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Hierarchical Bayesian methods estimate invasive weed impacts at pertinent spatial scales

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Abstract Invasive weed impact estimates are needed to determine whether or not weeds warrant costly control measures. Typically, land managers seek local weed impact estimates (e.g. ranches, parks) and policy-makers want to know how weeds are impacting entire regions. Our goal was to provide local and regional impact estimates for a ubiquitous invasive weed: leafy spurge (Euphorbia esula L.). The specific impacts we looked at related to desired species biomass production, livestock carrying capacities, and grazing land values. Our basic approach was to use an empirical model that characterizes weed biomass across the landscape in combination with another empirical model that predicts weed impact from weed biomass. Our investigation revealed that, without on-site plant biomass data, site-specific leafy spurge impacts are highly uncertain. Supplementing our general predictive model with small quantities of on-site data increased precision considerably. For the 17-state region we considered, 95% Bayesian credibility intervals

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indicated leafy spurge reduces cattle carrying capacities by 50–217 thousand animals a year and reduces grazing land values by 8–34 million dollars a year. Additional plant biomass data from randomly selected, leafy spurge-infested sites would shrink these fairly wide intervals.

Keywords Competition · Forage · Grassland · Impact assessment · Livestock · Model · Parameter estimation · Rangeland · Uncertainty · Weed management

Introduction

In selecting strategies for dealing with invasive weeds, resource managers compare predicted outcomes of multiple candidate strategies (Wilkerson et al. 2002; Odom et al. 2005). Intensive strategies (e.g. herbicides, revegetation, biological control) are selected when their costs and risks are considered mild in comparison to the severity of weed impacts. Conversely, when intensive weed management will have severe costs and risks, and weed impacts are comparatively mild, conservative strategies (e.g. reduced stocking rates, containment protocols, or inaction) are more sensible. Unfortunately, weed managers and policy-makers are usually not provided with accurate impact estimates for the relevant spatial scales, so it is difficult for them to decide whether

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intensive or conservative strategies are better in any given situation.

Some invasive weed management strategies, such as targeted grazing, herbicides, and desired species seeding, do not greatly impact areas surrounding sites of application. For example, when domestic sheep are used to control leafy spurge (Euphorbia esula L.) (Olson and Wallander 1998), no risks (e.g. overgrazing) or benefits (e.g. weed control) accrue outside the fence confining the animals. In cases like these, where weed management costs and risks are localized, site-specific weed impact estimates should drive decision-making (Luschei et al. 2001). Other weed management strategies (and policy measures) exact costs and provide benefits across entire regions, and in these cases regional weed impact estimates are of principle interest. Exotic arthropod biological control agents are a prime example (Stiling 2004; Louda et al. 2005). These agents spread from release sites, and over time their distribution can come to match or exceed that of the target weed (Baars and Heystek 2003).

Whether estimating local or regional weed impacts, data on weed density or biomass per unit area are needed, because a weed's competitive impact is strongly related to its abundance (e.g. Cousens 1985; Vila et al. 2004), and abundances vary widely from site to site (e.g. Lym and Messersmith 1990; Ortega and Pearson 2005). In addition to weed abundance data, models that predict impact from weed abundance are also needed (e.g. Spitters 1983; Jasieniuk et al. 2001; Grekul and Bork 2004).

Once an impact model and weed abundance data are in hand, estimating local weed impacts is conceptually straightforward. Commonly used statistical tools can be applied to random weed abundance samples and the resultant statistical estimates (e.g. mean weed abundances) can be plugged into impact models (e.g. Rinella and Sheley 2006).

In comparison to local weed impacts, sampling effort and analytical requirements are greater when regional weed impacts are the focus. To estimate regional impacts, random weed abundance samples must be collected from a random sample of weed-infested sites. In addition to being more practically burdensome to collect, this kind of two-level hierarchical dataset is more difficult to analyze. Assembling and analyzing hierarchical weed data is our central focus in this paper.

This paper describes how we used data from many sites to estimate local and regional weed impacts. The impacts of interest related to desired species biomass production, cattle carrying capacities, and grazing land values. To estimate local weed impacts, we applied a weed impact model to on-site weed biomass samples. In doing this, we paid careful attention to key sources of prediction uncertainty (i.e. uncertainty about impact model parameters, uncertainty about local leafy spurge and desired species biomasses). In estimating regional impacts, we focused on the coterminous 17-state area west of Minnesota to Texas. Leafy spurge is a high-profile invader in this region, hence a pool of spatially distributed biomass data are available. Additionally, Duncan et al. (2004) recently estimated the area infested by leafy spurge within the region, so we were able to scale our estimate to the appropriate infestation size (sensu Parker et al. 1999)

Materials and methods

We developed two models. The leafy spurge impact model characterizes leafy spurge effects on associated species biomass production. The plant biomass model describes leafy spurge and associated species biomass production at individual sites and averaged over a 17-state region. By plugging simulated values from the biomass model into the impact model, we estimated leafy spurge impacts at a specific site in North Dakota and across a 17-state region. The North Dakota analysis is used to show how on- and off-site data can be used together to estimate weed impacts for any site of interest. The regional analysis estimates some damages caused by leafy spurge in the western U.S.

