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Predicting foundation bunchgrass species abundances: model-assisted decision-making in protected-area sagebrush steppe

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Abstract. Foundation species are structurally dominant members of ecological communities that can stabilize ecological processes and influence resilience to disturbance and resistance to invasion. Being common, they are often overlooked for conservation but are increasingly threatened from land use change, biological invasions, and over-exploitation. The pattern of foundation species abundances over space and time may be used to guide decision-making, particularly in protected areas for which they are iconic. We used ordinal logistic regression to identify the important environmental influences on the abundance patterns of bluebunch wheatgrass (*Pseudoroegneria spicata*), Thurber's needlegrass (*Achnatherum thurberianum*), and Sandberg bluegrass (*Poa secunda*) in protected-area sagebrush steppe. We then predicted bunchgrass abundances along gradients of topography, disturbance, and invasive annual grass abundance. We used model predictions to prioritize the landscape for implementation of a management and restoration decision-support tool. Models were fit to categorical estimates of grass cover obtained from an extensive ground-based monitoring dataset. We found that remnant stands of abundant wheatgrass and bluegrass were associated with steep north-facing slopes in higher and more remote portions of the landscape outside of recently burned areas where invasive annual grasses were less abundant. These areas represented only 25% of the landscape and were prioritized for protection efforts. Needlegrass was associated with south-facing slopes, but in low abundance and in association with invasive cheatgrass (*Bromus tectorum*). Abundances of all three species were strongly negatively correlated with occurrence of another invasive annual grass, medusahead (*Taeniatherum caput-medusae*). The rarity of priority bunchgrass stands underscored the extent of degradation and the need for prioritization. We found no evidence that insularity reduced invasibility; annual grass invasion represents a serious threat to protected-area bunchgrass communities. Our study area was entirely within the Wyoming big sagebrush ecological zone, understood to have inherently low resilience to disturbance and resistance to weed invasion. However, our study revealed important variation in abundance of the foundation species associated with resilience and resistance along the topographic-soil moisture gradient within this zone, providing an important foothold for conservation decision-making in these steppe ecosystems. We found the foundation species focus a parsimonious strategy linking monitoring to decision-making via biogeographic modeling.

Key words: *Achnatherum thurberianum*; *Bromus tectorum*; decision-making; invasive plants; monitoring; national parks; *Poa secunda*; predictive modeling; proportional odds logistic regression; *Pseudoroegneria spicata*; sagebrush; *Taeniatherum caput-medusae*.

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Introduction

Foundation species are increasingly recognized as being of special importance to the functioning of ecosystems (Ellison et al. 2005, Gaston 2011). Foundation species are those structurally dominant members of ecological communities that stabilize and mediate ecological processes (Dayton 1972, Ellison et al. 2005). They build habitat and facilitate community assembly, provide critical ecosystem services and, in some systems, are thought to confer ecological resilience to disturbances like wildfire and resistance to biological invasions (Prevey et al. 2010, Angelini et al. 2011). Being common, foundation species are often overlooked as being at conservation risk but, as with other less prominent members of ecological communities, they may also be threatened from land use change, biological invasions, and over-exploitation (Gaston and Fuller 2007).

Given their importance to ecosystems, foundation species may be suitable foci around which to organize ecosystem restoration and management plans. In particular, the facilitative role that foundation species play in community assembly (Gaston and Fuller 2007) has motivated their use in ecosystem restoration (Byers et al. 2006, Gomez-Aparicio 2009, Angelini et al. 2011). The so-called "neighbor effects" documented in many plant communities dominated by foundation species (see review by Gomez-Aparicio 2009) have led to a paradigm shift in terrestrial restoration in which emphasis is increasingly on maintaining existing native vegetation or replanting desired foundation species for facilitation rather than on removal of competitive invaders (Gomez-Aparicio 2009). Also, because foundation species are structurally dominant and conspicuous, they typically are iconic to the landscapes in which they are found. This provides additional impetus and opportunity for conservation, particularly in parks and protected areas where viewsheds and visitor experiences are so dependent on healthy populations of foundation species. In protected area settings, these other values are often important to the management decision-making process, and so a focus on iconic foundation species may help align protected area management and restoration goals to the broader theme of biodiversity conservation.

