarios, and darker colored columns are simulations with MDN present. Values above the 0% line indicate percentage of years in which the sites were carbon sinks. Values below the 0% line indicate percentage of years in which the sites were sources of carbon to the atmosphere. The first two columns represent the upper elevation sites, and the second pair of columns represent the lower elevation sites.

3.5b Total Site Carbon response to MDN addition

Accumulation of total site C (vegetation, litter and soil C) showed a consistent increase at all six sites in the MDN simulations. Figure 3.7 shows that simulated study sites accumulate (1.0 ± 0.1 kg m^{-2}) more total site carbon by the end of the 110-year simulation with MDN than control simulations (a 2.8% increase). Upper elevation sites respond more to MDN addition than lower elevation sites (1.1± 0.09 kgC m^{-2}, and 0.8± 0.04 kgC m^{-2} increases in site C with MDN, respectively, or 2.6 and 3.0% increases, respectively).
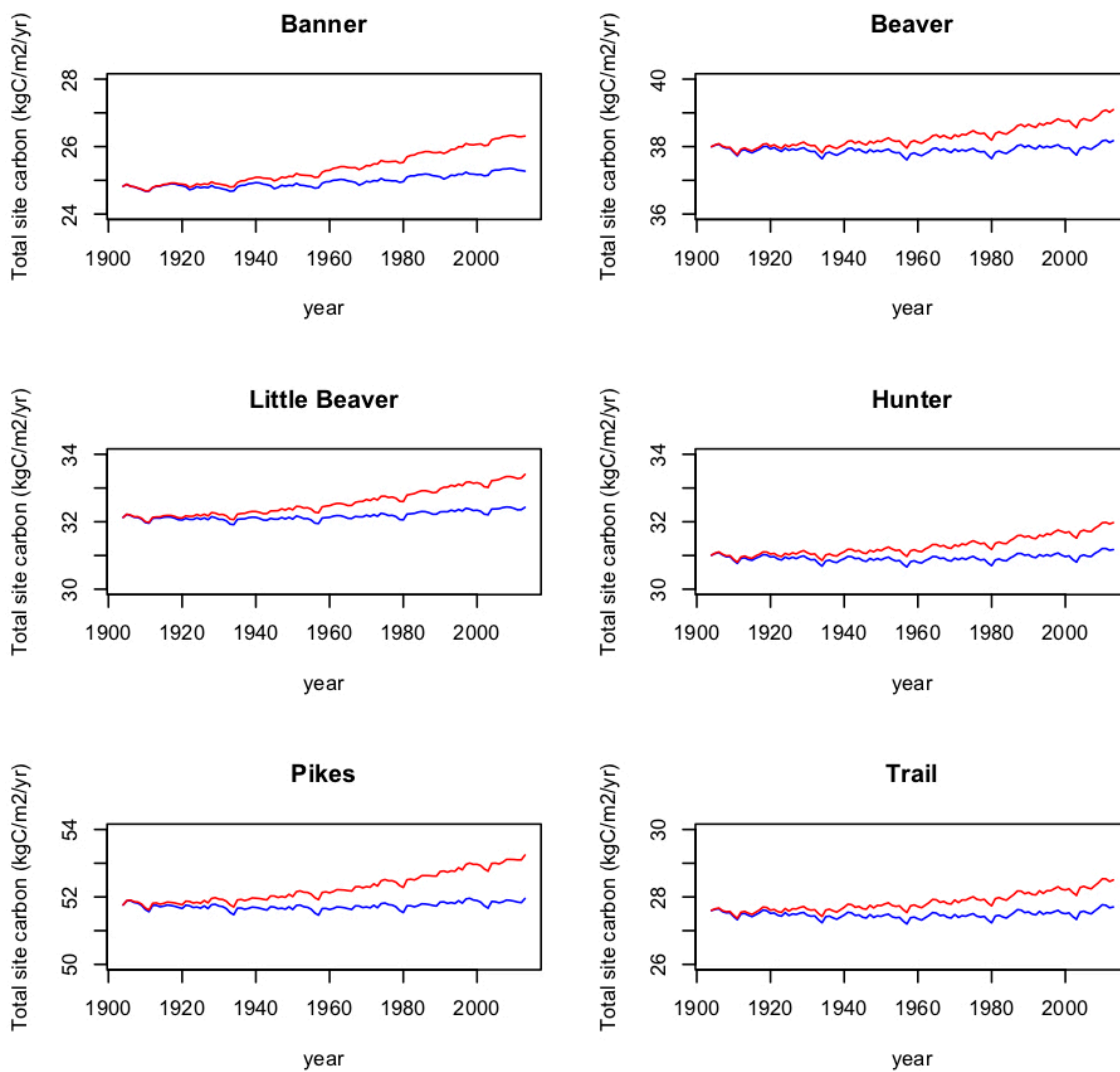
Figure 3.7. Total site carbon based on Biome-BGC simulations for control (blue lines) and MDN (red lines) scenarios at six sites in central Idaho from 1904-2013. Note difference in Y axis: scale is the same throughout but magnitude differs.

