DISSERTATION

WOLVES, ELK, AND WILLOWS: ALTERNATE STATES AND TRANSITION

THRESHOLDS ON YELLOWSTONE'S NORTHERN RANGE

Submitted by

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ABSTRACT

WOLVES, ELK, AND WILLOWS: ALTERNATE STATES AND TRANSITION
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The detection and prediction of alternate states of ecosystem configuration is of increasing importance in our changing world. Ecosystems may be perturbed by shifts in climate, or by human activity. Many perturbations to ecosystems can be reversed by reducing the initiating stressor. Sometimes shifts in ecosystem states are irreversible, and alternate configurations persist long after the initiating stressor is reduced. The reintroduction of wolves to Yellowstone National Park 17 years ago provided a rare opportunity to study whether the effects of predation could restore an ecosystem degraded by herbivory. Wolves were absent from the Yellowstone ecosystem for approximately 70 years. When wolves were absent, elk numbers increased and heavy herbivory degraded vegetation communities, particularly in riparian areas. Herbivory induced an alternate state in riparian vegetation, where willows, once dominant, were rare on the landscape and short in stature.

My dissertation research describes how the top-down effects of predation and herbivory interact with the bottom-up effects of resource availability in northern range riparian areas. My research addressed three questions: 1) How do water table depth and browsing intensity constrain willow height and annual production? 2) What is the role of landscape heterogeneity in determining spatial variation in the configuration of alternate states? 3) How have climate patterns interacted with trophic effects of ungulates and wolves over the last 40 years to shape willow canopy cover, growth, and establishment?

My work provides broad understanding of limitations to willow growth on the northern range, and revealed that wolf reintroduction has not restored riparian areas. A decade-long experiment showed that the effects of removing herbivory on willow height and production depend on water table depth. My second study showed that topography and temporal variation in water table depth influence willow height and growth more strongly than does herbivory. My third study found that

bottom-up effects of growing season length and precipitation drive patterns in willow height over four decades. Far less support existed for the effects of elk and wolves on willows through time. All of these studies led to the conclusion that bottom-up effects of resource limitation influence northern range willows more strongly than top-down effects of top predators or herbivores. Results from my research show that wolf reintroduction has not uniformly restored riparian areas along small streams on the northern range. Instead, water table depth, topography, and climate drivers influence willows more strongly than herbivory or wolves.

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1 Introduction

Lewontin (1969) and Holling (1973) developed the idea that ecosystems exist in states that are stable through time, and yet can be forced to transition into different configurations. The detection and prediction of alternative states and the transitions between them remains an important concept in ecosystem and community ecology four decades later. The ability to identify thresholds and feedbacks that push systems into one state or another have become increasingly necessary as global climate change pushes physiological limits of species and invasions and extinctions press ecosystems into new configurations (Vitousek et al., 1997; Scheffer et al., 2001).

Alternative states occur in a wide range of ecosystems including lakes, coral reefs, forests, shrublands, grasslands, and coastal marine ecosystems (see reviews by Scheffer et al., 2001; Beisner et al., 2003; Folke et al., 2004; Briske et al., 2005). Both biotic and abiotic factors my cause transitions between alternate states or reinforce existing states. In temperate lakes, the presence or absence of phosphorus can lead to a eutrophic or oligotrophic state (abiotic, Carpenter et al., 1999). In coastal marine ecosystems, overfishing of top predators has caused a potentially irreversible shift in which juvenile predators are out competed by their prey species (biotic, Walters and Kitchell, 2001). In African savannas, both abiotic and biotic forces dictate ecosystem configuration. There, grazing herbivores reduce the amount of vegetative fuel for fires, allowing trees to grow tall enough to escape vulnerability to fire. Reducing grazing allows grasses to accumulate and wildfires to persist on the landscape, along with tall trees (McNaughton et al., 1989; McNaughton, 1992; Rietkerk and vandeKoppel, 1997).

Identifying key feedbacks and thresholds within each state is imperative to understanding alternative states of ecosystems. A state is resilient if a perturbation pushes it away from its original configuration, but removing the perturbation allows the ecosystems to return to the original state (Holling, 1973; May, 1973). Alternatively, a large perturbation or change in environmental conditions may cause ecosystem reconfiguration that is then reinforced with new feedbacks. If the ecosystem does not return to the original state after the perturbation is removed, then the original

ecosystem state was not resilient. Alternative stable states occur when both alternate ecosystem states are resilient to perturbations. In the savanna example above, herbivore grazing caused an irreversible shift of grassland to forest, and therefore this system is not resilient to the impact of grazers.

Top-predators in many ecosystems control food web structure by reducing the abundance of herbivores or changing herbivore foraging behaviors. Reduced herbivory from either cause can increase net productivity by primary producers. Cascading trophic effects from top predators have been documented in both aquatic and terrestrial food webs around the world (Carpenter et al., 2008; Chase, 1996; Frank et al., 2005; Pace et al., 1999). Most examples of trophic cascades arise from removing predators from ecosystems, either intentionally or unintentionally (Estes et al., 2011; Paine, 1980; Myers et al., 2007; Schmitz et al., 2000). Far fewer examples have documented the ecosystem effects of reintroducing predators to their native ecosystems. Some have shown clear linear return of ecosystems to their original states (bass in a temperate lake,Mittelbach et al., 1995). Other studies found that removal of predators causes changes in ecosystem structure that are not reversed by predator reintroduction (spiders in meadows, Schmitz, 2004).

In this study, I focus on understanding how alternative stable states are created and reinforced in riparian areas of Yellowstone National Park. The removal and subsequent reintroduction of the gray wolf (*Canis lupus*) to Yellowstone offers a unique example of a long term perturbation that has been mitigated by reintroducing the predator. The absence of wolves led to dramatic degradation of vegetation communities caused by heavy herbivory by elk (Kay, 1997; Singer et al., 1994; Singer, 1995). My research explores whether wolf reintroduction has allowed disturbed riparian communities to return to their original state. Specifically, I investigated spatial and temporal variability in ecosystem states and the feedbacks that reinforced those states across a heterogeneous landscape.

Wolves were abundant in the Yellowstone area until the late 1800s, when they were heavily hunted for bounties and fur trading (Whittlesey and Schullery, 2011). Wolves were completely extirpated from Yellowstone around 1930. In the absence of a top predator, park management

culled the park's large elk (*Cervus elaphus*) herd until 1967 to maintain a relatively constant population size (Eberhardt et al., 2007). Park management adopted a natural regulation strategy starting in 1968. Lack of top-down control of the elk herd led to a five-fold increase in their population over the subsequent 25 years (Eberhardt et al., 2007). Heavy herbivory by elk during this time dramatically changed vegetation (Singer, 1995), particularly in riparian areas (Singer et al., 1994).

Riparian corridors support 80 percent of vertebrates during some stage of their life (Knopf et al., 1988). Willows (*Salix spp.*) are the dominant riparian plants in most montane ecosystems in the northern hemisphere. Willows provide numerous ecosystem services, from stabilizing stream banks and improving water quality with their roots (Wright et al., 2002), to providing habitat for song birds and food material to ungulates and beaver with their long stems (Medin, 1990; Baril et al., 2011). Willows covered most of the valley bottoms in the Northern Range during the 1920s (Warren, 1926; Meagher and Houston, 1999). Abundant, tall willow communities coincided with a high density of beaver colonies along small streams. After wolves were extirpated, heavy browsing pressure from elk in the absence of wolves led to declines in willow height and density on the northern range (Singer et al., 1994, 1998; Jonas, 1955; Kay, 1997). Willow decline, in turn, led to decreases in abundance of species that depend on them, in particular beaver (Jonas, 1955).

Beaver (*Castor canadensis*) and willow have a mutualistic relationship (Baker et al., 2005). Beavers use long willow stems for food and for building dams that interact with flooding and drought to benefit willows. Dams increase the magnitude of flooding both upstream and downstream along small streams (Westbrook et al., 2006), which aids in deposition of sediment farther from the stream channel. Willow seeds require bare moist sediment for germination (Cooper et al., 2006). Increasing the distance of sediment deposition increases the width of the riparian corridor by creating wider swaths of substrate available for willow establishment. Beaver dams also attenuate declining water table levels after the onset of late summer drought (Bilyeu et al., 2008). Higher water tables in late summer may lengthen the growing season by lessening willow drought-stress (Johnston et al., 2007).

Ungulate herbivory and the beaver-willow mutualism interact to create two alternate riparian ecosystem states along small streams on the northern range (Wolf et al., 2007). The ungulate-beaver-willow state occurs when ungulates and beaver both utilize the willow resource. Ungulate herbivory is low to moderate and beaver complexes are stable because a relatively small area of willows (4 ha, Peinetti et al. 2009) can sustain a beaver colony indefinitely. Positive feedbacks from beaver dams to willows increase the stability of this state. High levels of elk herbivory during the period of wolf absence on the northern range pushed the ecosystem into the alternate state, the ungulate-grassland state. Elk can out compete beaver for willow resources by continuously browsing and creating hedged plants. Short willows are unsuitable for beaver food caches and building material. Insufficient food may cause beaver to abandon complexes in search of more suitable habitat. Wolf et al. (2007) hypothesized that this state may be stabilized by the abandonment of beavers. Relatively small changes in water table depth caused by stream incision in the absence of beaver dams could have large impacts on willow stature and growth (Bilyeu et al., 2008). Therefore, reducing the stressor that caused state transition (browsing) may not allow the ecosystem to return to the original ungulate-beaver-willow state because the absence of beaver dams has led to bottom-up limitation of willows by water table depths (Bilyeu et al., 2008).

Studies have suggested that the restoration of wolves to Yellowstone has restored a trophic cascade that has released willows and other vegetation from herbivory and that the system has recovered to its original state (Ripple et al., 2001; Ripple and Beschta, 2003; Beschta and Ripple, 2010b, 2007; Beyer et al., 2007; Frank, 2008). Others have not found support for indirect positive effects of wolves on vegetation (Creel and Christianson, 2009; Kauffman et al., 2007, 2010; Kauffman, 2011). My research seeks to unify these disparate views by studying the distribution of current riparian ecosystem states across the northern range and describing the abiotic and biotic factors limiting state transition. I investigated feedbacks that reinforce the ecosystem in its current state and explored how these feedbacks varied across a heterogeneous landscape. Specifically, I addressed three questions: 1) How do water table depth and browsing intensity constrain willow height and annual production? 2) What is the role of landscape heterogeneity in determining

spatial variation in the configuration of alternate states? 3) How have climate patterns interacted with trophic effects of ungulates and wolves over the last 40 years to shape willow canopy cover, growth, and establishment? In each of the three studies that follow, I collected data on willow responses in the field and developed Bayesian hierarchical models to describe temporal and spatial variation in willow responses. Together, these studies provide a broad perspective on the role of wolf reintroduction in shaping willow communities on Yellowstone's northern range. My findings will add to growing ecological understanding of alternative states, thresholds, and transitions in heterogeneous landscapes.

2 Trophic and hydrologic controls on restoration of riparian ecosystems in Yellowstone

The loss of predators from food webs has degraded ecosystems throughout the world (Terborgh et al., 2001; Myers et al., 2007). Although reintroduction of predators can reverse effects of their loss (Estes and Duggins, 1995; Paine et al., 1985), this reversal may not occur when the loss of predators from food webs create conditions that are not easily changed by predator restoration (Schmitz, 2004; Chase, 2003). A central challenge for restoring ecosystems is to understand when and why the loss of predators initiates feedbacks that stabilize the conditions created by their absence (Suding et al., 2004).

The reintroduction of the gray wolf (*Canis lupus)* to the landscapes of the northern range of Yellowstone National Park created an unprecedented opportunity to understand how restructuring a food web acts to change the state of an ecosystem. Wolves were extirpated from Yellowstone during the early twentieth century. Their loss from the ecosystem is believed to have caused a state-change in riparian zones as a result of excessive browsing on the dominant shrub, willow (*Salix spp.*), by a population of elk released from control by predators (Singer et al., 1994; Singer and Cates, 1995).

Willow communities and populations of beaver interact symbiotically in ecologically complete, riparian ecosystems. Riparian zones dominated by willows support biological diversity far dispro-portionate to their area by providing habitat for many species of herbaceous plants as well as birds, insects, and mammals (Naiman et al., 1993; Wright et al., 2002). By offering essential food and dam building materials for an ecosystem engineer, the beaver (*Castor canadensis*), willows form a critical link in the riparian disturbance regime (Baker and Cade, 1995). Disturbance by beaver, in turn, creates conditions particularly well-suited to the life histories of willows (Baker et al., 2005).

Historically, beaver dams punctuated the stream network on the northern range (Warren, 1926). A third of mainstream reaches have evidence of sediment deposition related to beaver dams (Persico and Meyer, 2009), a process that has been occurring for millennia (Wolf et al., 2007). Excessive browsing of willows was implicated in the disappearance of beavers from small streams

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during the twentieth century (Jonas, 1955; Kay, 1997; Ripple and Beschta, 2004b). The loss of beavers from the northern range created indirect, harmful feedbacks on willows, amplifying the direct effects of herbivory by elk. The loss of beaver ponds from the stream network lowered water tables and compressed the area of bare, moist substrate needed for willow establishment. Unimpeded by beaver dams, many northern range streams increased in velocity, downcutting channels and disconnecting flood plains from their adjacent streams (Wolf et al., 2007; Persico and Meyer, 2009). Thus, the loss of wolves from the food web caused multiple changes in the ecosystem's biological and physical processes, creating an alternate state where herbaceous vegetation dominated riparian corridors, where willows were predominately sparse in distribution and short in stature, and where beaver, once abundant, were absent (Wolf et al., 2007).

Wolves were reintroduced to the northern range in 1995 to restore a complete food web. The growth of the wolf population during 1995-2010 coincided with a 70 percent decline in elk numbers. Observations suggest that restoration of wolves altered plant communities on the northern range via a trophic cascade (Frank, 2008; Ripple and Beschta, 2004a; Beyer et al., 2007). The trophic cascade hypothesis holds that by modifying foraging behavior of elk and by reducing their abundance, wolves released plants from top-down control by elk, allowing dramatic recovery in communities degraded by historically excessive herbivory. In particular, it has been argued that trophic effects of wolves have restored willow communities by moderating browsing and allowing willows to grow tall (Beschta and Ripple, 2007, 2010b).

Restoring an ecologically complete ecosystem on the northern range requires the return of tall willow communities to riparian zones and the reestablishment of disturbance by beaver. There is a clear threshold of willow height needed for ecosystem recovery– willow stands must exceed about 2 m in height (Keigley et al., 2002; Beschta and Ripple, 2007). This threshold is important because stems taller than 2 m can exceed the reach of browsing ungulates, thereby providing a reliable seed source for willow establishment and preventing complete consumption of the plant during severe winters (Keigley et al., 2002). Moreover, beavers need tall willows in stands with high biomass to provide food and structural materials for dam building (Baker et al., 2005).

Here, I test the hypothesis that moderating browsing alone allows willows to recover to their threshold heights relative to the alternative hypothesis that recovery depends on moderating browsing *and* restoring a beaver-modified hydrologic regime. My hypotheses are motivated by the following ideas. Although excessive browsing by elk released from predation by wolves was responsible for degrading willow communities, the attendant changes in the ecosystem, notably the loss of beaver dams, may have created conditions that cannot be rapidly reversed by restoring wolves to the food web. If reducing top-down effects of browsing is sufficient to allow willows to reach the height threshold for recovery, then there is evidence for the operation of a linear trophic cascade. Alternatively, if recovery depends on the interplay of trophic and hydrologic effects, there is evidence that a complete ecosystem cannot be quickly restored by reintroduction of wolves. This alternative hypothesis holds that the current state of the riparian ecosystem is determined by the interaction of top-down control from herbivory and bottom-up control by beaver-modified hydrology. Moderating elk herbivory by restoring wolves may be a necessary but insufficient condition for ecosystem restoration.

To test these hypotheses, I continued a ten-year, factorial experiment on the northern range ((Bilyeu et al., 2008), Figure2.1A, B). I measured willow height growth and biomass accumulation in response to two levels of water table depth (dammed and undammed) and two levels of herbivory (browsed and unbrowsed, Figure 2.1) at four replicated sites that were historically dammed by beaver on Yellowstone's northern range (Bilyeu et al., 2008). Experimental units were four plots per site, each 200 m^2 in area. Browsing was eliminated from half of the plots by surrounding them with 2.4 m high fences. Availability of water was enhanced on half of the plots by constructing dams that raised water tables adjacent to streams, simulating the effects of beaver. The two treatments (exclosures and dams) were crossed to total four plots per site, including a control representing ambient conditions.

In each plot, we quantified willow growth and browsing. Approximately 10-20 individuals per plot, representing three species (*Salix boothii*, *S. geyeriana*, and *S. bebbiana*), were marked permanently and monitored each year. In spring and fall, willow stature was recorded as height of

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the tallest stem perpendicular to the ground surface. In fall, I assessed annual above ground net primary production at peak standing crop by measuring lengths of a subset of shoots of the current year and converting them to mass using length-mass regressions (Bilyeu et al., 2008). During spring, these same stems were assessed for biomass remaining to estimate overwinter tissue loss from browsing and twig shedding (Bilyeu et al., 2007). I define net accumulated biomass as the current annual growth remaining after overwinter tissue losses (SOM 2.1).

A decade of total protection from browsing was not sufficient to allow willows to grow to threshold heights unless the water table was also raised. Mean heights of plants within exclosures with ambient water tables were well below the recovery threshold (Figure2.2A) and their growth rates were declining (Figures 2.2A, 2.3, S2.7). Exclosed, undammed willows were only nominally taller than browsed, undammed willows (mean = 159, 95% credible interval = [147, 172] cm vs 123 [114, 134] cm) and accumulated no additional net production (140 [109,181] g vs 130 [101,166] g, Figure 2.2A, C). The effect of exclosures on height of undammed willows was small, and the effect on their biomass was undetectable (Figure 2.2B, D).

The effect of removing browsing depended on the availability of water. Heights of dammed, exclosed plants exceeded the recovery threshold (244 [227,263] cm, Figure 2.2A). After ten years, browsed willows with raised water tables were 40 percent taller and accumulated 86 percent more biomass than browsed willows with ambient water tables (174 [161, 189] cm and 242 [189, 305] g vs 123 [114, 134] cm and 130 [100, 166] g, Figure 2.2A, C). The effect size of the exclosure + dams treatment on willow height was more than double the effect of removing browsing alone (Figure 2.2B). The effect size of the dam treatment on willow biomass accumulation was more than seven times greater than the effect size of removing browsing (Figure 2.2 D), offering clear evidence that bottom-up control of willow productivity by hydrologic conditions exceeded top-down control by herbivory.

According to the trophic cascade hypothesis, willows in my control plots should have grown rapidly because they were released from effects of browsing by behavioral and numeric effects of

wolves on elk. However, average heights of control plants increased only 23 cm in ten years and remained far below the recovery threshold (Figure 2.2A).

Willow heights in my experimental plots were representative of current variability in heights observed across sites historically occupied by beaver on the northern range (Figure 2.4). The frequency distribution of 2010 willow heights from 23 sites across the northern range was indistinguishable from the distribution of heights observed on the northern range prior to wolf reintroduction (p = 0.091, Figure 2.4, (Singer et al., 1994)). Tall willows have always been found on the northern range (Singer et al., 1994), but their abundance relative to short willows has not changed following wolf reintroduction.

Landscape-level restoration of riparian zones requires restoring physical structure contributed by tall willows as well as restoring the disturbance regime, notably damming of stream channels by beaver. I showed that heights of willows needed for restoration of an ecologically complete ecosystem occurred only when browsing was removed and water tables were elevated, refuting the hypothesis that a simple, linear trophic cascade has restored riparian zones across the northern range. Release of willows from top-down control alone is not adequate for restoration of riparian zones because alterations of the disturbance regime resulting from the loss of beaver from the small stream network have lowered water tables on floodplains, thereby amplifying bottom-up controls on willow growth. The current state of the landscape is resilient to the restoration of wolves because the absence of beaver opposes the return of tall willows and the absence of tall willows opposes the return of beaver.

Patches of willows showing increases in height after the restoration of wolves (Beschta and Ripple, 2007, 2010a) are not inconsistent with my findings. My experimental results imply that willows with access to shallow ground water would have experienced rapid increases in height during the past decade. Willows near my experimental plots that obtained > 70% of their water from ground water resembled height of willows in my experimental, dammed plots (Johnston et al., 2011). Other authors showed that sites occupied by tall willows had greater soil moisture and shallower groundwater than nearby short willow sites (Tercek et al., 2010). However, many

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areas of the current landscape with perennial shallow ground water, such as ground water seeps and portions of large river floodplains, are not suitable for beaver dams.

The elimination of wolves from Yellowstone nearly a century ago caused an alternative state to develop in riparian zones across the northern range landscape, but wolf reintroduction has not uniformly restored the historic state of the ecosystem. Beaver have not recolonized any of the sites that were active complexes in the 1920s (Warren, 1926). Seventeen years after restoration of wolves, heights of willows in my control plots (Figure 2.2) and at similar sites across northern range (Figure 2.4) remain far below the 2 m threshold needed for restoration. The frequency distribution of willow heights closely resembles the distribution observed before wolves were reintroduced (Figure 2.4). Landscape level restoration of historic conditions in willow communities is opposed by hydrologic changes in the riparian zone caused by beaver's continued absence. My results amplify the fundamental importance of conserving intact food webs because changes in ecosystems caused by removal of apex predators may be resilient to predator restoration.

Acknowledgments

2.1 Supporting Material

Materials and Methods

Experimental Treatments

Details on selection of sites and application of treatments were described by Bilyeu et al. (Bilyeu et al., 2008).

