Interactions among herbivory, climate, topography and plant age shape riparian willow dynamics in northern Yellowstone National Park, USA

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Summary

1. Understanding how the environmental context modifies the strength of trophic interactions within food webs forms a central challenge in community ecology.

2. Here, we demonstrate the necessity of considering the influence of climate, landscape heterogeneity and demographics for understanding trophic interactions in a well-studied food web in Yellowstone National Park, USA. We studied riparian willow (*Salix* spp.) establishment and stem growth reconstructed from tree rings on the northern range of Yellowstone over a 30-year period that included the reintroduction of a top predator, the grey wolf (*Canis lupus*).

3. We used climate variables (annual precipitation, stream flow and growing season length), herbivore abundance and landscape descriptors (elevation and topographic wetness index) to predict establishment and growth processes through time before and after the reintroduction of wolves. We fitted Bayesian hierarchical models to establishment data and time series of individual stem heights from 1980 to 2008.

4. Explaining variability in establishment required models with stream flow, annual precipitation and elk abundance.

5. Climate, trophic and landscape covariates interacted with stem age to determine stem height and growth rate through time. Growth rates of most stems ages (2+) declined after the reintroduction of wolves. However, stem growth rates naturally declined with age, and the decline we observed was coincident with faster growth rates for the youngest stems. Mean stem heights at age have remained relatively stable through time for most age classes. Estimated effects of landscape topography had approximately the same magnitude of effect on stem growth rate at age as elk abundance.

6. *Synthesis.* We show that the effects of modification of a food web cannot be predicted by studying trophic dynamics in isolation. No single driver explained patterns of willow establishment and growth over the past three decades in Yellowstone. Instead, interactions among trophic forces, inter-annual climate variability and landscape topography together shaped how the ecosystem responded to perturbations. Top-down effects of ungulates on riparian woody vegetation must be considered in the context of plant age, and climate and landscape heterogeneity.

Key-words: Bayesian state-space, beaver, elk, herbivory, plant population and community dynamics, riparian vegetation, tree rings, trophic cascade, willow, wolf, Yellowstone

Introduction

The green world hypothesis (Hairston, Smith & Slobodkin 1960) motivated decades of inquiry that sought to understand how trophic forces control the structure of ecological communities. A large and expanding literature offers evidence of top-down control of the population dynamics of prey by their predators (Terborgh *et al.* 2001; Myers *et al.* 2007; Estes *et al.* 2011; Ripple *et al.* 2014), as well as evidence of bottom-up control by resources (Borer *et al.* 2005; Shurin & Seabloom 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 (Power 1992; Menge 2000). In many ecosystems, the interaction of climate and

disturbance regimes with food web structure determines the direction and magnitude of trophic effects within the ecological community (Folke *et al.* 2004; Visser & Both 2005; Schweiger *et al.* 2008). Understanding how these forces interact to shape the emergent dynamics of consumers and producers within ecosystems remains a critical challenge in contemporary ecology.

Here, we report investigations of the dependence of food-web interactions on environmental context using elk *Cervus elaphus* and riparian willows *Salix* spp. along small streams on the northern range of Yellowstone National Park, Wyoming, USA as a model system. Specifically, we explore how willow establishment and growth processes have changed over a 30-year period spanning a major perturbation to the food web, the reintroduction of wolves. We examine the respective roles of climate variability and ungulate abundance in shaping willow establishment and growth. We also explore how trophic and climate effects on willow growth depend on stem age.

The grey wolf (*Canis lupus*) is one of the most studied top-predators in temperate terrestrial ecosystems (Mech 2012). Top-down effects of wolves on ungulate populations and plants have been described across North America and Eurasia (recent examples include: Ripple & Beschta 2012; Callan *et al.* 2013; Kuijper *et al.* 2013; Latham *et al.* 2013). Reintroductions and increased protections for wolves in recent decades have spurred studies investigating whether restoring a top-predator can restore ecosystem dynamics (Ripple & Beschta 2012; Callan *et al.* 2013; Marshall, Cooper & Hobbs 2013).

The history of the extirpation of wolves from Yellowstone in the 1920s, their reintroduction 70 years later and concurrent changes to the ecosystem has been detailed by many (Kay 1997; Singer *et al.* 1998; Eberhardt *et al.* 2007; Ripple & Beschta 2012; Marshall, Hobbs & Cooper 2013; Ripple *et al.* 2013). In brief, removing wolves led to increased elk abundance on the northern range (Eberhardt *et al.* 2007). The large elk herd exerted heavy browsing pressure on woody vegetation, especially during the 1980s and 1990s (Singer *et al.* 1998; NRC 2002). Wolves were reintroduced in 1995 to restore a complete ecosystem. Spirited scientific debate has focused on the net effect of reintroducing wolves on woody vegetation (e.g. Kauffman, Brodie & Jules 2010 and resulting comments). Studies in some areas of the northern range have found support for reduced browsing leading to increased height of woody vegetation since wolves have been returned to the ecosystem (Beyer *et al.* 2007; Ripple & Beschta 2012; Ripple *et al.* 2013). Studies in other areas of the northern range have failed to find lower levels of browsing or dramatically taller plants (Bilyeu, Cooper & Hobbs 2008; Marshall, Hobbs & Cooper 2013).

Willows are the dominant riparian woody vegetation in Yellowstone, and across the Rocky Mountains. Here, we focus on the effects of changing ungulate abundance and climate variability on willow establishment and growth. To motivate our work to understand these effects, we briefly outline dominant factors known to drive willow population dynamics.

Willow stands are tightly linked to hydrologic processes and herbivory by large mammals. Seedling establishment depends on the physical disturbance created by episodic flooding. Receding floodwaters leave behind bare mineral substrate, which is required for seedling establishment in both willows and cottonwoods (Gage & Cooper 2005; Polzin & Rood 2006). However, the timing of flooding with respect to seed sprouting is vital to plant reproductive success; spring floods that recede too quickly leave seedlings susceptible to drought, and large floods occurring after seeds sprout can also result in mortality due to scour (Mahoney & Rood 1998).

