

# LTREB: Understanding controls on state-transition on Yellowstone's northern range

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## Intellectual Merit

Understanding the feedbacks that create resilience in alternative states of ecosystems forms a central challenge in contemporary ecology, providing the conceptual basis for the practice of ecosystem restoration. The reintroduction of the gray wolf (*Canis lupus*) to the landscapes of the northern range of Yellowstone National Park offers an unusual 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, and the simplified food web that resulted is believed to have caused a state change in riparian ecosystems. Extensive observational evidence suggests that release of the population of elk (*Cervus elaphus*) from control by wolves and consequent elevated herbivory caused a shift in riparian plant communities from willows to grasslands. Coincident with these changes, a major source of disturbance—dam building by beaver—ceased to influence the hydrology of the small stream network. The loss of engineering by beaver degraded habitat for willows.

Wolves were reintroduced to Yellowstone in 1995. It has been hypothesized that behavioral and numerical effects of wolves on elk initiated a trophic cascade, causing a rapid and dramatic reversal of ecosystem state from grassland to willow. We have been working for a decade to test the trophic cascade hypothesis and to understand the role of top-down and bottom-up forces in controlling the state of riparian ecosystems on the northern range. A 10-year factorial experiment manipulating herbivory and water availability found little support for the operation of a linear, trophic cascade. Instead, we observed a composite of top-down and bottom-up controls and counter-intuitive feedbacks resulting from removing herbivory. Browsing intensity on willows remained static in the face of large reductions in the number of elk.

It is vital to the discipline of ecology and the practice of restoration that the feedbacks created by the reintroduction of wolves to Yellowstone be accurately understood over the fullness of time. The abundance of elk has only recently declined to levels that prevailed during the first half of the twentieth century, the period when state change is believed to have occurred. Thus, it is plausible that there has not been sufficient time for top-down effects of wolves on elk to release willows from effects of herbivory. Here, we propose long-term research to understand how climate, hydrology, and trophic dynamics act to control the state of riparian ecosystems on Yellowstone's northern range. We will continue our manipulative experiment, supplementing it with landscape-scale observations. We will assimilate our measurements in a fully Bayesian, state-space model to evaluate how ungulate numbers and patterns of predation risk explain spatiotemporal variation in browsing intensity and willow growth. We will use the model to determine how trophic effects are modified by climate and hydrology. Using our ongoing experiment, we will examine legacy effects of water stress on willows growing on historic floodplains as a potential, mechanistic explanation for time lags in trophic effects. We will determine if shifts in the composition of the community of large herbivores can explain temporally static patterns of browsing intensity or if those patterns are better explained by an absolute shortage of food created by snow accumulation during winter.

## Broader impacts

The demonstrated interest of citizens in the unfolding story of wolves, elk, and willows in Yellowstone assures that our results will have the opportunity to be communicated in the popular media. By extending understanding of community-level effects to the ecosystem, our proposed work will add value to an ongoing LTREB, "Yellowstone wolves: their ecology and community consequences" (DEB-0613730). We will collaborate closely with park staff in Yellowstone to offer citizen education to three million visitors to the park through interpretive programs. We will communicate our results to park staff to support interpretation and management. Graduate and undergraduate students will be trained. Our data will be made easily available to the scientific community.

## 1 Results from prior funding

Our previous work has been supported by an NSF predoctoral fellowship and by “Landscape Configurations in Yellowstone National Park: An Alternative State Stabilized by Herbivory?” (DEB 0717367, \$399,960, 09/01/2007- 08/31/2011). Four publications in core ecological journals acknowledge support from these awards (Bilyeu et al., 2007, 2008; Johnston et al., 2007, 2011) and five others are being prepared. The findings from our studies are summarized in section 3, *Motivation for proposed work*. Two Ph.D. students were supported by these awards and ten undergraduates were trained, including two REU students, one of whom will begin graduate school with Hobbs in 2012. The most recent graduate student, Kristin Marshall, has received specialized training in communicating science to the public at the Santa Fe Science Writing Workshop. Marshall gave guest lectures at the Wild Rockies Field Institute, Missoula, MT, taught a fifth grade class on tropic cascades at T. R. Paul Academy of Arts and Knowledge in Fort Collins, and participated in a curriculum-based Park Service program for 4th-8th graders visiting Yellowstone. Cooper and Hobbs routinely briefed staff of Yellowstone National Park on our findings to support park management.

## 2 Conceptual framework

One of the most important challenges in contemporary ecology is to understand how biotic processes interact with climate and the physical environment to determine the resilience of natural and human-dominated systems (reviewed by Scheffer, 2009). Resilience is a property of communities and ecosystems that determines their propensity to reorganize to their original condition after disturbance. Although we most often think of resilience in the context of sustaining desirable states, the concept applies equally to restoring degraded ones—in both cases resilient states resist change (Suding et al., 2004). In this proposal, we seek long-term support to understand how hydrology, climate, and the structure of food webs act to determine resilience of alternative states in a riparian ecosystem.

Lewontin (1969), and later Holling (1973), recognized that communities and ecosystems can exist in alternative states of biotic and physical organization, states that can shift abruptly, one to another. State change can be triggered by biotic or abiotic stress, leading to temporary or enduring re-organization of system structure and function. Of particular interest are alternative states that are resilient, that resist return to the original state even when the triggering stressor is removed. For example, in coastal marine ecosystems, over-harvest of top predators has caused a potentially irreversible change in fisheries because juvenile predators are outcompeted by their prey species. Although excessive harvest may have caused the state change, reducing the number of fish taken is not sufficient to recover the fishery (Walters and Kitchell, 2001). In grasslands throughout the world, heavy grazing has reduced plant standing crops and caused shifts in the composition of plant communities, producing feedbacks that reduced soil fertility and water infiltration. Although excessive grazing may have caused the state change, moderating grazing does not allow the original grassland to reorganize on dry, infertile soils (Scheffer et al., 2001; van de Koppel et al., 1997). Because anthropogenic activity is often responsible for moving ecosystems to degraded states (Cote et al., 2004; Osterblom et al., 2007; Moellmann et al., 2009), a central challenge for restoring ecosystems is to understand the feedbacks that create and maintain these states (Suding et al., 2004).

Alteration of the food web of the northern range of Yellowstone National Park during the last century has created a natural experiment with exceptional potential to understand the interplay of biotic, physical, and climatic controls on alternative ecosystem states. The landscapes of the northern range experienced dramatic changes in structure and function over the last century (reviewed by National Research Council, 2002). During the early 1900s, communities of willows predominated the

riparian zones of the northern range, extending up to 40 m laterally from stream margins. Beaver dams punctuated the stream network, flooded large areas of the landscape, and created hydrologic and soil conditions particularly well-suited to the life-history requirements of willows. During the latter half of the 1900s, willows declined in abundance and stature to the extent that they effectively disappeared from the landscape and were replaced by grasslands in riparian zones (Houston, 1982; Singer et al., 1994, 1998).

The change in riparian state from willow to grassland coincided with changes in the terrestrial food web and the disturbance regime. Throughout the 20th century, the northern range provided winter habitat for one of the largest migratory elk herds (*Cervus elaphus*) in North America (Houston, 1982). Historically, elk were the primary prey of the apex predator in the region, the gray wolf (*Canis lupus*). (National Research Council, 2002). However, wolves were extirpated from Yellowstone by the early 1920s. The loss of wolves from the system and the cessation of elk culling by park staff have been repeatedly implicated in the dramatic increases in the abundance of elk during the later part of the twentieth century (National Research Council, 2002)(Figure 1A).