I assessed overwinter biomass losses in unfenced and fenced plots. In unfenced plots, overwinter losses included mass lost to browsing and mass lost to shedding of new shoots (Raven, 1992). In fenced plots, overwinter losses consisted of shedding only. Overwinter loss (L) is defined as $L = 1 - \frac{m_{plot}^{spring}}{m_{plot}^{fall}}$ where m_{plot}^{fall} is the sum of current annual growth on all tagged stems in a plot assessed at the end of the growing season and m_{plot}^{spring} is the portion of that growth that has not been removed by browsing over the winter (Bilyeu et al., 2007). Current annual growth (CAG) was estimated by measuring lengths of a subset of new shoots on tagged stems (as described in Bilyeu et al. (Bilyeu et al., 2008)). Lengths were transformed to mass using a length/mass regression developed from 1200 shoots: log(mass) = -3.88 + 1.18*log(length) (R^2=0.92). In spring, I used the length/mass equation for unbrowsed shoots and measured browsed shoot diameters at the base and at the browse point. I converted browsed stem measurements to mass using an equation developed from 180 browsed shoots: log(mass) = -4.52 + 2.54*log(base diameter) + 0.95*log(base diameter - browse diameter) (R^2=0.85).

In order to differentiate between shedding and browsing in unfenced plots, I estimated the proportion of CAG shed from whole stems that were not browsed. This subset of stems in browsed plots changed each year, depending on which stems ungulates selected for browsing. Using this unbrowsed subset I estimated overwinter loss using the same methods as above. Together, browsed and unbrowsed stems in unfenced plots, and unbrowsed stems in fenced plots, represented the effects of my experimental treatments on shoot shedding and browsing (Figure S2.5).

I monitored the effects of dams on water table levels in monitoring wells in dammed and undammed plots over 10 years. Water tables in undammed plots averaged 121 +/- 6 (+/-1 SEM)

cm below ground in July. Dams increased water tables to 88 +/- 6 cm in July, a difference of 33 +/- 6 cm on average. Presence of dams has not affected water table levels in adjacent undammed plots. In only two years (2008 and 2009) undammed July water table depths were significantly different from pre-treatment depth (p<0.001), and this was attributed to relatively high flow and late run-off in those years.

Treatment effects after 10 years

I measured two responses: willow height (for years 2001 to 2010) and accumulated biomass (for years 2002 to 2005, and 2007 to 2010). I estimated accumulated biomass of individual plants by summing the net current annual growth in each year that I had browsing information:

$$M_{i,t} = M_{i,t-1} + m_{i,t}^{spring} \tag{2.1}$$

where $M_{i,t}$ is the mass of plant i at time t and is a function of its mass at the previous time step and $m_{i,t}^{spring}$ represents the remaining current annual growth after winter browsing and twig losses for plant i in the current year. I compared this accumulated mass to the height of the plants in the fall of 2010.

I examined treatment effects on height and biomass responses in 2010, the final year of observations. Thus, heights and biomasses observed during this year included the cumulative effects of a decade of treatment. To examine effects of treatments I used a Bayesian hierarchical model with a process model that predicted the true mean response of willows and a data model that included sampling variation.

The true, mean predicted height of plot j is a function of whether the plot was unbrowsed or dammed or both:

$$log(\mu_j^{pred}) = B_0 + B_1 R_j + B_2 W_j + B_3 R_j W_j \tag{2.2}$$

where R indicates whether the plot experiences herbivory and W is whether the plot is dammed.

Because height and mass are strictly positive values I modeled observations of plant height as log-normally distributed around the predicted mean for the plot such that:

$$\log(H_{ijk}^{obs}) \sim \text{Normal}(\log(\mu_j^{pred}), \sigma^2) \tag{2.3}$$

I constructed this same model using accumulated mass (M) as the response variable. I did not include additional covariates in my model such as site or species effects. I chose to pool across these effects to describe the mean response of willow stands on the northern range. I note that species specific responses were important in previous analyses of willow height (Bilyeu et al., 2008), however, my current analyses indicated that credible intervals on species differences strongly overlapped zero for all species pairs.

Treatment effects through time

In addition to modeling the decadal, accumulated effects of the experimental treatments on willow height recovery, I also modeled their effects through time using hierarchical Gompertz state-space models (Clark and Bjornstad, 2004). Sixteen states were predicted by site and treatment means through time, with a time-varying growth rate. The general form of the process model is:

$$\log(Y_{jk,t}^{pred}) = a_{jk} + c_{jk} * t + \log(Y_{jk,t-1}^{true}) \tag{2.4}$$

where $Y_{jk,t}^{pred}$ is the predicted height of site j, treatment k, at time t, a_{jk} is the growth rate for the state at time 0 (year 2001), c_{jk} is the site and treatment specific slope of the growth rate through time, and $Y_{jk,t-1}^{true}$ is the true unobserved height at the previous time step.

The true unobserved state of log(Y) is a normal random variable with a mean of the predicted state and a process variance:

$$\log(Y_{jk,t}^{true}) \sim Normal(\log(Y_{jk,t}^{pred}), \sigma_{proc}) \tag{2.5}$$

The initial growth rate for each state is a function of a site-specific intercept and treatment effects:

$$a_{jk} = a_{0,j} + a_1 R_k + a_2 W_k + a_3 R_k W_k \qquad (2.6)$$

The site-specific intercept is a random effect with a shared mean and variance $a_{0,j} \sim Normal(\mu_a, \sigma_a)$. Because residuals from constant growth rate models showed strong increasing trends through time, I fit a temporal trend in growth rate. The slope term was modeled as a function of site and treatment with a similar form as in 2.6:

$$c_{jk} = c_0 + c_1 R_k + c_2 W_k + c_3 R_k W_k \qquad (2.7)$$

A site-specific intercept was described by $c_{0,j} \sim Normal(\mu_c, \sigma_c)$. Individual observations of each plant i within each site-treatment combination at each time-step are normally distributed around the true-mean of the site-treatment combination, with an observation variance:

$$log(Y_{ijk,t}^{obs}) \sim Normal(Y_{jk,t}^{true}, \sigma_{obs}) \qquad (2.8)$$

Parameter estimation

I estimated all parameters using Bayesian methods. Models were fit using JAGS within R (Plummer, 2011). To ensure convergence, I ran three chains simultaneously for 5000 iterations, after a burn-in of 35000 iterations. In all cases, I fit the full model, and dropped terms when estimated coefficients were centered on zero, and refit the reduced model to obtain final parameter estimates. I used non-informative priors for all parameters (normal priors for all regression coefficients and global random effect means, uniform priors for standard deviation of site random effects, and gamma priors for precisions (inverse of variance) (Gelman, 2006).

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Comparing treatment effects to observational willow height

I compared heights of willows in my experimental plots with willow heights across the northern range to assure that my experimental results were reasonably representative. I measured 113 willow heights at 23 randomly selected sites at the end of the 2010 growing season. Sites were selected randomly from a population of stream reaches that were either known to have been occupied by beaver at some time during the 20th century, or of appropriate size for damming by beaver (Baker and Hill, 2003). Potential study streams were selected based on gradient (<10%) and stream order (3rd and 4th order), and I used a spatially balanced random sampling algorithm (RRQRR, (Theobald et al., 2007)) to select from the population of potential sites. Subplots were established within each site, and willows within subplots were selected at random for permanent marking. I compared these willow heights with willow heights in my experimental treatment, and with pre-wolf willow heights measured by Singer et al. in 1990 (Singer et al., 1994). I limited my comparison to Singer's data to those species that also appeared in my 2010 data set, resulting in 164 willows at 14 different sites across the northern range measured in 2001. His site descriptions are provided in (Singer et al., 1994). I compared the past and current distributions of willow height using a two-sided Kolmogorov-Smirnov test.

Table 2.1: Posterior mean and 95 percent credible intervals for height time-series model parameters

parameter	mean	.025	.975
μ_a	-0.012	-0.082	0.069
σ_a	0.053	0.01	0.217
a_1	0.103	0.072	0.137
a_2	0.068	0.035	0.099
μ_c	0.015	0.006	0.025
σ_c	0.005	0.0002	0.0201
c_1	-0.021	-0.029	-0.013
c_2	-0.014	-0.022	-0.007
c_3	0.006	-0.00004	0.012
σ_{proc}	0.0008	0.0019	0.0004
σ_{obs}	0.086	0.092	0.082

Figure 2.1: Study system and overview. A) We built fences to exclude browsing and B) artificial beaver dams to raise water tables.
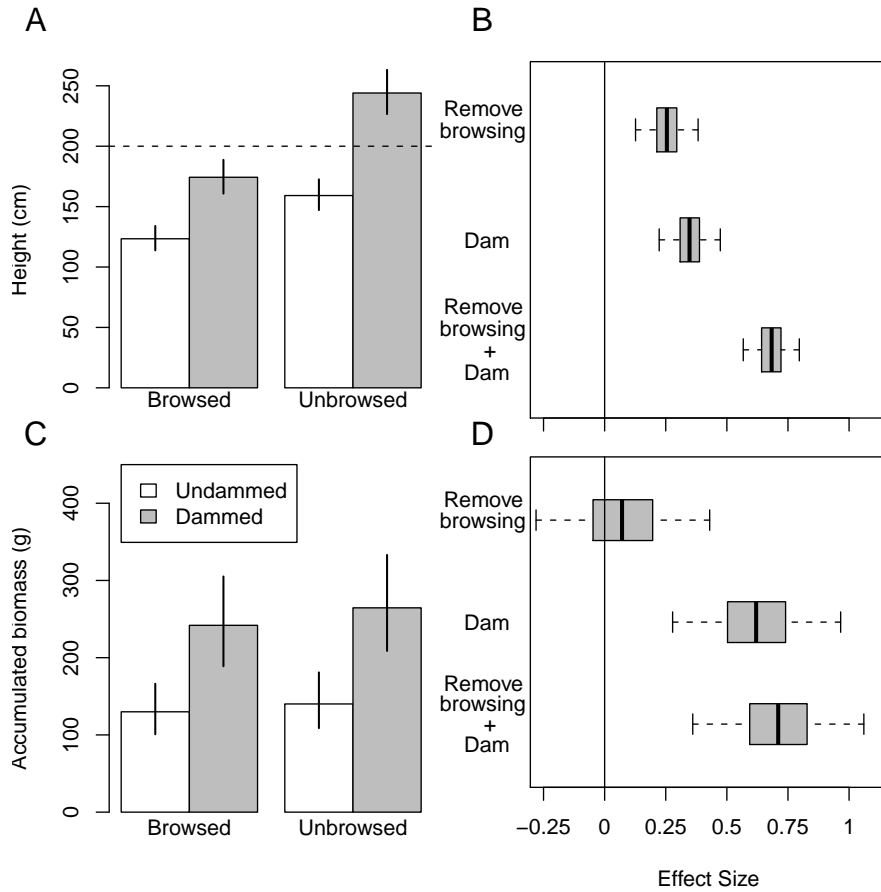
Figure 2.2: Willow responses after 10 years. A) Bars indicate posterior mean heights with error bars representing 95 percent credible intervals. Unbrowsed willows were taller than browsed willows, but raising water tables using simulated beaver dams increased height more than removing browsing did. Unbrowsed, dammed willows exceeded the 2 m height threshold (dashed line). B) We calculated effect size as natural log of the posterior mean height of plants in the treatment divided by the posterior mean height of control plants. Heavy line = mean, horizontal gray bars = 50 percent credible intervals, whiskers = 95 percent credible intervals. Dams and browsing removal had similar effects on height after 10 years. Dams increased the magnitude of the effect of browsing removal. C) Accumulated biomass over eight years showed no difference between browsed and unbrowsed plots. Biomass in dammed plots was more than double biomass in undammed plots. D) Effect size of dams on accumulated biomass was seven times greater than effect size of exclosures.
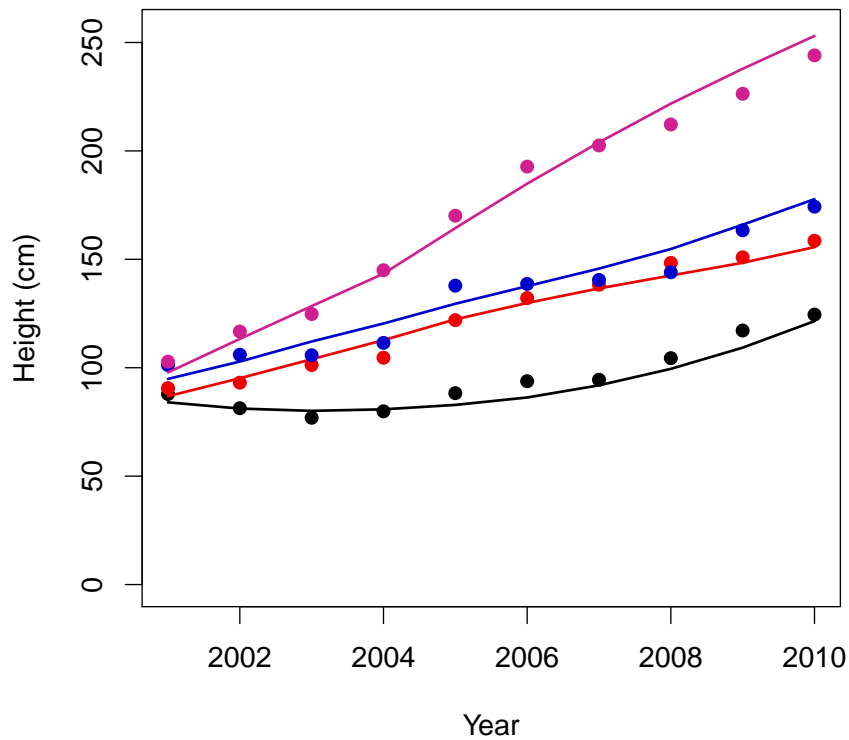
Figure 2.3: Willow height from 2001 to 2010. Lines indicate posterior means of the estimated true states, points represent observed means (browsed, undammed (control) = black; unbrowsed, undammed = red; browsed, dammed = blue; unbrowsed, dammed= magenta). Although all treatments showed increases in height through time, rates of growth were increasing in both browsed plots and decreasing in unbrowsed plots (see Supplementary Material).
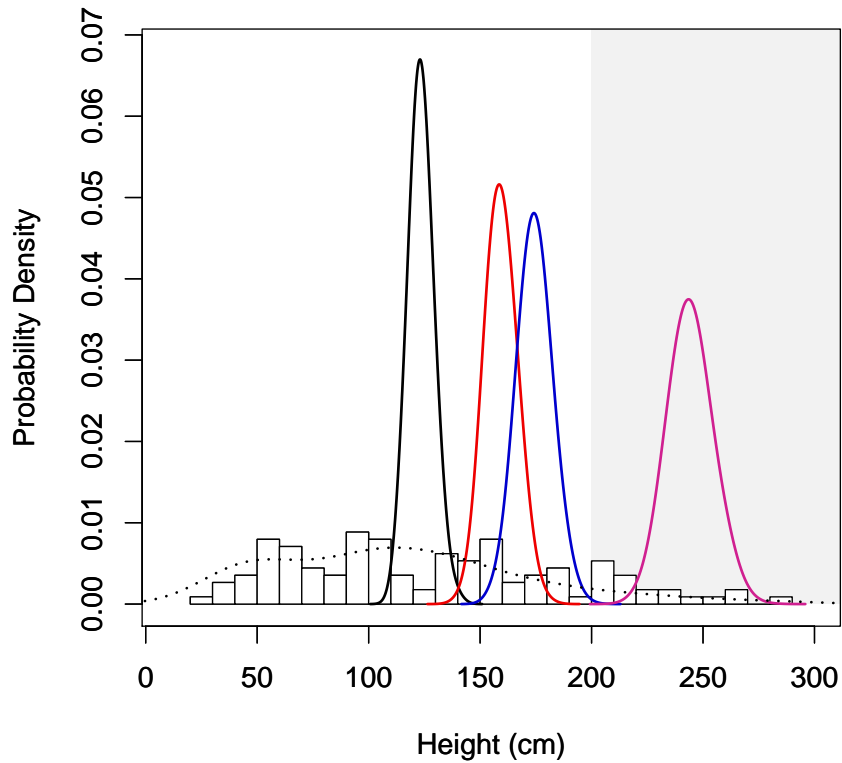
Figure 2.4: Distributions of willow height on the northern range. Normalized histogram represents end-of-growing-season heights of 113 permanently marked willows observed on the landscape at 23 randomly selected sites with historic or potential for beaver damming (see Supplementary Material). Dotted line represents kernel density of end-of-growing-season heights for 254 willows at 14 different sites measured before wolf reintroduction by Singer et al. in 1990 (Singer et al., 1994). Solid lines indicate posterior distributions of mean height at the end of 2010 growing season in experimental plots; colors as in Figure 2.3. Grey shaded area indicates 200 cm recovery threshold.
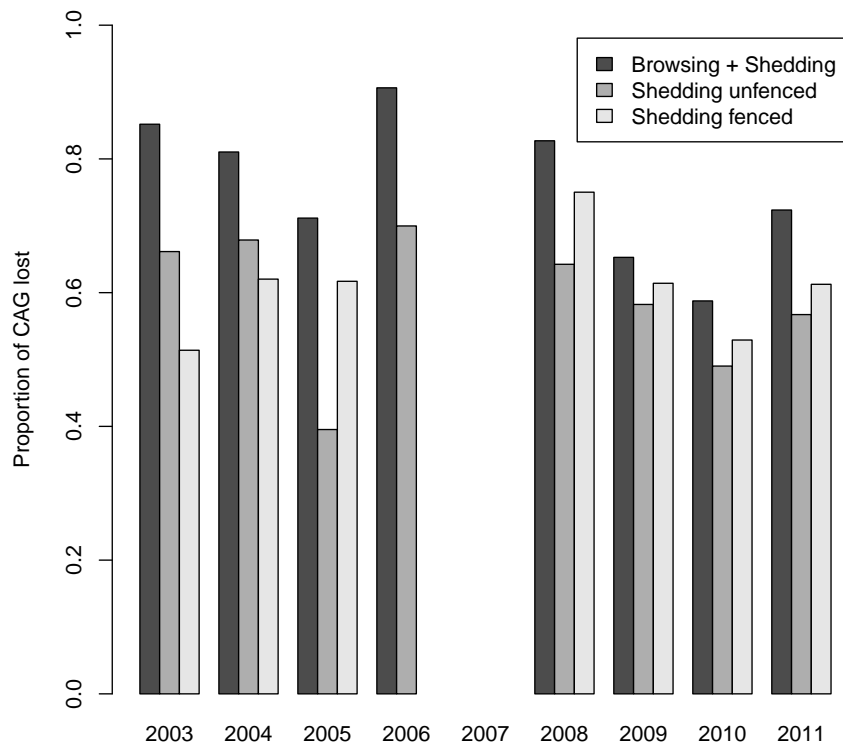
Figure 2.5: Overwinter losses to browsing and shedding. Plot-level proportion of current annual growth lost to shedding or browsing, averaged over sites and dam treatments. Fenced plots are missing in 2006 and all plots are missing in 2007 due to a break in data collection.
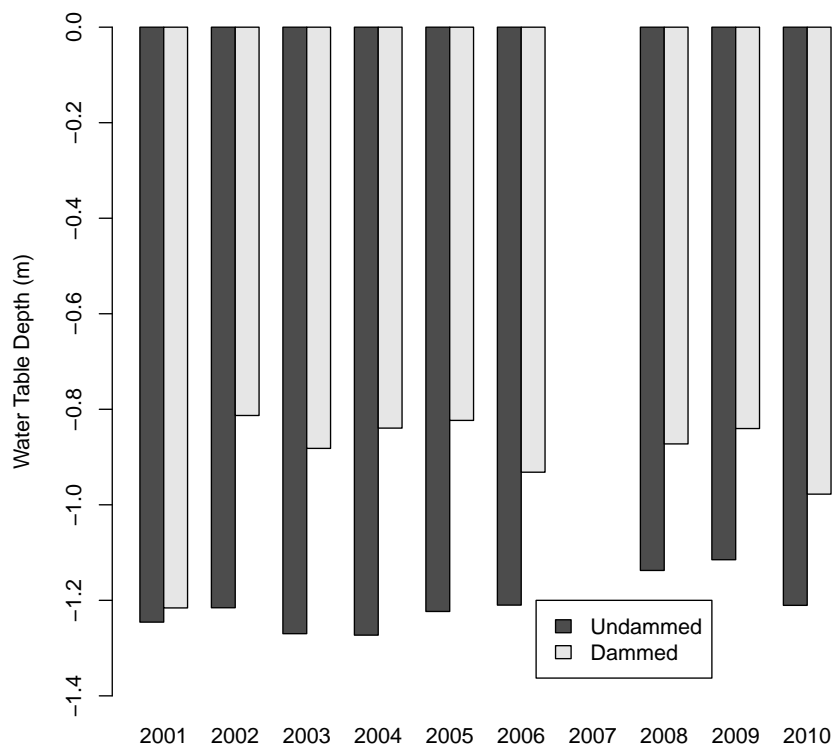
Figure 2.6: Dam effects through time. July water table depths, averaged across wells, sites, and plots, for dammed and undammed treatments. 2001 depths indicate pre-treatment water tables. Dark gray bars are undammed plots and light gray bars are dammed plots.
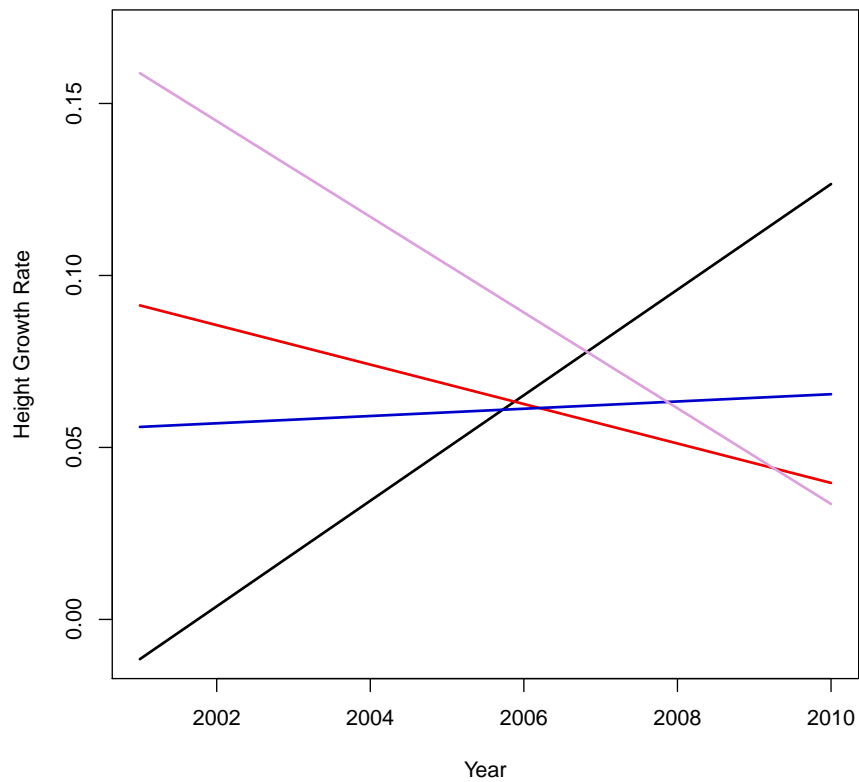
Figure 2.7: Growth rates of height through time as a function of experimental treatments. Lines represent posterior means of mean growth rate across sites by treatments: colors as in Figure 2.3. Growth rates declined for both unbrowsed plots and increased for both browsed plots over the ten years.