The leafy spurge impact model

Experimental design

To develop a model that predicts associated species biomass from leafy spurge biomass, we

used data from 2 field experiments (hereafter referred to as Experiment 1 and Experiment 2). These experiments were conducted at the Montana State University Arthur H. Post Research Farm near Bozeman, MT. In each experiment, 4 Kentucky bluegrass (Poa pratensisL.) and 6 western wheatgrass (Pascopyrum smithii Rybd.) seeding rates and 6 leafy spurge seedling densities were combined in 1.0×1.0 -m plots in every possible density combination (4 bluegrass seed rates \times 6 wheatgrass seed rates \times 6 spurge seedling densities \times 2 experiments = 288 plots). Kentucky bluegrass and western wheatgrass were used because they commonly grow in association with leafy spurge. Grass seeds were uniformly hand-sown into Experiment 1 plots in June 1998 and into Experiment 2 plots in August 2000. Leafy spurge seedlings were planted at even spacing in early May 2000, so grasses were established before leafy spurge in Experiment 1 and after leafy spurge in Experiment 2. Rinella and Sheley (2005b) explain Experiments 1 and 2 in full detail.

Data collection

Leafy spurge and grass biomass were harvested by clipping at ground level in August 2002 when repeated plant height measurements indicated plots were at peak standing crop. To avoid unrepresentative growing conditions near plot edges, only the inner 85×85 -cm plot area was harvested. Leafy spurge and grass biomass samples were weighed after drying to constant weight at 50°C.

Analysis

Because we used Bayesian statistics, the parameters of our models are estimated as probability distributions. We use quantiles to summarize these distributions. The 2.5–97.5% quantile interval (i.e. 95% Bayesian credibility interval) is similar to a 95% confidence interval, but with a more straightforward interpretation. The 95% credibility interval is interpreted simply as having a 95% chance of containing the true parameter value. Leafy spurge biomass, as well as several control variables (e.g. experiment, seeding rate), were evaluated as predictors in linear regression models. The response variable of the models was combined western wheatgrass and Kentucky bluegrass biomass. The two grasses were combined because they respond similarly to leafy spurge competition (Rinella and Sheley 2005c, b). The regression coefficient of interest was the one that multiplies leafy spurge biomass (β_w). Bayes factors were used to identify the model most consistent with the data (Kass and Raftery 1995).

As we had no prior knowledge of the model's parameter values, a standard noninformative probability distribution served as our prior distribution of regression parameters (Gelman et al. 2004, p. 355). With this prior, the posterior probability distribution of the beta coefficient vector (β) given the random error variance (σ^2) is multivariate normal (Gelman et al. 2004, p. 356):

$$p(\beta|\sigma^2) \sim N(\hat{\beta}, V_B \sigma^2)$$
 (1)

where $\hat{\beta}$ is the least-squares estimate of the regression coefficient vector and $V_{\beta} = (X^T X)^{-1}$. The matrix X is the $n \times (k + 1)$ (n = number of plots, k = number of predictors) predictor data matrix with a column of 1's prepended. It can be shown that the marginal posterior distribution of σ^2 given response data (y) has a scaled inverse chi-square distribution with n-k degrees of freedom and scale parameter equal to the regression mean square error (s^2):

$$p(\sigma^2|y) \sim \operatorname{Inv-}\chi^2(n-k,s^2)$$
 (2)

A random draw from the posterior distribution of regression parameters is obtained by sampling σ^2 from Equation [2], inserting this deviate into Eq. (1), and then sampling the distribution given by Eq. (1). No starting values or discarding of simulations (i.e. burn in) is required with this particular linear model. All simulations were done using Mathematica 5.1 (Wolfram 2003).

To determine if the impact model accurately describes leafy spurge impacts across a range of sites, we compared the 95% credibility interval for the leafy spurge biomass coefficient (β_w) to

coefficient estimates from 28 leafy spurge removal experiments conducted throughout the western U.S. We conducted some of the removal experiments with the explicit purpose of evaluating model performance. The other experiments, which we meta-analyzed to derive β_w estimates, were conducted by others for the purpose of testing leafy spurge herbicides (Maxwell 1984; Gylling and Arnold 1985; Lym and Messersmith 1985, 1994; Lym 2000; Markle and Lym 2001). Whereas the removal experiment data were helpful for testing the model, potential problems with the experiments dissuaded us from relying on them for model development. One prospective problem with the removal experiments was that herbicides were used to remove leafy spurge, and the specific chemicals used sometimes injure grasses. Rinella and Sheley (2005a) detail the plant removal experiments as well as our protocol for deriving beta estimates from these experiments.