Coincident with the loss of willows, beaver abandoned the small streams of the northern range (Warren, 1926; Jonas, 1955). Almost a third of mainstream reaches historically experienced beaver-related aggradation (Persico and Meyer, 2009) and the absence of their engineering transformed many areas of the riparian zone (Figure 1B,C). The loss of beaver dams lowered water tables and narrowed the area of exposed substrate and moist soils (Figure 1B) required by willows for establishment and growth (Wolf et al., 2007). Unimpeded by beaver dams, stream flows accelerated, causing locally significant incision that effectively disconnected channels from historic flood plains (Figure 1C). Competing explanations exist for the disappearance of beaver from the northern range. One idea is that increasing elk populations in the early 20th century excluded beaver through interspecific competition (Kay, 1990). Another possibility is that warmer temperatures and lower stream flows in recent decades may have initiated beaver abandonment (Persico and Meyer, 2009). Irrespective of its cause, loss of beaver dams from the landscape created feedbacks that increased the resilience of the alternative grassland state: the absence of willow removed an important resource for beaver, and the absence of engineering by beaver degraded habitat for willow (Wolf et al., 2007).

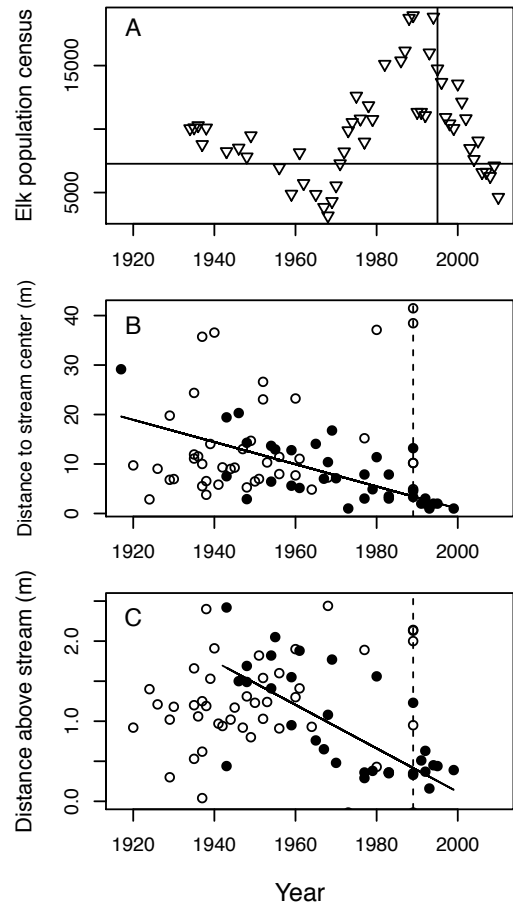


Figure 1: **A.** Elk census on the northern range during 1930-2010 (Houston, 1982; Taper and Gogan, 2002, Yellowstone National Park, unpublished). The horizontal line shows the mean population size during 1930-1970, the approximate time interval when state change occurred. The vertical line indicates when wolves were reintroduced. **B,C.** Dendrochronological studies (Wolf et al. 2007) show that after 1950, willows established primarily on alluvium (closed circles) adjacent to streams. Before that period, plants established on beaver pond margins (open circles) that extended up to 40 m from the current stream center. Regressions through points for alluvial establishment reveal **(B)** temporal trends in area of establishment habitat and **(C)** stream down-cutting. Exposed, fine-grained sediment following the fires of 1988 stimulated seedling establishment (dashed vertical lines).

It has been hypothesized that the prevailing grassland state along stream corridors has recently reorganized to the willow state as a result of a trophic cascade caused by the successful restoration of wolves to Yellowstone in 1995. The central idea in the trophic cascade hypothesis is that the direct effects of wolves on elk numbers and their indirect effects on elk foraging behavior have released willows from top-down control by herbivory and have promoted a rapid recovery in willow biomass, distribution, and stature (Ripple and Beschta, 2004, 2006; Beschta and Ripple, 2007; Beyer et al., 2007). The trophic cascade hypothesis holds that the grassland state is not resilient to the perturbation caused by adding an apex predator to the food web.

The trophic cascade hypothesis has been accepted as scientific fact in the popular press (e.g., Gugliotta, 2004; Robbins, 2005; Ward, 2010) and in the literature on conservation practice (e.g., Donlan et al., 2006, 2005; Soule et al., 2005; Beschta and Ripple, 2010). However, recent work (Creel and Christianson, 2009; Kauffman et al., 2010) casts serious doubt on behaviorally mediated trophic effects of wolves on deciduous woody plants (but also see Beschta and Ripple, in press). Although numerical effects remain possible, the release from top-down trophic control due to reductions in herbivore abundance might be a necessary but insufficient condition for state change (Wolf et al., 2007). It might be insufficient because the loss of engineering by beaver and a warming climate may have created bottom-up forces that prevent return to the willow state. The system may be locked in a resilient grassland state by changes in the availability of riparian habitat suitable for willow establishment and growth (Wolf et al., 2007) (Figure 1 B,C).

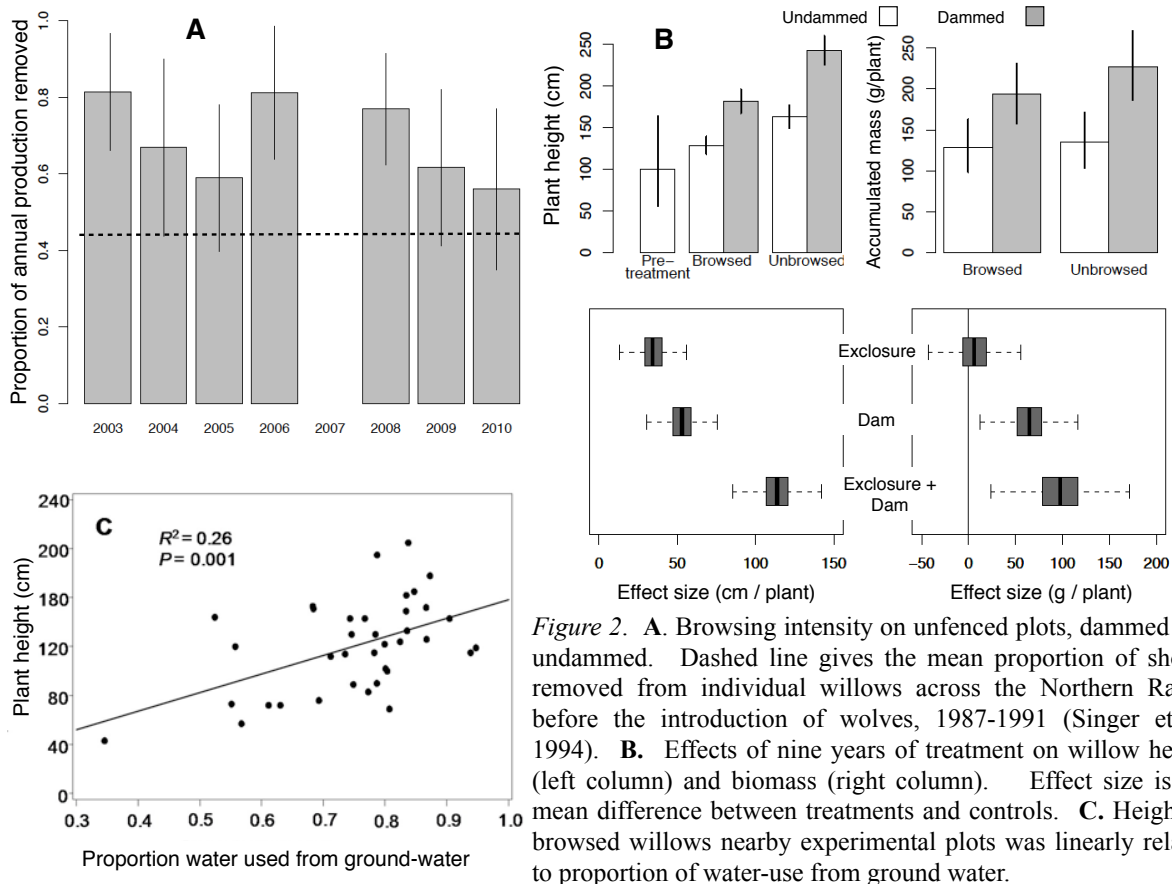
If a state-change has occurred as a result of the restoration of wolves to Yellowstone, then the following outcomes should have occurred along the floodplains of small streams during the last decade: 1) Ungulate herbivory on willows was moderate and declining; 2) Growth of willows that were artificially protected from browsing resembled growth of willows that were ostensibly protected from browsing by trophic effects of wolves; 3) Recovery of willows was not limited by availability of water or other resources, and most importantly, 4) Willows increased dramatically in height and biomass. The failure to observe these outcomes shows that the state of riparian ecosystems currently remains resilient to disturbance of the food web caused by the reintroduction of an apex predator.