Part 4: Discussion

4.1 Simulation Experiments: Effects of Marine Derived Nitrogen Addition on NPP and
NEP and Total C

Riparian Forest NPP increased by 7% after 106 years of MDN additions. However, the
magnitude of the effect varied with shifts in environmental limiting factors, seasonally,
among years, and with elevation. MDN had its greatest effects when environmental
conditions favored high NPP, when constraints from water availability, temperature, and
solar radiation lessened and N became a limiting factor. The simulations predict an
increase in NPP that exceeded the increase in heterotrophic respiration, so NEP
increased as well, resulting in the riparian forests becoming greater carbon sinks when
MDN was present. Simulations suggest that a loss of MDN in this region resulted in a loss
in C uptake and the capacity for C sequestration. First, we compare simulation results for
no-MDN and MDN scenarios to explore the varying response to MDN with limiting
factors, and their implications. Second, we discuss confidence in the model simulations.
Finally, we discuss assumptions and limitations of our approach.

Modeled NPP followed expected seasonal patterns for this region with high
productivity in spring and early summer, dipping dramatically during the summer
drought, and raising again somewhat in the fall before dropping off in winter (Figure
3.5). Not surprisingly, the response MDN is greatest during the peak in NPP period in the
spring and summer before the summer drought begins (Figure 3.5). This seasonal
pattern developed in response to seasonal variation in limiting factors: all sites were
limited in winter by low temperatures and low solar radiation, and in summer by low
soil moisture and high VPD (Boisvenue and Running 2010).

The overall 7% increase in NPP with MDN was underpinned by substantial
variation across seasons, years, and the landscape, with the greatest magnitude increase
occurring in years with high NPP at the upper elevation sites, and the lowest in years
with low NPP at the lower elevation sites. The upper elevation sites were consistently
more productive that the lower sites and therefore saw a greater magnitude increase in
NPP and NEP with MDN. Despite having a shorter growing season by, on average, 21

days (Table 3.4), the upper elevation sites had higher productivity throughout the growing season than the lower elevation sites. Figure 3.4 shows that, in no-MDN simulations, the upper sites had a longer spring period of high productivity than the lower sites, and that NPP, although low, remained almost entirely positive through the summer drought period. In contrast, at lower elevation sites, NPP became negative during the summer drought. While NPP was higher at the upper sites during the summer drought, it was the spring and early summer where MDN made the greatest difference (Figure 3.5). This pattern suggests that factors other than nitrogen were limiting in late summer, but that in spring, those factors were lifted enough that nitrogen became the limiting factor that could raise NPP. Importantly, MDN did not cause NPP to increase when other factors were limiting, such as in winter, when cold and low solar radiation inhibited production, and in the summer drought period, when drier soils and air caused a decrease in NPP by limiting stomatal conductance. In fact, at low elevation sites during low productivity years, MDN caused a temporary *decrease* in NPP during the summer drought period compared with no-MDN simulations (Figure 3.5). The increased productivity in spring of these years, however, outweighed this summer drop, and annually NPP still increased with MDN in these poorer conditions, though to a lesser extent. However, if the summer drought intensifies with climate change, this drop could increase and become greater than the spring increase, reversing the effect of MDN on NEP.

Interannual climate-driven changes were even greater than elevation effects. The increases in NPP and NEP with MDN were larger at both elevation groups in the high productivity years than the response at either elevation in low productivity years (Table 3.6). In simulations without MDN, NPP at upper and lower sites peaked at similar levels in high productivity years (409 and 402 gC/m^2/yr at upper and lower sites, respectively), . Without water limitation, MDN had a greater effect in these years (increasing by 34 and 27 gC/m^2/yr at upper and lower sites) than the more constrained low-NPP years (with increases of 22 and 17 g/m^2/yr at upper and lower sites. In low productivity years, however, NPP and summer precipitation were both substantially lower than in high productivity years (Table 3.6). However, total annual precipitation

was only 2% and 9% lower than in the high productivity years, at upper and lower sites, respectively.

Over the time of the climate record, the highest NPP occurred in years with greater growing season precipitation and lowest in years with low precipitation in the growing season. This pattern persisted despite the upper elevation sites receiving substantially more annual precipitation than the lower sites in all years (Table 3.6). Growing season precipitation thus appears to be a more important control on NPP than annual precipitation. In low NPP years, both upper and lower elevation sites actually received more non-growing-season precipitation than in the more highly productive years (Table 3.6). While many factors limited productivity at our sites (cold temperatures and low solar radiation in winter, water stress in summer), the factor most important to MDN response was precipitation during the growing season, because when cold temperatures and sun were not limiting, water availability constrained growth, and thus the forest's response to MDN.