Established willows also depend on water and can be negatively impacted by browsing ungulates. Experimental work in Yellowstone that raised water-tables and removed ungulate browsing showed that willow height was equally limited by herbivory and water-table depths and that plants compensate for herbivory when access to water is sufficient (Johnston, Cooper & Hobbs 2007; Bilyeu, Cooper & Hobbs 2008; Marshall, Hobbs & Cooper 2013). Willow height is also strongly related to plant water use; an observational study using oxygen stable isotopes showed that plants that obtained most of their water from groundwater were taller than plants using more water from upper soil layers (Johnston, Cooper & Hobbs 2011).

Understanding the food web containing willows in Yellowstone also requires understanding the role of beaver (*Castor canadensis*). Beaver are an important food-web component with direct and indirect feedbacks to riparian areas; they consume willows and use them to build dams. Beaver dams create a disturbance regime that supports the establishment and growth of willows (Naiman *et al.* 1994; Smith & Tyers 2012). Beaver were abundant along small streams on the northern range in the early 1920s (Warren 1926), but disappeared from the stream network across the northern range after wolves were eliminated (Jonas 1955). The disappearance of beaver has been attributed to excessive herbivory by elk occurring during the period after wolves were eliminated (Kay 1997; Wolf, Cooper & Hobbs 2007). Aerial surveys suggest beaver populations are increasing in larger rivers on the northern range; however, beaver have yet to recolonize small streams where they were abundant during the 1920s (Warren 1926; Smith & Tyers 2012). We have previously hypothesized that the return of beaver is precluded by insufficient willow stands along small streams (Wolf, Cooper & Hobbs 2007; Bilyeu, Cooper & Hobbs 2008; Marshall, Hobbs & Cooper 2013).

In this study, we explored how changing food-web structure and landscape and climate variability interact with two willow population processes along small streams on Yellowstone's northern range: plant establishment and stem height growth. A simple view of food-web interactions would suggest that ungulates should have negative effects on willows and that these effects should have diminished since wolves were reintroduced in 1995. In concert with this view, observational research has shown height and diameter increases in willows in some areas of the northern range that are attributed to reduced browsing (Beschta and Ripple, 2007; Beyer *et al.* 2007).

Evidence for cascading trophic effects requires two observations. We must observe reductions in abundance or constraints on behaviour of herbivores in response to a predator. Changes in herbivores, in turn, must translate into positive effects on plants. Here, we focus our investigation on the second requirement of a trophic cascade: that changes in the elk population following the reintroduction of wolves have enhanced willow growth and establishment. We justify this focus because census estimates of elk and wolves were highly correlated during the past three decades (1980 to 2010, $r = -0.84$) potentially creating misleading conclusions when alternative models are selected (Burnham & Anderson 1998). Moreover, the correlation between wolves and elk numbers in recent years may be in part spurious because of coincident changes in elk harvest in areas adjacent to the park and the co-occurrence of a prolonged drought (Vucetich, Smith & Stahler 2005). Thus, it is possible that the recent decline in elk may not be solely attributable to wolves. For all of these reasons, we decided that clear and statistically reliable results would be obtained by limiting our analysis to predictor variables that were not correlated and we focused on the direct effects of ungulate herbivores.

We sought to understand how trophic effects of elk depended on the spatial and temporal context created by climate and landscape heterogeneity. Multiple stages of the willow life cycle depend explicitly on hydrologic processes, which are driven by climate variability, landscape topography and beaver occupation. Therefore, we hypothesized that the effects of herbivory would vary across the landscape and through time depending on the hydrologic context created by underlying physical drivers. We tested this hypothesis by evaluating the roles of physical and landscape drivers in explaining variation in willow establishment and growth across Yellowstone's northern range in riparian areas historically occupied by beaver. We explored how all three sets of drivers (herbivory, climate and landscape) interact with plant age and stage using Bayesian statistical models.

Materials and methods

STUDY AREA

We worked along small streams on Yellowstone's northern range, ranging in elevation from 5717 to 7640 m, latitude 44.87 to 45.00 degrees and longitude -110.79 to -110.20 degrees (Fig. 1). Climate is temperate and semi-arid, with mean annual precipitation of around 250 mm and daytime average temperatures of 25 to 30 °C in summer and -20 to -5 °C in winter. Study watersheds were glaciated during the Pleistocene, and the landscape is dominated by rolling hills of glacial till.

SITE SELECTION

Sites were selected in riparian areas along small streams that were suitable for damming by beaver. Others have documented patterns of historic activity by beaver on the northern range (Warren 1926; Wolf, Cooper & Hobbs 2007; Persico & Meyer 2009). These previous beaver surveys were not complete censuses of northern range streams.

Therefore, we developed a population of sites from which to sample based on stream geomorphology identified as suitable for beaver habitat (Allen 1983; Persico & Meyer 2009). This population of sites consisted of all third- and fourth-order northern range stream reaches with low gradients (<10 per cent). We created 50-m buffers surrounding these potential streams, and assigned probability of sampling according to accessibility on foot. Stream sections identified as previously occupied by beaver (Warren 1926; Wolf, Cooper & Hobbs 2007; Persico & Meyer 2009) were also assigned a higher probability of selection. The buffered stream layer was converted to raster format with 1-hectare pixels. The RRQRR package in ArcGIS (Theobald *et al.* 2007) was used to generate an ordered list of random pixels using these criteria. Each 1-hectare site was visited in order, and those that did not meet the minimum density of at least five willow plants of non-clonal species occurring in a 15×15 m square area along the stream channel were eliminated. We visited potential sites in order until 23 suitable study sites were selected. We sampled willows at all 23 sites, and 16 of these sites showed conclusive evidence of historic occupation by beaver (Warren 1926; Persico & Meyer 2009).