We have been working for ten years to test the trophic cascade hypothesis and, more importantly, to understand the relative roles of herbivory and hydrology in controlling the state of willow communities on the northern range of Yellowstone. We examined the strength of top-down controls relative to bottom-up controls in an experiment manipulating water availability and browsing intensity.

### **3 Motivation for proposed work**

#### **3.1 *Experimental studies of state change***

During spring of 2001, we initiated a decadal experiment on the northern range to examine the response of willow height and biomass accumulation to ungulate browsing and disturbance of the water table (Bilyeu et al., 2008). We chose four replicate sites in areas that were historically occupied by beaver. After a year of pre-treatment observations, we constructed simulated beaver dams to raise water tables along stream corridors and built exclosures to prevent herbivory by ungulates in a two by two factorial design (browsed and unbrowsed crossed with dammed and undammed). Each of the four replicates consisted of four 0.02 ha plots. Each plot was randomly assigned to a treatment combination. The undammed, unfenced plots represented the ambient condition, and we will refer to these as controls. In the experiment, we annually measured height gains, over-winter losses to browsing, and biomass accumulation in 255 permanently marked individuals of three species (*Salix boothii*, *S. geyeriana*, and *S. bebbiana*) (Bilyeu et al., 2007, 2008).



*Figure 2. A. Browsing intensity on unfenced plots, dammed and undammed. Dashed line gives the mean proportion of shoots removed from individual willows across the Northern Range before the introduction of wolves, 1987-1991 (Singer et al. 1994). B. Effects of nine years of treatment on willow height (left column) and biomass (right column). Effect size is the mean difference between treatments and controls. C. Height of browsed willows nearby experimental plots was linearly related to proportion of water-use from ground water.*

We chose height as a response variable because the stature of willows is an important indicator of reorganization to the historic condition. Tall willows are needed by beaver for dam construction (Baker et al., 2005). Moreover, their upper branches extend above the level that can be browsed by elk. Because they remain mostly unbrowsed, the upper stems of tall willows reliably produce catkins, assuring a seed source for establishment of seedlings. The threshold height for these effects has been estimated as about 2-2.5 meters (Keigley and Frisina, 1998; Beschta and Ripple, 2007). If willows reach this height, then the recovered willow state can be reasonably expected to be resilient to ungulate herbivory, even in the face of episodically extreme levels of browsing during severe winters. In addition to willow height, biomass is an important indicator of state reorganization because beaver cannot reoccupy areas they historically colonized without an adequate food supply provided by willow and other woody deciduous plants. Moreover, beaver must have access to stems of sufficient length and thickness to build and maintain dams (Baker et al., 2005).

Our experiment revealed multiple controls on willow growth, some of which were unintuitive. Annual browsing intensity averaged 55 - 81% of above-ground production (Figure 2A). Although our measurements are not strictly comparable with measurements of browsing taken before the introduction of wolves (Singer et al., 1994), it appears qualitatively that browsing intensity has not declined below pre-wolf levels (Figure 2A).

Average height of willows experiencing ambient browsing and moisture conditions (i.e., controls) increased 28 cm relative to pre-treatment means, an average rate of increase of only 3.4 cm / year (Figure 2B). At this rate of growth, willows in control plots would require an additional 34 years to reach the 250 cm resilience threshold. It is important to remember that these plants were ostensibly “released” from browsing by trophic effects of wolves. Height increases of unbrowsed willows with

ambient water tables were more than double the control values (mean increase relative to pre-treatment = 63 cm, 90% credible interval = 47, 79). Raising water tables<sup>1</sup> allowed browsed willows to increase by 81 cm (90% CI = 64, 97). The combined effects of raised water tables and protection from browsing caused the average height of willows to increase by 142 cm (90% CI = 117, 169), permitting these plants (and only these) to reach the resilience threshold (Figure 2B).

Effects of treatments on accumulated biomass paralleled the effects on height except that we observed no difference in biomass between the browsed and unbrowsed treatments at the end of the experiment, a result discussed in more detail below. Despite high levels of browsing in unfenced plots, the enclosure effect size was small relative to the dam effect size (Figure 2B) because willows in dammed, browsed plots grew rapidly despite intense browsing.

These patterns are explained in part by findings of *negative* feedbacks from protection from browsing to growth rate of willows on historic floodplains. Similar to Alstad et al. (1999), we found that unbrowsed willows experienced greater moisture stress than browsed willows did (Johnston et al., 2007). Unbrowsed, undammed plants had lower photosynthetic rates and lower stomatal conductances than browsed, undammed plants (Johnston et al., 2007). We discovered that increased moisture stress resulted from effects of protection from browsing on plant architecture. Unbrowsed plants had narrower stems and more age and branch junctions between the soil and the leaves than browsed plants did, and these morphological differences reduced water-use efficiency by unbrowsed plants relative to browsed ones. As a result, *removing* browsing *amplified* the water stress experienced by willows on flood plains disconnected from streams. These effects likely explain the similar levels of biomass accumulation between browsed and unbrowsed willows (Figure 2B). Although rates of biomass accumulation in unbrowsed willows with ambient water tables were rapid early during years 1-4, they slowed dramatically after nine years of protection from browsing, while rates of biomass accumulation of dammed plants almost tripled in both the browsed and unbrowsed plots during the same time interval. This feedback suggests that the alternative, grassland state is resilient because removal of the presumed initiating stressor (intense browsing) strengthens feedbacks opposing state transition (moisture stress resulting from lowered water tables).

Interpretation of the effects of our simulated beaver-dam treatments was reinforced by observations of total height and growth rate of browsed plants nearby our experimental plots (Figure 2C)(Johnston et al., 2011). Analysis of stable isotopes of oxygen revealed that heights and growth rates of these plants were linearly related to their access to groundwater. Heights of browsed plants that obtained 70-90% of their total water budget from groundwater resembled heights of willows in browsed, dammed plots.