3 Spatial variation in riparian landscape configuration on Yellowstone's Northern Range

3.1 Introduction

Lewontin (1969) and Holling (1973) developed the idea that ecosystems can exist in multiple states of organization, states that can shift abruptly one to another. Since then, a large body of evidence reinforced their ideas by showing that ecosystems can be moved among alternative configurations by changes in disturbance regimes, climate, or the composition of food webs (Scheffer and Carpenter, 2003; Scheffer, 2009). Alternative states have become a particularly important organizing concept in ecology because human actions frequently push ecosystems well beyond their historic ranges of variation. Ecosystem restoration depends on understanding controls on these state transitions.

Landscape heterogeneity is one important factor driving state transitions. Theory portrays alternative states as homogeneous; ecosystems are predicted to exist in one state or another, with state changes occurring uniformly over space. However, some of the best known empirical examples of state transitions show marked spatial variation. For example, sea otters off the west coast of Vancouver Island prey on urchins, causing a trophic cascade that releases kelp forests from otherwise heavy herbivory (Estes and Duggins, 1995; Watson and Estes, 2011). In areas where otters have been continually present, urchins are predictably absent and kelp forests dominate. In areas continually without otters, urchins are abundant and kelp are absent. However, the rates of transition between these two stable states, occurring when otters are excluded, or invade previously unoccupied areas, are highly variable over space (Watson and Estes, 2011). Transitions occur rapidly in some areas, while change is very slow in other areas (Watson and Estes, 2011).

The reintroduction of the gray wolf (*Canis lupus*) to the northern range of Yellowstone National Park provided an unparalleled opportunity to understand how perturbing a food web caused state change on a heterogeneous landscape. In particular, it created a natural experiment well-suited to understanding sources of spatial heterogeneity in state transitions. Wolves are top predators whose presence or absence may exert cascading effects on lower trophic levels. Wolves were extirpated

from Yellowstone during the 1920s, and were absent until park management reintroduced them in 1995. During the 75 years wolves were absent, Yellowstone's largest elk (*Cervus elaphus*) herd grew five fold (Eberhardt et al., 2007). Intense herbivory by the expanding elk population had dramatic effects on woody deciduous plants. In particular, heavy elk herbivory created an alternate state in northern range riparian areas by reducing willow stature and density (Wolf et al., 2007).

Willows (*Salix spp.*) are the dominant shrubs in montane riparian zones of Western North America and they form a critical link in riparian disturbance regimes through their mutualism with an ecosystem engineer, the beaver (*Castor canadensis*). Beaver use tall willow branches for food and dam building materials (Baker and Hill, 2003). Willows along small streams benefit from beaver dams because dams raise water tables, thereby increasing water availability for willows. Beaver dams also promote flooding, which deposits sediments on the flood plain and creates bare surfaces required for establishment of willow seeds (Cooper et al., 2006). This beaver-willow mutualism led to tall, dense willow communities along the small stream network of Yellowstone's northern range during the 1920s(Warren, 1926). Tall, dense willows tolerate low to moderate ungulate browsing, creating an ecosystem state where elk, beaver, and willows coexist. This ungulate-beaver-willow state is stable because the tips of tall willow stems are past the reach of ungulates, and willow have sufficient water to attenuate browsing by ungulates and utilization by beaver.

Heavy browsing by ungulates, released from predation by wolves, converted tall willow stands to short willow stands in Yellowstone. Reduction in willow height and abundance was implicated in beaver's disappearance (Jonas, 1955; Baker et al., 2005; Kay, 1997). Beaver require tall willows for food and dam building; short willows are insufficient (Baker and Hill, 2003). Overbrowsing of willows and the lack of positive feedbacks from once abundant beaver led to a riparian ecosystem state where herbaceous vegetation dominated and willows were short and sparse (Singer et al., 1994). This elk-grassland state has been reinforced by ungulate herbivory because short willows can be kept hedged by even modest browsing (Baker et al., 2005). The absence of beaver dams on small streams led to deepening of water tables and downcutting of channels along more than one-fourth of reaches that previously had beaver dams (Persico and Meyer, 2009). These changes to

stream geomorphology decreased water availability to willows at all life stages, further hindering their growth and reproduction (Wolf et al., 2007).

Wolves were reintroduced to Yellowstone in 1995. Rapid growth of the wolf population during the subsequent 15 years coincided with a 70 percent drop in the northern range elk herd (Eberhardt et al., 2007; Smith et al., 2011). Some observations suggest that the behavioral and numeric effects of wolves on elk have created a trophic cascade, releasing woody deciduous plants from excessive browsing, promoting rapid growth (Beschta and Ripple, 2010b; Ripple and Beschta, 2007; Frank, 2008; Beyer et al., 2007). Others failed to find evidence consistent with trophic effects of wolves on woody plants (Kauffman et al., 2010; Creel and Christianson, 2009; Wolf et al., 2007; Tercek et al., 2010; Bilyeu et al., 2008). Beaver numbers have increased on large streams and rivers on the northern range (Smith and Tyres, 2008), but beavers have not returned to any of the sites they occupied on small streams in the 1920s (Warren, 1926).

State transition along small streams in Yellowstone requires tall willows. The relationships between ungulate browsing and the beaver-willow mutualism lead to a clear willow height threshold for state transition on Yellowstone's northern range. Willows taller than 2-2.5 m are much less susceptible to pressure from herbivory because parts of the plant can escape from browsing (Keigley et al., 2002). These tall stems can serve as seed sources for new individuals, and dam building material for beaver. Furthermore, beaver colonies can sustain indefinitely on tall willow stands of suitable density and size (Peinetti et al., 2009).

I hypothesize that state transition from the ungulate-grassland state to the ungulate-beaver-willow state is currently precluded by insufficient willow stature and density to support beaver along small streams. Willows may be too short or too sparse to support beaver colonies for two reasons. The first possibility is that ungulate browsing is still too high to allow willows to grow taller than the 2 m height threshold for state transition. Therefore, they are limited from the top down by upper trophic levels. The second possibility is that ungulate browsing has abated, but willows are not growing taller because they are limited from the bottom up by resources such as water or light. I showed in an experiment that both water table depth and browsing by ungulates

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contributed to willow height and producivity through time (Marshall et al., Bilyeu et al., 2008), and I suspect both factors may be important across the northern range landscape. Landscape heterogeneity may lead to variable rates of state transition by causing variation in either top-down or bottom-up effects, or both.

To evaluate these hypotheses, I developed a network of observational study sites to document willow height and growth as a function of top-down and bottom-up effects across a heterogeneous landscape. Here, I ask what features of the northern range landscape drive heterogeneity in willow responses across space? My objectives were to 1) describe the patchiness of riparian ecosystem states across small streams on the northern range, 2) describe variation in states and transition rates as a function of top-down and bottom-up controls, and 3) identify relevant scales of heterogeneity in state transition.

Study Design

Following from my objectives, I chose a suite of riparian study sites to document the current ecosystem states and rates of state transition on the northern range. I targeted small streams that had the potential to support beaver dams because state transition from the ungulate-grassland state to the ungulate-beaver-willow state requires restoring the disturbance regime created by beaver dams. In the following sections I outline how I selected study sites, defined ecosystem states, and estimated rates of state transitions. I used willow height compared against the 2 m threshold for state transition as a snapshot of the ecosystem state at each site during 2008 to 2010. Willow production and height growth during 2009 and 2010 represented the dynamic rate of state transition. I developed models to predict the state of the ecosystem and the rate of state transition across a heterogeneous landscape as a function of top-down and bottom-up effects.

Both top-down and bottom-up factors can affect riparian ecosystem state and the rate of state transition. I define top-down effects as those resulting from upper trophic levels, in particular ungulate herbivores. Ungulate browsing occurs primarily in winter, and may have positive or negative effects on willows. Low to moderate browsing may stimulate willow growth the following year (Johnston et al., 2007; Bilyeu et al., 2008), but high levels of browsing can lead to net loss

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of woody material. Bottom-up effects consist of physical factors that influence ecosystem state or transition rate. For example, the availability of light, water, or heat may increase or decrease photosynthesis, and therefore affect willow growth rate or willow height (Tercek et al., 2010; Bilyeu et al., 2008). It follows that landscape heterogeneity may affect riparian ecosystem states and state transitions by driving a patchy mosaic of top-down and bottom-up factors across the northern range landscape.

3.2   Methods

Site selection

I focused site selection on small northern range streams suitable for damming by beaver. A beaver survey conducted in the 1920s documented widespread beaver activity on a number of northern range streams (Warren, 1926). Recent studies of historic beaver occupation identified additional streams with evidence of past beaver dams (Persico and Meyer, 2009; Wolf et al., 2007). None of these prior studies were complete censuses of beaver activity, however. My goal was to make inferences to the full population of potential beaver-willow sites on northern range small streams. Therefore, I pooled the beaver sites documented by others and used current landscape features to create a population of potential riparian areas.

I developed a hierarchical set of criteria to determine site suitability from current landscape features. I first identified all low gradient (< 10 percent), 3rd and 4th order small stream reaches contained within the northern range and park boundaries. Beaver dams are typically found on relatively narrow, low gradient streams(Allen, 1983; Persico and Meyer, 2009). Streams meeting these characteristics were then buffered by 50 m on each side, and assigned probabilities of selection based on accessibility (e.g. distance from roads or trails: < 1 km P = 1, 1-2 km P = 0.75, 2-3 km P = 0.5, >3 km P = 0.25). I converted the buffered stream layer into a raster with 100 x 100 m pixels. I used a spatially balanced random sampling algorithm (RRQRR, Theobald et al., 2007) to create an ordered list of pixels, weighting more highly the sites shown by others as previously occupied by beaver (Warren, 1926; Persico and Meyer, 2009; Wolf et al., 2007). In the field, I

visited each site in order to determine whether willows were present. Sites were excluded if they had fewer than 5 willows in any 15 m x 15m area adjacent to the stream channel.

At each selected study site, I set up 15 x 15 m subplots adjacent to the stream channel. I randomly selected one subplot containing a minimum of 5 willows, instrumented the plot with 1-4 groundwater monitoring wells, and a staff gauge. I randomly selected 5 plants within the subplot and permanently tagged 3 stems at random on each plant.

Defining Current Riparian Ecosystem States

I documented the current riparian ecosystem state at each of the 23 study sites using the mean height of tagged willows. State transition was defined by the willow height threshold of 2 m. If tagged willows had a mean height above 2 m, then the site had transitioned from the ungulate-grassland state to a state that could support beavers (a precursor to the ungulate-beaver-willow state). I measured the stature of each tagged plant each year during 2008 to 2010. Stature was measured at the end of the growing season as the height of the tallest stem perpendicular to the ground.

Characterizing Rate of State Transition

The rate of transition between the ungulate-grassland state and the ungulate-beaver-willow state is controlled by the rate of net accumulation of willow height and/or biomass. I measured height growth and annual production on each tagged willow at the end of the growing season in 2009 and 2010. Willow growth increment was the change in stature from one fall to the next, integrating over-winter losses due to browsing and gains in the growing season. I estimated annual production at peak standing crop by measuring lengths of a subset of new shoots on each tagged stem (Bilyeu et al., 2007). I used mass-length regressions to covert shoot lengths to biomass (Marshall et al., unpublished), and scaled up to the stem level by dividing by the proportion of shoots measured. I scaled from stem to plant by summing mass across the three tagged stems and again dividing by the proportion of stems tagged on that plant.

Top-down effects

Top-down effects on willows consist of biomass removal by upper trophic levels. Browsing by ungulates removes willow biomass primarily in winter on the northern range. Elk browsing occurs almost exclusively in winter, but bison and moose browsing may occur throughout the year. In my study sites, the vast majority of losses due to browsing that I observed occured overwinter. I estimated losses due to overwinter browsing using the biomass comparison method (Bilyeu et al., 2007). This involves re-measuring shoots on tagged stems in the spring and comparing the biomass remaining in spring to the biomass available in fall. In spring, I measured lengths of unbrowsed shoots and diameters of browsed shoots, and converted them to mass using regression equations I developed through destructive sampling of non-marked plants (Bilyeu et al., 2007). I defined browsing intensity as the proportion of production removed by ungulates over winter. Note that browsing intensity, as I define it, also includes overwinter losses due to twig shedding.

Bottom-up effects

I estimated bottom-up factors by measuring water table levels at each study site, and by developing a suite of landscape covariates that described heterogeneity in topography, slope, aspect, and position of each study site within its watershed. I measured groundwater levels biweekly during the growing season and surveyed the height of the ground surface at each plant, well, and staff gauge, in order to interpolate well measurements to individual plants using inverse distance weighting. I summarized variation in water table depths through the growing season using July mean water table depth and standard deviation during the growing season. Average depth in July represented the mid summer water table at a site, which was less influenced by interannual variation in magnitude and timing of peak flow than a season-long average. Preliminary analysis suggested that a quadratic relationship existed between water table depth and plant responses, because water table depths were very close to the surface at some sites, and perennially high water tables may drown willow roots, therby retarding growth. Variance in water table depth through the growing season

may capture the magnitude of late summer drought and/or the magnitude of peak flow, both of which may play an important role in willow growth.

I developed landscape covariates for elevation, slope, aspect, and topographic wetness index. Elevation may affect growth through its correlation with temperature, aspect affects solar exposure or light, and slope affects water accumulation. Topographic wetness index combines the position of a site in its watershed with the slope at a site to represent relative soil moisture. I developed landscape covariates from a 10 m resolution digital elevation model (DEM, Yellowstone Park Spatial Analysis Center) in ArcGIS 9.0. I extracted the mean elevation at each site, and calculated slope and aspect for each plant. Aspect was transformed to "southness", on a -1 to 1 scale (-cosine(aspect), (Roberts, 1986)). I also calculated topographic wetness index, a broad scale metric of water accumulation (Beven and Kirkby, 1979). Topographic wetness index is a function of slope and upstream watershed area, calculated as ln(a/tan(b)), where a is the area upstream, and b is the slope of the site. To determine area upstream, I delineated watersheds and calculated area upstream of each site using the watershed tool in ArcGIS. Watersheds corresponded roughly to hydrologic unit code (HUC) 12 sub-watersheds from the National Hydrology Dataset.

Bayesian hierarchical models for states and transitions

I explored variation in ecosystem state and rates of transition using Bayesian hierachical models. Ecosystem state was determined by mean willow height, and rates of transition were represented by willow growth rates (growth increment and annual production), as described above. I analyzed each of the three responses (height, growth increment, and production) using hierarchical models with three levels representing spatial variation at the site and plant level, and temporal variation at the plant level. At the top level of the hierarchy, I modeled variation between sites using the two covariates that varied at the site-level, elevation and topographic wetness index:

$$\mu_i = \alpha_1 W_i + \alpha_2 E_i + \alpha_3 E_i^2 \tag{3.1}$$

where μ_i is the mean response of site i, W_i is the topographic wetness index, E_i is elevation, and αs are site-level regression coefficients. I modeled elevation as a quadratic function to incorporate the idea that some optimal elevation range may exist for willow growth in my study area, with sites above and below that being less optimal. Each site was allowed to vary around the predicted site variation with an overall site variance term: $\gamma_i \sim Normal(\mu_i, \sigma_{site})$.

The second level of the hierarchy described variation between plants as a function of slope and aspect:

$$\mu_j = \beta_1 A_j + \beta_2 S_j + \beta_3 S_j^2 \tag{3.2}$$

where μ_j is the mean response of plant j, A_j is aspect, S_j is slope, and βs are plant-level regression coefficients. Each plant varied around the predicted mean with an estimated variance term: $\gamma_j \sim Normal(\mu_j, \sigma_{plant})$. The idea that topography may influence willow growth within and between sites follows from the somewhat random process of seed dispersal. Because willows do not control the location of germination, natural gradients of more and less suitable micro-sites are likely to occurr.

Finally, the third level of the model described temporal variation in willow response as a function of water table depth and browsing intensity estimated at the plant level. The predicted response of plant j at site i in year t is given by:

$$\mu_{ijt} = \gamma_i + \gamma_j + \gamma_t + \delta_1 D_{jt} + \delta_2 D_{jt}^2 + \delta_3 V_{jt} + \delta_4 B_{jt} + \delta_5 B_{jt}^2 \tag{3.3}$$

where D_{jt} is the water table depth under plant j in year t, V_{jt} is the variance in water table depth during the growing season, B_{jt} is the browsing intensity on plant j in the year t (the previous winter), and γ_t is a fixed effect for year.

Willow height and production were assumed to be distributed log-normally because they were strictly positive values and exhibited long right-handed tails. I modeled growth increment as normally distributed because it could take on positive or negative values. All predictors were standardized prior to model-fitting by subtracting the mean from each observation and dividing by

the standard deviation. Standardized regression coefficients are interpreted as the change in the dependent variable per unit change in the standard deviation of a predictor.

I fit models for each response using R and Jags (Plummer, 2011). I used non-informative, flat priors for all parameters (gamma for precision/inverse of variance, normal for regression coefficients, and uniform for random effect standard deviations, Gelman, 2006). In all cases, I fit the full model, and eliminated coefficients when their posterior probabiliy was not at least 90 percent above or below zero. I retained linear coefficients when associated quadratic terms were retained.

I investigated residuals for evidence of spatial autocorrelation by fitting variogram models using the R package geoR (Ribeiro Jr. and Diggle, 2001). In all cases the saturated model reduced spatial autocorrelation such that the effective range parameter was estimated to be 25 km or greater. From this, I concluded modeling spatial autocorrelation was not necessary.

To evaluate the proportion of variation explained at each level of the model, I estimated a Bayesian R^2 for each level (Gelman and Pardoe, 2006). These values are based on variance estimates from the posterior distributions of residuals at each level. I also estimated the pooling factor for each random effect, which describes how much each grouping (plant or site) is pulled toward the global mean. Values closer to one indicate strong pooling, while values close to zero indicate that groups are more independent.

I used posterior estimates from the final model to estimate the probability of finding willows taller than the 2 m height threshold on small northern range streams. Site-level landscape predictors within the range observed at my study sites were combined with uncertainty associated with site and plant random effects. I used these predictors plus uncertainty to produce a probability surface combining information about multiple landscape predictors.

3.3 Results

Current Riparian Ecosystem States

Fifteen years after wolf reintroduction, only 3 of 23 study sites had transitioned from the elk-grassland state. All three sites with a mean willow height above 2 m were in one drainage, Blacktail

Creek (Figure 3.1). Six additional sites contained at least one plant over 2 m, for a total of 17.9 percent of measured willow plants showing evidence of state transition. Average willow height across all study sites was 117 (+/- 6 SE) cm, which is well below the 200 cm state transition threshold (Figure 3.1).

Predicting Heterogeneity in Ecosystem States

Willow height was correlated with landscape covariates and water table effects, but not with previous winter's browsing. After eliminating potential predictors with coefficients whose posterior weight was not at least 90 percent above or below zero, willow height was explained by bottom-up factors: topographic wetness index, aspect, elevation, and water table standard deviation (Table 3.2). Overall, this model described 91 percent of height variation across sites, plants, and years (Table 3.1).

Site, plant, and temporal variation influenced willow height. Mid-elevation sites with greater water accumulation (as predicted by topographic wetness index) were associated with taller willows (Figure 3.2). Topographic wetness index and elevation had the largest magnitude standardized coefficients, and along with the random site intercept explained 13 percent of variation between sites (Table 3.2 and 3.1). At the plant level, aspect (southness) and the individual plant intercept explained 39 percent of variation between plants (Table 3.1). Temporal variation in the form of increased variance in the water table during the growing season was also associated with taller willows (3.2). I investigated the trend in water table depth during the growing season at sites with high water table variance and tall willows and found that the high variance was due to high water table depths in the spring that declined steadily through the growing season.