The plant biomass model

Biomass data

To estimate leafy spurge and associated species biomasses across the 17-state region, we searched the literature and amassed data or sample statistics from nearly 100 leafy spurge-infested sites. In addition to being necessary for estimating regional weed impacts, this meta-dataset also improved impact estimates for the individual North Dakota site. Only 4 on-site plant biomass samples were available for the North Dakota site. It would be virtually impossible to estimate local plant biomass means, variances, and covariances from only 4 samples without statistically 'borrowing strength' from off-site data (i.e. the meta-dataset).

Several culling criteria were applied to the meta-dataset to ensure the data were gathered under realistic field conditions and contained minimal bias. These criteria were: (1) leafy spurge biomass had to be measured, as opposed to stem density or cover; (2) no tilling or mowing of study sites; (3) plant biomass measured around the time of peak standing crop; and (4) plant biomass not a criterion in site selection. Employing criterion (4) required us to contact each researcher and ascertain their site selection criteria. Data were omit-

ted if weed density or biomass was a criterion for selecting research sites; e.g. some research protocols called for "densely leafy spurge-infested sites". After culling, our dataset contained data or sample statistics from 19 sites (Table 1). The original study objectives varied but were irrelevant to our analysis, because we exclusively used data from units that were not experimentally manipulated (the untreated controls).

Most study sites were measured during multiple growing seasons. Because some of the multiyear studies averaged data over years, we could not estimate year effects. Therefore, our analysis averaged over annual variation. It was possible to construct 'by year' scatter plots for some of the sites, and these plots showed that between-year variation within a site was small in comparison to variation among sites. Therefore, incorporating year effects would not appreciably alter our results.

Ouadrat size varied between studies. Given that the leafy spurge impact model is based on 1.0-m² plots, raw quadrat values from quadrats that were smaller than 1.0 m², were added together such that each data point ultimately came from an area as close to 1.0 m² as possible. Quadrats that were combined were spatially clustered; they were sub-samples from the same plot or adjacent samples from the same transect. When raw data were not provided and quadrats were not 1.0 m^2 , sample size was adjusted so that means reflected 1.0-m² equivalents. Scaling measurements to 1.0 m² provided sampling variances of similar magnitude. This is favorable because our plant biomass model assumes between-quadrat variances are similar across sites.

Analysis of biomass data

Since data from some study sites were incomplete (Table 1), we used a multiple imputation routine to simulate missing data values (Congdon 2001; Gelman et al. 2004). Multiple imputation uses available data to simulate the distributions of missing data. We simulated 25 sets of missing data values and analyzed each of these. By averaging over the imputation datasets, uncertainty about missing data values was incorporated into our analysis.

A hierarchical one-way normal random effects model was used to estimate plant biomass parameters (Gelman et al. 2004). This model allowed us to jointly estimate regional and local plant abundances. For our analysis, the model relied on bivariate normal distributions. The first dimension of the distributions describes leafy spurge biomass and the second dimension describes associated species biomass. We used a standard noninformative prior distribution for the model parameters (Gelman et al. 2004 Chapter 5.4). With this prior, and conditional on the data (y)and all other parameters, the posterior distribution of the site *j* mean (θ_j) is independent of the other site means and is bivariate normally distributed

$$p(\theta_j|\mu, \Sigma, \Lambda, y) \sim \mathbf{N}(\hat{\theta}_j, V_{\theta_j})$$
 (3)

where:

$$\hat{\theta}_j = \left(\Lambda^{-1} + n_j \Sigma^{-1}\right)^{-1} \left(\Lambda^{-1} \mu + n_j \Sigma^{-1} \bar{y}_j\right) \tag{4}$$

and:

$$V_{\theta_j} = \left(\Lambda^{-1} + n_j \Sigma^{-1}\right)^{-1} \tag{5}$$

Sample size for site *j* is given by n_j , and \bar{y}_j is the two-dimensional site *j* sample mean. Other symbols, which are described in detail below, represent within-site covariance (Σ), between-site covariance (Λ), and the mean of the θ_j 's (i.e. μ).

The conditional posterior distribution of the overall mean (i.e. the mean of the site means) is bivariate normal:

$$p(\mu|\theta, \Sigma, \Lambda, y) \sim \mathbf{N}(\hat{\mu}, \Lambda/J)$$
 (6)

where:

$$\hat{\mu} = \frac{1}{J} \sum_{j=1}^{J} \theta_j \tag{7}$$

and the total number of sites is given by J.