Our results (Bilyeu et al., 2008; Johnston et al., 2007, 2011, and unpublished data reported here) are not consistent with the hypothesis that the northern range of Yellowstone National Park has experienced a state change resulting from a trophic cascade following the reintroduction of wolves. Despite dramatic reductions in elk numbers during the course of our studies (Figure 1A), browsing on unfenced plots remained intense and did not differ qualitatively from pre-wolf levels. Willows experiencing ambient browsing and water tables increased nominally in height. After almost a decade of complete protection from browsing, growth rates of willows in enclosed plots with ambient water tables were decelerating and their heights remained far below the 200-250 cm resilience threshold. There was strong evidence for bottom-up limitation of willow growth by availability of water. We revealed complex feedbacks creating resilience in system state: eliminating browsing amplified moisture stress and retarded photosynthetic rate of willows on historic flood plains. Thus, none of the four outcomes consistent with the trophic cascade hypothesis (i.e., page 3,

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<sup>1</sup>Wells in each plot revealed that average water tables depths were 0.4 m higher in plots with dams relative to plots without dams.

paragraph 3) were unambiguously realized in our experiment. Instead, we showed clear evidence of the simultaneous operation of top-down and bottom-up controls on state change in the riparian zone of the northern range. Our results are reinforced by the observational studies of Tercek et al. (2010) who also found evidence of bottom-up control; sites with tall willows had greater water availability, more rapid net soil nitrogen mineralization, greater snow depth, lower soil respiration rates, and cooler summer soil temperatures than nearby sites with short willows.

### 3.2 Observational studies of state change

During 2008, we initiated studies to understand the results of our fine-scale, manipulative experiment in the context of variation in willow growth at large scales of time and space. To enhance our understanding of controls on willow growth at larger spatial scales, we established 23 plots at sites historically occupied by beaver across the northern range using spatially balanced random sampling (Theobald et al., 2007). On each plot, we permanently marked 8 to 15 stems on 4 to 6 plants (318 stems on 115 plants across all sites) and measured annual increments in willow height and biomass, browsing intensity, and water table depth using the same methods as used in our experiment (Section 3.1).

Observations of willow heights in the control plots of our experiment were representative of variation at the landscape scale (Figure 3). The posterior distribution of mean heights in control plots (experiencing ambient browsing and water) fell in the center of the distribution of individual heights of willows on the landscape (Figure 3). The posterior distribution of mean height in the dammed, browsed treatment spanned much of the upper tail of the landscape distribution of heights. This comparison shows that the variation in willow growth caused by treatments in our experiments was also seen at the landscape scale, suggesting that although the average response of the system offered evidence of resilience to perturbation, the average response belied variation indicating that state change may be occurring in some locations (also see Tercek et al., 2010).

To understand large-scale temporal variation in willow height, we used dendrochronological methods to estimate age of willows differing in height across the 23 sites. Using samples of plants varying in age, we obtained data on willow height at different points in time by sectioning stems every 10 cm and counting growth rings on each section. Using relationships between stem age and height, we reconstructed establishment and growth of 298 willow stems, spanning establishment years from 1972 to 2006. We used a Bayesian hierarchical model to examine controls on willow height at the landscape scale, evaluating the strength of evidence for models predicting height growth over time from plant age and corresponding annual counts of elk, wolves, and bison, total annual precipitation, duration of the growing season (as growing degree days), and random effects for site, willow species, and year.

We found overwhelming support for a model predicting willow height based on stem age, elk numbers, growing degree days, and the interaction of age with elk numbers and growing degree days ( $\Delta\text{DIC}$  to next best model = 80). This model is consistent with the hypothesis of a numerically mediated trophic cascade caused by reductions in abundance of elk due to predation by wolves, but also shows that willow growth depended on the climatic context. A multi-year trend toward longer

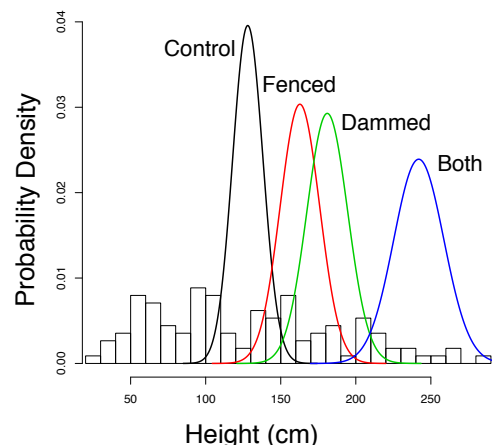


Figure 3: Posterior distributions of mean height of willows at the end of the growing season in experimental plots and normalized histogram of end-of-growing-season heights of 115 permanently marked willows observed on the landscape at 23 sites historically dammed by beaver.



growing seasons allowed greater height growth during the spring and summer for older stems (>14 years), but decreased growth rates of younger stems. We also observed an intriguing interaction between elk numbers and stem age: the effect of elk numbers on growth rate of young stems (<8 years old) was *positive*, suggesting that browsing may stimulate growth rates when stems are young. Thus, the results of our large-scale analyses amplify the central result of our experiment, that state change is likely to be controlled by the interplay of top-down and bottom-up forces, that the climatic context matters, and that trophic feedbacks do not operate in a simple, linear fashion. However, the large-scale analysis also reinforces the possibility that a numerical trophic cascade can be discerned.

#### 4 Why is long-term research needed?

The reintroduction of wolves to Yellowstone’s northern range represents one of the most significant natural experiments in the history of ecology, offering an exceptional opportunity to understand how disturbance of food webs interacts with climate and the physical environment to determine the state of an ecosystem. It is important to the discipline of ecology and the practice of conservation that this story be told fully and accurately.

The response of the ecosystem to perturbation of the food web remains uncertain (e.g., compare Kauffman et al., 2010; Beschta and Ripple, in press). It remains unclear if the northern range will return to a resilient willow state, and if it does, what forces will drive or oppose that transition. Our observational and experimental work suggest a complex set of controls on alternative ecosystem states, a pattern largely inconsistent with the linear trophic forcing that has been hypothesized (Ripple and Beschta, 2004; Beschta and Ripple, 2007, 2010). However, we do *not* argue that our work refutes the idea that restoration of an apex predator has fundamentally modified feedbacks controlling the state of the ecosystem. Rather, we contend that these feedbacks remain only partially understood, and that a full understanding depends on measuring them as they unfold over time and space. It is imperative to recognize that the abundance of elk has only recently reached levels that are below the number that were present during the period when the state-change is believed to have occurred (Figure 1A). Thus, it is entirely plausible that a numerically-mediated trophic cascade has not had sufficient time to be manifest, let alone observed. The change in riparian state from willow to grassland required the better part of a century (Wolf et al., 2007)(Figure 1B,C). Why would we think that its reversal would be plainly revealed 15 years after restructuring of the food web?

#### 5 Predictions and questions

Two, competing predictions motivated by our previous work frame a decade of future experimentation and observation:

1. The grassland state will be replaced by the willow state. The addition of a top predator to the food web has not yet caused responses in height and biomass of willows because there has been insufficient time for numerically-mediated effects on elk to become evident and because a legacy of shallow root development of willows on historic floodplains has retarded their growth. During the coming decade, we will observe widespread return of the willow state to the small streams of the northern range.
2. Alternatively, the grassland state is resilient to the addition of a top predator and will not be replaced by willow. Resilience is created by effects of hydrologic processes and climate. In addition, an increasing bison population may compensate for the top-down effects of wolves on elk. Slow progress toward the willow state will be episodically reversed by winter weather that amplifies browsing intensity and resets the landscape to the grassland condition.