Seasonal and interannual patterns in site carbon exchange (NEP) in response to MDN were similar to that of NPP, with the largest effect of MDN occurring in spring, in high productivity years, and with upper elevation sites outperforming the less productive lower elevation sites overall. In the no-MDN scenarios, the upper elevation sites were net carbon sinks in 83% of years, and the lower elevation sites were sinks in 57% of years. With MDN, these percentages increased to 87% and 65% at upper and lower sites, respectively. A potentially important caveat to these sink/source estimates is the structure of our simulations, in which the model reaches a steady state (thus, no NEP leading to C accumulation) as a baseline for the MDN experiment. This condition assumes a mature forest with little disturbance at the beginning of the MDN and No-MDN scenarios. Given the history of logging and grazing in the region, and that present day forests are of mixed age (See Table A.1, Appendix), the starting point magnitude of NEE (0 kgC/m^2/yr), and following accumulation, must be considered with caution. The relative magnitude of increase in NEP with MDN, however, remains a useful measure of anadromous-fish nitrogen on forest carbon uptake. At both elevations, and in high and low productivity years, even when NEP was negative (thus a carbon source), NEP was

higher in the presence of MDN (Figure 3.6), though smaller in magnitude at the low elevation sites.

Simulations suggest that MDN additions caused NPP to increase at a rate roughly double that of heterotrophic respiration (Figure 3.6), leading to a net increase in NEP, or atmospheric carbon taken up by the riparian forest ecosystem. NEP fluctuated more widely at the lower elevation sites because while simulated HR remained relatively stable, NPP dropped considerably more at the lower sites when conditions were less favorable (Figure 3.4). Future climate change scenarios predict longer growing seasons for this region and drier summers (Boisvenue and Running 2010, Hu et al. 2010, Payne et al. 2004). The lower elevation sites and their ability to respond to MDN may suffer more greatly under these conditions, given that NEP became negative under current conditions in years with low precipitation during the growing season. Our simulations suggest that, in this ecosystem, at least in conditions similar to the present, MDN would contribute positively to both productivity and carbon sequestration, even when NPP is low. The greatest effect, however, would be in years with high precipitation during the growing season, especially at the upper elevation sites. Even though upper elevation sites were more productive overall, they were only a slightly greater carbon sink. This is primarily due to similar rates of HR across sites but more widely varying NPP with elevation in the lower productivity years, when water was most limiting. If climate change differentially affects NPP and heterotrophic respiration, the effects on NEP could vary substantially, and could be similarly evaluated with a modeling approach.

Higher NEP increased the total carbon pool present on the sites relative to no-MDN scenarios. Simulations indicate that our study sites would contain up to 3% more site carbon at present day had anadromous fish runs continued at historical sizes to present day. That translates into roughly 4.4 tons more carbon per kilometer of stream (assuming a 20-m riparian zone on either side of the stream) at the upper elevation sites and 3.9 tons C per km of stream at the lower elevation sites. While this increase is a small percentage of a relatively large site C pool, it is a substantial absolute addition of carbon storage across the landscape. Literature supports chronic N deposition increasing C storage in soil (Pregitzer et al. 2008), and while the mountains of central Idaho do not receive large amounts of atmospheric N deposition, MDN may stand in for a

similar effect. A potentially important limitation of our study is the seasonal timing of N release. Biome-BGC does not allow specific discrete timing of N deposition, but applies it evenly throughout the year. Actual salmon runs, however, are seasonal (late summer and fall in our study area). A more realistically modeled seasonal distribution of MDN may change the effects, but given that MDN deposited in late summer persisted in the soil into the following growing season in Wheeler's (2017) field studies in Idaho, the lack of seasonality of nutrient availability is somewhat attenuated.

These patterns and magnitudes of site response to MDN may change, however, with climate change, especially regarding projected increases in CO_2 and temperature, and changes in timing and amount of precipitation. Field studies have shown that CO_2 uptake can be limited by low N availability, and that elevated CO_2 often increases N uptake by forests (Finzi et al 2006, Reich et al. 2006), so MDN may facilitate greater CO_2 uptake from the atmosphere as levels continue to rise. Warming temperatures generally enhance photosynthesis (Saxe et al. 2001) as well as soil respiration (Rustad et al. 2001), so the relative increases in these processes may lead to somewhat different outcomes in NEP response to additional nitrogen. Moderate increases in tree growth are predicted in the next few decades (Hyvonen et al 2007), but if precipitation decreases with rising temperatures, as predicted in the interior west, growth could be expected to lower (Boisvenue and Running 2006), and MDN effects may be moderated. Additionally, climate change is expected to further limit the possibility of successful salmon production in the Columbia River basin and thus the potential for natural MDN deposition (Barnett et al. 2004). MDN or nutrient mitigation responses in future climate scenarios could be further assessed with follow-up modeling experiments.

