A Bayesian Threshold Model of Willow (*Salix*) Height and Seed Production

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1 Abstract

The removal of a top predator leading to an alternative stable state is a major area of ecological research. The movement into the alternative state is often caused when the ecosystem crosses a critical threshold. In many situations, it is the objective of managers to revert that ecosystem back to its historical state. This is accomplished by identifying a threshold for restoration. Yellowstone National Park is an iconic example of a system that shifted into an alternative stable state following the removal of wolves (*Canis lupus*) in the early 1900s. Wolves were then reintroduced in 1995 with the goal of transitioning the ecosystem back to its original state. However, after almost 20 years of wolf presence in Yellowstone, the willow (*Salix*) populations in Yellowstone's riparian areas have not recovered. There may be several reasons for this phenomena, but one problem may be that willow are not producing enough seeds. A willow height threshold for restoration has been proposed for Yellowstone National Park's willow (**?**). Here, we present a Bayesian, zero-inflated Poisson regression which uses height and seed rain data from 21 randomly selected observational site across Yellowstone's Northern Range to estimate a willow height threshold for restoration. We found that the threshold height for willow seed production is very close to 200 cm from stem base to tallest stem. This model gives managers a new perspective on estimating ecological thresholds as well as rigorous basis for a willow height threshold for restoration.

2 Introduction

An ecological threshold can be an important management tool when used to determine whether or not an ecosystem is moving into an alternative stable state (?). It is well known that large populations of mammalian herbivores can cause a severe decline in riparian vegetation which may force a system beyond a threshold and into an alternative state (??). If willows (*Salix*) are inhibited from recruitment or if they simply do not survive, their population can decrease substantially, even beyond the point of reestablishment to their original stable state. Willows will not be able to recruit new plants if either they have become too damaged to produce catkins or the ground surrounding the seed producing willows is not fit for seedling establishment (?). Willows become viable when they begin producing seeds; therefore, it is useful to determine a threshold for seed production to know when soil for establishment can also be a factor in new willow growth.

Willow reestablishment has become a forward issue on the Northern Range in Yellowstone National Park. Wolves (*Canis lupus*) were not present in Yellowstone from the early 1900s until their reintroduction in 1995. This allowed elk populations to grow exponentially and nearly wipe out riparian willow communities. The reintroduction of wolves has significantly reduced elk herbivory of riparian willows, but the keystone species, beaver, have not recovered. Beaver and willow depend on each other for growth and recruitment. Beaver eat willow and also use willow to build dams which raises the water table to an ideal level for willow growth (?). Eventually, the beaver dam will break, draining a water pool and leaving exposed soil which is essential for willow seedling establishment (?). Without beaver activity there is minimal soil for willow reestablishment along the riparian corridors. Willows also play an important role in the structure of the stream banks, which can become incised and further decrease the area of feasible willow habitat.

It has been shown that due to extirpation of wolves, heavy elk browsing, and a decreased beaver population a new stable state has arisen known as the elk grass state (?). Tall willows that were ubiquitous in the early 1900s are now rare and lowered water tables have made it difficult for them to return to a tall willow community. This new stable state may have also prevented willows from reestablishing because there may be a lack of seed production. Data from our observational study suggests that most willow on Yellowstone's Northern Range are between 50cm and 200cm (Figure 1). This suggests that their is a missing older age class among willows that are still recovering from overabundant herbivore populations.

Even if beaver populations were reintroduced to Yellowstone's Northern Range and began to thrive, willow reestablishment would still depend on seed production. It has been hypothesized that willows will not produce seeds until they reach a threshold height (**?**) and was also suggested in our initial analysis (Figure 2), but there has yet to be any objective basis for that claim. Here, we provide a model that uses data collected from 21 randomly selected riparian sites across Yellowstone's Northern Range to rigorously estimate the threshold height for willow reestablishment. This model also has broader implications for restoration biology because it can be used by any manager who seeks to estimate a threshold for recovery with or without previous information.