Individual plant deviations from the mean were slightly larger than site deviations (σ_{site}= 0.35 and σ_{plant}= 0.23, Table 3.4), suggesting that individual plants within a site were at least as different from each other as they were from plants at other sites. Pooling factors also suggested inter-plant variation may be more important than inter-site variation (0.54 for plant, 0.39 for site, Table 3.1).

The highest predicted probability of a willow >200 cm was 0.221, occurring at a site of mid-elevation and high topographic wetness index (Figure 3.3). Although elevation and topographic

wetness index were the strongest linear predictors to describe height, overlaying study site loca-
tions on the probability surface showed that other factors also contributed to height. The three sites
with the tallest mean height were in areas of relatively high probability of having tall willows. The
two sites with the most optimal topographic wetness index and elevation did not have the tallest
willows, however.

Transition rates: growth increment

State transition rate as represented by growth increment was explained by landscape covariates
and water table effects (Table 3.3). However, browsing intensity described meaningful variation
in the transition rate (growth increment), but did not influence the state itself (willow height).
The increment model described a much lower proportion of the total variance in increment than
the height model, with less than 25 percent of variance explained by the full model (Table 3.1).
Also, the increment model did not have plant-specific intercepts because the observed data did not
support including them (posterior probability of plant variance was very small).

Both top-down and bottom-up effects shaped growth increment, but bottom-up effects were
more influential. Like the height model, topographic wetness index and elevation were the strongest
predictors of increment (Table 3.3). Together with site-specific intercepts, these predictors ex-
plained 36 percent of variation in growth increment among study sites (Table 3.1). After the site-
level predictors, the next most influential predictors were water table variance and slope. Variance
in water table depth during the growing season had a positive effect on increment, like height (Fig-
ure 3.4). Slope was quadratic, like elevation, with the highest willow growth increment on patches
with a slope of 25 to 30 percent (Figure 3.4). Browsing intensity was also quadratic; browsing
was associated with increasing growth increments up to about 35 percent of annual production and
increments declined as browsing intensity increased about 40 percent (Figure 3.4).

Transition rates: annual production

The rate of state transition, as described by willow annual production, was most strongly influ-
enced by landscape covariates, followed by annual water table effects. Browsing intensity was the

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least influential predictor (Table 3.4). The production model shared several predictors with both the height and growth increment models. All three willow responses were correlated with elevation and water table variance during the growing season. Production and height were both higher with south-facing aspects, and production and increment were both associated with browsing intensity. Overall, the production model explained 93 percent of variation in annual production (Table 3.1).

Aspect was the most influential predictor for willow production (Table 3.4, Figure 3.5). This was the only predictor for the plant level of the model, and together with the individual plant variation explained 13 percent of variation between plants (Table 3.1). After aspect, elevation had the next largest magnitude. Elevation combined with the site effect explained 3 percent of variation between sites (Tables 3.1 and 3.4). The standardized coefficient for water table variance was nearly the same magnitude as the quadratic term for elevation. As with the other models, increased water table variance was correlated with increased willow annual production (Figure 3.5). The coefficient for browsing intensity indicated it was only about 30 percent as influential as elevation and water table variance (Table 3.4). Intermediate levels of browsing were associated with increases in annual production and high levels led to declines in production, but the overall change in production over the range of browsing intensity was quite small (Figure 3.5).

Site and plant level variations were about the same magnitude (Table 3.4), which suggests that plants within a site are about as different from each other as different sites are from each other. The pooling factors estimated for sites and plants further supported this (0.3 and 0.31, respectively, Table 3.1), suggesting that sites and plants behave relatively differently from one another, and significant structure exists at both levels.

3.4 Discussion

I showed that heterogeneity in physical features of the landscape explained the preponderance of variation in current ecosystem states and the rate of state transition on Yellowstone's northern range. Interannual variation in water table variance also affected the state and transition rate. Browsing was a far less important predictor compared with landscape and temporal effects. The relatively small effect of browsing on willow responses suggests that state transition is prohibited

to a greater extent by bottom-up forcing from resources needed for growth, rather than top-down forcing from herbivory.

Overall, mean willow height was 83 cm below the 2 m threshold for state transition on the northern range. However when I found tall willows, they were more likely to occur on mid-elevation, low gradient sites with a large contributing upstream area. Of the sample sites with tall willows, all three occurred within the Blacktail Deer Creek drainage near the geographic center of the northern range. Regardless of the larger geographic context of sites, plants with greater south-facing exposure, and with higher variance in water table depth during the growing season were taller than plants with north-facing exposure and/or low water table variance.

The strength and direction of the influence of topography on both the ecosystem state and the rate of transition was somewhat surprising. In the northern hemisphere, south-facing slopes are generally associated with lower soil moisture because evaporation occurs more rapidly with higher solar radiation. I found a positive effect of south-facing slopes on willow height, height growth, and annual production, however. One possible explanation is that aspect captures important variation in light availability or temperature that strongly influences willow growth in my sites. All of my study sites were located in riparian areas in valley bottoms. In these relatively flat areas, aspect may be less correlated with soil moisture than to temperature and solar radiation.

My finding that the riparian ecosystem state has not shifted since wolves were reintroduced to the northern range might appear to conflict with the observations of others that trophic effects control willow height (Beschta and Ripple, 2007; Beyer et al., 2007). However, Beschta and Ripple (2007) documented increasing willow height in the Blacktail creek drainage, where I also observed the tallest willow stands. Beyer et al. (2007) found evidence for increasing ring area of willow stems subsequent to wolf reintroduction. Similar to my findings, they found elevation played a significant role in describing willow variability across the northern range, with higher elevation sites demonstrating lower growth rates. However, stem growth ring area may not correlate to willow height, which is more indicative of willow stand structure and state transition.

In order to more fully understand the current riparian ecosystem states of the sites I studied, I can compare current willow heights to those from years before wolf reintroduction. Singer et al. (1994) measured willow height at 14 sites across the northern range in 1988-1990. Their sites do not coincide with my sites, but nontheless provide insight into willow heights before wolves were reintroduced. During summer 1990, willows had a mean height of 114 cm, which is very close to my 2010 mean of 117 cm. However, Singer et al. measured one site in the Blacktail drainage, and found plants there were representative of mean northern range willow height at the time (106 cm). In 2010, however, I found that willow heights in the Blacktail drainage were taller than the northern range mean, which suggests state transition is occurring in this drainage. Part of this state transition may have resulted from trophic effects of wolves.

My transition rate models for growth increment and annual production indicated it was unlikely that increased height in the Blacktail drainage was due to release from herbivory alone, however. Landscape covariates demonstrated that recovering sites have better growing conditions than sites with short willows. Experimental findings have suggested both browsing and water table depths affect height accumulation, but water availability plays a stronger role (Bilyeu et al., 2008). Observational work has also demonstrated the importance of bottom-up factors influencing willow height, with heterogeneity occuring over small spatial scales (Tercek et al., 2010). I showed that factors affecting light availability (aspect) and water availability (topographic wetness index and water table variance) were the most important controls on willow growth increment and annual production. Browsing influenced willow growth, but its effect was *positive* when browsing removed less than 40 percent of annual production, and negative only when browsing exceeded 40 percent. Moreover, the magnitude of the effects of browsing was much lower than the landscape covariates or water table variance, providing further support for the limited role of herbivory.

I found that tall plants and more growth were associated with sites with higher water table variance, which was somewhat unexpected. I offer two potential explanations. One possibility is that several sites had perennially high water tables (low water table variance) and short, slow growing plants, potentially because willow roots had drowned, leading to limited above ground

growth. The second possibility is that water table variance describes temporal variation in peak flows at each site. In this case, higher water table variance would be capturing early summer water table depths closer to the soil surface, with less variation in the late summer low flows.

Mean July water table depths did not affect willow height or growth. Experimental evidence on the northern range has shown that raising water tables increases willow height and annual production (Bilyeu et al. 2008, Marshall et al. unpublished). However, observational studies have shown that water table depths do not necessarily describe a large proportion of variation in height (Johnston et al., 2011; Beschta and Ripple, 2007). Ground water use, as shown through stable isotope studies, explained 26 percent of variation in willow height (Johnston et al., 2011). Water table depths and plant water use may not always be correlated, because water use depends specifically on root architecture and shallow-rooted willows may not reach the water table and could be more water stressed.

Although my models explained a large proportion of the variation in height and production, site and plant level differences indicated that additional variation remains to be explored. The magnitude of the variation between plants at a site was similar to, or larger than, the variation between plants at different sites. This suggests that factors that vary across fine spatial scales (less than 15 m) may have strong influences on ecosystem state and the rate of state transition. Tercek et al. (2010) found that small scale variation was important in determining bottom up controls on short and tall willow patches, and suggested that microtopography and changes in elevation and aspect may explain differences in soil moisture and soil temperature they observed.

In this paper I showed that riparian ecosystem state transition from ungulate-grassland to ungulate-beaver-willow has not occurred along most northern range streams, and tall willow stands are currently limited to a single drainage. My landscape models showed that growing conditions are variable across the landscape, and variation in aspect, slope, and water table variance within a site contributes to plant growth responses. My work is the first to explicitly describe spatial variation in drivers of willow height growth on the northern range, and to identify the relative im-portance of top-down and bottom-up controls on Yellowstone's willows. Given the limited impact

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of browsing intensity on willow growth and lack of a browsing effect on height, I do not find evidence of widespread, uniform cascading trophic effects of wolves on willows. Instead I found that landscape heterogeneity shapes willow growing conditions, thereby explaining the patchy nature of state transitions occurring at fine scales on the northern range. The effects of wolf reintroduction on Yellowstone's willows has been a contentious topic in the primary literature and the popular press, and my research provides a clear spatial context to unify these disparate views.

Table 3.1: Model summaries for riparian ecosystem state, and the rates of state transition. R^2 describes the proportion of variance explained by each level of the model and pooling factors describe how strongly observations at that level are pulled toward the mean (0 represents strongly pooled, 1 represents independent observations).

Level	Ecosystem State: Height		Transition Rate: Growth Increment		Transition Rate: Annual Production	
	R^2	pooling factor	R^2	pooling factor	R^2	pooling factor
Site	0.13	0.24	0.36	0.58	0.03	0.3
Plant	0.39	0.54	NA	NA	0.13	0.31
Full	0.91	0.39	0.23	0.12	0.92	0.58

Table 3.2: Parameter estimates for willow height model, posterior mean and 95 percent credible intervals. Linear coefficients are standardized.

Predictor	Coefficient	mean	0.025	0.975
Topographic Wetness Index	α_1	0.15	0.00012	0.28
Elevation^2	α_3	-0.12	-0.21	-0.023
Aspect	β_1	0.092	0.0031	0.18
Elevation	α_2	-0.076	-0.2	0.048
Water table variance	δ_3	0.038	0.004	0.072
—	γ_1	4.73	4.57	4.86
—	γ_2	4.79	4.65	4.92
—	γ_3	4.87	4.73	5
—	σ_{plant}	0.35	0.29	0.41
—	σ_{site}	0.23	0.13	0.38
—	σ_{resid}	0.14	0.13	0.16

Table 3.3: Parameter estimates for growth increment model

Predictor	Coefficient	mean	0.025	0.975
Topographic Wetness Index	α_1	6.07	0.15	11.58
Elevation^2	α_3	-3.95	-8	0.49
Water Table Variance	δ_3	3.82	-0.72	8.8
Slope^2	β_3	-3.65	-7.61	-0.01
Browsing Intensity	δ_4	-3.34	-7	0.2
Browsing Intensity^2	δ_5	-2.46	-5.06	0.08
Slope	β_2	1.84	-3.51	7.41
Elevation	α_2	-0.73	-6.36	4.84
—	γ_2	14.87	6.67	22.73
—	γ_3	22.04	13.96	29.8
—	σ_{site}	8.53	1.9	15.66
—	σ_{resid}	18.48	16.43	20.91

Table 3.4: Parameter estimates for willow production model

		mean	0.025	0.975
Aspect	β_1	0.39	0.07	0.69
Elevation^2	α_3	-0.24	-0.61	0.13
Water Table Variance	δ_3	0.22	-0.02	0.46
Elevation	α_2	0.1	-0.44	0.64
Browsing Intensity	δ_4	-0.08	-0.2	0.05
Browsing Intensity^2	δ_5	-0.08	-0.17	0.02
—	γ_2	4.86	4.22	5.49
—	γ_3	5.1	4.46	5.72
—	σ_{site}	1.09	0.73	1.66
—	σ_{plant}	1.01	0.84	1.22
—	σ_{resid}	0.48	0.4	0.58
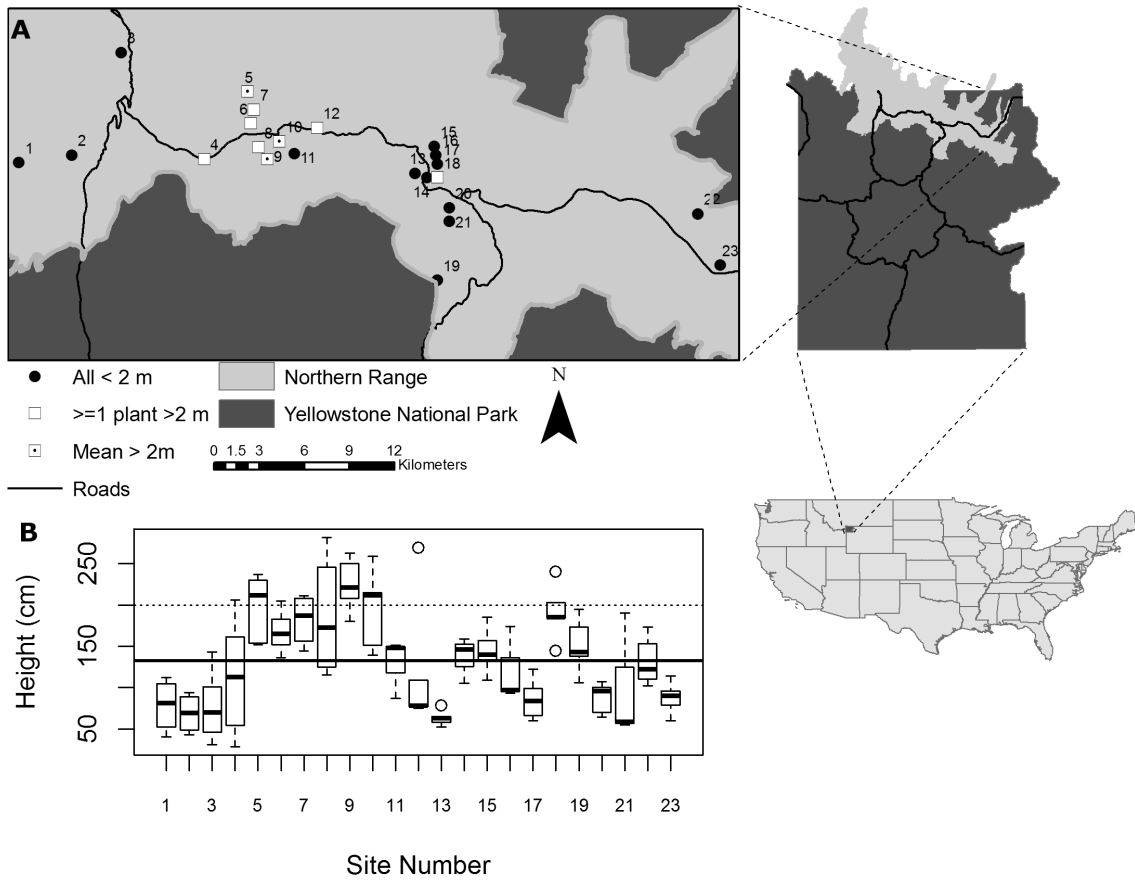
Figure 3.1: Overview of study area. A) Study site locations across Yellowstone's Northern range. Site symbology represents 2010 willow height as follows: black circles indicate no tagged willows were 2 m in fall 2010, white squares indicate at least on willow was taller than 2 m, and white squares with black dots indicate the mean of observed willow height was above 2 m. B) Box plot of 2010 willow height at 23 study sites. Overall mean height indicated by solid black line, threshold for state transition indicated by dashed line.