4.2 Summary of Measured Site Data and Evaluation of Model Performance

4.2a: Comparison of Biome-BGC output with field measurements
The sites chosen for this study represented a range of biological and physical factors in the region, which results in a range of species composition among the six study sites (Table 3.2), with upper elevation sites dominated by Engelmann spruce and lodgepole pine, and lower elevation sites dominated by ponderosa pine and Douglas-fir, at an

elevation range of 1329 to 1666 m. Annual and seasonal variability in limiting factors and resulting NPP and NEP were incorporated using 23 years of daily climate data for each study site. The meteorological record includes years in which MDN did not greatly impact NPP and NEP, and years when it did. Simulated annual NPP of 246 gC/m^2/yr ±12 SE at lower sites in low NPP years to 409 gC/m^2/yr ±19 SE at upper sites in high NPP years was within expected range for this forest type, measured by various methods, including biomass (allometry), turnover estimates, and modeling (Arthur and Fahey 1992, Comeau and Kimmens 1989, He et al. 2012, Law et al. 2003, Boisvenue and Running 2010). Thus, we were confident in the breadth of our simulations to capture the varying conditions in this ecosystem.

Comparisons of LAI and soil water content simulated in Biome-BGC with measurements made in the field show that simulations performed satisfactorily in representing the study system and its primary drivers of NPP. Simulated maximum LAI for the study sites capture the range and heterogeneity measured in the field (Table 3.2). While Biome-BGC predicts slightly higher maximum LAI values than measured LAI at both upper elevation sites (Table 3.2), this is expected given we only measured LAI of trees and these sites contained significant amounts of shrubs and grasses in the understory that were not included in the LAI measurements. The simulated soil VWC data follow closely the measured pattern and magnitude at Beaver Creek, the only site with a complete VWC record. The simulated VWC is an average across the full effective rooting depth (soil depth minus rock fraction, 55cm), while measured VWC covers only the top 30 cm of whole soil (Figure 3.2). In the three years recorded, there was a lag in the first year's spring rise in soil VWC, but after that the timing and magnitude of modeled periods of high and low soil moisture track measured patterns well (R^2 = 0.73, see Figure 3.2). Magnitude of longer high and low periods in VWC were similar between modeled and measured values despite some mismatch in timing and magnitude peaks (Figure 3.2). Overall, the modeled results match well with field measurements and we were confident to use the results in simulated experiments to understand the magnitude of and mechanisms involved in forest productivity response to MDN. Measured soil water content and LAI agree with values predicted by Biome-BGC, lending confidence to simulation experiments.

The adjustment we made to the model structure lowering the T_{min} thresholds limiting stomatal conductance could be described as the main "tuning" element in our simulations (see methods). Preliminary simulations with site and species-specific EPC values for some of the upper elevation sites resulted in simulations failing to spin up to steady state conditions. Given that this occurred at the colder, upper elevation, we surmised a cold hardiness in the trees in our region. In comparing stomatal closure temperature values measured in other higher elevation conifer forests, Smith et al. (1984) reported a range of stomatal responses to T_{min}, from which we adopted a mid-range estimate for our simulations.

4.2b Ecophysiology parameters:

We chose to adjust as many of the default EPC values as possible since we wanted to represent the species heterogeneity across the landscape. Therefore it is important to discuss the relative strengths of the measurements and data selected.

Maximum stomatal conductance can be difficult to capture, as measurements must be made when environmental factors are least limiting. Our measured g_{smax} was within the range of values reported in White, et al (2000), so we believe them to be accurate. The relatively high measured C:N_{leaf} values may be indicative of nitrogen limitation in this ecosystem (Billow, et al. 1994). PLNR can be a problematic input parameter, as productivity outputs in Biome-BGC are quite sensitive to this essential component of C assimilation. However, field measurements of PLNR are not widely reported. We found several more measured values in the literature beyond those reported in White et al (2000) and incorporated them (Table 3.1). This should provide a more accurate PLNR estimate.

We may not have captured complete variability of the soil composition at these sites, having only dug one soil pit at each study site. However, the sites were consistently very high in sand content (Table 3.3; this was also noted when digging pits for soil moisture sensors) suggesting this is the dominant pattern for the riparian areas in the region. Effective soil depth varied considerably more than total soil depth due to varying rock fraction, and simulations may benefit from more data points. Model sensitivity to soil depth and variance in that data may contribute to uncertainty in soil moisture

output and related processes. In fact, in the theoretical background of Biome-BGC (Golinkoff 2010), soil depth is described as a "tuning dial" as much as a physiological component.