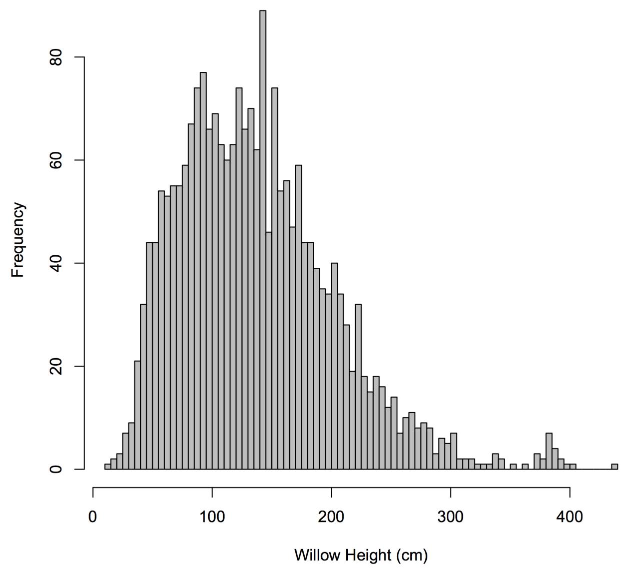

Figure 1: A histogram of the willow heights from over 2200 willows (*Salix*) randomly sampled across Yellowstone's Northern Range.

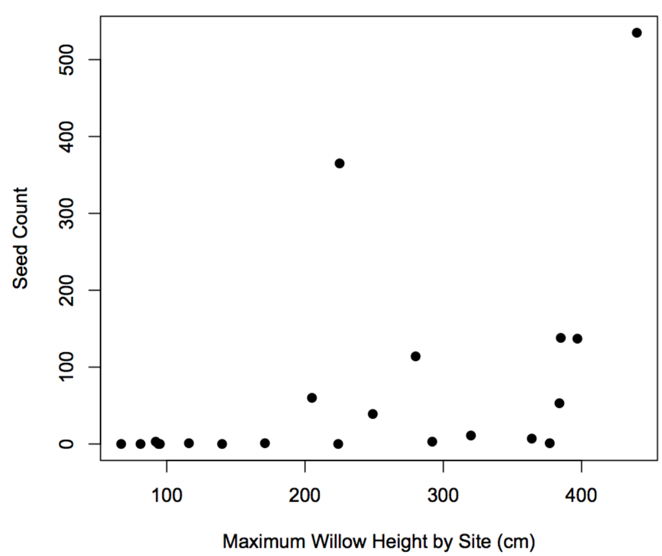

Figure 2: Raw data of maximum willow height versus seeds collected at each site from 21 randomly selected observational plots on Yellowstone's Northern Range. It has been hypothesized that willows will not produce seeds until they are 200 cm tall. Here we see that there had to be at least one tall willow in the plot or we did not detect any seeds.

3 Materials and Methods

3.1 Study Area

Data used in this analysis were collected from 21 randomly selected riparian areas in the northern range of Yellowstone National Park in June and July of 2010. These 21 observational sites originated from a database of stream sections that were either historically known to have beaver or were hypothesized to be a potential habitat for beaver based on gradient and stream order (?). The sites were selected using a spatially balanced random sampling algorithm (RRQRR). Each observational site was measured 100m by river length and extended 25m away from the river.

3.2 Data Collection

3.2.1 Seed Traps

Willow seeds were collected using seed traps made with an adhesive called Tree Tanglefoot© on plywood boards which were staked into the ground using shelf brackets. Two seed traps (measuring 30 cm^2 and 60 cm^2) were placed 25 m from the margin of the 100 m river length transect line within 5 m of the river bank. These seed traps capture the ambient seed rain for the entire site. A third trap (measuring 30 cm^2) was placed on an area within the transect determined optimal for seedling establishment. Willow seeds at each site were counted then removed from all traps each week during the willow seed production season. We will use the sum of the seeds counted from each site in our model.

3.2.2 Willow Height

Every willow within each site was measured from the center of the root base to the highest branch in centimeters.