The within-site covariance matrix (Σ) is comprised of the leafy spurge variance (σ_w^2), associated species variance (σ_g^2), and the covariance

between leafy spurge and associated species (σ_{wg}) .

$$\sum = \begin{pmatrix} \sigma_w^2 & \sigma_{wg} \\ \sigma_{wg} & \sigma_g^2 \end{pmatrix}$$
(8)

This matrix describes quadrat-to-quadrat variation within a site. It is assumed that withinsite variances and covariances do not change from site to site. This is a rather minor assumption for our purposes, and it greatly reduced the number of parameters to be estimated. The conditional posterior distribution of \sum is an inverse-Wishart distribution with *n* degrees of freedom (*n* = total number of data points):

$$p\left(\sum |\theta, \mu, \Lambda, y\right) \sim \text{Inv-Wishart}_n(\hat{\Sigma})$$
 (9)

where:

$$\hat{\sum} = \frac{1}{n} \sum_{j=1}^{J} \sum_{i=1}^{n_j} \left(y_{i,j} - \theta_j \right) \left(y_{i,j} - \theta_j \right)^T \tag{10}$$

and the $y_{i,j}$ are the two-dimensional data points.

The between-site covariance matrix (A) is comprised of the between-site leafy spurge (τ_w^2) and associated species (τ_g^2) variances, and their covariance (τ_{wg}) .

$$\Lambda = \begin{pmatrix} \tau_w^2 & \tau_{wg} \\ \tau_{wg} & \tau_g^2 \end{pmatrix} \tag{11}$$

Eq. (11) describes site-to-site variation in mean leafy spurge and associated species biomasses. The conditional posterior distribution of Λ is an inverse-Wishart distribution with *J*-1 degrees of freedom:

$$p(\Lambda|\theta,\mu,\sum,y) \sim \text{Inv-Wishart}_{J-1}\begin{pmatrix}\wedge\\\Lambda\end{pmatrix}$$
 (12)

where:

$$\hat{\Lambda} = \frac{1}{J-1} \sum_{j=1}^{J} \left(\theta_j - \mu\right) \left(\theta_j - \mu\right)^T \tag{13}$$

We used Gibbs sampling to simulate the joint posterior probability distribution of plant biomass

model parameters $p(\theta, \mu, \Sigma, \Lambda|y)$ (Gelman et al. 2004). To draw from this distribution, we assigned sample means and variances as starting values and then sequentially drew from the marginal posterior distributions (Eqs. (3), (6), (9), (12)). Simulation convergence was assessed by monitoring two Gibbs sequences (Gelman et al. 2004, Chapter 11.6).

Simulating leafy spurge impacts

In simulating the probability distribution of leafy spurge impacts for site *j*, we repeated the following steps until estimates of interest (i.e. quantile values) converged: (1) Insert a drawn value of β_w into the impact model; (2) Use drawn values for the site mean (θ_i) and within-site covariance matrix (\sum) to simulate a large number (i.e. 500) of quadrat-level biomass values as: $y_{i,j} \sim N(\theta_i, \Sigma)$; (3) Insert each of the 500 sets of biomass values $(y_{i,i}'s)$ into the impact model and compute 500 leafy spurge impact estimates $(I_i's)$; (4) Average over the I_i 's to calculate the expected value of weed impact $(E(I_i))$. The 500 quadrat-level draws were needed to stabilize $E(I_i)$ for a given value of θ_i and \sum . If the impact model were linear without transformation (it is not), no quadrat-level draws would be needed. In the linear case, inserting θ_i into the impact model would directly simulate $E(I_i)$. But because the impact model is non-linear, Jensen's inequality necessitates quadrat-level $E(I_i) =$ draws: $E(f(y_i)) \neq f(E(y_i))$ where $E(y_i) = \theta_i$ (Jensen 1906).

The procedure for simulating regional leafy spurge impacts is analogous to that for simulating site-specific impacts. We repeated the following steps until convergence: (1) Draw a large number (i.e. 500) of site means as: $\theta \sim N(\mu, V_{\theta_j})$; (2) follow steps 1–5 of the last paragraph for each drawn θ value; (3) compute the expected value of regional impact by averaging over the 500 sitespecific impact estimates.

Results

The leafy spurge impact model

Bayes factors indicated that the following model best describes Experiment 1 and 2 data (Fig. 1):



Fig. 1 Predicted versus observed graph for model that predicts grass biomass from leafy spurge biomass in two field experiments. Predicted values were obtained by fixing model parameters at the mode of their joint probability distribution

$$\ln(g) = \ln(g_{\max}) - \beta_w w + \beta_2^* E^* \ln(R+1) + \varepsilon$$
(14)

where g is associated species (in this case grass only) biomass, g_{max} is associated species biomass in the absence of leafy spurge, w is leafy spurge biomass, β_w describes the impact of w on $\ln(g)$, E is 0 for Experiment 1 and 1 for Experiment 2, R is western wheatgrass seeding rate, β_2 describes the effect of the site by western wheatgrass seeding rate interaction, and $\varepsilon \sim N(0, \sigma^2)$ is random error. Natural log transformations were used to better meet linear regression assumptions. The E and Rterms adjust for seeding rate effects and experiment-specific g_{max} (Rinella and Sheley 2005b). There is no clear need (or mechanism) for conditioning on E and R when using the model for prediction. Therefore, the relevant model is simpler:

$$\ln(g) = \ln(g_{\max}) - \beta_w w + \varepsilon \tag{15}$$

The vast majority of β_w values from leafy spurge removal experiments throughout the western U.S. are very similar to the β_w credibility interval values estimated from Experiment 1 and 2 (Fig. 2). This suggests that Eq. (15) will fairly accurately predict leafy spurge impacts throughout the western U.S. Also, several grass species grew at the removal experiment sites, and this