Figure 3.2: Predictors of willow height. Each panel shows the isolated relationship between the predictor and height response, holding all other covariates at their mean values (mean=0 for standardized predictors). A heavy black line indicates the posterior mean, with 95 percent credible intervals in the shaded grey region. The dashed line indicates the height threshold for state transition. Elevation had a quadratic relationship with height (A). Water table standard deviation (B), topographic wetness index (C), and aspect (D), all had positive correlations with willow height. Browsing intensity was not included in the final model because the probability of its coefficient being greater than zero was less than 10 percent.
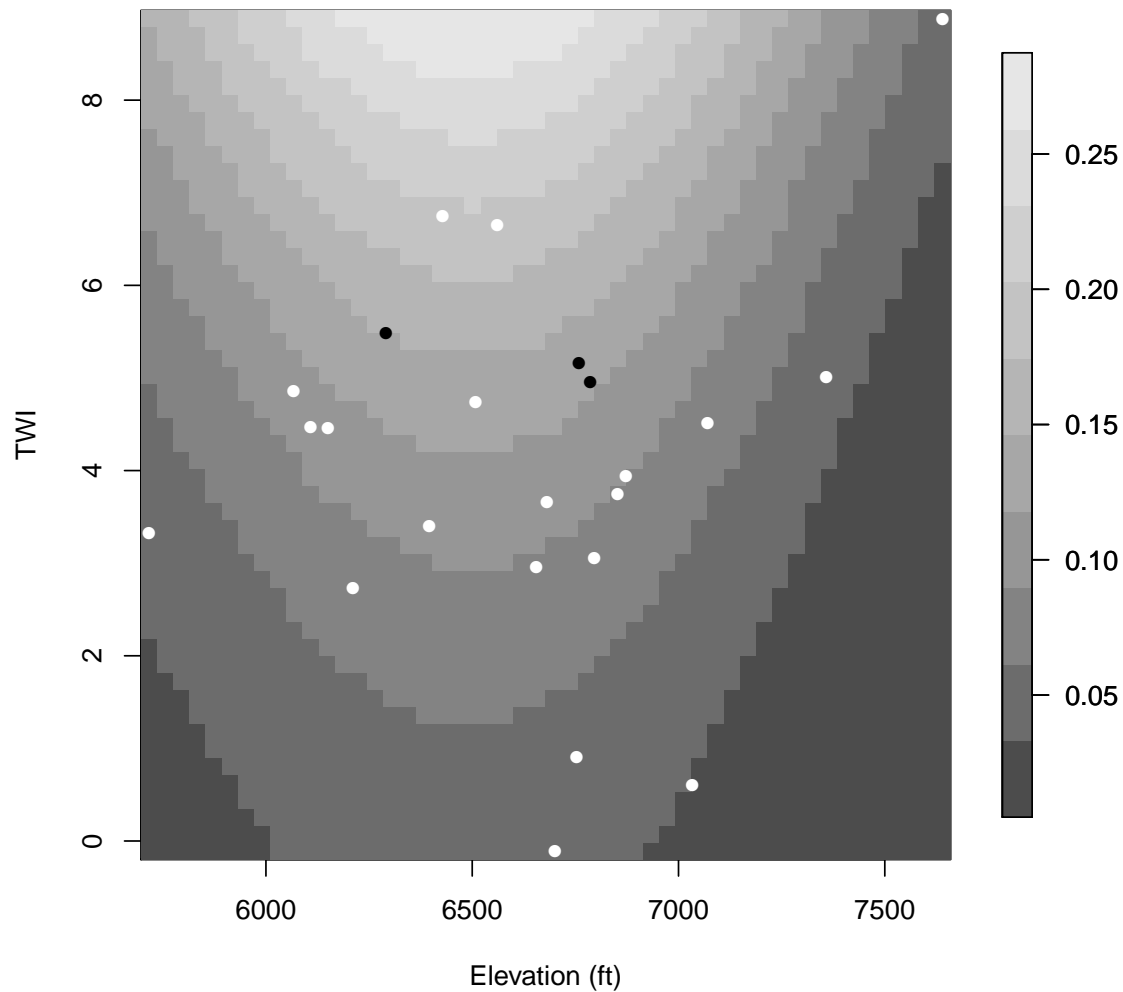
Figure 3.3: Surface plot of site-level landscape factors contributing to willow height on the northern range. Shaded areas represent a gradient of probability of a random willow taller than 200 cm at a randomly selected new site. Darkest areas represent probability of 0 to 2.5 percent, and lightest areas represent 22.5 to 25 percent. Each predictor was scaled between 0 and 1, with high values at the labeled vertex of the triangle, and low values along the opposite edge from the labeled vertex. Each point represents one of the 23 study sites, with sites in black having mean height > 200 cm and sites in white have mean height <200 cm.
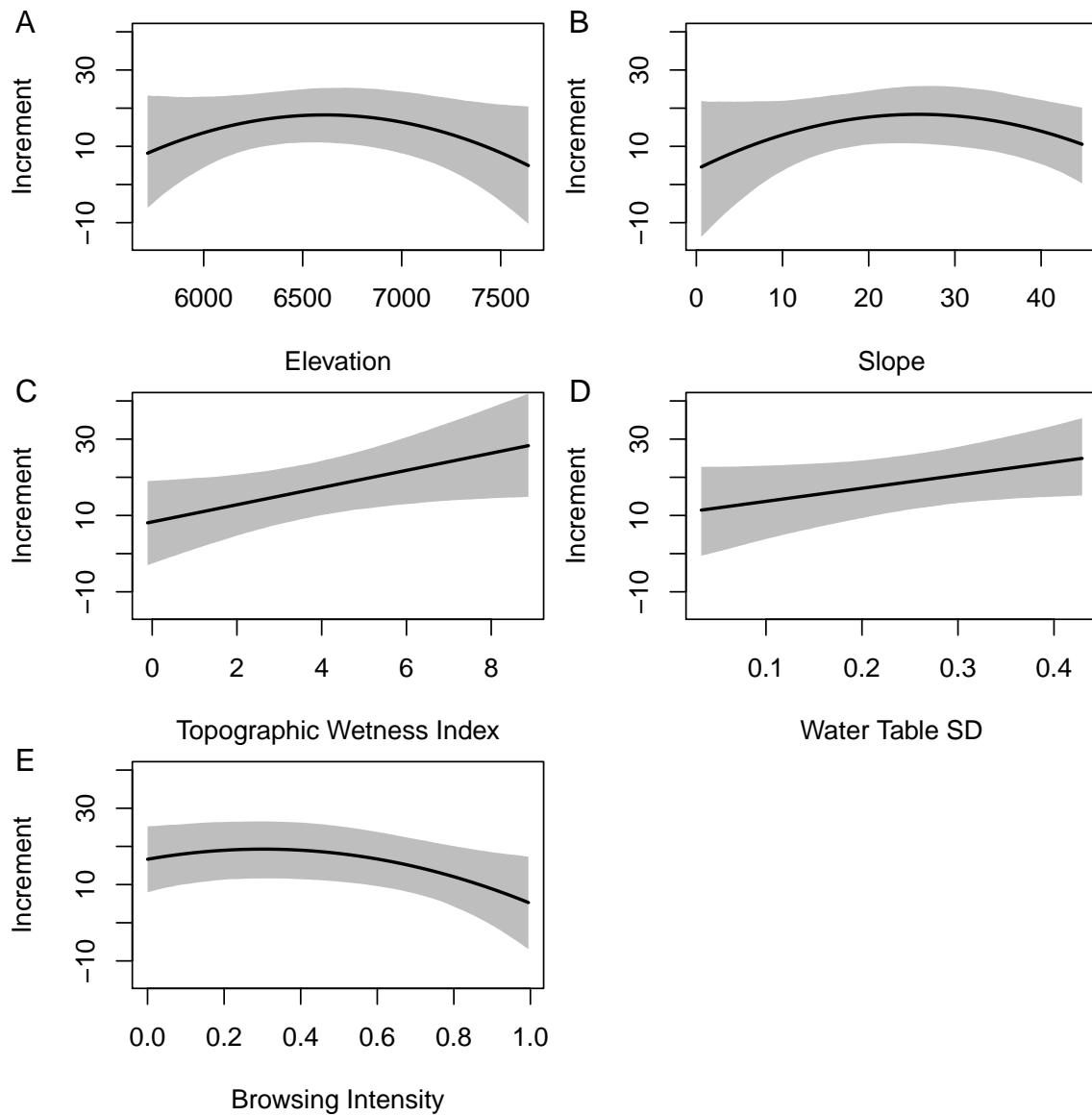
Figure 3.4: Predictors of state transition rate in terms of growth increment (cm). Each panel shows the isolated relationship between the predictor and height response, holding all other covariates at their mean values (mean=0 for standardized predictors). A heavy black line indicates the posterior mean, with 95 percent credible intervals in the shaded grey region. Elevation (ft, A) and slope (percent, B) both had quadratic relationships with growth increment. topographic wetness index (C) and the standard deviation of water table depth during the growing season (D) were positively correlated with height growth. Browsing intensity (E) was quadratic, positively correlated with increment at low levels of browsing (< 30 percent), and negatively correlated with increment for higher levels.
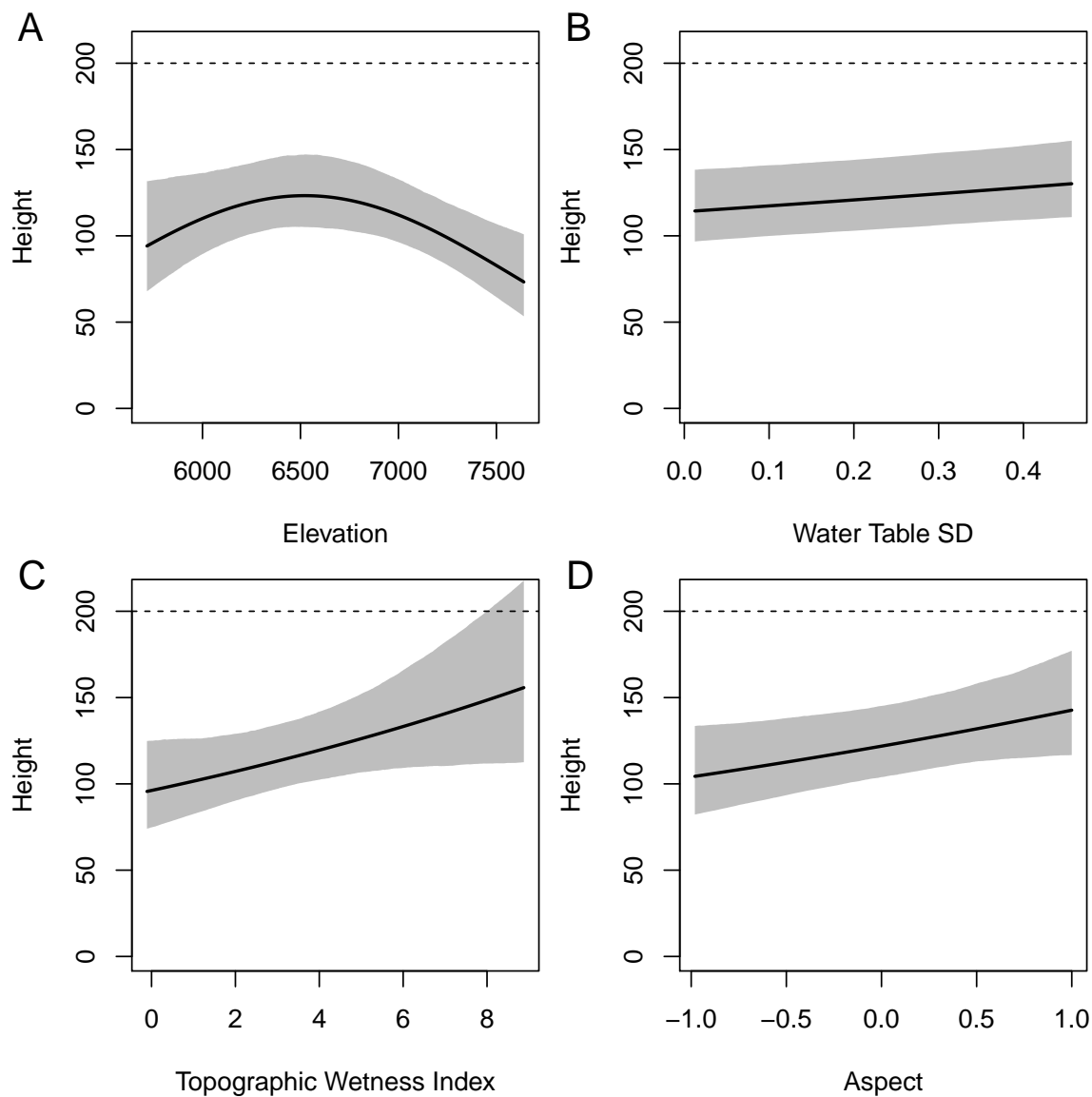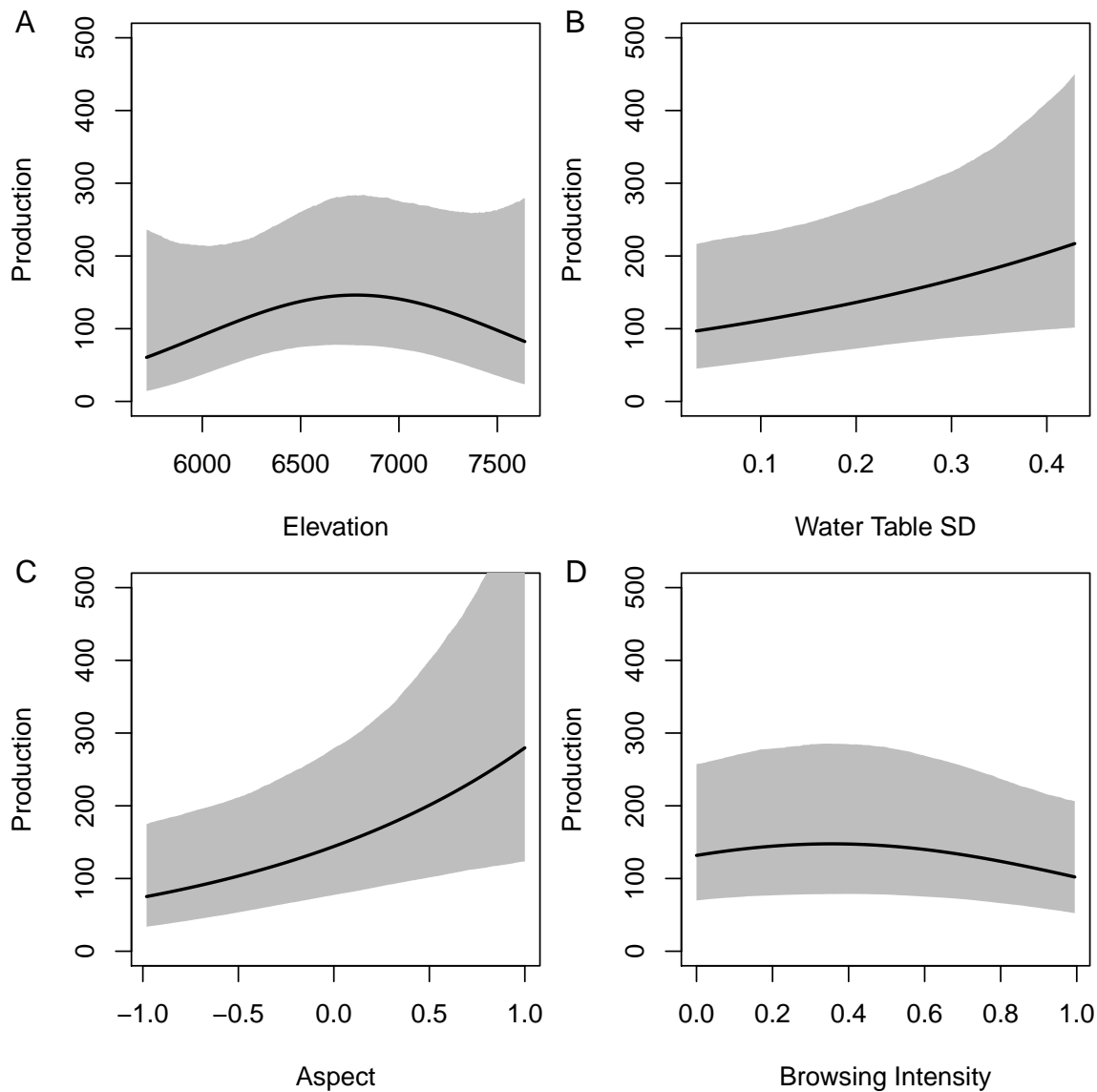
Figure 3.5: Individual predictors of willow production (g). Each panel shows the isolated relationship between the predictor and height response, holding all other covariates at their mean values (mean=0 for standardized predictors). A heavy black line indicates the posterior mean, with 95 percent credible intervals in the shaded grey region. Elevation (ft) had a quadratic relationship with annual production (A). Water table variance (B) was positively correlated with production, and south-facing locations had higher production than north-facing locations (C). Browsing intensity had a quadratic relationship with annual production (D).

4 Climate interacts with food web structure to shape willow establishment and growth in Yellowstone

4.1 Introduction

The green world hypothesis (Hairston et al., 1960) motivated decades of inquiry seeking to understand trophic forces controlling the structure of ecological communities. A large and expanding literature shows evidence for top-down control of the population dynamics of prey by their predators (Estes et al., 2011; Myers et al., 2007; Terborgh et al., 2001), as well as evidence of bottom-up control by resources (Shurin and Seabloom, 2005; Borer et al., 2005). A central finding of this work is that the number of trophic levels in a food web is rarely sufficient to predict the direction of controls (Menge, 2000; Power, 1992). Instead, the context created by climate and disturbance are likely to determine the direction and magnitude of trophic effects within ecological communities (Folke et al., 2004; Visser and Both, 2005; Schweiger et al., 2008). A key challenge in contemporary ecology is to understand how disturbance, the physical environment, climate, and food web composition interact to shape the dynamics of consumers and producers within ecosystems.

The elimination of the gray wolf (*Canis lupus*) from Yellowstone, and its subsequent reintroduction nearly 70 years later, provided a unique opportunity to study the reversibility of changes in communities caused by simplification of the food web. Wolves were extirpated from Yellowstone in the 1920s and were reintroduced in 1995. During the 75 year absence of these top-predators, the northern range elk (*Cervus elaphus*) population increased nearly five fold to a peak abundance in 1993 of just over 25000 individuals (Eberhardt et al., 2007).

Elevated herbivory associated with increased elk numbers is believed to have caused dramatic changes in vegetation communities, particularly in riparian areas (Singer et al., 1994; Kay, 1997). Riparian communities support biodiversity disproportionate to their area (Naiman and Decamps, 1997), providing food, cover, and access to freshwater for vertebrate and invertebrate species. Willows (*Salix spp.*) are the dominant riparian woody plants in most montane ecosystems in western

North America, including Yellowstone. Heavy browsing by elk following the extirpation of wolves markedly reduced the stature of willows and decreased their abundance on the landscape (Houston, 1982). Reducing the standing crop of willow had secondary effects on other species that depend on willows for cover and food (Jonas, 1955; Kay, 1997), particularly beaver.

Beaver have a mutualistic relationship with willow along small streams, a relationship that was a signature of Yellowstone's northern range in the 1920s (Warren, 1926). Beavers dam small streams to create habitat that is secure from predation (Baker and Hill, 2003). They use willow stems for building dams and lodges and for food. Beaver dams raise water tables along streams, which increases water availability to willow roots that tap directly into groundwater. Dams also increase flooding upstream and downstream (Westbrook et al., 2006). Flooding deposits bare soil required for germination of willow seeds. Willows require the disturbance regime provided by beaver dams to create wide riparian corridors along small streams. Beaver disappeared from the network of small streams across the northern range after wolves were eliminated (Jonas, 1955). The disappearance of beaver has been attributed to habitat degradation due to excessive herbivory by elk (Wolf et al., 2007; Kay, 1997).

Wolves were reintroduced to Yellowstone in 1995 and their presence coincided with numerous changes in lower trophic levels. The northern range elk population declined to 30 percent of its peak size during the 15 years after wolf reintroduction. Increased mortality resulted from predation by wolves, hunting outside of the park, and severe drought (Eberhardt et al., 2007; Smith, 2004). Woody vegetation increased in height and cover in a few areas of the northern range during this period. These increases have been interpreted as evidence of indirect trophic effects of wolves on willows resulting from behavioral and numeric effects of wolves on elk (Beschta and Ripple, 2007; Beyer et al., 2007). However, willow height is highly variable across the landscape (Marshall et al., Tercek et al. 2010) and beaver dams remain absent from northern range streams suitable for damming (Smith and Tyres, 2008). These observations suggest that the reintroduction of wolves and declining elk abundance are not the only factors controlling northern range willows.

The effect of beaver dams on water table depth and the importance of water table depth as a bottom-up force limiting willow growth was demonstrated with a ten year experiment on the northern range (Bilyeu et al. 2008, Marshall et al.) and by observational studies (Tercek et al., 2010). Simulated beaver dams and removal of ungulate browsing showed that willow height is limited by both herbivory and water, but that effects of water limitation are stronger, especially for productivity (Bilyeu et al., 2008). The absence of bare substrate created by beaver dams inhibits willow establishment on the floodplain. The majority of willow establishment on the northern range since the 1940s has occurred only on point bars in the channel, or during or after rare large floods that deposit sediment up on the flood plain (Wolf et al., 2007).

In addition to local deepening of the water table caused by the absence of beaver, shifts in climate over the past century may also affect willows. The northern range is currently experiencing a multi-decade drought (McMenamin et al., 2008). Significant wetland drying has been attributed to decreased annual precipitation and increased temperature over the last 60 years (McMenamin et al., 2008). Average winter snow depths have declined and springs have started earlier (Wilmers and Getz, 2005). Reduced snow could lead to reductions in ungulate browsing (Creel and Christianson, 2009). Longer growing seasons could increase willow growth, if summer drought doesn't limit plant production.

In this paper I explore the relative importance of climate drivers and food web structure on willow communities along small streams on Yellowstone's northern range over the past 40 years. I use three retrospective data sets on willow responses to evaluate support for the idea that wolf reintroduction has restored willow communities through their trophic effects on elk abundance and browsing. If wolves protected willows from the negative effects of elk browsing, I should expect to see increased willow growth since 1995, when wolves were reintroduced. Alternatively, if climate drivers and hydrology played a stronger role in determining changes in willows through time, I should expect to see correlations between recent warmer and drier years and willow responses. Discerning between climate and trophic effects on willows is possible because long changes in climate began before wolf reintroduction occurred.

I evaluated changes in willow patches in to evaluate these hypotheses. I explored change in percent cover of willows from 1969 to 2009, and also reconstructed willow height through time using relationships between stem age and height. I investigated recent patterns of establishment to evaluate whether changes in establishment can be attributed to changes in upper trophic levels. I describe temporal trends in these responses using Dynamic Factor Analysis and Bayesian hierarchical models. I explain variation in willow responses with the trophic effects of wolf, elk, and bison abundance and the climate effects of river flow, annual precipitation, and growing season length.

4.2 Methods

Site Selection

My work focused on riparian areas along small streams that were conducive to damming by beaver. Others have documented patterns of historic activity by beaver or had evidence of relict beaver dams (Warren, 1926; Persico and Meyer, 2009; Wolf et al., 2007). These previous beaver surveys were not complete censuses of northern range streams. Therefore, I developed a population of sites from which to sample based on stream geomorphology identified as associated with beaver habitat (Persico and Meyer, 2009; Allen, 1983). This population of sites consisted of all third and fourth order northern range stream reaches with low gradients (< 10 percent).

I selected 23 study sites from the larger population using spatially balanced random sampling. I created 50 m buffers surrounding these potential streams, and assigned probability of sampling according to accessibility on foot. Sites identified as previously occupied by beaver were also assigned higher probability of selection. The buffered stream layer was converted to raster format with 1 hectare pixels. I used the RRQRR package in ArcGIS (Theobald et al., 2007) to generate an ordered list of random pixels using these criteria. I visited each selected 1 hectare site in order, and eliminated those that did not meet a threshold willow density of at least five willows in a 15 x 15 m square area along the stream channel.

Willow Canopy Cover

I obtained a time series of aerial photographs from Yellowstone Center for Resources Spatial Analysis Center for the years 1969, 1991, 1998, 2006, and 2009 to analyze of changes in willow canopy cover over time. The 1969 photos were true color and taken between August 1969 and July 1971 at a scale of 1:15840. Photos from 1991 were also true color and taken between August 1990 and August 1992 at a scale of 1:56000. The 1998 photos were infrared, and taken between September and October 1998 at a scale of 1:24000. Aerial photographs were scanned at a resolution of 2031 dpi. Images from 2006 and 2009 consisted of NAIP imagery. Using ArcMap, the aerial photographs were clipped to just outside the areas of each of the 23 plots and georeferenced to the 2006 NAIP imagery to obtain an accuracy of < 1 m. The 2009 NAIP imagery did not line up within the desired 1 meter accuracy, so the imagery was clipped into smaller areas surrounding the plots and georeferenced to the 2006 NAIP imagery. Using the extension Hawth's Tools (Beyer, 2004), a 1,000 point grid was created for each of the one hectare plots. The 23 grids were combined into a single layer for each year of analysis. Display qualities of the imagery were adjusted in order to maximize visibility of willows. The grid layers for each year in the time series were displayed over the imagery and presence/absence was determined for each point in the grid. Willow presence/absence was determined first for the 2009 and 2006 NAIP imagery, then for the aerial photos in a reverse time sequence. Google Earth was used as a second resource to identify willows in areas where distinguishing between willows and non-willows was difficult.

I ground-truthed 2006 NAIP imagery in summer 2008 to determine the plausibility of identifying willows on aerial photos through time. I performed a double-blind test and selected 25 grid points at random from four sites. I visited the GPS coordinate for each grid point and determined whether the one square meter around that location was at least 50 percent covered by willow. Of 100 points visited, 80 were in agreement between photo and ground identification. Of the 20 that were mismatches, 18 were identified as willow from aerial photo but not on the ground, and two were identified as willow on the ground but not from the photo.

I modeled willow cover using Dynamic Factor Analysis (DFA), which is similar to Principal Components Analysis (PCA), but for time-series data (Zuur and Bailey, 2003). DFA is a state-space approach that discerns common trends from multivariate time-series data. Common trends are analogous to axes in PCA, and the number of trends presented is determined by model selection with AIC such that the most parsimonious model supports the smallest number of trends that adequately represent the data (Zuur and Bailey, 2003). I standardized the willow cover time series at each site and fit the DFA using the R package MARSS (Holmes et al., 2012), evaluating models with up to three shared trends. Although multiple covariance structures are possible with DFA, I only fit models with a single covariance parameter ("diagonal and equal" covariance matrix). I chose this simplified covariance form because the data time series spanned 40 years (1969 to 2009), but consisted of only five years with photos. Therefore, the model estimated states for 35 missing years for each time-series. I removed one site from the analysis (site 1), because no willows were observed in aerial photos from any year.