WILLOW ESTABLISHMENT

Willow root crowns were excavated to investigate recent patterns of willow establishment. All willow species we sampled (*S. geyeriana, S. boothii, S. bebbiana, S. drummondiana* and *S. pseudomonticola*) exclusively reproduce sexually in our study region and elevation range (Cooper *et al.* 2006; Wolf, Cooper & Hobbs 2007). Wolf, Cooper & Hobbs (2007) documented willow establishment from the 1940s through the 1990s at three sites on the northern range with a known history of beaver occupation. They demonstrated that younger age classes of willows were severely under-represented in their random sample of plants. Therefore, we focused our sampling on small plants that appeared to be young in order to increase the odds of sampling individuals that established before and after the reintroduction of wolves in 1995. We aged above-ground stem growth using annual growth sections identified by terminal bud scars (Keigley & Frisina 1998) and sampled randomly from plants with less than 10 years of above-ground growth.

We collected up to five root crowns per site, sampling no more than 10 per cent of willow saplings within each 1-hectare site. The root crown was sectioned horizontally to find the point of germination, contained in the cross section with pith on one site and no pith on the other (Scott, Friedman & Auble 1996; Cooper, Andersen & Chimner 2003). Sections were successively cut until the root crown was isolated in a 2–3 cm section. The top and bottom surfaces were sanded progressively finer, and the growth rings on both surfaces were counted. If the two counts were inconsistent, we used the maximum count as the age of the plant.

Willow establishment over the last 29 years was modelled using negative binomial regression. The negative binomial distribution was used over the Poisson because the data were overdispersed (mean of 2.13 and variance of 12.36). Using the negative binomial distribution was the more conservative choice because the distribution of willow establishment was skewed to the right. Establishment was modelled using Jackman's (2009) parameterization of the negative binomial distribution such that $W_t \sim$ negative binomial(p_t, r) where $p_t = \frac{r}{r+\lambda_t}$ and $\lambda_t = \exp(X_t B)$. Here, W_t is the number of willow plants observed to establish in year t, r is the overdispersion parameter of the negative binomial, and λ_t represents the predicted number of willows establishing as a function of the product of the vector of linear covariates (X_t) and their coefficients B.
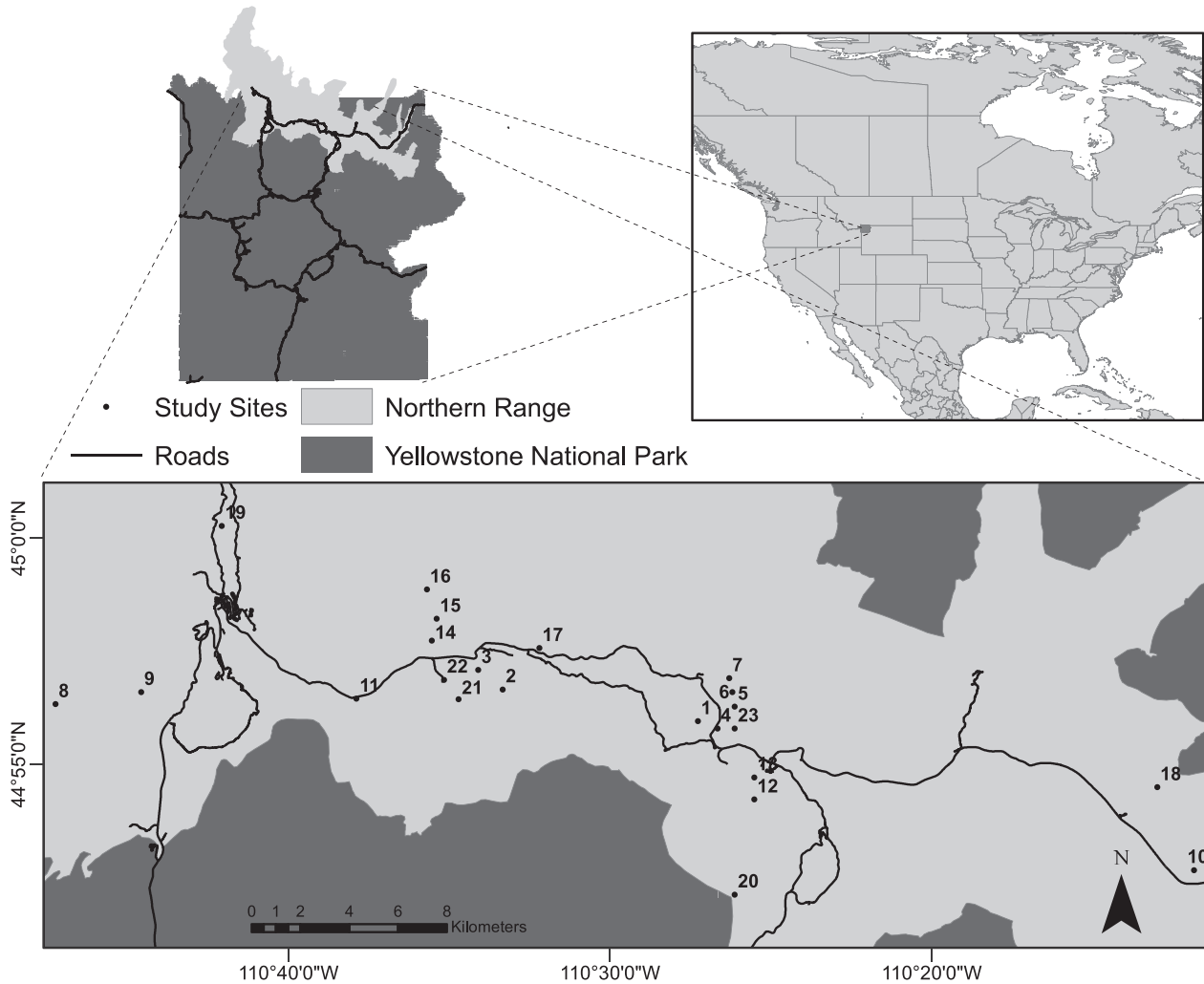
Fig. 1. Map of study sites on Yellowstone's northern range.