Fig. 2 Estimates of leafy spurge competitive impact parameter from two planting experiments conducted near Bozeman, MT. (horizontal bar) and from 28 leafy spurge removal experiments conducted throughout the western U.S. (histogram). The horizontal bar denotes the 95% credibility interval for the impact parameter (β_w), and the histogram represents point estimates for the parameter from the removal experiments

suggests model accuracy is similar regardless of grass species composition.

We believe the major factors Eq. (15) does not account for (i.e. the major contributors to ε) are measurement error and productivity variation between quadrat locations. Productivity variation is in part regulated by site characteristics, while measurement variation stems from differences between observers, and differences between measurement devices. Leafy spurge and grasses were established under uniform conditions in Experiments 1 and 2 (i.e. tilled fields), and the experiments were measured by a small number of people. Therefore, ε is not a broadly applicable error term for predicting leafy spurge impacts in the highly heterogeneous grasslands where the weed naturally occurs. Instead, the relevant sources of productivity and measurement variation are more logically included by estimating sampling variation, which we did with our plant biomass model. Because ε is redundant with sources of variation captured by our plant biomass model, we excluded this term from the remainder of our analysis.

Solving Eq. (15) for ln (g_{max}) , dropping ε , and exponentiating gives:

$$g_{\max} = g e^{\beta_w w} \tag{16}$$

Eq. (16) is biomass production in the absence of

leafy spurge. Subtracting associated species biomass production in the presence of leafy spurge (g) gives our leafy spurge impact model:

$$I = g e^{\beta_w w} - g \tag{17}$$

We define leafy spurge impact (*I*) on associated species biomass production as associated species biomass with leafy spurge absent $(ge^{\beta_w w})$ minus associated species biomass with leafy spurge present (g).

The plant biomass model

Averaged over the 19 sites in our plant biomass dataset, grasses produced the most biomass (66%) followed by leafy spurge (33%) and other forbs and shrubs (7%). Because forb and shrub biomasses were low, we combined these plant groups with grasses for analysis. In a second analysis we omitted forbs and shrubs from the dataset instead of combining these plant groups with grasses. Results from this second analysis were extremely similar to the results we obtained by lumping forbs and shrubs with grasses. Thus we do not present results from the analysis with forbs and shrubs omitted.

It was necessary to transform the biomass data to meet normality assumptions. We used a square root transformation because it often works well for plant abundance data (Kuehl 1994). To evaluate the reasonableness of the transformation, and our plant biomass model in general, we simulated seven datasets. Simulated datasets were compared to the raw data (Fig. 3). Simulated datasets tended to contain small numbers of values somewhat larger than the largest values in the raw data. Other than this minor disparity, we detected no systematic differences between simulated and actual data. Therefore, we concluded that the model reasonably depicts plant biomass means, variances, and covariances.

The biomass model was used to estimate plant abundance parameters for each site in the dataset as well as the entire 17-state region (Table 1). Inspecting these parameter estimates yields insight into model performance. Model parameters that are means (μ_w , μ_g , θ_w , θ_g) are presented in Fig. 3 Raw data (a) describing leafy spurge and grass biomass production at 13 sites distributed throughout the western U.S., and draws (b) from the posterior predictive distribution of new data from these same sites



Leafy Spurge Biomass (g m⁻²)

back-transformed units (g m⁻²), while variances and covariances remain untransformed ($\sqrt{\text{g m}^{-2}}$) (Table 1). Site means are estimated as covariance matrix-weighted averages of within-site sample means (\bar{y}_j) and the overall mean (μ) (see Eq. (4)). The between-site covariance matrix (Λ) had considerably larger parameter estimates than the within-site covariance matrix (Σ) (Table 1). As a result of between-site variation being greater than within-site variation, posterior medians for particular sites resemble the corresponding sample means, especially for sites with large sample size (Table 1). If Σ parameters were greater-valued,

posterior medians would be more appreciably pulled toward the overall mean.