Willow Establishment

I excavated willow root crowns to understand recent patterns of willow establishment. I collected up to five root crowns per site, but never more than 10 percent of willow saplings within the one hectare site. I focused my sampling on small plants that I perceived to be less than 30 years old because previous willow establishment research on the northern range demonstrated missing willow age classes for young plants (Wolf et al., 2007). Willow stem height or thickness is not necessarily a reliable indicator of plant age because stems may die back and re-sprout from the same root mass. However, I aged the aboveground growth by counting annual growth sections as indicated by the branching pattern and bud scars evident on the stems(Keigley and Frisina, 1998). I sampled randomly from plants that had less than 10 years of aboveground growth. Because I targeted young plants, I limited my analysis to plants that established in 1980 or later. This resulted in dropping nine plants from the analysis, leaving 63 established willows across 17 study sites.

After excavating the root crown, I sectioned the root and shoot material cross-sectionally to find the point of germination. Plant root material does not contain pith, while stems do. The point

of germination is contained in the cross section with pith on one site and no pith on the other (Scott et al., 1996). I successively cut sections until the root crown was isolated in a 2-3 cm section. I sanded the top and bottom surfaces with progressively finer sandpaper, finishing with 10 micron, and counted the growth rings on both surfaces. If the two counts were inconsistent, I used the maximum count as the age of the plant.

I analyzed willow establishment over 29 years using Poisson regression, following the methods of Wolf et al. (2007). I evaluated the relative importance of climatic and trophic covariates using standardized predictors. I first regressed each covariate individually, eliminating predictors that had correlations greater than 0.7 (retaining the predictor that explained more deviance). I combined remaining predictors to find the most parsimonious groupings of predictors to explain willow establishment over the last 30 years. I modeled dispersion hierarchically, such that

$$W_t \sim Poisson(exp(X_t\beta + \theta_t))$$

where the number of willows established in year t is a Poisson random variable, with a mean described by linear predictors and their associated coefficients, XB, plus an optional overdispersion parameter, θ_t. Overdispersion in each year was a normal random variable with an estimated precision parameter: $\theta_t \sim Normal(0, \tau)$ (Gelman and Hill, 2006).

I estimated all parameters using Bayesian methods in JAGS with R (Plummer, 2011), and compared models using DIC (Spiegelhalter et al., 2002). Due to the low sample sizes at each site, I pooled across all sites.

Willow height

I collected up to three stems per plant on eight willow plants at each of 20 sites (278 stems total) to analyze the relationship between willow height and age. To maximize the length of stem height-age time series, I selected plants with at least one thick stem (that I estimated to be >10 years old). I cut the largest stem at the ground surface and roughly verified its age in the field. If the thickest stem from the plant was less than 8 years old, I did not select further stems from the

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plant. Otherwise, I cut two more stems that represented the size distribution of stems on that plant. I never sampled more than 10 percent of stems at a site to minimize my impacts on willow stands.

I reconstructed stem height through time by sectioning willow stems in 10 cm increments, from the ground surface to the tallest point of the stem. I sanded each section using progressively finer sand paper and counted the rings present. For each section, the height of the stem represented a minimum height of the stem give that year of the stem's life. When consecutive stem increments were the same age, I used the maximum height for that age. In this way, I reconstructed height at age for all willow stems.

Using these data, time-series of height were created from each stem. The height of stem j in site k in year t was a function of the height of that stem in the previous year (without observation error) plus a site, year, and age-specific growth rate:

$$log(H_{jkt}^{pred}) = log(H_{jkt-1}^{true}) + a_{jkt}$$

where a_{kt} is the growth rate for the stem at that time and site. Growth rate was an exponential function of site characteristics and trophic and climate covariates by year, which constrained growth to be positive:

$$a_{jkt} = \exp(a_0 + a_a A_{jt-1} + \mathbf{a_b T_t} + \mathbf{a_c C_t} + \mathbf{a_d S_k})$$

where a_0 is the intercept, A_{jt-1} is the age of the stem in year t-1, $\mathbf{T_t}$ are trophic effects, $\mathbf{C_t}$ are climate effects for that year, and $\mathbf{S_k}$ represent site-specific linear covariates. Observed height for each stem at each site and year was a function of the unobserved true height plus observation error: $log(H_{jkt}^{obs}) \sim Normal(log(H_{jkt}^{true}), \sigma_{obs})$. The unobserved true height was a function of the predictions plus process error: $log(H_{jkt}^{true}) \sim Normal(log(H_{jkt}^{pred}), \sigma_{proc})$.

I used trophic and climate predictors with no time-lags, as described below. Trophic covariates included elk, bison, and wolf numbers. I used growing season length and annual precipitation for climate covariates. Site covariates included mean elevation derived from a 10 m resolution digital elevation model (DEM), cumulative upstream area, and topographic wetness index. All predictors

were standardized and predictors whose correlation score was greater than 0.70 were removed from the model, which resulted in dropping bison because it was too correlated with wolf numbers over the time period covered by the data (1972 to 2008).

As with establishment models, I estimated parameters using Bayesian methods in JAGS and R (Plummer, 2011). I standardized all regression predictors by subtracting the mean from each observation and dividing by the standard deviation. I used noninformative priors: all regression coefficients were distributed normally with a mean of 0 and standard deviation of 10 (not informative because predictors were standardized), and precision parameters were gamma distributed with shape and scale parameters equal to 0.001 (Gelman, 2006). I ran the MCMC algorithm for a minimum of 10000 iterations, with a burn-in of 5000. I fit the full model with all potential two-way interactions, and dropped interaction terms if their 95 percent credible intervals overlapped zero. I maintained all main effect terms that were involved in interactions, regardless of their credible intervals.

Climate effects

I developed climate covariates related to growing season length, precipitation, and Yellowstone river discharge. For growing season length, I estimated growing degree days on the northern range from temperature records from two National Climate Data Center weather stations (Mammoth and Tower). Growing degree days were calculated for each day using the difference between the mean temperature and a threshold of 32 F, and summed over each day from March to October. I averaged the growing degree days estimate from each station to provide a single indicator of growing season length for the northern range.

I used precipitation data from the same weather stations to estimate total annual precipitation by summing over the water year (starting in October). Like with growing season length, I averaged over the two weather stations in each year to provide a single indicator of annual precipitation for the northern range. In addition to a single year's precipitation, I also estimated cumulative precipitation for up to four previous years.

Yellowstone River discharge data was used to capture annual variation in flow. Wolf et al. (2007) showed previously that Yellowstone River discharge highly correlated with flow in smaller tributaries on the northern range. Since the Yellowstone has a continuous time series of flow during the period of interest, I used the USGS gauge information at Corwin Springs to represent interannual variability in flow across the northern range. I investigated both peak discharge as well as mean annual discharge. Like precipitation, I created cumulative predictors for mean annual discharge summing up to four previous years.

Trophic effects

I used abundance data for elk, bison, and wolves on the northern range to explore the effects of upper trophic levels on willow establishment and growth. A complete census of bison and wolves exists for each year during the period of interest (1970 to 2009, P.J. White, unpublished, Smith et al. 2011). To obtain a complete time series for elk, I used published abundance data from aerial counts (Eberhardt et al., 2007; Smith et al., 2011) and interpolated missing years using an auto-regressive time-series model fit in the package MARSS (Holmes et al., 2012).

4.3 Results

Willow Canopy Cover

Overall, willow canopy cover declined from 1969 to 2009, which did not provide support for positive trophic effects of wolves on willows (Figure 4.3). If wolves had decreased elk numbers and/or browsing pressure on willows, I should have seen widespread increases in willow cover since 1995. Model selection among DFA models with 1, 2, or 3 shared trends among cover time series supported a model with a single shared trend. The common trend indicated little change in cover from 1969 to 1991, and a sharp decline in cover from 1991 to 2009 (Figure 4.3).

Over half of the sites indicated a decreasing trend in canopy cover over the 40 year time series, declining more steeply from 1991 to 2009 (13 of 22 sites, loadings > 0.2, Figures 4.3, 4.4). Less than one third of sites (7 of 22 sites) indicated increasing willow cover (negative loading). These

sites showed steep increases in cover from 1991 to 2009. Two sites showed little support for a positive or negative trend in willow cover.

Willow Establishment

The 63 willows in my sample established from 1980 to 2008 (Figure 4.5). At least one plant established during each year, with the exceptions of 1981, 1988, 1990-1992, and 2008. Establishment peaked in 2003, with 17 plants germinating in that year.

Willow establishment over the past three decades was better predicted by trophic effects than climate and hydrologic drivers. My individual predictor regressions showed correlations between most trophic and climate predictors and establishment, however wolf and elk abundance explained the greatest proportion of deviance and had the largest magnitude standardized coefficients (Table 4.1). Wolf abundance was positively correlated with establishment (median +/- 95 percent credible intervals = 0.974 [0.724,1.255]), while elk abundance had a negative effect (-0.616 [-0.849,-0.383]). Bison abundance was positively correlated with willows establishing (0.191 [-0.042,0.399]).

Despite the stronger trophic covariates, climate predictors did explain substantial variation in willow establishment when regressed individually (Table 4.1). Higher peak flows the year prior to establishment and lower peak flows the year following establishment were correlated with higher establishment rates (0.249 [0.013,0.472] and -0.383 [-0.669, -0.106]). I observed a negative effect of mean annual flow in the current year and year after establishment (-0.312 [-0.612, -0.034] and 0.607 [-0.927, -.0309]), as well as negative effects of cumulative flow up to three years prior to establishment (-0.253 [-0.555,0.022]). Annual precipitation in the year prior to establishment and cumulative annual precipitation up to 4 years prior had negative effects on willow establishment (-0.196 [- .443, 0.056] and -0.331 [-0.613, -0.061]).

Model selection using combined predictors also suggested trophic predictors were more important than climate predictors in explaining recent establishment patterns (Table 4.2). After eliminating correlated predictors, I used a single predictor each for annual precipitation, mean annual flow, and peak flow to describe climate variation in a multiple regression model. Wolf and bison abun-

dance represented the trophic covariates. The ten best models with combined predictors included were all within two DIC units of each other, suggesting they were indistinguishable from each other in terms of fit. However, the model with the lowest DIC score also had the lowest number of effective parameters, and included elk and bison abundance, but no climate covariates.

Willow Stem Height

Collected stems ranged in age from 5 to 36 years old in 2009. The median year of stem initiation was 1996, and I observed stems sprouting in every year from 1972 to 2004 with the exception of 1973 and 1976 to 1980 (Figure 4.7). Models fit observed height changes quite well, with exceptions in the years that were data limited (e.g. 1976-1980, Figure 4.9). Stem age strongly influenced height growth rate (-0.347 [-0.397, -0.304], Tables 4.3 and 4.4, Figure 4.9). Height growth rate declined with age, with younger stems growing at much faster rates than older (e.g. 10 year old) stems. None of the site covariates (elevation, topographic wetness index, or cumulative upstream area) explained meaningful variation in stem height and they were not retained in the final model.

I estimated the overall mean height for the collected stems from 1972 to 2008 (Figure 4.6). Mean height for these stems has increased through time. Rates of increases in height accelerated during recent years. If elk herbivory had severe impacts on stems, I should have seen very low growth rates during the period of highest elk abundance. Instead I saw an increasing trend in height that began around 1985, ten years before wolf reintroduction (Figure 4.6). Despite the increasing trend, however, my sample of stems had only reached a mean height of about 150 cm by 2008.

Stem height time series suggested that both biotic and abiotic factors affected stem growth, depending on the age of the stem. After dropping coefficients with posterior distributions over-lapping zero by 5 percent or more, my willow height time-series model included all main effects except for site covariates, and some interactions. Interactions between age and elk (-0.155 [-0.194, -0.102]), age and wolves (-0.196 [-0.246, -0.14]), age and precipitation (-0.078 [-0.123, -0.026]), and growing season length and precipitation (0.249 [0.157, 0.341]) were retained in the final model

(Table 4.3). For stems younger than two years, elk abundance, wolf abundance, and precipitation were all correlated with higher height growth rates. For stems older than two years, all three of these factors had negative effects on height growth. Growing season length increased stem growth rate, regardless of stem age. Growing season length interacted with annual precipitation, however, such that the effect of a longer/warmer growing season was lessened when annual precipitation was low (Table 4.4).

The strength of evidence supporting control by upper trophic levels or climate drivers also depended on stem age. Growing season length was the single most influential predictor for stems less than four years old (coefficient in an average precipitation year = 0.359, Table 4.4). Stems older than four years were more influenced by elk and wolf abundance (coefficients declined from -0.489 to -1.666 with stem age). Growing season length could shift the age at which stems switch from being more bottom-up to top-down limited during extremely wet years. For example, in a somewhat dry year, the height of three year old stems would be more strongly correlated with wolf abundance (-0.292) than with growing season length (0.22). The stem height-age model revealed complex interactions among variables controlling stem height. During any one year, the relative influence of trophic effects depended on stem age and climate.

4.4 Discussion

Canopy Cover

Willow cover over the last 40 years showed limited evidence for trophic effects attributable to reintroduction of wolves. If wolves had released willows from browsing pressure, I should have seen widespread increases in canopy cover through time along small streams. Instead, willow cover has declined at most of my study sites. I saw little change in cover during 1969 to 1991 at any sites, a period when elk abundance increased seven fold. Willow canopy cover declined from 1991 to present at two-thirds of my study sites, while the elk population declined to 30 percent of its peak size. The dramatic changes in elk numbers with little change in willow canopy cover suggests that cover was not particularly sensitive to changes in elk numbers.

Baril et al. (2011) used the same aerial photos as us to estimate height change in willow stands from 1991 to 2006 at different locations on the northern range. Baril (2009) showed that regardless of on the ground canopy cover estimates, only willows taller than 100 cm could be seen from the aerial photos. This 100 cm height threshold for detection occurred because willows shorter than 100 cm did not provide enough relief from background herbaceous vegetation. Therefore, plants that were once hedged short but grew taller than the 100 cm threshold appeared as "new" plants on aerial photos. Alternatively, new plants that established could be detected denovo once they were taller than 100 cm. Recent willow establishment patterns documented in this study suggested that new plants have germinated in recent years, which could explain some of the increases in cover I detected. In contrast, decreases in cover that I detected may indicate height declines or increased mortality of willow plants.

The patchy pattern of increasing cover I observed is similar to what Baril et al. found using the 1991 and 2005 aerial photos. They detected increases in cover ("release") at three of seven sites they studied. Notably, one of their sites was on Blacktail creek, where several of my study sites were located. However, of seven sites I studied on Blacktail creek, only two showed increased willow cover through time. Their work and my shows that changes in willow cover over time has been remarkably variable across the landscape. Differences in the direction and magnitude of change occurred among stands within a single drainage.

Establishment

Willow establishment appears to have increased since 1999. Changes in abundance of herbivores following wolf reintroduction were correlated with these increases. The positive correlation between wolf abundance and recent willow establishment may provide evidence for a trophic cascade. Wolf and elk abundances were highly correlated. Wolf numbers were a stronger predictor of establishment events than elk numbers, which may suggest that changes in establishment are not due solely to changes in elk numbers, leaving behavioral effects (Ripple and Beschta, 2004a) as a potential explanation.

Despite relatively small effects of climate on willow establishment, my findings on the links between climate and establishment agree with previous work. Wolf et al. found that establishment followed periods of drought, and my establishment data supported this finding. Cumulative annual precipitation and cumulative mean annual flow of the Yellowstone river for 3-4 years prior to germination was negatively correlated with willow establishment (Table 4.1 and Figure 4.5). I also found that high flows during the year following germination were negatively correlated with successful establishment. Scouring during high flow events has been shown to negatively impact survival of willow seedlings (Gage and Cooper, 2004).

Increased willow establishment was not correlated with increased willow cover on the northern range. Although I did not survey seedling locations, previous work showed that willows established increasingly closer to the stream channel from 1941 to 1999 (Wolf et al., 2007). The absence of beaver dams and associated fine-grained sediment limited the spatial extent of recent willow establishment (Wolf et al., 2007). Almost all of my excavated root crowns were located within 5 m of the stream channel, suggesting that willow establishment I observed continues to be limited by a lack of beaver dams along small streams.

Stem height

I found mixed support for indirect trophic effects of wolves in my stem height time series. The negative slope of coefficients for elk and wolf numbers was not consistent with the idea that willows were protected by increasing predator abundance. If wolves were protecting willows from browsing, I should have seen a positive effect of wolf numbers on stem growth. The negative effect of elk on stem growth suggests that greater numbers of elk browse willows more heavily. The negative effect of wolves on stem growth may be explained by behavioral effects of wolves that intensify elk browsing on willows. Creel et al. (2009) found that elk increased browsing on willows in the presence of wolves. Observed stem growth rates may reflect this pattern. Although elk abundance decreased after wolf reintroduction, the smaller number of elk may have increased browsing on willow stems in response to wolf presence.

The negative effect of high precipitation on willow stem growth may also be an indirect signal of negative trophic effects of elk. Increased elk browsing rates have been linked to deeper winter snow (Kay, 1997; Christianson and Creel, 2007; Creel and Christianson, 2009). Therefore, if annual precipitation correlates with greater winter snow depths, precipitation in my model may actually describe variation in winter browsing patterns.

Ours is the first study to investigate the role of stem age in the relative importance of top-down and bottom-up controls. Young stems were more strongly influenced by growing season length than by trophic effects of elk or wolves. Relatively lower trophic effects may indicate that young stems were not browsed as heavily as older stems. In their first few years of age, young stems are typically shorter than older stems on the same plant. Therefore, young stems could be protected from browsing during winter by being buried under the snow. Alternatively, ungulates may have a harder time accessing young stems in the middle of a willow clump compared to older taller stems on the upper and outer periphery of the clump.

Conclusions

I show clear evidence for the simultaneous operation of bottom up and top down controls on willow establishment, canopy cover, and height during the past 4 decades on small streams on Yellowstone's northern range. I found support for the operation of a trophic cascade in negative correlations between willow establishment and elk numbers and positive correlations between willow establishment and wolf numbers. I also found evidence that climate change, particularly increasing periods of drought and fewer high flow years have accelerated willow establishment. Height growth for willow stems appeared to be most strongly shaped by increased growing season lengths during the 1980s, an effect that was independent of stem age. I failed to observe dramatic changes in stem height or canopy cover coincident with wolf reintroduction. Instead, I found that increases in growth rates for young stems and increased mean height began a decade before wolves were reintroduced to Yellowstone. This longer term trend implicates climate change as the cause for changes in growth patterns. Overall, my work demonstrates the importance of multiple con-

trols on growth of willows and casts doubt on the operation of a linear trophic cascade as the sole influence on Yellowstone's willows.

Table 4.1: Results of Poisson regressions for single parameter models predicting establishment as a function of climatic and trophic independent variables. The median and 95 percent credible intervals of posterior estimates are given, as well as the posterior weight greater than or less than zero. I estimated pseudo R^2 as the proportion of deviance explained by the predictor over the null model with an intercept alone. Posterior weights greater than 90 percent are indicated by * and predictors included in combined model selection indicated by 1.

Predictor	Time	Median	0.025	0.975	$P > 0$ or $P < 0$	Pseudo R^2
Peak Flow	t	0.141	-0.104	0.379	0.8714	0.0082
	t+1	-0.383	-0.669	-0.106	0.9971*	0.0468[1]
	t-1	0.249	0.013	0.472	0.9803*	0.0277
Mean Annual Flow	t	-0.312	-0.612	-0.034	0.9859*	0.0307
	t+1	-0.607	-0.927	-0.309	1*	0.107[1]
	t-1	-0.172	-0.454	0.09	0.8943	0.0092
	$\sum$t-1 and t	-0.312	-0.622	-0.03	0.9865*	0.0289
	$\sum$t-2 to t	-0.469	-0.823	-0.167	0.9999*	0.0563[1]
	$\sum$t-3 to t	-0.253	-0.555	0.022	0.9622*	0.0189
	$\sum$t-4 to t	0.005	-0.261	0.244	0.5147	0
Annual Precipitation	t	-0.145	-0.398	0.102	0.8742	0.0132
	t+1	-0.14	-0.395	0.113	0.86	0.007
	t-1	-0.196	-0.443	0.056	0.9402*	0.015
	$\sum$t-1 and t	-0.264	-0.536	-0.004	0.9769*	0.0235
	$\sum$t-2 to t	-0.364	-0.641	-0.106	0.9962*	0.0459
	$\sum$t-3 to t	-0.503	-0.814	-0.227	1*	0.0799[1]
	$\sum$t-4 to t	-0.331	-0.613	-0.061	0.992*	0.0374
Wolf abundance	t	0.974	0.724	1.255	1*	0.3866[1]
Bison abundance	t	0.191	-0.042	0.399	0.9475*	0.0178[1]
Elk abundance	t	-0.616	-0.849	-0.383	1*	0.1619

Table 4.2: Strength of evidence for alternative models predicting willow establishment. WOLF and BISON are abundances, AFLOW2 is cumulative mean annual flow from the current and two previous years, CPRCP3 is cumulative precipitation from the current and three previous years, NFLOW is the mean annual flow for the year following establishment, PFLOW is peak flow in the previous year.