The relative importance of hydrologic and trophic covariates was assessed by standardizing covariates, using the same set of hydrologic predictors as in Wolf, Cooper & Hobbs (2007). First, we regressed each covariate individually against establishment rate for direct comparison with Wolf, Cooper & Hobbs (2007). We then built multivariate models, after eliminating all predictors that had pairwise correlation coefficients greater than 0.7 (retaining the predictor that explained more variation in the response). We combined the remaining predictors to find the most parsimonious groupings that explained willow establishment over the last 30 years. It is important to note that the three decades in our study span 16 years prior to the reintroduction of wolves and 13 years after their reintroduction. Two model selection analyses were performed: the first using only the hydrologic predictors and interactions among them, and the second using hydrologic predictors, elk abundance and their interactions. The variance explained by the best models from each of these analyses was calculated using a Bayesian R-squared (Gelman & Pardoe 2006).

We estimated all parameters using Bayesian methods in JAGS using the package rjags in R (Plummer 2011; R Core Team 2012), and compared models using DIC and DIC weights (Spiegelhalter *et al.* 2002). We used Bayesian methods over maximum-likelihood methods to be consistent with the subsequent analysis for stem heights. The stem height analysis required a Bayesian state-space

model to estimate missing covariates and latent states. Details of model fitting and comparisons are provided in the Supporting Information (see Appendix S1 in Supporting Information). Because we targeted young plants with our sampling, we limited our analysis to plants that established in 1980 or later. This resulted in dropping nine plants from the analysis, leaving 63 willow root crowns across 17 study sites. Due to the low sample sizes at each site, we pooled establishment across all sites.

WILLOW HEIGHT

Up to three stems per plant were collected from eight willow plants at each of 20 sites (279 stems total) to analyse the relationship between willow height and age. To maximize the length of stem height-age time series, we selected plants with at least one thick stem (that we estimated to be >10 years old). We cut a large stem and two other representative stems from each plant (unless the thickest stem indicated the plant was less than 8 years old, in which case we stopped sampling that plant). We never sampled more than 10 per cent of stems at a site to minimize our impacts on willow stands.

Stem height was reconstructed through time by sectioning willow stems in 10-cm increments, from the ground surface to the tallest point of the stem. Each section was sanded to allow rings to be

counted. For each section, the height of the stem represented a minimum height of the stem during that year of the stem's life. When consecutive stem increments were the same age, we used the maximum height for that age. Time series of stem height were generated for 276 stems. We removed the three oldest stems from the analysis because a large gap in the observed time series occurred between 1976 and 1982, which strongly influenced the estimation of the model parameters. 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:

$$\log(H_{jkt}^{\text{pred}}) = \log(H_{jkt}^{\text{true}}) + a_{jkt} \qquad \text{eqn1}$$

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

$$a_{jkt} = \exp(a_0 + a_a A_{jt-1} + a_b E_t + a_c \boldsymbol{C_t} + a_d \boldsymbol{S_k} + \gamma_{\text{species}}) \qquad \text{eqn2}$$

where a_0 is the intercept, A_{jt-1} is the age of the stem in year $t-1$, E_t is elk abundance in year t, $\boldsymbol{C_t}$ are climate effects for that year, and $\boldsymbol{S_k}$ represent site-specific linear covariates. We included willow species as a random effect where $\gamma_{\text{species}} \sim \text{Normal}(0, \sigma_{\text{species}})$ Observed height for each stem at each site and year was a function of the unobserved true height plus observation error: $\log(H_{jkt}^{\text{obs}}) \sim \text{Normal}(\log(H_{jkt}^{\text{true}}), \sigma_{obs})$. The unobserved true height was a function of the predictions plus process error: $\log(H_{jkt}^{\text{true}}) \sim \text{Normal}(\log(H_{jkt}^{\text{pred}}), \sigma_{\text{proc}})$.

Climate covariates included growing season length and annual precipitation (see Appendix S1). Site covariates included mean elevation and topographic wetness index at each site, derived from a 10-m resolution digital elevation model (DEM).

After standardizing all predictors, we fit a Bayesian height model using JAGS and the rjags package in R (Plummer 2011; R Core Team 2012). We fit the full model with all potential two-way interactions, then dropped interaction terms if their 95 per cent credible intervals overlapped zero. All main effect terms that were involved in interactions were included, regardless of their credible intervals. We investigated model fit to the data using Bayesian P-values. Details of model fitting and evaluation are provided in the Supporting Information (see Appendix S1).

We estimated mean stem height at age for the 25th, 50th and 75th quantiles of ages observed (age 4, 7 and 11) to disentangle the effects of the changing demographics of our sample of stem ages from the observed stem heights. To do this, we simulated new height trajectories for stems beginning in each year from 1982 to 2008 up to the age of interest, including parameter uncertainty for all time-varying parameters. We held site-specific covariates and the species random effect at their mean values (0), and did not include process or observation errors in age-specific height estimates through time.

We also show the mean effects of interactions between the covariates on stem growth rate at age. We fixed each covariate at two different levels (± 2 standard deviations of the mean), and fixed all other covariates and the species random effect at their mean values (0). We then estimated the mean growth rate at age from stems age 0 to 10.

We explored how the effects of elk abundance and climate variability have influenced stem growth rates through time. We show these combined effects for three fixed ages (0, 1 and 2) by presenting posterior means and 90 per cent credible intervals of combined effects through time. Climate effects included main effects and interactions that included only climate covariates. Similarly, trophic effects included elk abundance and its interactions. We also present the resulting posterior mean growth rates (and credible intervals) through time for those fixed age stems.

Results

WILLOW ESTABLISHMENT

Sixty-three willows in our sample established during 1980 to 2008 (Fig. 2). 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. The root crowns for almost all plants were close to the soil surface, and the wood was solid with well-developed annual rings.