The between-site covariance τ_{wg} is positive (Table 1), suggesting that both leafy spurge and its inter-specific competitors respond positively to the same environmental factors (e.g. soil depth, soil water, nitrogen). Within-site covariance σ_{wg} is slightly negative. This suggests that, at individual sites, inter-specific competition is intense enough to override the positive covariance. Similarly, Hagar and Vinebrooke (2004) found a negative relationship between weed and associated species biomass when they studied the invasive weed

T uti utili	I ocation county state	Sample size	Available data	Sample mean	Ollanti	PS.			
		- - -		-	2.5%	25%	Median	75%	97.5%
0. 					6.5	7.5	8.1	8.7	10.1
σ _{wg}					-2.7	-2.0	-1.6	-1.3	-0.6
σ_{ρ}^2					4.6	5.2	5.6	6.1	7.1
1 2 12					6.8	10.8	14.0	18.5	32.9
Twg					1.9	5.5	8.0	11.3	22.2
25					6.6	10.3	13.3	17.5	31.5
μ					50.1	69.1	79.6	90.9	116.9
μ_g					64.5	85.8	97.0	108.9	135.6
Gylling and Arnold $(1985)\theta_w$	Sanborn, SD	8	mean	114.0	68.1	95.9	113.4	133.8	190.4
Gylling and Arnold $(1985)\theta_g$	Sanborn, SD	8	mean	140.0	89.7	117.7	133.4	149.4	180.9
Hein and Miller (1991, 1992) θ_{w}	Fergus, MT	32	mean	85.5	61.3	75.3	83.1	91.4	109.6
Hein and Miller (1991, 1992) θ_g	Fergus, MT	32	mean	57.8	41.3	53.8	59.5	65.3	76.5
Lym and Messersmith $(1994)\tilde{\theta_w}$	Barnes, ND	8	raw data	14.8	4.2	10.7	15.3	20.8	33.9
Lym and Messersmith (1994) θ_g	Barnes, ND	8	raw data	14.8	5.7	11.8	15.8	20.4	30.8
Lym and Messersmith (1994) $\ddot{\theta}_{w}$	Cass, ND	8	raw data	5.3	0.4	3.6	6.5	10.2	19.5
Lym and Messersmith (1994) θ_g	Cass, ND	8	raw data	15.1	5.7	11.7	15.7	20.5	31.0
Lym $(2000)\theta_w$	Richland, ND	4	raw data	221.3	122.4	161.7	184.3	208.6	260.1
$Lym (2000) \theta_g$	Richland, ND	4	raw data	187.2	107.5	138.0	155.8	174.7	213.5
$Lym (2000) \theta_w$	Ransom, ND	4	raw data	216.9	133.5	174.3	197.8	222.8	275.7
$Lym (2000) \theta_g$	Ransom, ND	4	raw data	215.1	149.7	185.9	206.9	228.7	273.5
$Lym (2000) \theta_w$	Stutsman, ND	4	raw data	218.7	130.0	170.3	193.6	218.7	271.5
$Lym (2000) \theta_g$	Stutsman, ND	4	raw data	233.7	159.7	198.3	219.6	242.1	288.6
Maxwell $(1984)\theta_w$	Fergus, MT	30	raw data	52.3	33.6	41.7	46.3	51.2	61.3
Maxwell (1984) θ_g	Fergus, MT	30	raw data	153.6	129.0	142.1	149.0	156.2	170.3
Prosser and Sedivec (unpublished) θ_w	Carter, MT	24	raw data	52.9	36.5	45.8	51.2	56.7	68.5
Prosser and Sedivec (unpublished) θ_g	Carter, MT	24	raw data	173.0	140.5	155.6	163.9	172.2	188.6
Rees (unpublished) θ_w	Custer, ID	7	raw data	69.7	28.1	43.4	52.7	63.0	85.0
Rees (unpublished) θ_g	Custer, ID	7	raw data	37.8	20.1	32.3	39.1	46.6	62.7
Rees (unpublished) θ_w	Ransom, ND	8	raw data	105.0	65.1	86.5	98.7	111.6	138.7
Rees (unpublished) θ_g	Ransom, ND	8	raw data	93.3	63.2	80.5	90.5	101.0	122.3
Rees $(unpublished)\theta_w$	Valley, MT	6	raw data	83.7	43.9	60.8	70.5	80.9	103.1
Rees (unpublished) θ_g	Valley, MT	6	raw data	93.1	61.6	78.1	87.2	97.0	117.3
Rees (unpublished) θ_{w}	Brown, NE	4	raw data	25.3	8.4	20.7	29.3	39.4	63.0
Rees (unpublished) θ_g	Brown, NE	0	none ^a		15.8	39.8	55.3	73.5	118.0
Rees (unpublished) θ_{w}	Rio Blanco, CO	6	raw data	117.6	67.3	87.6	99.3	111.8	137.7
Rees (unpublished) θ_g	Rio Blanco, CO	6	raw data	58.9	35.7	48.6	56.1	64.1	80.6
Rees $(unpublished)\theta_w$	Fergus, MT	5	raw data	128.8	68.1	95.1	110.9	128.4	165.4
Rees (unpublished) θ_g	Fergus, MT	5	raw data	52.9	30.7	46.7	56.4	67.0	89.6
Samuel $(2003)\theta_w$	Golden Valley, ND	60	raw data	31.2	18.0	22.2	24.6	27.1	32.3