3.3 Model

3.3.1 Overview of Modeling Approach

We constructed a Bayesian, zero inflated Poisson model to account for process variance and observation error in our analysis of the effect of willow height on seed production. We estimated the marginal posterior distributions of parameters, specifically, the threshold height for willow seed production. A comprehensive representation of the model follows:

$$P(\boldsymbol{z}, p, \boldsymbol{\beta}|\boldsymbol{y}) \propto P(\boldsymbol{y}|\boldsymbol{\lambda})^{\boldsymbol{z}} P(y=0)^{\boldsymbol{z}-1} P(\boldsymbol{z}|p) P(p, \boldsymbol{\beta}) \quad (1)$$

$$\boldsymbol{\lambda} = \boldsymbol{X}\boldsymbol{\beta} \quad (2)$$

The vector $\boldsymbol{z}$ represents our prediction of the true state of willow seed count that we observed in vector $\boldsymbol{y}$ where either $z = 0$ or $z > 0$. The true state is derived from a process model when $y > 0$ and $z > 0$. Otherwise when $y = 0$, $z = 0$ with probability 1. The process model is formed by a deterministic regression shown in equation 2 where $\boldsymbol{X}$ is a matrix of covariates multiplied by $\boldsymbol{\beta}$ a vector of parameters. We estimate these parameters in a parameter model. Equation 1 will serve as a guide to our methods section. First we will outline the models of the data, $P(\boldsymbol{y}|\boldsymbol{\lambda})^{\boldsymbol{z}} P(y = 0)^{\boldsymbol{z}-1}$. Then, we will describe models of the process $P(\boldsymbol{z}|p)$ that determines the true state of willow seed production. Next, we will explain our choice of the parameter models, $P(p, \boldsymbol{\beta})$. Finally, we will assemble the full model.

This three sub-model structure allows us to represent uncertainty associated with data collection in the data model, account for the underlying mechanisms from which the data are drawn in the process model, and define prior distributions of the parameters in the parameter model.

3.3.2 Data Model

We chose a zero-inflated Poisson regression model because some sites (i) had no seeds. Thus, our data model is represented below:

$$y_i \sim \begin{cases} 0 & , x_i = 0 \\ \text{Poisson}(\lambda_i) & , x_i > 0 \end{cases} \tag{3}$$

where x_i is our prediction of the true state and y_i are the seed count data for site i.

3.3.3 Process Model

We seek to estimate a threshold height for willow seed recruitment, but we also recognize that the number of willows in a plot among other things should effect seed production. To estimate the effect of willow height and numbers of willow in the plot on seed recruitment, we created an indicator variable x_i to count the number of willows in each plot above a threshold height $\left(\tilde{h}\right)$ with an interaction effect with total willow height h_{ij} for the site such that

$$x_i = \sum_{i=1}^{J_i} 1_{\{h_{ij} \geq \tilde{h}\}} h_{ij} \tag{4}$$

where j is an index for the individual willow. Then, to compute the intensity (λ_i), we used the following regression model:

$$\lambda_i = \beta_0 + \beta_1 \log(x_i) \tag{5}$$

The vector x_i was only calculated when $y_i > 0$ because as stated in the previous section if $y_i = 0$, $x_i = 0$ with probability 1.

3.3.4 Parameter Model

There are three parameters in this model, $\tilde{h}, \beta_0$, and β_1. Previous evidence suggests that the threshold height for willow seed recruitment is 200 cm (**?**), so we assigned an informative prior to $\tilde{h}$ by moment matching a gamma distribution with mean = 200 and variance = 50.

$$\tilde{h} \sim \text{gamma}(4, .02)$$

We gave the coefficients in our regression model vague priors with mean = 0 and variance = 50. We assumed that β_0 and β_1 were independently and identically distributed.

$$\boldsymbol{\beta} \sim N(\boldsymbol{\mu}_{\boldsymbol{\beta}}, \sigma^2 I)$$

3.3.5 Posterior

The full posterior and joint distributions are given by

$$\left[\boldsymbol{\beta}, \tilde{h} \,\middle|\, y_i\right] \propto \prod_i \left(1_{\{y_i=0\}}^{1_{\{x_i=0\}}} \text{Poisson}\left(y_i \,\middle|\, \lambda_i\right)^{1_{\{x_i>0\}}} \right) \\ \times \text{Multivariate Normal}\left(\boldsymbol{\beta} \,\middle|\, 0, 50\right) \text{Gamma}\left(\tilde{h} \,\middle|\, 2, 0.04\right) \quad (6)$$

3.4 Implementation

Marginal posterior distributions of states, parameters, and model predictions were estimated using Markov chain Monte Carlo (MCMC) methods in the R computing environment (?). Parameters were estimated using a random walk metropolis-hastings algorithm with normal proposal distributions. Three chains were chosen for each estimated quantity. Initial values of chains were each chosen to vary 20% in either direction relative to posterior distributions (?). Convergence was assured by inspection of trace plots and by the diagnostics of Gelman and Rubin (?). All code for this model can be found in the supplementary materials.