It is a relatively straightforward problem to discriminate between these predictions, if not the mechanisms they represent. Prediction 1 is refuted if there is no rightward shift in the height

distribution of individually-marked willows (Figure 3). Prediction 2 is refuted if such a shift occurs. An additional decade of observations of willow height and biomass of willows at our experimental and observational sites will allow us to differentiate among these futures, an important result in itself. However, a far more important goal is to understand the mechanisms that give rise to the future condition of the landscape. This understanding depends on answering three questions:

1. How do climate and hydrology modify the effects of a restructured food web to explain spatial and temporal variation in willow growth?
2. Are willows on historic floodplains locked into a slow growing state as a result of changes in hydrology or are they approaching change-points in above-ground growth allowed by root development?
3. Why has browsing pressure remained largely unchanged despite the addition of wolves to the food web and their top-down effects on elk numbers?

## 6 Proposed work

### 6.1 Question 1: How do climate and hydrology modify the effects of a restructured food web to explain spatial and temporal variation in plant growth?

Past work on effects of disturbance of the food web on the northern range has focused on the question “Has a trophic cascade occurred?” (Ripple and Beschta, 2004; Beyer et al., 2007; Beschta and Ripple, 2007). In the work proposed here, we recast this question to ask about the relative strength and interdependencies of trophic, hydrologic, and climatic controls on ecosystem state. To address this question, we will model the dynamics of willow growth over time and space using a fully Bayesian, state-space approach (Figure 4, Box 1). Our model-data framework allows us to examine controls on browsing intensity during winter<sup>2</sup> (ungulate population numbers, predator numbers, predation risk, snow characteristics) with influences on growth during spring and summer (access to ground water, duration of growing season, spring and summer precipitation, previous winter’s browsing intensity). In so doing, it provides a way to quantify the relative strength of top-down and bottom-up controls within a changing context created by climate. Although it is simple, our modeling approach is able to portray change-points that result from changes in the balance between growth and removals. The model can represent complex feedbacks; for example, browsing can retard growth during winter and accelerate growth during the subsequent growing

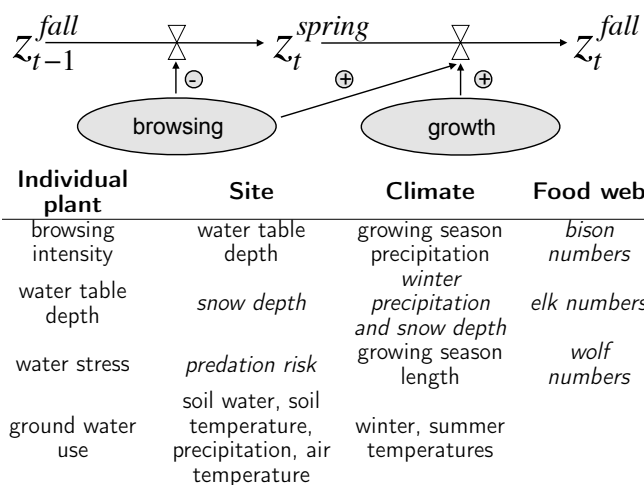


Figure 4: Spatio-temporal model of trophic, climatic, and physical controls on height or biomass accumulation ( $z_t$ ) of willows on Yellowstone’s northern range. Covariates to be measured are tabulated; effects on browsing are shown in italics, effects on growth in plain text. For statistical implementation of this model, see Box 1.

<sup>2</sup>An increasing bison population that remains on the northern range during the spring and summer (Figure 5, Section 6.3, below) may lead to significant browsing during the growing season. Currently, only 2% of the stems we measured were browsed during summer. We conclude these effects are minor. If the intensity of summer browsing increases, we are prepared to include summer browsing in our measurements and model.)

season (Figure 4, Johnston et al., 2007). Missing observations resulting from differences in times spans of responses and covariate data can be accommodated (Clark and Bjornstad, 2004).

We are particularly interested in using our analysis to address competing hypotheses explaining observed spatial variation in willow growth (Figure 3). The first hypothesis is that browsing intensity varies over space in response to spatial variation in predation risk and that browsing intensity, in turn, explains spatial variation in willow growth (Beschta and Ripple, 2007; Ripple and Beschta, 2006). An alternative hypothesis is that spatial variation in willow growth is largely determined from the bottom-up by water availability (Tercek et al., 2010; Johnston et al., 2011). To evaluate these alternatives, our model includes a spatially explicit covariate for predation risk derived from an updated version of the Kauffman et al. (2007) risk map. It will also include covariates for water table depth and groundwater use, allowing us to evaluate strength of evidence in data for the two competing hypotheses for the first time.

We will use two sampling regimes, one extensive the other intensive, to provide the data needed to estimate parameters and to evaluate evidence for alternative models. In the extensive regime, we will use 20 years of data from our experimental plots (10 past, 10 future) and 13 years of data from our landscape-scale plots. Thus, our extensive sample will include more than 500 individually marked plants, at 39 sites. Responses will include a spatially replicated time series of willow height and willow biomass at two time points per year (Box 1). Covariates will include annual weather data (collected at the National Climatic Data Center station at Mammoth, Wyoming), browsing intensity<sup>3</sup>, water table depth, elk population size, bison population size, wolf population size, modeled predation risk and modeled snow depth. The experimental sites are critical to this analysis because: 1) they will span 20 years, and 2) they provide reference, manipulated conditions for browsing intensity and water availability.

We will also deploy an intensive sampling regime that will more clearly reveal mechanistic controls on willow growth and that will offer greater spatial resolution in observations of climate. This regime will include all of the measurements obtained in the extensive sample, but will also include isotopically measured groundwater use, plant moisture stress, and detailed, local-scale climatic measurements. The intensive regime will be limited to the experimental sites and 10 additional observational sites chosen in a stratified design from the full range of sites (Figure 3) to maximize variation in willow heights among sampled sites.

Data required for responses and covariates in both sampling designs (Figure 4, Box 1) will be obtained as follows. Willow heights, biomass accumulation, browsing intensity, water table depths, ground-water use and plant moisture stress will be measured following Bilyeu et al. (2007, 2008) and Johnston et al. (2007, 2011). To quantify local climate, we will establish a meteorological station in each of the four long-term experimental sites and the ten intensive observational sites. These stations will be used to quantify the duration of the growing season, soil temperature, soil water content, water table depth (using existing wells), and precipitation. Growing season duration will be quantified as the period from bud burst to leaf drop using plant cams that take one photo per day of each plot. Soil temperature and soil water content will be measured in a vertical array at 20 and 50 cm depth using Decagon 5TM soil temperature and moisture sensors. Water table depth will be measured daily using a submersible pressure transducer (In-Situ Rugged Troll 100) installed into ground water monitoring wells. Precipitation during the growing season will be measured using a recording tipping bucket rain gauge (Onset Instruments). Snow depth will be measured with a permanently installed measuring pole photographed daily with a field installed digital camera. Snow water content will be measured periodically to estimate snow water equivalents.

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<sup>3</sup>Browsing intensity can serve as a predictor or a response in the model. See Box 1 and section 6.3.