Table 1 continued									
Parameter	Location county, state	Sample size	Available data	Sample mean	Quantil	es			
					2.5%	25%	Median	75%	97.5%
Samuel (2003) θ_{σ}	Golden Valley, ND	60	raw data	160.1	136.8	146.2	151.3	156.3	166.4
Scholes $(1996)\theta_w^3$	Marshall, SD	6	mean	130.5	74.6	106.6	126.7	149.6	197.5
Scholes $(1996)\theta_{g}$	Marshall, SD	6	mean	113.0	71.2	100.2	117.9	137.1	179.8
Vore $(1984)\theta_w$	Crook, WY	0	none		49.3	72.0	85.2	9.66	128.7
Vore $(1984)\theta_g$	Crook, WY	16	mean	93.7	70.4	86.4	96.0	106.2	127.3
Vore $(1984)\theta_w$	Johnson, WY	0	none		56.4	94.9	118.9	144.2	294.6
Vore $(1984)\theta_g$	Johnson, WY	5	mean	172.8	102.7	141.2	163.1	186.8	234.6
^a A multiple imputation model estin	mated quantile values when r	no data were avi	ailable						

Lythrum salicaria L. at several sites within a twocounty region.

Site-specific estimates of plant densities and leafy spurge impact

We use data from Fargo, ND to demonstrate how the impact and biomass models can be used in concert to estimate local leafy spurge impacts (Lym and Tober 1997). The Fargo data were omitted from our overall analysis because the site was tilled. If it is known that leafy spurge occupies the Fargo site, but no plant biomass data are available, n_i is set at zero in Eqs. (4) and (5). In this way, plant densities at Fargo are estimated from the 19 measured sites. Because variation between the 19 sites was extensive (i.e. μ was imprecisely estimated and Λ parameters are large), the 19 sites provide limited information about the mean of any one unmeasured site. Consequently, biomass estimates for the unmeasured site are quite imprecise (Table 2, rows 1 and 5). In exploring effects of adding to the dataset only leafy spurge (w) or associated species (g) samples, our imputation routine was used to fill in the missing data values. When estimating leafy spurge biomass, 4 on-site leafy spurge samples reduced the uncertainty (i.e. shrank quantile interval width), as did 4 associates species samples, but if leafy spurge samples were included, associated species samples did not further reduce the uncertainty (Table 2, rows that begin with w). Analogous results were obtained for associated species biomass (Table 2, rows beginning with g).

When estimating leafy spurge impact at Fargo, 4 on-site leafy spurge samples reduced uncertainty about I, as did 4 associated species samples (Table 2). When leafy spurge samples were used in estimating impact, associated species samples did not further reduce the uncertainty.

Estimates of leafy spurge impact on a 17-state region

In this section, we consider the monetary forage value of plants displaced by leafy spurge in a large region. Working with monetary forage values enabled us to estimate weed impacts on cattle

Variable	On-site data	Sample mean	Quantile	s			
			2.5%	25%	Median	75%	97.5%
g	none	95.6	19.4	72.3	100.2	132.3	210.3
g	w samples	95.6	12.8	41.3	59.6	82.0	128.8
g	g samples	95.6	58.3	82.4	96.2	110.9	142.2
g	w and gsamples	95.6	56.8	81.8	93.8	108.5	140.2
w	none	71.0	8.4	47.5	79.7	118.8	213.2
w	w samples	71.0	31.9	53.9	67.1	81.5	114.5
w	g samples	71.0	31.0	60.3	81.0	105.8	161.3
w	w and gsamples	71.0	35.9	57.4	70.6	85.2	117.3
Ι	none		10.1	33.3	54.9	92.4	231.4
Ι	w samples		9.5	21.6	31.2	45.0	90.3
Ι	g samples		19.7	37.4	53.1	74.8	140.9
Ι	w and g samples		20.3	34.6	47.7	58.5	102.7

Table 2 Quantiles characterizing annual leafy spurge w and associated species g biomass production (g m⁻²) and leafy spurge impact on associated species biomass production $I(g m^{-2})$ at site near Fargo, ND

carrying capacity and grazing land values (Table 3). Cattle are an effective conversion factor for expressing leafy spurge impacts because these animals typically do not consume the weed (Lym and Kirby 1987), and cattle are the region's predominate class of livestock. Sheep are a distant second to cattle with cattle outnumbering sheep about 12–1 (USDA 2004c, b). Basing our analysis on sheep would drastically reduce the impact estimates, because sheep can consume considerable quantities of leafy spurge without experiencing detrimental health effects (Landgraf et al. 1984; Lym et al. 1997).