We developed site-specific temperature histories for each stream, thus capturing greater variability among locations. We were unable to adjust precipitation in a similar fashion, so all upper elevation sites have the same precipitation as Mores Creek SNOTEL and all low elevation sites share the Graham Guard SNOTEL precipitation data. This led to our grouping sites by upper and lower elevation for analysis and data presentation.

There are many potential sources of error when estimating historical salmon population and distribution, as precise measurements are not available. To minimize this error, our MDN estimate was constructed using the smallest region for which we could find population estimates, the Snake River above Hells Canyon Dam (Chandler, 2001), and estimates of riparian area width and total N per salmon (Table 2.2) that were regional, and fraction of salmon transported by bears from coastal and intact Alaska systems (Quinn, et al. 2009).

Our value of total nitrogen per salmon carcass was based on modern hatchery spawning salmonids, which were measured to have body mass of approximately 3.2 kg (Wheeler and Kavanagh 2017). Historically, Columbia River salmon and steelhead averaged 6.75 kg each (NPPC 1986). Not accounting for the historically larger body size of pre-development tributary-spawning fish may mitigate an overestimation of N transfer to the system. Gende (2007) estimates that approximately two thirds of total nitrogen from a salmon carcass enters the plant-available N pool, suggesting our calculation is not a gross overestimation of MDN deposition in this region.

Using the upper end of population and carcass deposition estimates created a high-end estimate for MDN levels deposited in the study area (0.53 gN/m^2/yr), which allowed for clarity of effects and mechanisms using model simulations. While our estimates may be at the high end of the range of possible MDN amounts historically present, there were also factors that suggest the estimate is still somewhat conservative. Fly larvae, for example, which often comprise a large fraction of the decomposing carcass material, were not included in some of Wheeler's (2017) nutrient deposition analyses, and yet many of these insects remain in the ecosystem and contribute MDN by

excretion or decomposition. Our estimate also does not account for all nutrient deposition pathways such as via hyporheic flow. Ashkenas (2004) discusses additional pathways not included in our analysis, such as hyporheic flow, direct uptake by bryophytes and mosses, emergence of aquatic invertebrates, and vertebrate consumers including amphibians. Other estimates of MDN deposition found in the literature confirm the conservative nature of our estimate. Reported estimates range from 1.4 to 2.2 $gN/m^2/yr$ in Alaskan systems (Quinn et al, 2009; Gende, et al. 2007). Both of these studies assumed a 10m riparian area width; had they assumed 20m as at our sites, their rates would be halved, to 0.7 to 1.1 $gN/m^2/yr$, close to our estimate. Marcarelli et al (2014) estimates an upper end 2.1 $gN/m^2/yr$ MDN deposition rate in central Idaho.

Part 5: Conclusions

Carbon sequestration is an important ecosystem process provided by forests. MDN mitigation or preservation of existing salmon populations in similar ecosystems may be a useful component in increasing or maintaining a positive carbon balance. Our simulation experiments suggest that riparian forests in central Idaho saw a relative decrease in annual NPP of 7-8% after a century without MDN. Over time, the loss of this nutrient subsidy has caused a relative decrease in NEP and a slowing of carbon accumulation on the landscape, resulting in a reduction of 4.4 tons C per km of 20m riparian forest with the loss of MDN. However, the magnitude of the increase was highly dependent on the environmental variables limiting riparian forest productivity. The largest effects were seen when conditions already favored high productivity, primarily in wetter years, and at the cooler, wetter upper elevation sites. Therefore, a comprehensive model is a preferable method when estimating the magnitude of the effect.

Simulated ecosystem response to MDN at varying elevation and in different annual conditions can inform how managers plan for nutrient mitigation in current conditions and help predict response to climate change. For current mitigation efforts, carcass or nutrient application is likely to be most effective in years and sites with otherwise high productivity; in this region, years with higher growing season precipitation and longer growing season, and at higher elevation sites.

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Appendix A: Additional data

A.1. Soil water potential data

Biome-BGC overpredicted summer peak water stress (at the driest point) measured by soil water potential at one of the two sites where it was measured, even while simulated VWC closely tracked measured values and patterns. At Pike's, modeled Ψ_{soil} at the summer minimum in 2010 was more negative than measured, -1.7 MPa and -1.2 ± 0.3 MPa, respectively. At Trail, modeled and measured Ψ_{soil} at the summer minimum were not different, at -1.3 and -1.2 ± 0.3 MPa, respectively.

Soil water potential is an important driver of biological processes, such as stomatal opening, photosynthesis, and decomposition, so overestimation of soil water stress may have a limiting effect on modeled processes, causing productivity to be somewhat underpredicted during the brief period when water potentials reach their minimum.