Predictors	Effective number of parameters (pD)	Deviance	DIC	△DIC
WOLF, BISON	3.453	82.09	85.54	0
WOLF, BISON, AFLOW2*CPRCP3	6.1	80.08	86.18	0.64
WOLF, BISON, AFLOW2	4.092	82.21	86.3	0.76
WOLF, BISON, CPRCP3	4.417	81.94	86.36	0.82
WOLF, BISON, NFLOW	4.53	82.17	86.7	1.16
WOLF, BISON, INT	4.695	82.21	86.91	1.37
WOLF, BISON, PFLOW	4.119	83.05	87.17	1.63
WOLF, BISON*CPRCP3	5.216	82.24	87.46	1.92
WOLF*NFLOW, BISON, NFLOW*CPRCP3	6.845	80.7	87.54	2
WOLF*NFLOW, BISON	5.26	82.29	87.55	2.01

Table 4.3: Parameter estimates for models predicting stem stem height over time. Predictor variables are age of the stem (AGE), growing degree days (GDD), elk abundance (ELK), wolf abundance (WOLF), and annual precipitation (PRCP).

	median	0.025	0.975
intercept	-0.003	-0.115	0.098
AGE	-0.347	-0.397	-0.304
GDD	0.359	0.239	0.493
ELK	0.174	0.091	0.257
WOLF	0.296	0.212	0.381
PRCP	0.087	0.021	0.151
AGE*ELK	-0.155	-0.194	-0.102
AGE*WOLF	-0.196	-0.246	-0.14
AGE*PRCP	-0.078	-0.123	-0.026
GDD*PRCP	0.249	0.157	0.341
Observation error s.d	0.045	0.035	0.062
Process error s.d.	0.388	0.376	0.401

Table 4.4: Effects of climate and trophic effects on stem growth rate as a function of stem age. Standardized coefficients for elk abundance (ELK), wolf abundance (WOLF), and precipitation (PRCP) reflect the main effect plus the interaction effect with stem age. Growing season length (GDD) interacts with annual precipitation (GDD avg. PRCP), and dry and wet years were defined by 0.25 and 0.75 quantiles of the precipitation data from 1972 to 2008.

| AGE	ELK	WOLF	PRCP	GDD (avg. PRCP)	GDD (dry year)	GDD (wet year)
0	0.174	0.296	0.087	**0.359**	0.22	0.456
1	0.019	0.1	0.009	**0.359**	0.22	0.456
2	-0.137	-0.096	-0.069	**0.359**	0.22	0.456
3	-0.292	-0.292	-0.147	**0.359**	0.22	0.456
4	-0.448	**-0.489**	-0.225	0.359	0.22	0.456
5	-0.603	**-0.685**	-0.303	0.359	0.22	0.456
6	-0.758	**-0.881**	-0.381	0.359	0.22	0.456
7	-0.914	**-1.077**	-0.459	0.359	0.22	0.456
8	-1.069	**-1.274**	-0.537	0.359	0.22	0.456
9	-1.225	**-1.47**	-0.615	0.359	0.22	0.456
10	-1.38	**-1.666**	-0.693	0.359	0.22	0.456
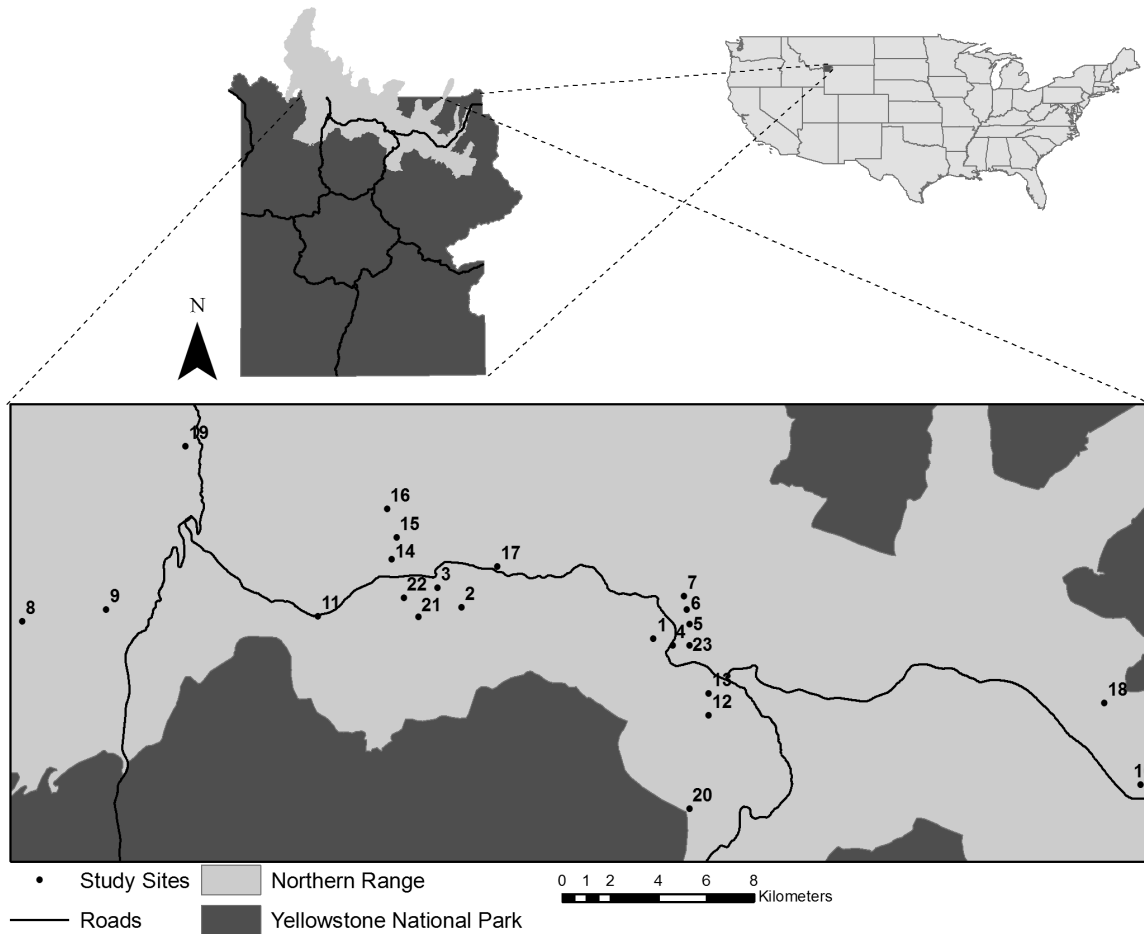
Figure 4.1: Map of study sites
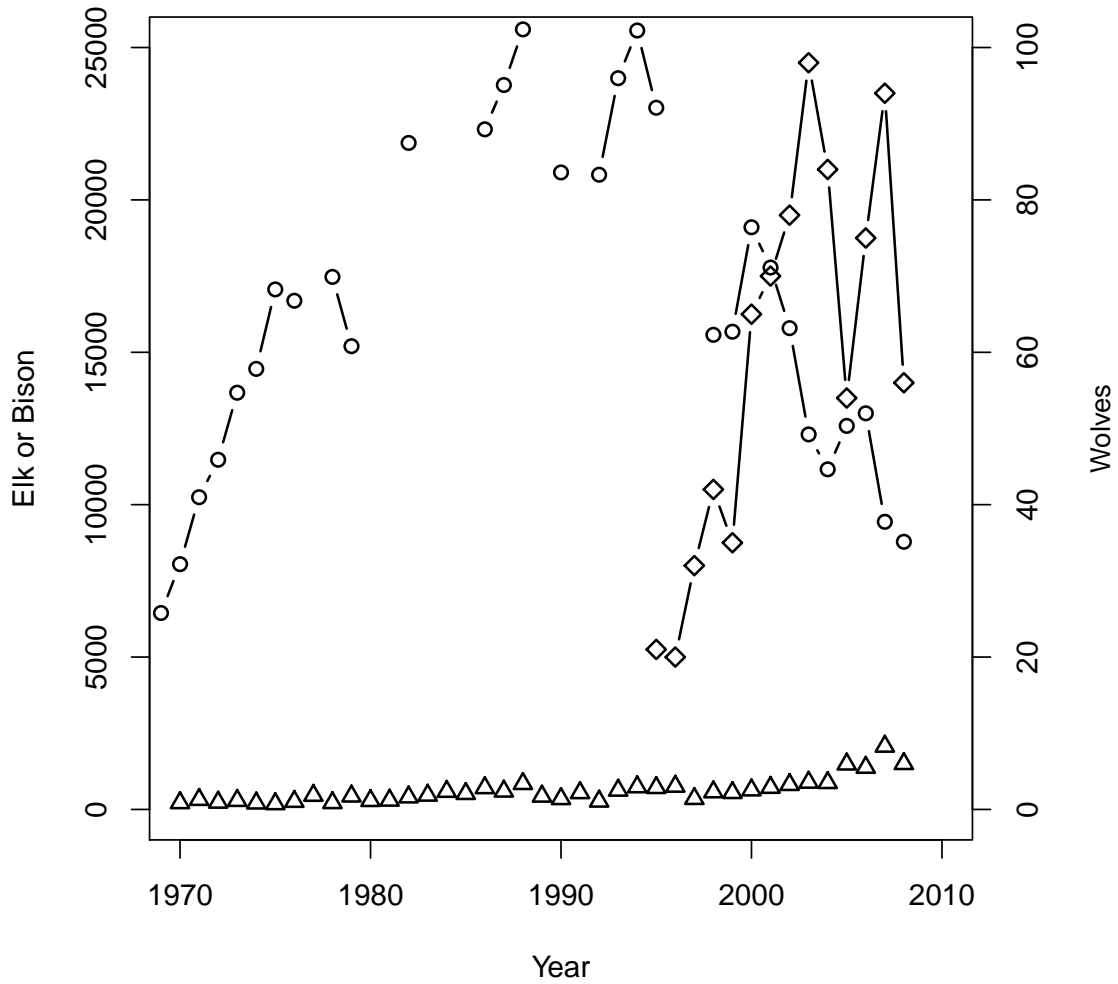
Figure 4.2: Elk, wolf, and bison abundance on Yellowstone's northern range 1970 to 2009. Elk (circles) and bison (triangles) abundance are represented on the left y-axis, while wolf abundance (diamonds) is on the right y-axis.
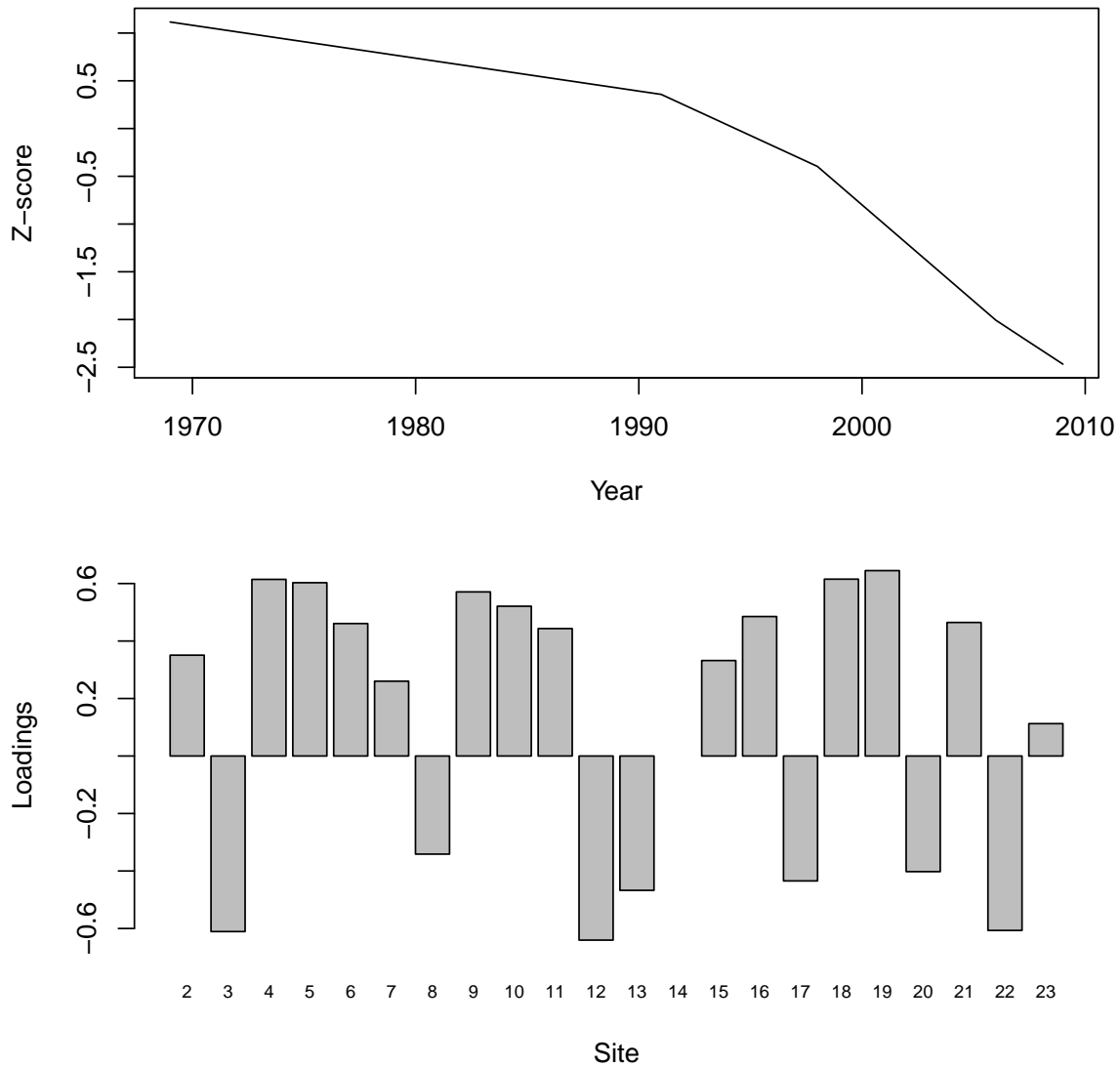
Figure 4.3: Results from dynamic factor analysis of willow canopy cover trends from 1969 to 2009. Common trend from dynamic factor analysis (upper panel) indicates canopy cover decreased at most sites during the four decades. Site loadings (bottom panel) illustrate how well the common trend describes the dynamics at each site. Positive loadings indicate the site follows the common trend and negative loadings indicate the site follows the inverse of the common trend (increasing canopy cover through time). Only site loadings greater than 0.1 were plotted.
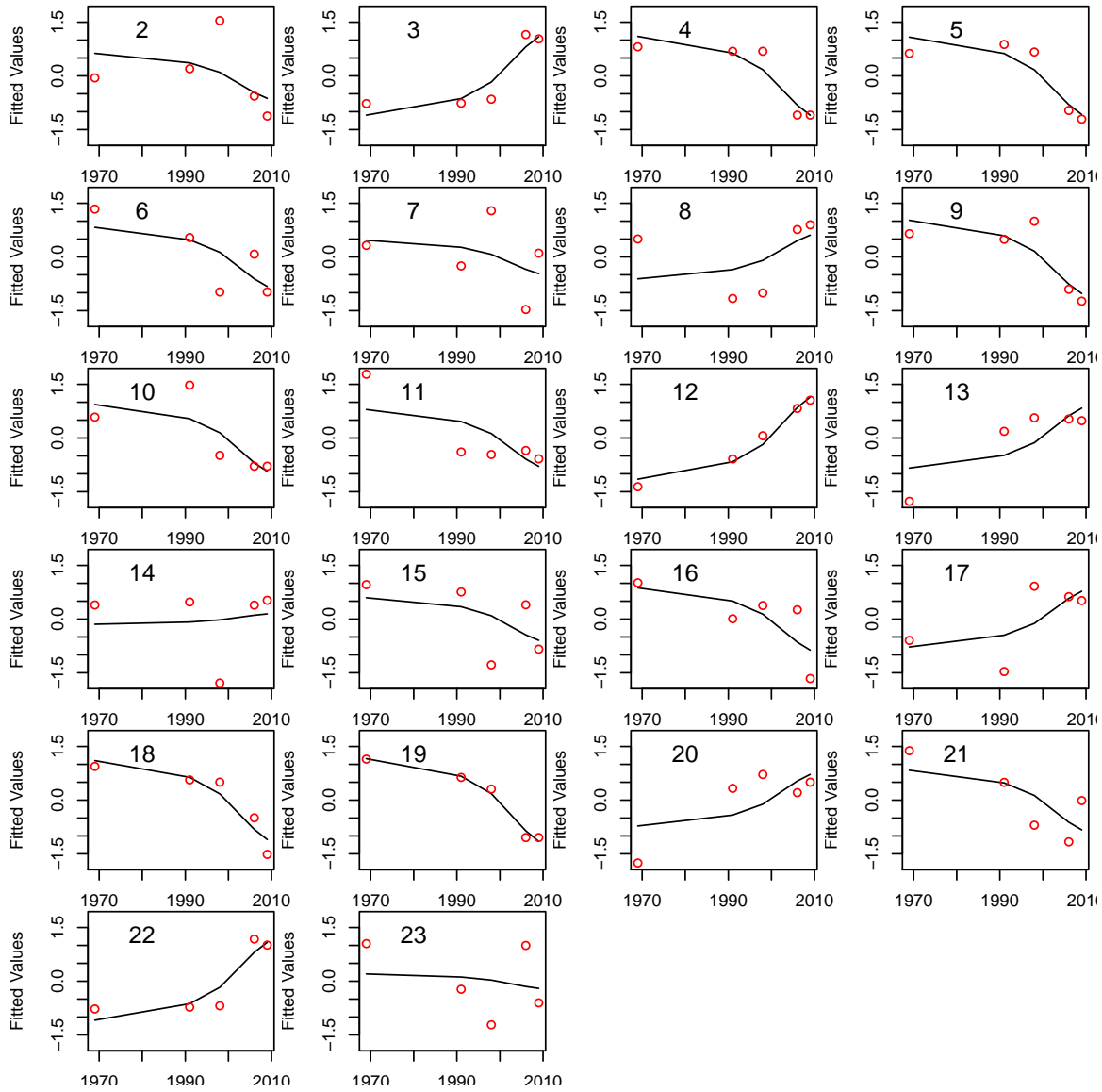
Figure 4.4: Dynamic Factor Analysis fits to willow cover data at 22 study sites from 1969 to 2009. Observed data were plotted as points, while the model fit was plotted as a line. Each trend line combines the common trend and the site loadings indicated in Figure 3.
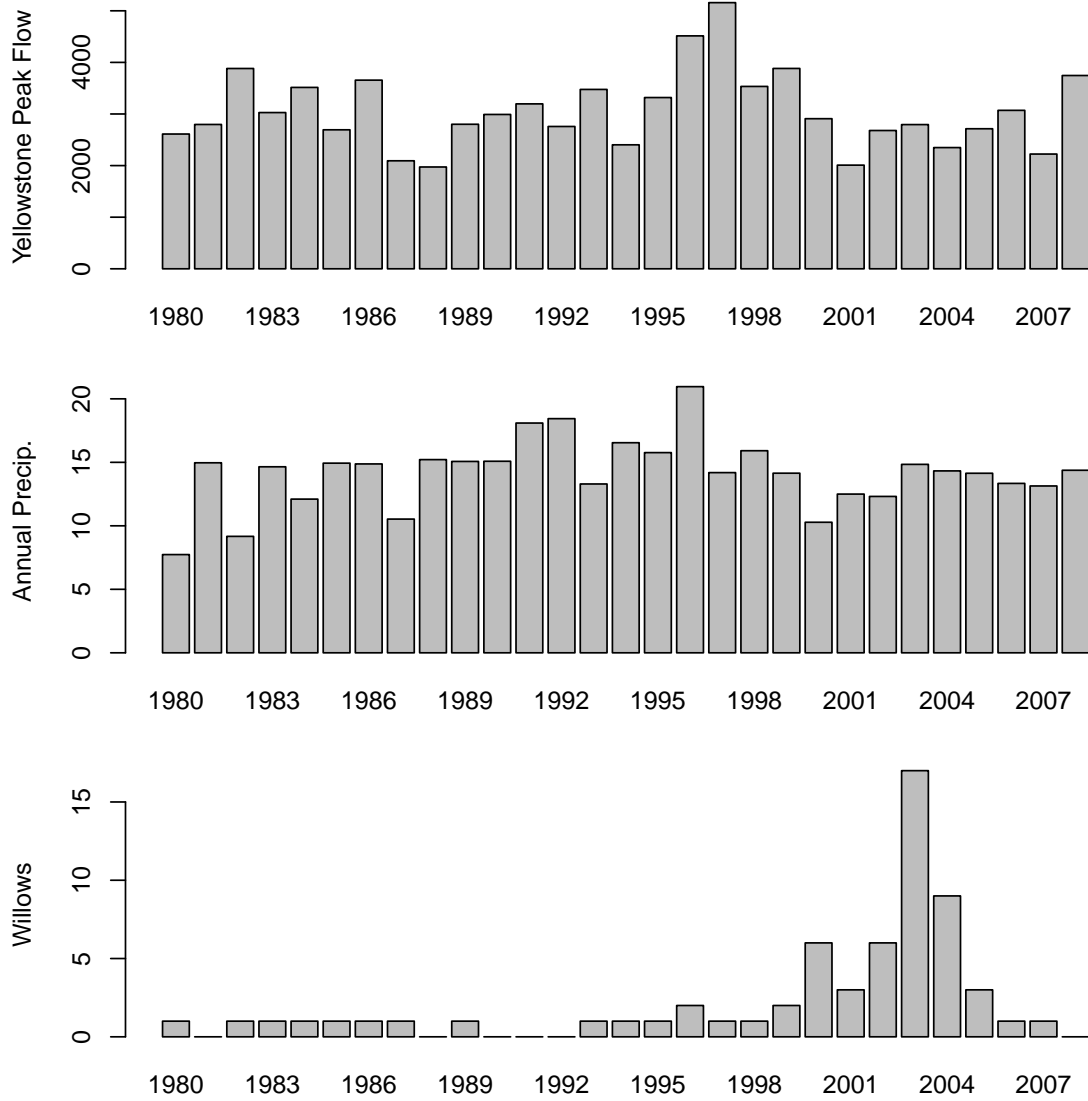
Figure 4.5: Peak discharge of the Yellowstone River (cubic feet per second), northern range annual precipitation (inches per year), and willow establishment from 1980 to 2008.
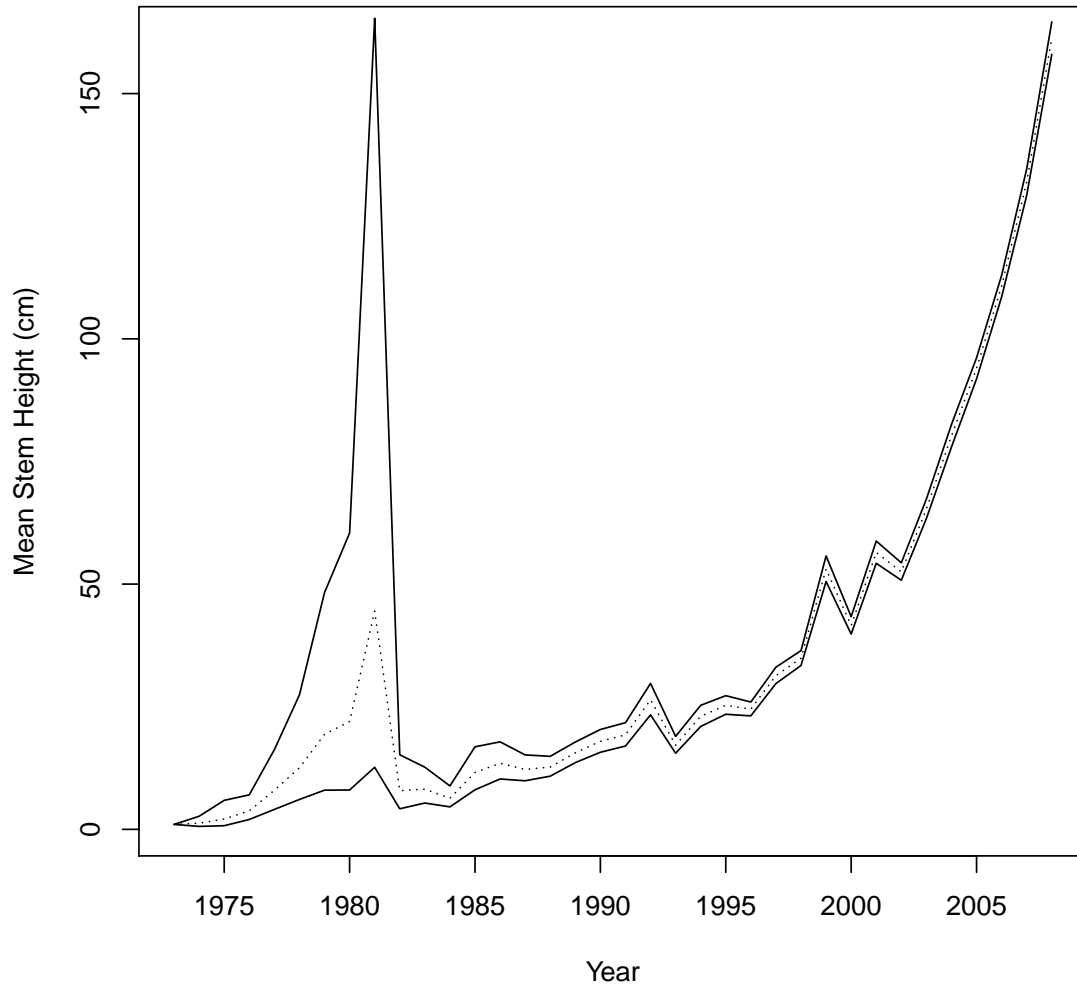
Figure 4.6: Mean height of all stems 1972 to 2008. Posterior predictive mean height with 95 percent credible intervals.
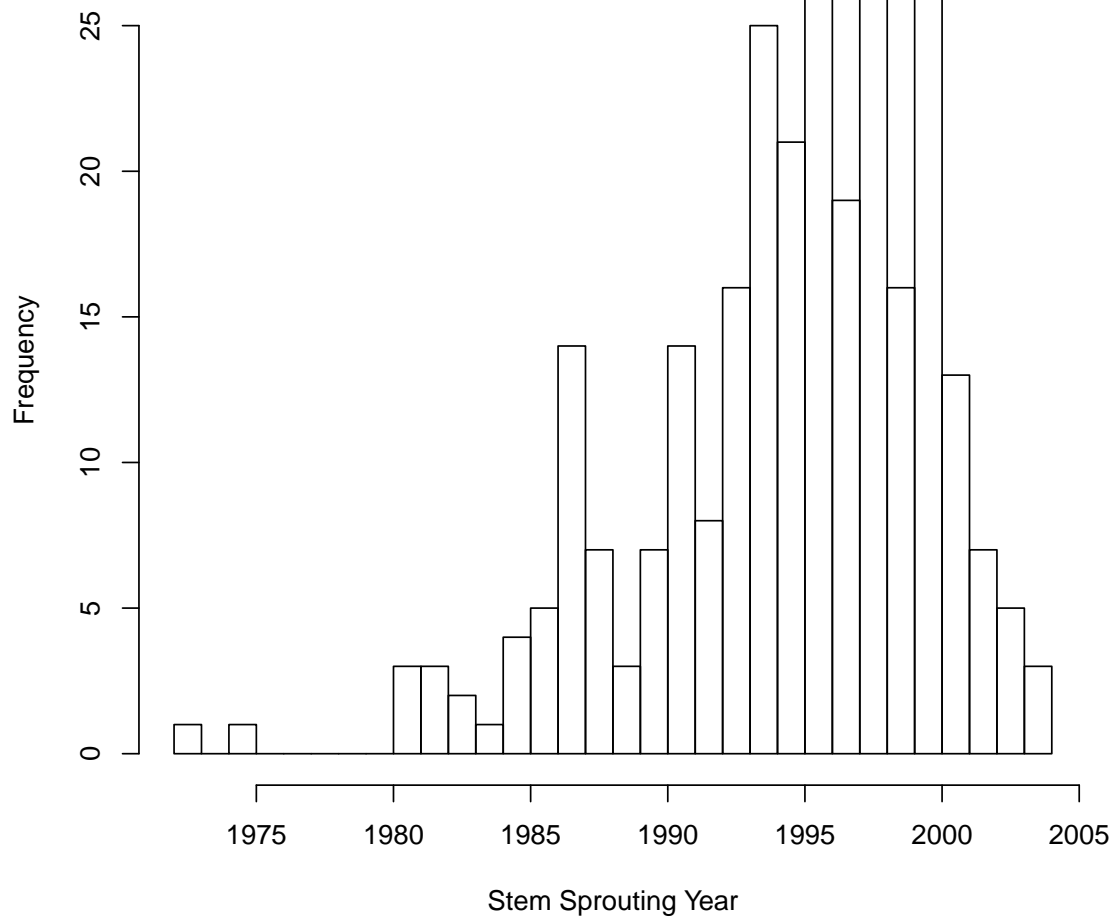
Figure 4.7: Frequency distribution of stem initiation years for collected willow stems.
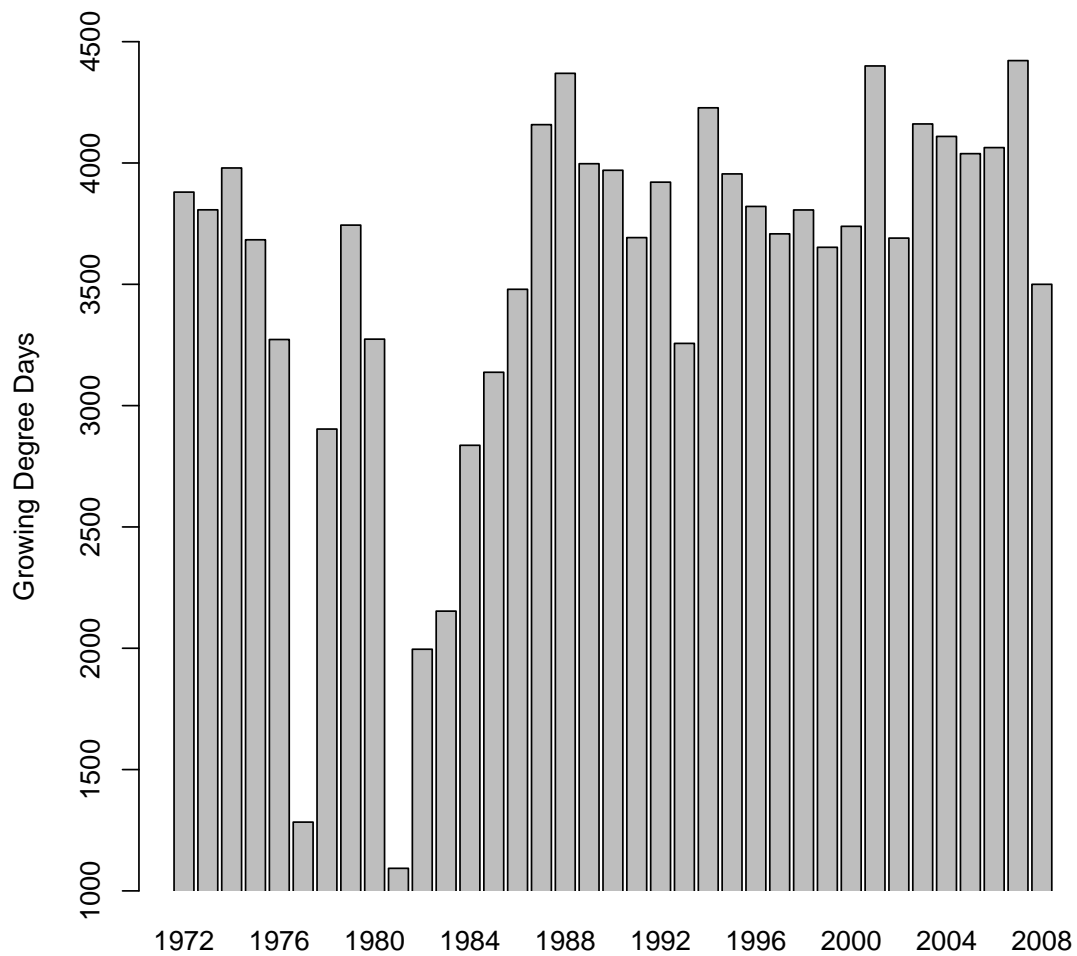
Figure 4.8: Growing season length on the northern range 1972 to 2008. Growing season length is represented by growing degree days, calculated with a 32 F threshold.
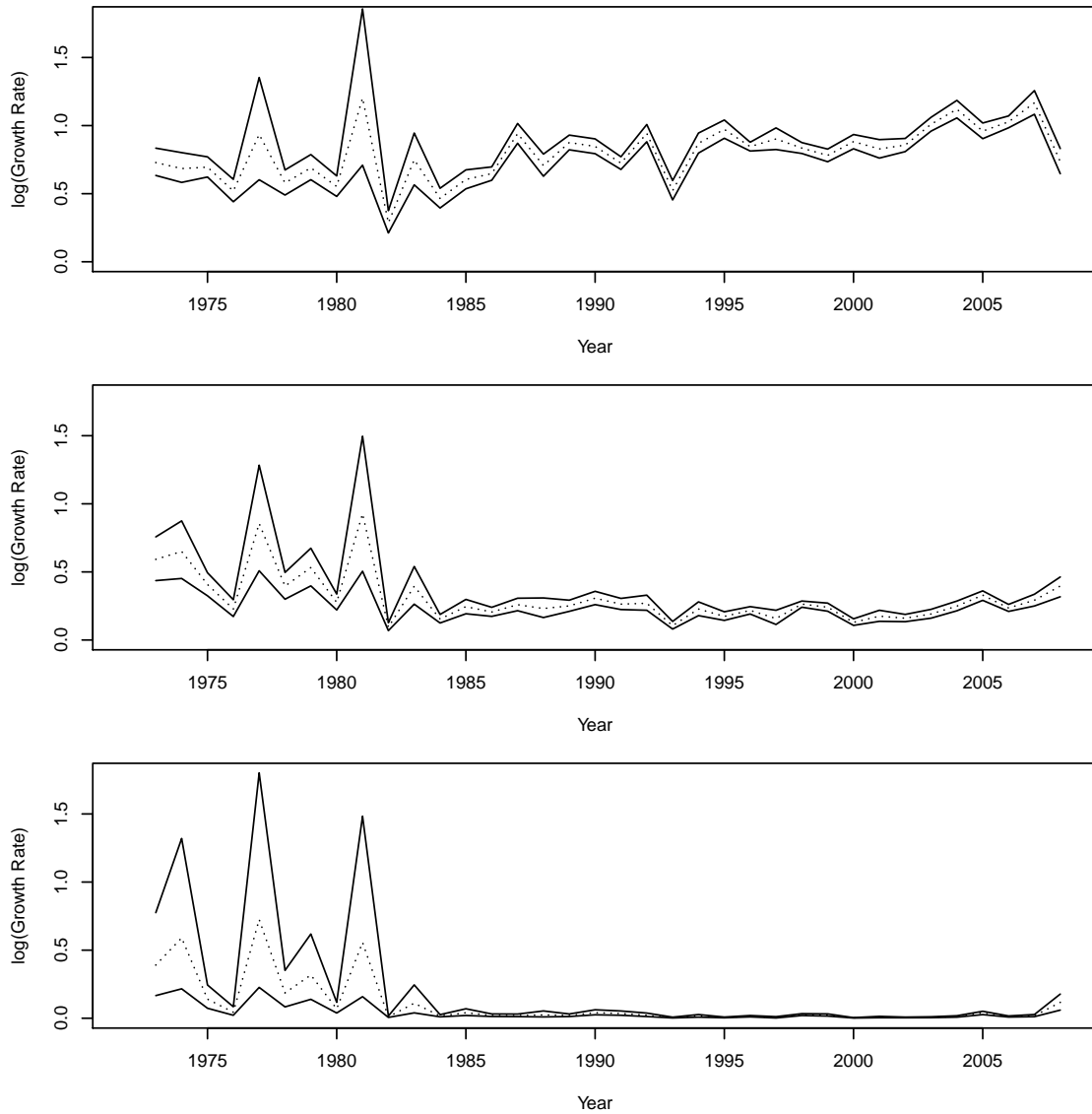
Figure 4.9: Predicted stem height growth rates 1972 to 2008 for stems age 1 (upper), 4 (mid), and 10 (lower). Dotted line represents the posterior estimate of the mean growth rate. Solid lines show 95 percent credible intervals on the mean.