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**Box 1** Overview of state-space implementation of the conceptual model depicted in Figure 4.

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As a starting point for analysis, we will use the deterministic, process models  $\log(z_{i,t}^{spring}) = \log(z_{i,t-1}^{fall}) + d_t^w \mathbf{X}_{i,t} \beta$  and  $\log(z_{i,t}^{fall}) = \log(z_t^{spring}) + d_t^g \mathbf{W}_{it} \gamma$ , where  $i$  indexes individual plants and  $t$  indexes years (Figure 4). Thus,  $z_{i,t}$  is the true state (height or biomass) of plant  $i$  at time  $t$ ,  $d_t^w$  is the duration of winter,  $\beta$  is a vector of regression coefficients describing controls on browsing intensity (Figure 4),  $d_t^g$  is the duration of the growing season,  $\gamma$  is a vector of coefficients describing controls on growth rate, and  $\mathbf{X}_{i,t}$  and  $\mathbf{W}_{it}$  are corresponding matrices of covariates predicting browsing intensity and growth (Figure 4). The quantity  $\mathbf{X}_{i,t} \beta$  represents the removal rate from the  $i$ th plant on the log scale and the quantity  $\mathbf{W}_{it} \gamma$  represents the growth rate on the log scale. We will estimate the posterior distributions of states and parameters using the stochastic model:

$$\begin{aligned}
 P(\mathbf{Z}, \gamma, \beta, \sigma, \alpha, \nu, | \mathbf{Y}, \mathbf{X}, \mathbf{W}) &\propto & (1) \\
 \prod_{i=1}^n \prod_{t=1}^T & \text{N} \left( y_{i,t}^{spring} | z_{i,t}^{spring}, \sigma_1 \right) \text{N} \left( y_{i,t}^{fall} | z_{i,t}^{fall}, \sigma_2 \right) \cdot \\
 \prod_{t=2}^T & \text{N} \left[ \log \left( z_{i,t}^{spring} \right) | \log \left( z_{i,t-1}^{fall} \right) + d_t^w \mathbf{X}_{i,t} \beta + \alpha_{j[i,t]}, \sigma_3 \right] \cdot \\
 & \text{N} \left[ \log \left( z_{i,t}^{fall} \right) | \log \left( z_t^{spring} \right) + d_t^g \mathbf{W}_{it} \gamma, + \nu_{j[i,t]}, \sigma_4 \right] \text{N} \left( \alpha_{j[i,t]} | 0, \sigma_5 \right) \cdot \\
 & \text{N} \left( \nu_{j[i,t]} | 0, \sigma_6 \right) \cdot \text{appropriate priors}
 \end{aligned}$$

where  $n$  is the total number of plants,  $T$  is the number of years in the time series, N abbreviates the normal probability density function,  $\mathbf{Y}$  is the observation matrix of willow heights or biomasses,  $\alpha_{j[i,t]}$  and  $\nu_{j[i,t]}$  are random effects for site, and the  $\sigma$ 's represent standard deviations for the process model, observation model, and random effects. Initial conditions ( $z_{i,0}^{fall}$ ) will be estimated as parameters. Data models will be included to represent uncertainty in estimates of responses and covariates.

Equation 1 provides an initial framework for analysis. We will evaluate elaborations on this initial model, including non-linear functional forms, change-points, coefficients modeled hierarchically as functions of site level measurements, and spatially structured random effects. All models will be evaluated using posterior predictive checks to assure that they reasonably represent the data (Gelman and Hill, 2009; Gelman et al., 2004). A set of candidate models (6 - 10 total) will be composed *a priori* to represent a continuum of hypotheses about the roles of top-down and bottom-up control of state change. We will calculate the probability of each model conditional on the data and associated Bayes factors. Comparison of coefficients of standardized regressors and Bayes factors will be used to evaluate evidence for top-down effects mediated through browsing and bottom-up effects mediated through growth (Figure 4). Our hierarchical approach also lends itself to Bayesian structural equation modeling (Lee, 2007; Mysterud et al., 2008). For example, we can estimate the latent quantity true browsing intensity using observed browsing intensity in a data model. True browsing intensity can then be modeled as a function of herbivore population density, which, in turn, can be portrayed as a function of wolf density.

PI Hoeting has extensive expertise in Bayesian spatio-temporal modeling (e.g., Farnsworth et al., 2006; Hoeting, 2009; Webb et al., 2010) and model selection (Hoeting et al., 1999, 2006). She will oversee the analysis.

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We will use the Watson snowpack model (Watson et al., 2006a,b) and snow depth measurements at each site to assess snow characteristics at multiple scales surrounding each site and to estimate snow compaction and snow water equivalents. The snowpack model was specifically developed

to enhance understanding of controls on ungulate dynamics in Yellowstone National Park (e.g., Bruggeman et al., 2006; Geremia et al., 2011). The model simulates snowpack accumulation and depletion at grid-cell scales as small as 28.5 m at a daily time-step. At each grid cell, the model simulates a full water and energy balance including processes such as precipitation, sublimation, evaporation, melt, and snowpack compaction. By carefully calibrating the model using site level measurement of snow depth and snow water equivalents, we will be able to use its predictions as covariates for the full extensive sample.

Spatial and temporal variation in predation risk will be estimated using an updated version of the model of Kauffman et al. (2007). In brief, the model estimates predation risk to elk from wolves using logistic regression with a matched case-control design (Hosmer and Lemeshow, 2000), where relative probability of a kill on the landscape is estimated from the differential landscape attributes of locations where elk were killed by wolves compared to random locations. New data on wolf pack territories and elk kill locations needed to update the model will be provided by a collaborating LTREB project and by Yellowstone National Park (see Section 8.1). Landscape attributes used to build the model include the annual distribution of wolf packs (based on cumulative kernel densities and weighted by pack size), relative elk density (based on the habitat model of Mao et al., 2005), and the landscape features of proximity to streams, proximity to roads, habitat openness (forest vs. grassland), slope, and snow depth (Kauffman et al., 2007). In addition to providing a robust measure of predation risk to evaluate willow growth responses, the updating to the Kauffman et al. (2007) risk map with an additional decade of wolf kills will provide the most extensive time series of spatial predation patterns known to the PIs. This is important because spatial and temporal inconsistencies of cues for risk generated by wide ranging predators such as wolves can erode the behaviorally mediated signal of trophic cascades (Fortin et al., 2005; Kauffman et al., 2010).

Populations of bison and elk on the northern range are censused from low flying aircraft each winter by Yellowstone National Park staff. Data models have been developed to account for uncertainties associated with failure to detect all animals during census (Eberhardt et al., 2007). Wolves are censused by complete counts of radio-collared packs (Smith et al., 2004) and augmented by frequent ground counts. Yellowstone National Park will share these data (Supplemental Documents).

## **6.2 Question 2: Does root development create a time lag for state transition?**

A compelling explanation for our observations of slow growth in willows is a legacy effect created by shallow root development interacting with herbivory. Willows that established on flood plains around beaver ponds (Wolf et al., 2007) likely experienced shallow water tables and in response, developed roots near the surface of the flood plain, root systems that assured plants would experience moisture stress when water tables declined following beaver dam abandonment (Johnston et al., 2007; Bilyeu et al., 2008). The concomitant stress of excessive herbivory may have prevented established willows from growing deeper root systems in response to declining water tables.