4 Results

Here we describe the results of our MCMC output. We accumulated 100,000 samples from each chain and discarded 20,000 iterations as the burn-in to ensure convergence of parameter chains. In Figure 3, we show the marginal posterior distributions of the model parameters, and in Table 1 we report the means and 95% credible intervals of each parameter. The parameters converged after 100,000 iterations of the MCMC Sampler as indicated by the Gelman Diagnostics of 1.00 for all parameters with a 20,000 iteration burn-in.

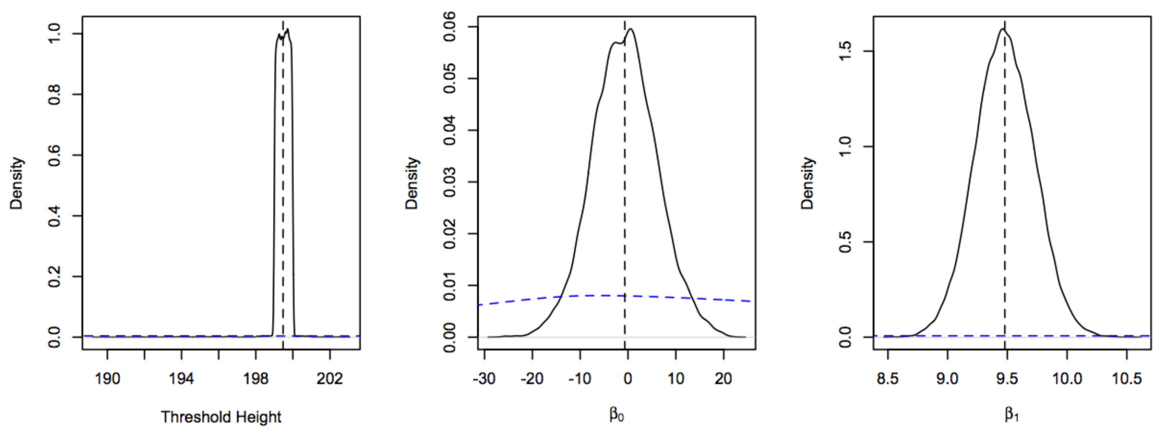

Figure 3: The marginal posterior distributions of the parameters. The dotted horizontal line is the prior distribution we defined for the parameter, and the dotted vertical line is the mean of the marginal posterior distribution of each parameter.

Parameter	Lower 95% Credible Interval	Mean	Upper 95% Credible Interval
$\tilde{h}$	199.04	199.48	199.98
β_0	-11.41	-0.29	13.50
β_1	9.07	9.48	9.97

Table 1: The means and 95% credible intervals for each parameter estimated in the model.

5 Discussion

5.1 The Willow Height Threshold

Ecological thresholds have important implications for ecosystem management and ecological theory. Yellowstone National Park has been a premier example of a major shift over a critical threshold from one alternative stable state to another following the extirpation of a top predator (**?**). The reintroduction of the wolf reduced elk populations by 70% supposedly paving the way for riparian willow recovery (**?**). However, alternative evidence suggests that wolves are not the only species needed to restore the area's original willow populations. Beaver depend on willow for nourishment and protection, so following the extreme decrease in the willow population beavers vacated Yellowstone. Now without beaver, willows have been unable to reestablish because beaver dams raise the water table which is essential for willow growth, and when the dams break, they also create establishment soil for seedlings. This positive feedback has caused researchers to conclude that Yellowstone has shifted to an elk grassland stable stage (?). We know that beavers are critical in the process of shifting Yellowstone's ecosystem back to its historical stable state, but we do not know when willows will be able to produce seeds in order to begin the reestablishment process. With this model and randomly collected data, we proved that the threshold height for willow seed production on Yellowstone's Northern Range is very close to 200 cm.