5 Synthesis

My dissertation research described how top-down and bottom-up effects on willows control alternate states in riparian communities across a heterogeneous landscape in Yellowstone National Park. My work provides broad understanding of limitations to willow growth on the northern range, and revealed that wolf reintroduction has not restored riparian areas. I used a decade-long experiment to explore the relative influences of water table depths and ungulate herbivory on willow height and net annual production. I applied the findings from this experiment to explore gradients of top-down and bottom-up control across the landscape and made predictions about where willow recovery may occur more quickly and where beavers may be likely to re-colonize northern range streams. I also evaluated relative support for trophic and climatic effects controlling willow growth and establishment over the past four decades. All of these studies led to the conclusion that bottom-up effects of resource limitation influence northern range willows more strongly than top-down effects of top predators or herbivores. This strong evidence for bottom-up limitation suggests that the alternative ecosystem state induced by the 70 year absence of wolves is not easily reversible. My findings on the thresholds associated with willow recovery and beaver occupation are applicable beyond Yellowstone, to wild and managed lands across the western U.S. More broadly, this work will add to growing ecological understanding of alternative states, thresholds, and transitions in heterogeneous landscapes.

I showed that water table depth limits willow height and annual production more than ungulate browsing in a manipulative experiment in Chapter 2. After 10 years of total protection from browsing, the riparian ecosystem remained locked in the ungulate-grassland state unless water tables were raised by an artificial beaver dam. Removing browsing had no effect on net annual production by willows regardless of water table depth. Heights of willows in my experimental treatment were representative of the current height distribution of willows on small streams across the northern range. More importantly, the current distribution of willow heights on the northern

range did not differ from the willow height distribution observed in 1990, five years prior to wolf reintroduction.

In chapter 3, I showed that riparian ecosystem states and rates of transition between states were heterogeneous across the northern range landscape. Bottom-up effects driven by landscape heterogeneity were stronger than the top-down effects of herbivory on willow height and growth. Study sites at mid-elevation with shallow slopes and large contributing watershed areas had taller willows than sites at high or low elevation with steep slopes, and small contributing areas. Topography within and across sites controlled the current state of the ecosystem and its rate of transition. Temporal variation in water table variance during the growing season contributed to willow height and growth responses. This provided evidence that willows were adapted to a hydrologic regime described by spring floods and low flows in late summer.

The trends in willow canopy cover, stem growth, and establishment over four decades presented in chapter 4 reinforced what I found in chapters 2 and 3. Top-down effects of wolves and ungulates may influence willow responses, but bottom-up controls associated with climate have stronger influences on northern range willows. Willow canopy cover has increased in only 7 of 23 study sites since 1969. Wolf and elk abundances influenced the growth rate of willow stems younger than four years, but growing season length and annual precipitation had stronger impacts on stems older than four years. Of all the data sets presented in all three chapters, only willow establishment was more strongly controlled from the top down by wolves and elk than by bottom-up effects dictated by climate.

Together, these results clearly show that the operation of a linear trophic cascade resulting from wolf reintroduction has not restored riparian communities on Yellowstone's northern range. Instead I found that trophic effects must be considered within their climate and landscape context. Wolf predation on elk may cause ecosystem state transition in areas where water is not a limiting resource, or during particularly wet years. However, cascading effects of wolf presence on the northern range have not uniformly caused dramatic shifts in willow height.

The goal of reintroducing wolves to Yellowstone was to restore a complete ecosystem. Restoring riparian ecosystems on the northern range requires beavers to recolonize small streams. Three possibilities explain the continued absence of beaver dams on the northern range. The first possibility is that willow height and density is insufficient to support beaver colonies over multiple years. My landscape study found that willow height was taller than the transition threshold at three sites in the Blacktail Creek drainage. Those sites may be suitable for beaver occupation. However, I studied willow heights at seven sites in that drainage and less than half of them had willows of sufficient heights for beavers. A patchy distribution of tall willows over a drainage basin may be insufficient to establish and support beaver complexes over multiple years.

A second possible explanation for the continued absence of beaver is that the source population is too small or too distant for beaver to recolonize suitable areas. Reintroduction of beaver on public lands outside the park has led to established populations in upper Slough creek, upper Hellroaring Creek and the Buffalo Fork. Beavers have dammed both of these rivers outside of the park boundary, and individuals have moved down into Slough Creek inside park boundaries. They have yet to dam the main stem of slough creek inside the park for more than a single season, at least in part because the river is too large and active. Beavers have built bank dens along Slough Creek, Soda Butte Creek, and occasionally along the Lamar River and Gardner River over the past decade. The presence of bank denning beaver suggests that a source population is available and beaver are moving around the ecosystem. Perhaps the distance between these edges of the northern range and the areas where willows are increasing in height in the Blacktail Creek drainage is a barrier to beaver dispersal. A beaver was discovered in one of our experimental sites on Blacktail Creek in 2003 (D. Cooper, pers. comm.), making use of the artificial dam and pond. It did not overwinter in the site, however. Beavers have occupied (in small numbers) the western edge of the northern range in the upper Gardner river and Glen Creek . Two of our study sites occurred in these drainages, but no evidence of beavers occurred in those sites. My landscape study suggested that perennially high water tables limited willow growth in these areas, and beaver appear to utilize sage brush in their dams along those streams. These individuals may be exceptions to the idea that beavers

require tall willows to survive, but their small numbers and limited activity suggest that they have low reproduction and high turnover of individuals over time.

A third reason that beavers are absent from small streams on the northern range is that wolves may prey on dispersing beavers. Wolves consume beaver in other temperate ecosystems, but no evidence exists of wolf predation on beavers in Yellowstone. Predation may be unobserved because beaver are rare on the landscape. Intensive surveys of wolf predation occur in summer and winter, but may not coincide with the timing of juvenile beaver dispersal.

Management implications of my research reach beyond Yellowstone's borders. Wolf populations have radiated from Yellowstone since they were reintroduced in 1995, spilling over into Montana, Wyoming, and Idaho. Wolves have also moved south from British Columbia and established populations in Washington and Oregon. As wolf abundance increases in these areas, predation may reduce ungulate browsing of riparian shrubs by reducing ungulate populations or modifying their foraging behaviors. My research suggests that reductions in browsing may lead to increases in willow height and annual production in areas that are not limited by water availability. Any riparian community response will likely occur in discrete patches. Willow responses will be greater under the most optimal growing conditions, and lower less suitable sites. Predator reintroduction should be viewed as a necessary, but insufficient condition for restoring extensive riparian ecosystems.

Beyond direct implications for the effects of wolves on riparian areas, my study provides a novel example in a growing body of work demonstrating that the effects of removing a top predator are not easily reversible. Restoring native species to their native ranges is an attractive conservation effort. Not only does predator reintroduction lead to more intact ecosystems, but the public connects with charismatic predators more than other species. Resource for conservation are always limited, and trade-offs are unavoidable. My research suggests more value may be gained from conserving intact ecosystems than from reintroducing predators because restoring predators may be insufficient to restore processes that stabilize desirable ecosystem states.

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