Since 1980, willow establishment was higher during and after periods of low annual precipitation, low mean annual flow and low elk abundance. All lags and cumulative predictors for these three sets of predictors that met our criteria for inclusion in the model had negative signs (90 per cent of the posterior weight fell left of zero, Table 1). The relationship between peak flow and establishment depended on the time-lag considered. There was a negative effect of high peak flow on establishment in the year after establishment [-0.330 (-0.801, 0.152)]. The sign of this effect switched
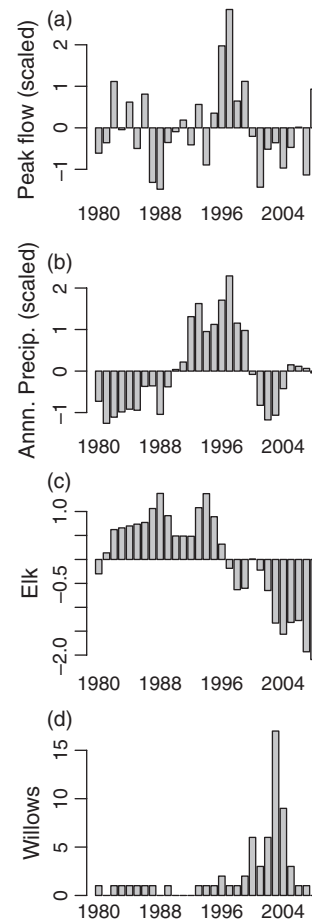

Fig. 2. Climate and trophic effects on willow establishment. Peak discharge of the Yellowstone River (a), index of northern range annual precipitation (b), northern range elk abundance (c) and willow establishment (d) observed from 1980 to 2008. Note y-axes for panels (a–c) show standardized values.

Table 1. Results of negative binomial Poisson regressions for single parameter models predicting establishment as a function of flow, precipitation and elk. The median and 95 per cent credible intervals of posterior estimates are given, as well as the posterior weight greater than or less than zero. Posterior weights greater than 90 per cent are indicated by * and predictors included in combined model selection indicated by bold font

Covariate	Year	0.5	0.025	0.975	$P > 0$ or $P < 0$
Peak Flow	T	0.156	−0.346	0.695	0.275
	t + 1	−0.330	−0.801	0.152	0.080*
	t − 1	**0.401**	**−0.145**	**1.007**	**0.076***
Mean Annual Flow	T	−0.322	−0.858	0.217	0.116
	t + 1	**−0.543**	**−1.070**	**−0.071**	**0.012***
	t − 1	−0.190	−0.720	0.351	0.239
	$\sum_{t-1}^{t}$	−0.300	−0.804	0.229	0.127
	$\sum_{t-2}^{t}$	**−0.353**	**−0.832**	**0.124**	**0.068***
	$\sum_{y-3}^{t}$	−0.179	−0.612	0.285	0.214
	$\sum_{t-4}^{t}$	0.019	−0.421	0.493	0.466
Annual Precipitation	T	−0.470	−0.963	0.032	0.033*
	t + 1	−0.442	−0.958	0.050	0.040*
	t − 1	−0.434	−0.944	0.086	0.048*
	$\sum_{t-1}^{t}$	−0.486	−0.966	−0.025	0.020*
	$\sum_{t-2}^{t}$	−0.473	−0.946	0.002	0.026*
	$\sum_{y-3}^{t}$	−0.443	−0.915	0.022	0.029*
	$\sum_{t-4}^{t}$	**−0.411**	**−0.891**	**0.059**	**0.041***
Elk Abundance	T	−0.751	−1.253	−0.277	0.003*
	t + 1	**−0.809**	**−1.315**	**−0.356**	**<0.0001***
	t − 1	−0.668	−1.243	−0.175	0.004*

Table 2. Strength of evidence for alternative models predicting willow establishment, using flow and precipitation covariates only: avnxt is the mean annual flow for the year following establishment, pkprev is peak flow in the previous year, prevprcp4 is cumulative precipitation from the current and three previous years, and avprev2 is cumulative mean annual flow from the current and two previous years

Covariates	DIC	ΔDIC	w_{DIC}
int, avnxt, prevprcp4, avnxt*prevprcp4	101.9	0	0.32
int, avnxt, prevprcp4, pkprev, avprev2, avnxt*prevprcp4	103.9	2	0.12
int, avnxt, avprev2, avnxt*avprev2	104.6	2.7	0.08
int, avnxt, pkprev	104.7	2.8	0.08
int, pkprev, prevprcp4, pkprev*prevprcp4	104.8	2.9	0.08
int, pkprev, prevprcp4	104.8	2.9	0.08
int, avnxt	105	3.1	0.07
int, avnxt, prevprcp4, pknxt, avprev2, avprev2*prevprcp4, avnxt*prevprcp4, avnxt*avprev2	105.1	3.2	0.07
int, avnxt, pkprev, avnxt*pkprev	105.4	3.5	0.06
int, pkprev	105.7	3.8	0.05

Table 3. Strength of evidence for the top 10 models predicting willow establishment using flow, precipitation and elk abundance predictors: elknxt is elk abundance the year after establishment, avnxt is the mean annual flow for the year following establishment, pkprev is peak flow in the previous year, prevprcp4 is cumulative precipitation from the current and three previous years, and avprev2 is cumulative mean annual flow from the current and two previous years

Covariates	DIC	ΔDIC	w_{DIC}
int, elknxt, pkprev, avnxt, prevprcp4, avprev2, avnxt*avprev2, avnxt*prevprcp4, elknxt*prevprcp4	94.82	0	0.23
int, elknxt, pkprev, avnxt, prevprcp4, elknxt*prevprcp4	94.91	0.09	0.22
int, elknxt, pkprev, avnxt, avprev2, prevprcp4, elknxt*prevprcp4	95.58	0.76	0.15
int, elknxt, pkprev, avnxt, prevprcp4, avprev2, avnxt*prevprcp4, elknxt*prevprcp4	96.43	1.61	0.10
int, elknxt, avnxt, prevprcp4, elknxt*prevprcp4, avnxt*prevprcp4	96.91	2.09	0.08
int, elknxt, pkprev, prevprcp4, elknxt*prevprcp4	96.93	2.11	0.08
int, elknxt, pkprev, avnxt, prevprcp4, avprev2, avnxt*avprev2, elknxt*prevprcp4	97.03	2.21	0.07
int, elknxt, avnxt, prevprcp4, avprev2, avnxt*avprev2, avnxt*prevprcp4, elknxt*prevprcp4	97.91	3.09	0.05
int, elknxt, avnxt, prevprcp4, elknxt*prevprcp4	100.9	6.08	0.01
int, elknxt, avnxt, prevprcp4, avprev2, avnxt*avprev2, elknxt*prevprcp4	101.1	6.28	0.01

when using the peak flow the year prior to establishment, which was positively correlated with establishment [0.401 (−0.145, 1.007)].