However, it is possible that slow but positive above-ground growth in ambient willows (Figure 2B) belies root expansion below ground. This is important because our experimental studies revealed that plants with access to groundwater could withstand high levels of browsing; they rapidly accumulated canopy height and biomass despite removals of more than half of their production each winter (Johnston et al., 2007; Bilyeu et al., 2008, Marshall et al. unpublished.). If root growth increases access to groundwater in plants with ambient water tables, then these plants might be approaching a threshold when they can tolerate browsing, thereby creating positive feedbacks accelerating growth. If plants in the ambient condition are approaching this threshold, we predict the proportion of their water budget contributed by groundwater will increase over time, and their water stress will decrease. We predict that growth rates of plants on sites with deep water tables will approach growth rates of plants on sites with shallow water tables, leading to local state transition.

Our ongoing experiment is poised to test these predictions by allowing a long-term comparison between willows with ambient water tables and willows with elevated water tables. In each plot of the experiment, we will continue to measure willow growth and browsing intensity on 270 permanently marked individuals as we have done in the past (Bilyeu et al., 2007, 2008). Although we could attempt to observe root growth directly (e.g., Ruess et al., 2003), we choose instead to observe its functional outcome: access to groundwater. To determine the proportion of each plant’s water budget contributed by ground water during the growing season, we will collect samples of: 1) ground-water from 6-10 existing wells at each site, 2) an integrated soil sample from the upper 50 cm of soil, and 3) suberized stems from each plant in each study plot. Water will be extracted from soil and plants using cryogenic distillation methods. Water samples will be analyzed for  $\delta^{18}\text{O}$  on a mass spectrometer. We will determine the proportion of ground water use following the methods in Johnston et al. (2011). Sampling will occur annually during mid- and late summer.

Willows with greater access to ground water, and therefore a more reliable and consistently available water source, should experience less water stress and higher mid-day and pre-dawn xylem pressure potentials ( $\psi_{xpp}$ ), stomatal conductance ( $g_s$ ), and photosynthesis rates. We will measure pre-dawn and mid-day  $\psi_{xpp}$  on a randomly selected group of ten willows in each plot, twice during each summer using a Scholander type pressure bomb. Stomatal conductance and photosynthesis will be measured during mid-day twice each summer using LiCor 6400 equipped with an external light source that will allow measures regardless of ambient light conditions. Details of methods can be found in Johnston et al. (2007).

We will test the hypothesis that ground-water use and other physiological responses in the control plots will approach the responses in the browsed, dammed plots using a Bayesian hierarchical model with coefficients for intercept, treatment (dammed vs undammed), year, and the year x treatment interaction. Treatment will be analyzed as a fixed effect and year as a random effect using plots as a grouping variable. Our conclusions will be based on the posterior distribution of the interaction, which, under our hypothesis, should show diminishing effects of treatment with time. These mechanistic, experimental studies will provide a strong compliment to the long-term observational work proposed for Question 1.

### **6.3 Question 3: Why has browsing remained intense?**

One of the most counter-intuitive results of our studies was the finding that browsing intensity remained virtually constant during 2003-2010 and resembled pre-wolf browsing intensity observed during 1987-1991 (Figure 2A). This result implies that browsing intensity is largely insensitive to elk numbers. It has been suggested that browsing on willows is better explained by behavioral effects of wolves on elk than by numerical effects. However, recent work showed that effects of predation risk on behavior are in the opposite direction of those predicted by a behaviorally mediated trophic cascade (Creel and Christianson, 2009; Kauffman et al., 2010), leaving changes in elk numbers as the best, mechanistic explanation for trophic control (but also see Beyer et al., 2007; Beschta and Ripple, in press). This produces a seeming paradox—although numbers of herbivores declined dramatically (Figure 1A), the proportion of willow production browsed remained consistently high (Figure 2A).

There are two potential explanations for this paradox. The first is that a shift in the composition of the food web has caused total demand for plant biomass by large herbivores to remain largely unchanged (Figure 5). Although the number of elk on the northern range declined steeply during the past decade in response to predation by wolves, drought, and hunter harvest outside the park (Vucetich et al., 2005; Eberhardt et al., 2007), the number of bison (*Bison bison*) on the northern range concomitantly increased (Figure 5), possibly as a consequence of reduced interspecific competition with elk (White and Garrott, 2005). The body mass of bison is roughly twice the mass

of elk, so increases in bison numbers allowed total herbivore biomass to decline only slightly in the face of steeply declining elk numbers (Figure 5). Because daily dry matter intake of ruminants is directly proportionate to their body mass (Demment and Van Soest, 1985), we would expect that browsing pressure would remain approximately constant if bison consume willow. American bison are considered to be predominantly grazers (as are elk, Christianson and Creel, 2007). However, willow can dominate bison diets (Waggoner and Hinkes, 1986). Thus, a parsimonious explanation for constant browsing pressure is that bison maintained removal rates as the elk population declined.

The second explanation is that there are periods during winter when there is an absolute shortage of food for large herbivores on the northern range. During winter, the herbaceous layer can be episodically covered by deep and compact snow. There is a substantial literature showing that elk increase consumption of woody plants when accumulated snow blocks access to the herb layer (reviewed by Christianson and Creel, 2007; Creel and Christianson, 2009). During these episodes, the total supply of plant biomass available to large herbivores may be less than the total intake requirements of even a small herbivore population (e.g., Wallmo et al., 1977; Hobbs, 1989). Under these circumstances, removal rates would be uncoupled from herbivore abundance.

These two explanations are not necessarily competing, and we will evaluate evidence for both. To understand how restructuring of the food web may influence the strength of top down control of willows, we need to know which herbivore species are responsible for browsing removals. We will use molecular techniques to determine the species of ungulates consuming willows. When browsers crop bites, small amounts of saliva containing buccal cells are left on residual stems. Co-PI Spong has developed techniques for extracting sufficient DNA from browsed stems for analysis by diagnostic polymerase chain reaction (PCR) methods. Based on mitochondrial sequence data, Spong’s lab has designed species specific genetic markers that amplify only the target species. DNA can be successfully extracted from twigs for up to four months after browsing, and the extraction is successful on about 70% of samples. We have tested the methods on willows browsed by bison and elk in a blind, controlled experiment and were able to correctly identify the browser on all successfully amplified samples. All samples are extracted by a Qiagen® robot using a protocol optimized together with Qiagen’s application laboratory. Samples are currently run on RT-PCR machines from Applied Biosystems®. We will sample four willow browsed stems from different plants from each of our study sites during early January and late March of each winter (n = 60 per date) and will determine the proportion of browsing that is attributable to elk and bison.