We used the following information to derive the regional impact estimates of Table 3. An animal unit month (AUM) is the amount of forage needed to sustain a cow and a calf for one month. One AUM is defined as 359 Kg of air dry forage, and the estimated value of one privately owned AUM is \$13.10 (USDA 2004a). On grazing lands in the western U.S., the "take half, leave half" guideline is widely used to limit overgrazing. Managers that employ this guideline allow livestock to remove approximately 50% of the net annual primary production. Therefore, in estimating weed impacts on cattle carrying capacity (Table 3, row 3) and grazing land value (Table 3, row 2), we assumed cattle would be allowed to utilize 50% of the forage increase that results from leafy spurge removal. Finally, Duncan et al. (2004) estimated that leafy spurge infests an area 1,487,237 ha in size in the region.

Discussion

An earlier analysis by Leitch et al. (1996) estimated that leafy spurge reduces cattle carrying capacity by 90,000 cows in the 4-state region of North Dakota, South Dakota, Montana, and Wyoming. This estimate is based on a 657,000ha infestation size. If this estimate is scaled to the infestation size we used, the carrying capacity reduction is estimated to be 204,000 cows.

 Table 3 Quantiles characterizing annual leafy spurge impacts on forage production, cattle carrying capacity, and grazing land value within a 17-state region

Variable	Quantile	5			
	2.5%	25%	Median	75%	97.5%
Impact on forage production (millions of Kg) Impact on grazing land value (millions of dollars) Impact on carrying capacity (thousands of cattle)	446 8 51	678 12 79	862 16 100	1,121 21 130	1,942 36 225

Whereas this estimate does reside within our 95% credibility interval (51,000–225,000 cows) it is more than double our median estimate (100,000 cows). Lietch et al. (1996) caution that, "Relationships and models used in [their] study lack direct empirical foundations." Our leafy spurge impact estimate is likely more reliable than the older estimate because it is based on empirically derived models that represent key sources of uncertainty.

Whereas our analysis accounted for important sources of error that will naturally hinder any attempt to quantify invasive species impacts, we did ignore uncertainty about some parameters. Most importantly, it is highly unlikely that leafy spurge infests exactly 1,487,237 ha (Duncan et al. 2004).

While our regional leafy spurge impact estimates are informative, considerable uncertainty remains (Table 3). What information is needed to more precisely estimate the costs of this invasive species? When simulating regional impacts, the only parameters that caused uncertainty were β_w and the overall site mean (μ) and variance (Λ); all other parameters were averaged over in simulating the expected value of weed impact $(E(I_i))$. The β_w parameter was estimated very precisely. In fact, when we fixed β_w at the posterior distribution mode and reran the analysis, quantile interval widths didn't shrink appreciably. Therefore, uncertainty about β_w plays a minor role, and more precisely estimating regional leafy spurge impacts will require more precisely estimating μ and Λ . The only readily apparent way to reduce uncertainty about these parameters is to collect additional biomass data from randomly selected, leafy spurge-infested sites.

The hierarchical model was very useful for quantifying regional plant abundances and weed impacts. To see why this model is likely superior to other potential models, it is helpful to consider an alternative approach for estimating regional weed impacts. The alternative approach would construct 19 nonhierarchical models; one for each site in the meta-dataset. Then, regional leafy spurge impacts would be estimated by averaging over simulated quadrat-level values for just these 19 sites. An important limitation of this nonhierarchical approach becomes apparent by conceptualizing data from 19 newly measured sites. If the nonhierarchical analysis were repeated on data from 19 newly measured sites (i.e. a new sample of sites), the new results would certainly differ somewhat from the original results. Nonhierarchical models would ignore this sample-to-sample variation. In contrast to nonhierarchical models, the hierarchical model employs a probability distribution of site means (i.e. Eq. (3)) to account for sample-to-sample variation (i.e. variation among samples of sites).

The hierarchical model also proved advantageous for estimating local plant biomass parameters and weed impacts. An alternative approach to estimating local weed impacts would forgo the precision weighting (Eq. (4)) and use exclusively site j data to estimate site j parameters. At a glance, this seems rational because it eliminates the chance of off-site data distorting site-specific parameter estimates. The problem with such an approach is that, presumably, resource managers will not take the time to gather large numbers of on-site samples. And, unless off-site data are factored into the analysis, a small number of on-site samples will be insufficient for estimating the necessary on-site parameters (i.e. $\theta_w, \theta_g, \sigma_w, \sigma_g, \sigma_{wg}$). Only by borrowing strength from off-site data were we able to reasonably estimate the necessary site-specific parameters.

Without information on invasive weed impacts, costs and benefits of weed management actions cannot be compared. Over the last few decades, considerable data have amassed on some of the more notorious invasive weeds. Many of these data describe weed abundances, and with some weeds, a few of the data describe impact per unit weed abundance. Collectively, these data can tell us something of the toll invasive weeds exact across various spatial scales.

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