Models with elk abundance and hydrologic predictors clearly provided better fits to the data than models with hydrologic predictors alone or models with elk abundance alone. All DIC values for the top ten models including elk and hydrologic predictors were lower than the top ten models including hydrologic predictors alone (Tables 2 and 3). Six models using only hydrologic predictors made up 76 per cent of the total DIC weights for the first model selection analysis (Table 2). The best-fit model was given 32 per cent of the DIC weight and explained 21 per cent of the variation in willow establishment and included mean annual flow the year following establishment, accumulated annual precipitation in the 4 years prior and their interaction (Table 2). The top four models using hydrologic predictors and elk abundance together made up 70 per cent of the DIC weight for the second set of models; however, the top two models' weights were similar (0.23 and 0.22, Table 3). Of these, the simpler model included peak flow, mean annual flow and the interaction between elk abundance and cumulative annual precipitation. This model explained nearly four times more variation in willow establishment than the best model with hydrologic predictors alone ($R^2 = 0.81$). The interaction between precipitation and elk was positive [0.644 (0.28, 1.00)], indicating that the negative correlation between elk abundance and willow establishment diminished during wet periods.

WILLOW STEM HEIGHT

Stem age ranged from 5 to 27 years at the time of collection (2009). We observed new stem initiation in every year from 1982 to 2004 (Fig. 3a). There was no evidence of lack of fit in the final model of observed height changes (Bayesian
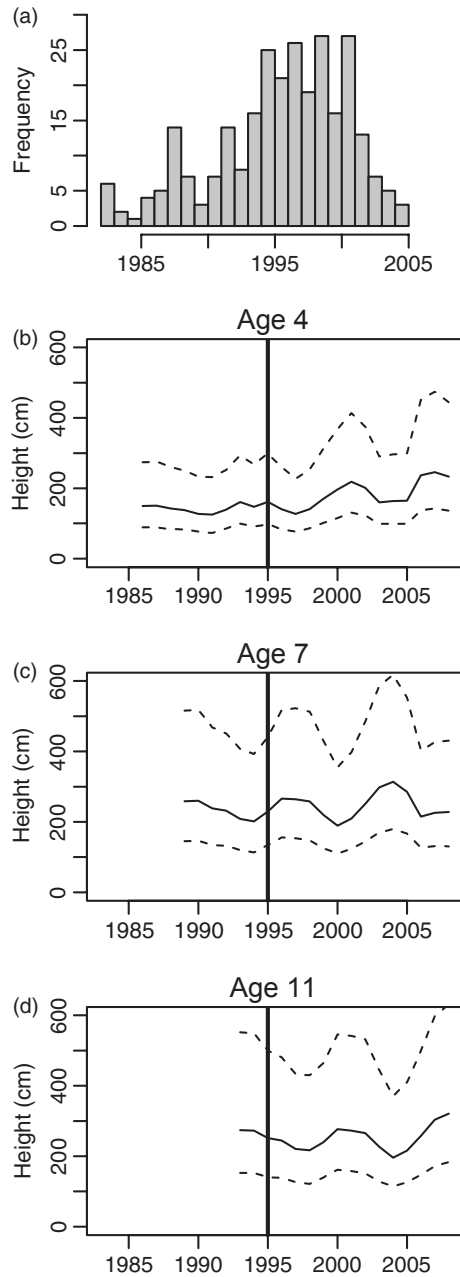
Fig. 3. The distribution of maximum ages of sampled stems and stem height at age through time. Frequency distribution of the year of stem sprouting for 275 collected willow stems shows most stems initiated after the 1995 reintroduction of wolves (a). Panels (b–d) show mean height of stems of age 4, 7, and 11. Vertical line indicates the year of wolf reintroduction (1995).

Table 4. Parameter estimates for models predicting stem height over time. Predictor variables are age of the stem (AGE), elk abundance (ELK), growing degree-days (GDD), annual precipitation (PRCP) and topographic wetness index (TWI). Estimates also provided for the estimated value of growing degree-days in 1983 and 1984, the standard deviation for the species random effect, and observation and process error

Parameter/Covariate	0.5	0.025	0.975
Intercept	1.148	1.054	1.257
AGE	−0.818	−0.855	−0.783
GDD	0.012	−0.017	0.040
ELK	−0.090	−0.127	−0.056
PRCP	0.013	−0.009	0.034
TWI	−0.022	−0.058	0.013
AGE*ELK	0.096	0.050	0.141
AGE*TWI	0.067	0.020	0.115
PRCP*GDD	0.034	0.007	0.060
GDD_{1983}	0.099	−1.302	1.441
GDD_{1984}	−0.016	−1.376	1.290
$\sigma_{species}$	0.128	0.058	0.331
σ_{obs}	0.047	0.035	0.068
σ_{proc}	0.449	0.435	0.464

−0.78)]. Due to this large age-dependent effect on growth dynamics, interactions with stem age were also dominant. During periods of low elk abundance, stems of younger ages grew more quickly and reached asymptotic heights (growth rate dropped to zero) more quickly than stems growing during periods of high elk abundance (Fig. 4a). Stems growing at sites with predicted high and low soil moisture, as described by the topographic wetness index, had similar growth rates in the first 2 years, but sites predicted to be dry were associated with lower growth rates than wet sites for all other ages (Fig. 4b). The interaction between growing degree-days and precipitation had very small overall effects on stem growth rate.

Predicted mean height of stems at age has not shifted for most ages of stems over the past three decades (Fig. 3b–d). Heights of young stems (age 4) in recent years may be increasing compared with the height at age in the 1980s and 1990s (Fig. 3b). There has been no apparent trend in height at age for moderate-to-older stems (Fig. 3c,d).

Climate effects on stem growth rate averaged across all stem ages were smaller and more variable over time than the effects of elk abundance (Fig. 5a,d,g compared with b,e,h). Credible intervals on coefficients for climate effects did not include 0 during 6 years. Climate effects were negative during years with short growing seasons or that were particularly dry (1988, 1993, 1995, and 2003). Climate effects were positive during wet years with long-growing seasons (1994 and 1998).