The increase of riparian willow is the key to the restoration of Yellowstone, but it cannot occur until more willows are producing seeds. In this study the heights of over 2200 willow were measured and only 16% of willow were above the threshold height of 200 cm (Figure 4). In spite of this low percentage, 13 of the 21 sites had tall willows present and most sites had several up and coming willows between 50 - 200 cm. We suggest that willows are beginning to produce seeds and that they will continue to grow because herbivore populations have decreased. Although there are tall willows in more than half of the sites, there do not yet seem to be enough tall plants to allow the willow communities to expand to historic levels. The seeds produced at a site are not simply a function of the number of tall plants. We are also interested in the effect of the sheer number of willows present. This is why our indicator variable in the process model includes an interaction factor between number of tall willows and cumulative willow height at the site (h_{ij}). The estimated value of our slope coefficient in our regression model suggests that this interaction effect is very important ($\beta_1 = 9.48$). Thus, a tall and large willow community that facilitates seedling recruitment will allow for willow recovery, but returning to this state may be impossible without more water and exposed soil for seedling establishment in the riparian corridors.

5.2 Threshold Modeling: Generalizations for Management

We have provided a Bayesian structure that can allow managers to input their own knowledge through data, informed priors, and increased number of covariates in a intuitive and rigorous way to determine a threshold value in their own system and to quantify the uncertainty associated with those estimates. This gives the manager and the researcher a Bayesian alternative to the piecewise regression described in **?**. Our use of an indicator variable in the process model signals to the flexibility of this methodology.

These types of models are becoming more critical as our world continues to change. Shifts in ecosystems are occurring rapidly. It will be important for managers to understand ecological thresholds and have a quantitative basis for estimating their values. Thresholds often form the basis for management action plans as well as interpreting the type of stable state an ecosystem is realizing. Mistakes in these estimations could lead to mismanagement which could lead to further ecological harm. In Yellowstone National Park, managers need to know these types of critical details for willow reestablishment in order to return the ecosystem to its historical stable state. They have taken courageous steps to reduce the herbivore population by reintroducing wolves, and now they seek to know more about what needs to happen to reconstruct their riparian corridors. Knowing an ecological threshold and the inherent uncertainty is one step in a very complicated problem that can help managers and researchers further understand the transition from one stable state to another.

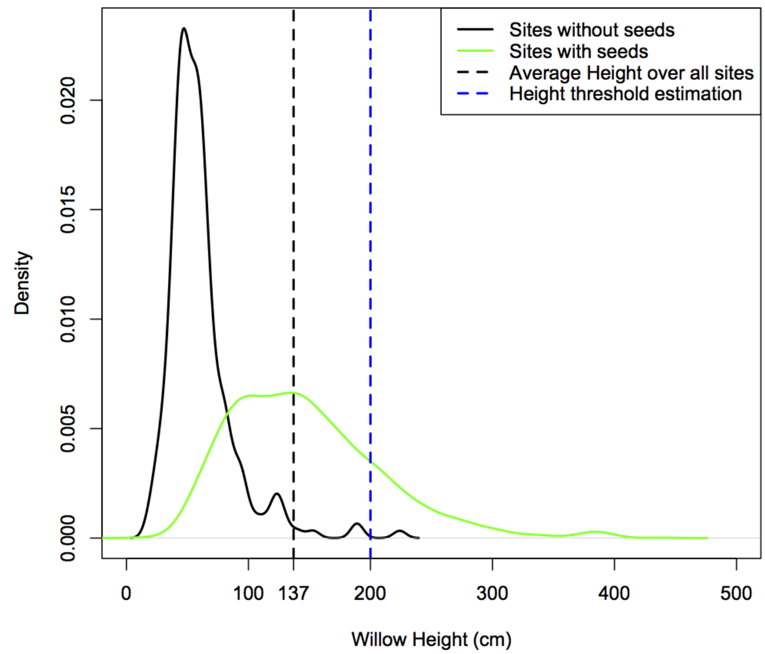

Figure 4: This is a plot of the frequency of the willow heights measured in this study. The black curve is the frequency of willow heights for sites that did not produce seeds. The green curve is the frequency of willow heights for the sits that did produce seeds. The black dotted line is the overall average willow height, and the blue dotted line is the estimated height threshold $\left(\tilde{h}\right)$. The majority of willows (84%) are below the estimated threshold height for seed production (200cm).