Upslope vs Riparian predawn water potential

We measured predawn water potentials in both riparian streamside trees (those in the valley bottom near the stream) and upslope trees (those located high enough on the hill to be above the given species' rooting depth's distance from the riparian zone. Values were adjusted to account for height of foliage sample above ground to estimate soil water potential. Interestingly, the upslope and streamside predawn water potential measurements were not significantly different (Figure A.1), despite minimal understory vegetation. Trees were of patchy lower density on the hillslopes. These circumstances along with equivalent predawn water potentials suggest that the upslope trees may be depending on preferential water flow paths in the soil.
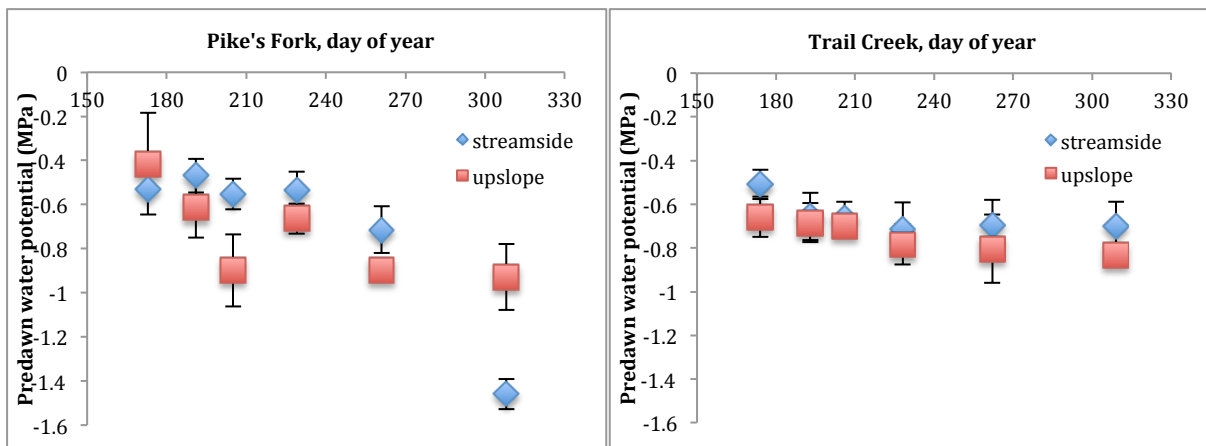

Figure A.1. Summer soil water potential data for six dates in May-November 2010 at two riparian forest sites in the North Fork Boise River basin. Blue points are streamside locations, in the riparian valley bottom, and red points are upslope locations, on adjacent hillsides higher than the rooting depth above the riparian zone.

A.2 Site-adjusted temperature data

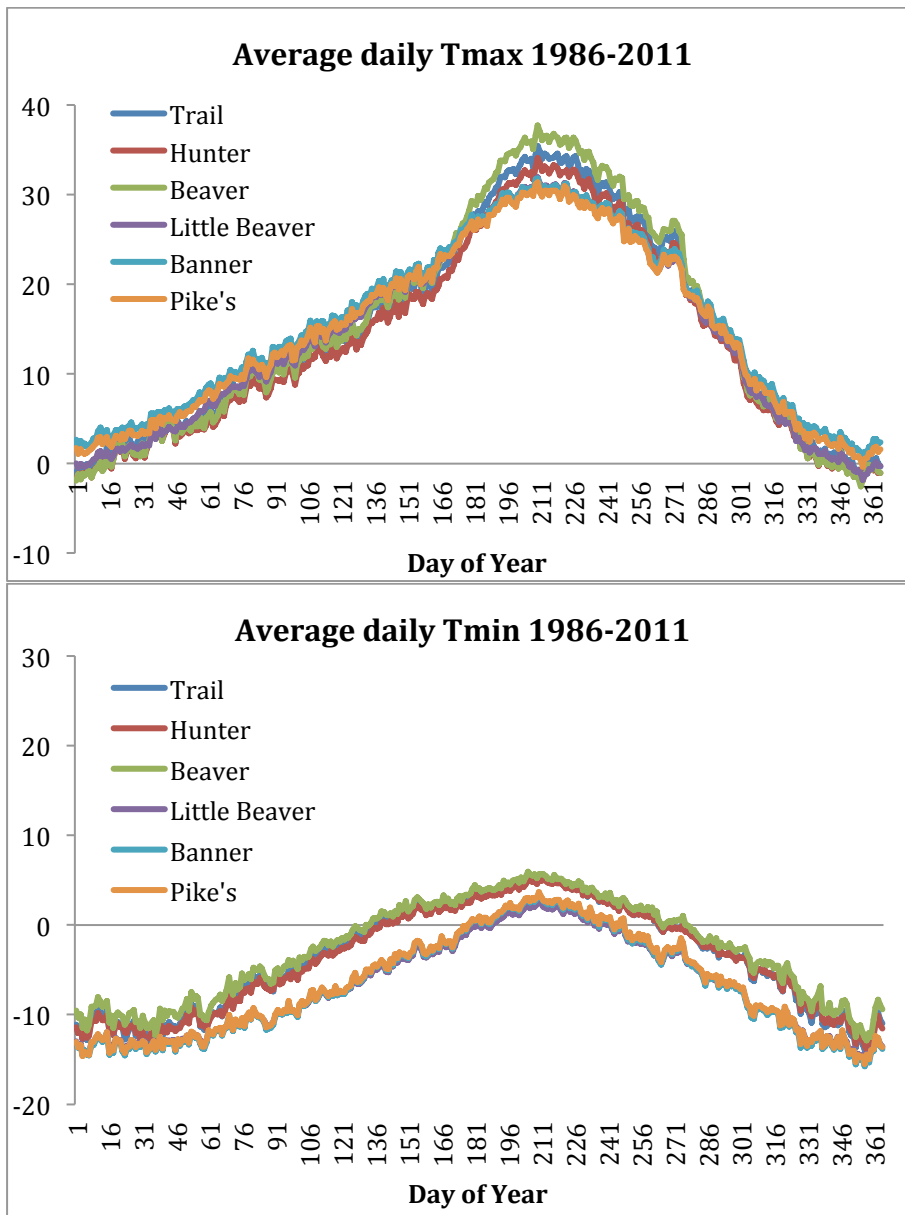Figure A.2. Average daily T$_{max}$ (top) and T$_{min}$ (bottom) in °C for six sites in the North Fork Boise River watershed. 1989-2011 daily SNOTEL station data from two stations were adapted to each site using 3 year local temperature records (Graham Guard station for Trail, Hunter and Beaver) and More's Creek Summit station for Little Beaver, Banner and Pike's).