Combining the effects of elk and climate variables on growth rate, growth rates for stems aged 2+ indicate a declining trend since 1995 (Fig. 5i). Growth rates for stems age 0 have increased, and remained stable for age 1 stems. Anomalous climate years (e.g. 1993) had stronger effects on stem growth rate than elk effects for young stems (Fig. 5c,f,i). In
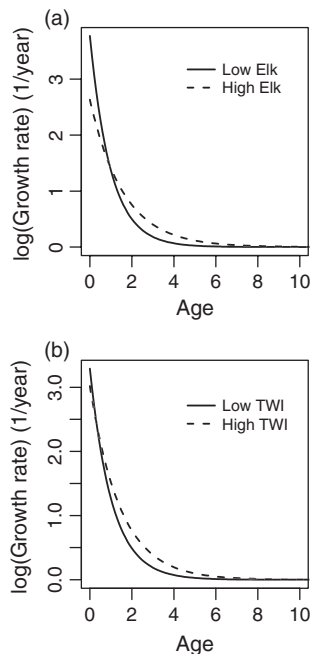
P-value = 0.546). Our final model included all main effects and multiple interactions between them: age and elk abundance, age and topographic wetness index, precipitation and growing degree-days, and precipitation and elevation (Table 4).

Growth rates of willow stems were strongly driven by stem age. We cannot directly interpret the magnitudes of the coefficients of the model because of the numerous interactions; however, the coefficient of the age effect was an order of magnitude larger than any of the others [−0.82 (−0.86,

Fig. 4. Interactions between elk abundance and age (a) and topographic wetness index and age (b) influence stem growth rate. Lines indicating low and high levels of the covariate indicate ±2 SD in both panels.

most years, however, the effects of changing elk abundance were more evident in stem growth rates than the effects of climate variability (Fig. 5).

Discussion

Establishment and growth of woody riparian vegetation has been influenced by the climate-driven hydrologic cycle, temperature and the abundance of browsing ungulates on the northern range of Yellowstone National Park during three decades spanning a strong trophic disturbance, the reintroduction of wolves. These factors interact over the course of a plant's multidecade life cycle to influence willow height dynamics across Yellowstone's northern range. Top-down effects of elk are clearly important drivers of willow establishment and growth, but these effects must be considered within the greater context created by interannual climate variability and landscape topography.

Willow establishment has increased along small streams on Yellowstone's northern range since 1999. Our models suggest this increase is due to favourable climate conditions that were coincident with reduced elk abundance on the northern range. The establishment of woody riparian vegetation is closely linked to hydrologic disturbance regimes across the US Rocky Mountain region (Scott, Auble & Friedman 1997; Shafroth, Stromberg & Patten 2002). Along small streams on the northern range, however, large flood events do not currently drive establishment. Wolf, Cooper & Hobbs (2007) found that willow establishment on the northern range followed periods of drought through the 1990s, and our models provide support for this finding through the 2000s. Our

finding that high flows during the year following germination were negatively correlated with establishment supports existing evidence that flood scouring negatively impacts willow seedling survival (Gage & Cooper 2004). The link between willow establishment and periods of drought occurs because willows are establishing on point bars adjacent to channels, rather than on the broader flood plain (Wolf, Cooper & Hobbs 2007). Seedlings in the channel are subject to greater risks of flood scour over their life span. Establishment is limited to point bars because the lack of beaver dams during the past half-century allowed streams to incise and become disconnected from their floodplains (Wolf, Cooper & Hobbs 2007; Persico & Meyer 2009).

The effects of elk abundance on willows clearly depend on plant age. Successful establishment of willow plants was negatively correlated with elk abundance during the year after the plant established, but only during dry periods. This suggests elk browsing can, in some contexts, have strong negative effects on willow survival in the early part of the plant's life (though negative effects of ungulate trampling may provide an alternative explanation, E. Gage, pers. comm.). After plants established, newly sprouting stems had higher growth rates when elk abundance was low. When elk abundance was high, growth rates of new stems were lower, but their growth rates declined more slowly with age. Taken together, stems sprouting and growing during periods of low elk abundance (after 1996) reached asymptotic heights more quickly than stems growing during periods of high elk abundances (prior to 1996). It is important to note that the overall height of stems of a given age varied across the period of study, but monotonically increasing trends have not occurred, except perhaps for young stems (e.g. age 4). This observation means that any observed height changes in willows on the northern range are likely due a changing age distribution of willow stems, not changes in height of existing stems.

Our findings generally agree with a previous study in Yellowstone investigating changing willow growth using growth rings. Beyer *et al.* (2007) studied growth ring area of willow stems collected in 2002 from 18 sites along small streams and large rivers on the northern range. They found, as we did, that both trophic and climate variables were required to explain changes in growth ring area through time.

Food-web theory predicts that numerically mediated trophic cascades are more likely to occur than behaviourally mediated trophic cascades when generalist herbivores are preyed upon by cursorial predators as in the wolf–elk system in Yellowstone (reviewed by Schmitz 2010). However, no one has been able to demonstrate numerical effects of elk on willows on Yellowstone's northern range. Ours is the first analysis to show clear correlation between elk population size and willow growth and establishment.