We will evaluate the variation in browsing intensity explained by snow at our experimental and observational sites. The effects of snow on ungulate foraging are widely assumed to be important (Hobbs, 1989; Turner et al., 1993, 1994; Tyler, 2010), but the functional relationship between characteristics of snow and effects of browsers on plants remains unknown. Understanding how temporal

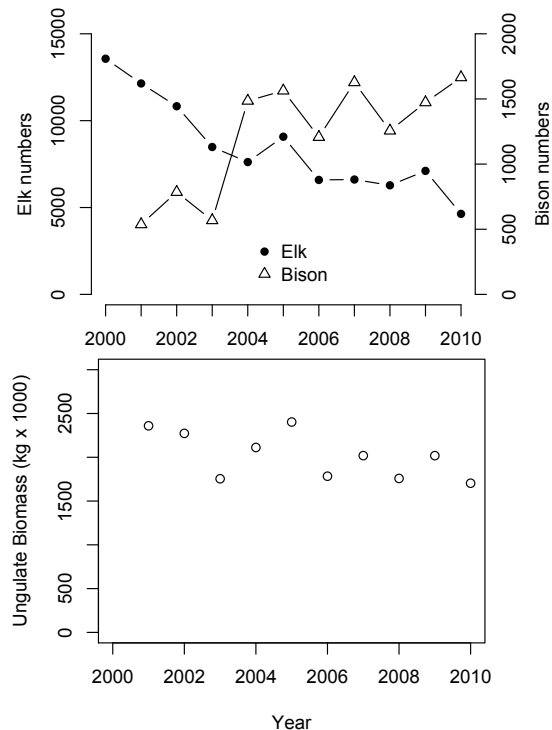


Figure 5: Numbers of elk and bison (upper panel, Yellowstone National Park, unpublished) and total biomass of elk + bison (lower panel) on Yellowstone’s northern range during 2000 - 2010. Biomass is calculated from age and sex specific body masses weighted by demographic composition of the populations.

variation in snow characteristics influences browsing requires that we supplement the annual observations of browsing intensity obtained for the willow growth model (see Section 6.2) with more frequent observations. To that end, we will make bi-weekly measurements of mass removed from willows at our intensive sampling sites using the procedure of Bilyeu et al. (2007).

We will evaluate models of the influence of snowpack on browsing at annual and biweekly time scales. The candidate set of models will include: 1) monotonic relationships where increasing snowpack leads to increasing browsing, 2) change-points, where threshold snow characteristics lead to qualitative shifts in browsing, and 3) modal relationships, where increases in snowpack eventually lead to declines in willow browsing as plants become inaccessible. Independent variables will include snowpack depth and water equivalents (SWE) computed as mean, peak, and time-integrated values.

## 7 Decadal research plan

### 7.1 *What we know now*

A decade of work has revealed an alternative state in Yellowstone and a set of feedbacks that currently stabilize that state. Despite the addition of wolves to the food web and a dramatic reduction in elk numbers (Figure 2A), browsing on willows remains intense (Figure 1A). The absence of beaver dams has compressed habitat for willows (Wolf et al., 2007) and has caused water stress on willows that established on flood plains along channels historically dammed by beavers (Johnston et al., 2007). Water stress retards willow growth, even when they are totally protected from browsing (Bilyeu et al., 2008; Marshall et al., in prep.), and removing browsing amplifies the growth-inhibiting effects of water stress (Johnston et al., 2007). We detected effects of reduced elk numbers and an expanding growing season on willow growth at the landscape scale (Marshall et al., in prep.). However, these effects are not simple; both depend on plant age. We have shown that there is enormous spatial variability in heights of willows (Figure 3).

### 7.2 *What we will know in five years*

The abundance of elk on the northern range has only recently fallen below levels implicated in state transition (Figure 1A). Five more years of research will almost certainly double the number of observations of the effects of elk at these low levels, thereby giving a numerically mediated trophic cascade an honest chance to be observed. Moreover, our experiment will allow us to determine if the current, slow growth of willows is due to legacy effects of shallow root development. We will be able to test competing hypotheses on the role of predation risk and water availability in controlling spatial variation in willow growth. We will know if bison are contributing to browsing pressure on willows. Finally, we will have the data to resolve important climate effects, particularly the effects of snow, that now remain uncertain. In five years, we will have 232 data points (12 years x 4 experimental sites + 8 years x 23 observational sites) on browsing intensity paired with site-specific, instrument-calibrated, model estimates of a suite of snow characteristics. We will also be able to exploit an unusually important opportunity created by the 2010-2011 winter. Some locations on the northern range had the deepest snows recorded since snow-pit observations were established in 1994 (Halfpenny, 2011). Accumulated snow water equivalents were double the average of the previous ten years (Watson, unpublished). Preliminary analysis of browsing data obtained during May of 2011 suggests two things: there was large variability over space in browsing intensity, and some plants lost more than *three years* of accumulated growth to browsing. It is vital to understand the impact of this extreme climatic event.

### 7.3 *What we will know in ten years*

Analysis of auto-regressive time series (Box 1) provides a proven approach to understanding controls on dynamics of ecological systems. However, these analyses require decades of data to resolve



interactions and main effects. At the conclusion of our work, we will have 20 years of observations of willow growth extensively replicated over space with known reference conditions provided by a manipulative experiment, allowing us to examine rigorously how climate and hydrology modify trophic effects. Our collaboration with park biologists at Yellowstone (including investigators Smith and Renkin) assures that we will be able to evaluate browsing and climatic effects against equally long trends in abundance of wolves, elk, and bison as well as annual patterns of predation risk. During year eight of our future work, we will repeat the dendrochronological studies of Wolf et al. (2007) on willow establishment and Marshall et al. (in prep.) on plant height-age relationships, thereby providing a view of willow demographics and growth spanning multiple decades before and after the reintroduction of wolves. Moreover, an additional ten years of research creates a valuable opportunity to exploit unplanned events—for example, declines in the bison population that might result from prey switching by wolves (Garrott et al., 2007) or the return of engineering by beaver. Our observational sites were chosen in areas of historically occupied by beaver. If beaver return to these sites, we will have a before-and-after-controlled-impact design (Stewart-Oaten and Bence, 2001) in place to learn from the disturbances they create. The value of ten more years of research does not depend on serendipity, but we are poised to learn from the unexpected.

## **8 Broader impacts**

### **8.1 *Collaboration with an existing LTREB***

Our proposed work will add value to an ongoing LTREB, “Yellowstone wolves: their ecology and community consequences” (DEB-0613730, PIs J. Vucetich, D. Smith and R. Peterson), which focuses on impacts of wolves on the elk and bison populations of the northern range. Our work will illuminate the effects of elk and bison on the state of riparian zone, thereby extending understanding of community processes to the ecosystem. The two projects will co-author publications, as appropriate, and will share data. In particular, the wolf project will provide data on wolf locations, elk locations, and kill locations needed to assess predation risk (Figure 4, Box 1). One the PIs on the wolf project (Smith) is a senior investigator on our proposed work (Supplemental Documents).

### **8.2 *Collaboration with Yellowstone National Park***

Yellowstone National Park hosts over three million visitors annually, providing an unusual opportunity for educating citizens of all ages. We will work closely with interpretive staff to prepare educational materials featuring the results of our work. We will continue our contribution to "Expedition: Yellowstone!" a curriculum-based Park Service program for 4th-8th graders visiting the park. We will meet with park staff to support decisions on policy and management. A resource manager for the Park (Renkin) is a senior investigator (Supplemental Documents) and will act as a liaison between the project and park management and interpretive staff. Yellowstone National Park is committed to working with us on the research permitting process, providing ungulate and wolf census data, and working with us to contribute to interpretive programs (Supplemental Documents).

### **8.3 *Education***

We will support at least two Ph.D. students over a ten year research project and will offer training to a dozen undergraduates. In addition, the demonstrated interest of the public in the story unfolding in Yellowstone creates opportunity for citizen-education through the popular media. Hobbs is an Aldo Leopold Fellow and is committed to working with journalists to make our findings accessible to citizens. As we have done with our current student, Kristin Marshall, we will assure that our future students become adept at communicating science to the public by attending specialized training, participating in K-12 education, and by offering talks on our research to visitors and residents in the greater Yellowstone ecosystem.

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