A.3 Tree data collected from 9-11 plots at each of the six study stream reaches

Site	Species	# Trees	DBH (cm)		Height (m)		Crown depth (m)		Tree age (yr)		SW area (m^2)		Total SW area (m^2)
Banner	DF	18	3.1	(2.4)	2.2	(1.0)	2.2	(1.0)	23.7	(9.4)	0.001	(0.001)	0.024
	LP	140	5.2	(9.5)	3.4	(5.1)	2.4	(3.1)	17.1	(17.9)	0.006	(0.021)	1.922
	SAF	1	6.0		2.8		2.8		30.0		0.003		0.003
Beaver	DF	34	9.2	(13.6)	5.8	(7.5)	4.2	(4.8)	40.6	(35.7)	0.008	(0.016)	0.480
	LP	1	0.0		0.8		0.8		9.0		0.000		0.000
	PP	39	12.2	(19.9)	6.9	(9.9)	4.1	(5.0)	35.8	(34.4)	0.023	(0.049)	1.708
Hunter	DF	23	14.5	(19.8)	7.3	(8.7)	4.4	(5.5)	45.9	(65.1)	0.012	(0.029)	0.378
	ES	1	1.0		1.5		1.5		22.0		0.000		0.000
	LP	35	3.6	(8.8)	2.7	(2.6)	2.4	(1.7)	11.0	(3.9)	0.001	(0.003)	0.159
	PP	13	32.4	(19.9)	15.7	(8.1)	9.9	(4.3)	70.5	(43.9)	0.055	(0.039)	0.719
	SAF	9	9.6	(8.4)	5.9	(4.3)	5.4	(3.7)	21.0	(9.9)	0.003	(0.005)	0.026
Little Beaver	DF	6	5.5	(10.3)	2.8	(3.7)	2.2	(2.6)	31.3	(30.9)	0.005	(0.011)	0.042
	LP	94	8.2	(12.2)	5.6	(7.5)	3.8	(4.8)	27.1	(26.4)	0.007	(0.017)	1.181
	SAF	10	6.6	(5.3)	3.9	(2.8)	4.0	(2.8)	37.8	(9.6)	0.004	(0.004)	0.043
Pike's	DF	4	20.3	(21.6)	10.8	(10.0)	10.3	(9.5)	77.8	(54.1)	0.020	(0.024)	0.079
	ES	11	13.8	(22.5)	5.5	(7.0)	4.7	(5.9)	39.0	(38.4)	0.025	(0.052)	0.429
	LP	38	8.0	(9.5)	5.2	(6.4)	3.7	(4.3)	26.3	(24.3)	0.006	(0.013)	0.259
	PP	1	4.8		3.0		2.7		27.0		0.001		0.001
	SAF	5	3.1	(5.7)	2.9	(4.0)	2.7	(3.4)	26.1	(20.7)	0.002	(0.005)	0.030
Trail	DF	48	19.3	(25.0)	9.6	(12.1)	7.1	(8.6)	59.5	(58.4)	0.020	(0.034)	1.210
	ES	1	28.8		14.6		12.7		70.0		0.055		0.055
	LP	25	1.7	(5.8)	2.2	(4.0)	1.8	(2.2)	11.8	(13.8)	0.001	(0.007)	0.219
	PP	9	6.2	(16.6)	3.7	(7.6)	3.1	(5.8)	21.1	(44.4)	0.015	(0.046)	0.324
	SAF	57	10.7	(15.0)	5.8	(7.7)	5.0	(6.9)	40.2	(31.4)	0.006	(0.012)	0.368
All sites	DF	133	12.6	(19.1)	6.8	(9.2)	4.9	(6.4)	45.5	(48.8)	0.011	(0.025)	2.2
	ES	13	13.9	(21.7)	5.8	(7.0)	5.0	(5.9)	39.7	(37.2)	0.025	(0.050)	0.5
	LP	333	4.8	(9.5)	3.5	(5.2)	2.6	(3.2)	16.7	(18.3)	0.004	(0.015)	3.7
	PP	62	13.3	(20.4)	7.2	(9.7)	4.6	(5.4)	36.9	(39.6)	0.025	(0.048)	2.8
	SAF	82	8.9	(12.7)	5.0	(6.5)	4.5	(5.8)	35.8	(27.2)	0.005	(0.010)	0.5