We did not observe overriding effects of climate variability on willow stem growth in this study, but the potential exists for extreme events to affect riparian willow dynamics. Over the three decades that we observed willow growth, only a handful years exhibited large effects of climate variables. However, the northern range is currently experiencing a
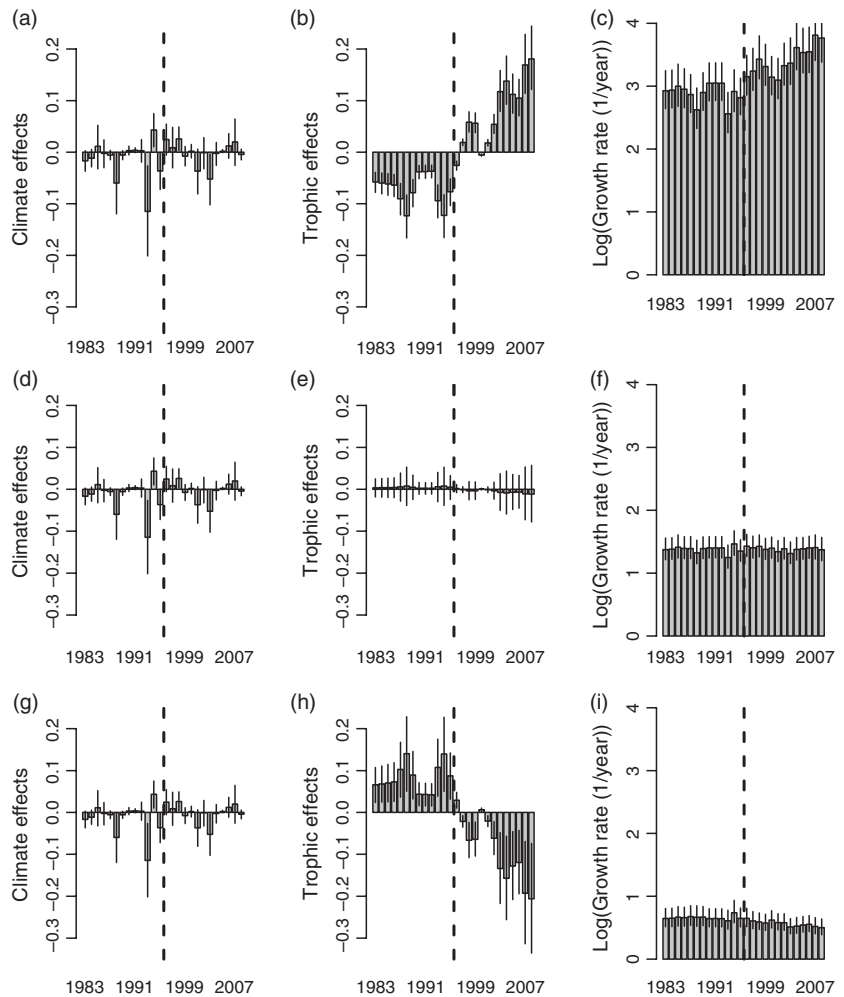
Fig. 5. Climate and trophic effects interact with stem age to influence interannual variability in growth rate from 1980 to 2008. We define 'effect' through time as the product of the posterior of the estimated coefficient and the value of its associated predictor in each year. Each row of panels represents a single age of stem (0 in the top row, 1 in the middle row, and 2 in the bottom row). In each row, climate effects (a, d, g) sum with trophic effects (b, e, h) to influence growth rate (c, f, i). Climate effects included precipitation, growing season length and their interaction. Trophic effects included elk abundance, stem age and their interaction. Note that climate effects do not change with stem age and panels (a), (d), and (g) are identical.

multidecade drought (McMenamin, Hadly & Wright 2008). Significant wetland drying has been attributed to decreased annual precipitation and increased temperature over the last 60 years (McMenamin, Hadly & Wright 2008). These slowly changing climate conditions combined with the long life spans of willow plants suggest our estimates of the strength of the links between climate drivers and willow growth are really minimum estimates. Alternatively, the range observed in elk abundance over the past three decades is much more representative of the full range of that population since elk surveys began in 1930 (Eberhardt *et al.* 2007).

All observational studies share the same central limitation: there is the potential to misinterpret correlation for causation. Causation can only be attributed using carefully designed, manipulative experiments. However, the correlations we observed in the work reported here are entirely consistent with experimental work that *does* permit attribution of cause and effect. Marshall, Hobbs & Cooper (2013) and Bilyeu, Cooper & Hobbs (2008) found that height growth and biomass accumulation of willows was controlled by the simultaneous effects of water availability and browsing. These results align with our finding that the strength of the relationship between elk numbers and willow growth and establishment depended on a spatial and climatic context that

influences availability of water to willows. Thus, our findings are useful in providing a large-scale compliment to the fine-scale experimental work we reported earlier (Bilyeu, Cooper & Hobbs 2008; Marshall, Hobbs & Cooper 2013), and the experiment provides a plausible mechanism for the correlations we observed.

Conclusions

Here, we show that climate and landscape heterogeneity modify the strength of trophic effects of elk on growth and establishment of willows. Climate and landscape variables that controlled water availability in small streams determined whether trophic effects were detected in any given year. Our work demonstrates that climate, topography and plant age structure act in concert to shape how plants respond to a modified food web.

In addition to the landscape heterogeneity and climate variability we considered here, other factors may also affect riparian willow dynamics in Yellowstone. Over the past three decades, the impacts of other ungulate species (e.g. moose *Alces americanus* and bison *Bison bison*) on willows were likely to be very small because the northern range elk herd was so large. However, these species could contribute more

to browsing pressure if elk numbers continue to decline (Painter and Ripple 2012). Also, the effects of fire can interact with flooding to change willow establishment (Wolf, Cooper & Hobbs 2007). Further investigation into these additional factors is warranted as the ecosystem continues to respond to on-going changes.

Our results contribute to a growing body of evidence showing that changes in growth of woody deciduous plants following the reintroduction of wolves cannot be explained by the trophic cascade model alone (Beyer *et al.* 2007; Kauffman *et al.* 2007; Wolf, Cooper & Hobbs 2007; Bilyeu, Cooper & Hobbs 2008; Creel & Christianson 2009; Eisenberg, Seager & Hibbs 2013; Marshall, Hobbs & Cooper 2013). Applying straightforward theoretical models (such as a tritrophic cascade) to real ecosystems is a necessary step towards simplifying a complex system and understanding the dominant forces and patterns governing ecosystem dynamics. However, it is equally important to consider complexity and potentially interacting effects of ecosystem drivers to more fully understand how ecosystems respond to perturbations to food-web structure.

Acknowledgements

Data Accessibility

Willow establishment data, stem height data, and coordinates of study site locations are deposited in the Dryad repository (Marshall, Cooper, & Hobbs 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary Methods.