Table A.1. Field measurements of tree data by site and species. Measurements include diameter at breast height (DBH, cm), total height (m), crown depth (m), tree age (years), and sapwood area (SW area, m^2). Values are averages, with standard deviation in parentheses, except for total sapwood area, which is a sum. Tree species are as follows: Douglas-fir (DF), Engelmann spruce (ES), lodgepole pine (LP), ponderosa pine (PP), and subalpine fir (SAF).

A.4. Simulated NPP vs precipitation falling in the growing season and the rest of the year

Simulated NPP is more strongly responsive to precipitation that falls during the growing season than it is to precipitation falling the rest of the year.
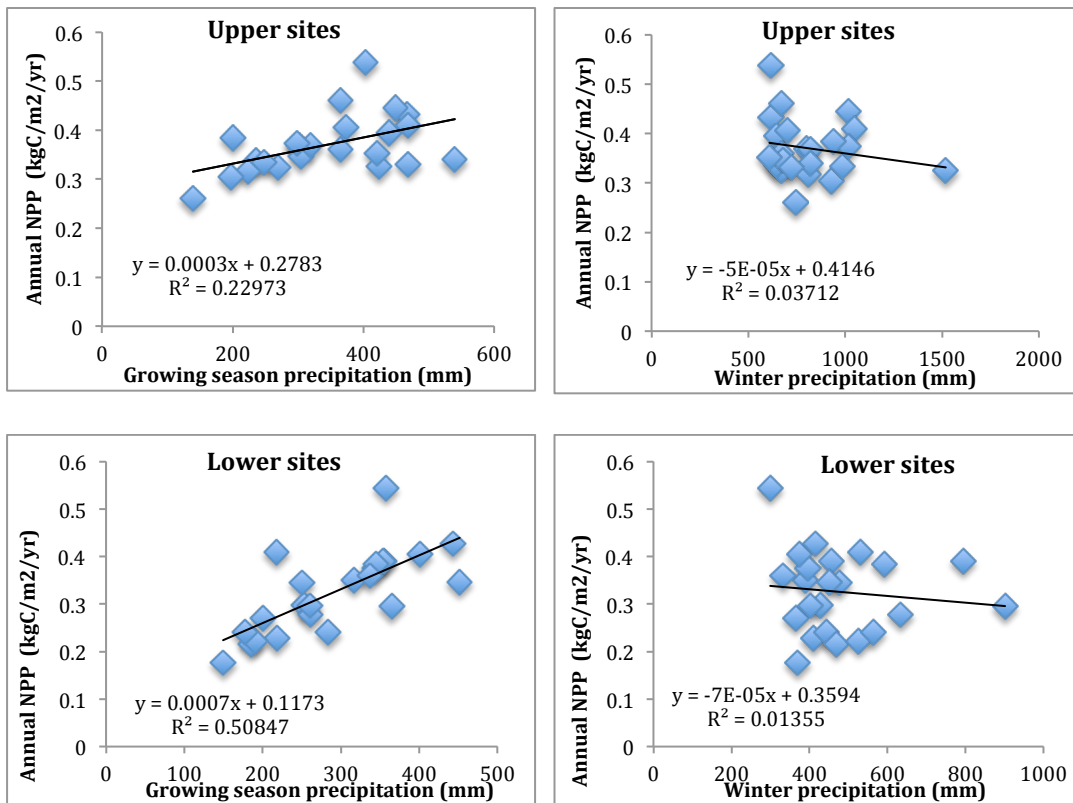

Figure A.3. Net primary productivity (NPP) vs. growing season precipitation (precipitation which fell on days 89-310) and precipitation which fell during the rest of the year ("winter precipitation"), by elevation group (Values are averages of three sites at each elevation).