In the sagebrush biome of western North America, widespread declines in the abundances of foundation shrubs, particularly big sagebrush (*Artemisia tridentata*), and perennial bunchgrasses such as bluebunch wheatgrass (*Pseudoroegneria spicata*) are occurring in the wake of over-exploitation, altered fire regimes, and associated invasions by Eurasian annual grasses such as cheatgrass (*Bromus tectorum*) (Davies et al. 2011). These declines have cascading ecological effects, characterized by positive feedback loops between community invaders and fire, with irreversible changes in ecosystem structure and function (D'Antonio and Vitousek 1992, Brooks et al. 2004, Balch et al. 2013). The abundances of these steppe foundation species correlate strongly with resilience to fire and resistance to invasion (Chambers et al. 2007, Brooks and Chambers 2011, Condon et al. 2011, Davies et al. 2011, Davies et al. 2012, Reisner et al. 2013). The uptake of soil nitrogen and water by big sagebrush and by bunchgrasses has been shown through removal experiments to reduce community invasibility (Chambers et al. 2007, James et al. 2008, Mata-Gonzalez et al. 2008, Prevey et al. 2010). Additionally, the severity of infestations of cheatgrass and another invasive annual grass, medusahead (*Taeniatherum caput-medusae*), are inversely correlated with the abundances of pre-existing native perennial bunchgrasses (Davies 2008, Condon et al. 2011, Davies et al. 2012, Reisner et al. 2013). Tall tussock-type bunchgrasses like bluebunch wheatgrass seem to effectively reduce dispersal of medusahead seeds, and therefore robust stands of these bunchgrasses may contain incipient infestations (Davies 2008). Collectively, the aforementioned studies suggest that abundances of large stature bunchgrasses and bluebunch wheatgrass, in particular, can be used as a proxy indication of potential resilience to disturbance and resistance to invasion (e.g., Miller et al. 2013).

In general, because of the non-linear threshold dynamics and positive feedback loops associated with degraded sagebrush steppe (Suding et al. 2004, Bestelmeyer 2006), restoration of heavily degraded sites is expensive and rarely successful (Davies et al. 2011, James et al. 2013). This is particularly so when emphasis is on eradication of heavy infestations (Sheley et al. 2006). Accordingly, recent recommendations are to prioritize remnant intact steppe for protective efforts and, only where success is likely, should investments in restoration be made (Chambers and Wisdom 2009, Davies et al. 2011, Davies and Sheley 2011, Chambers et al. 2014). This is consistent with a broader paradigm shift in restoration ecology towards "positive" interventions encouraging neighbor effects and facilitative interactions among desired species (Gomez-Aparicio 2009). In order to operationalize these recommendations, however, some means of predicting and mapping conditions on the ground that meet the criteria of prioritization is needed. A focus on foundation species may facilitate such an effort, and lead to more effective management and restoration decisions.

Drawing on an extensive dataset from a rapid-assessment monitoring protocol (Yeo et al. 2009), we used ordinal logistic regression to identify the important environmental influences on the abundances of three foundational bunchgrass species and to predict and map the abundances of these species across the John Day Fossil Beds National Monument, a rugged 5800-ha unit of the US National Park Service in north central Oregon. Using predictors developed in a GIS, we constructed models to reflect hypotheses about bunchgrass community resilience to disturbance (particularly fire) and resistance to annual grass invasion. We used our maps to produce a prioritization of the Monument landscape for strategic implementation of a weed management and restoration decision-support tool. The tool, Ecologically-Based Invasive Plant Management (EBIPM; James et al. 2010, Sheley et al. 2010), is based on successional theory (Kreuger-Mangold et al. 2006, Sheley et al. 2006) and describes a series of steps, guided by ecological principles, which lead to specific choices about tools and strategies. However, it provides limited guidance on how to prioritize restoration and management activities across large landscapes. Qualitative rangeland health assessments (Pyke et al. 2002, Pellant et al. 2005) are being integrated into EBIPM to inform managers about which processes that drive plant community change are in need of repair (Sheley et al. 2011). But these assessments do not provide explicit direction on exactly *where* action is most needed or likely to be successful, leading managers to make ad hoc prioritization decisions.

As is the case with many protected-areas in western North America, restoration across such large landscapes is prohibitively expensive and tools such as rangeland drills are of limited use. Much of the Monument is infested by cheatgrass and medusahead as well as several species of invasive forbs, but remnant stands of native bunchgrass steppe can be found throughout and are an important part of both the historic character and ecological integrity of the Monument. Notably, a very small proportion ($<5\%$) of the North American sagebrush steppe biome is represented in protected areas (Caicco et al. 1995, Noss et al. 1995, Storms et al. 1998), underscoring the importance of demonstrating effective conservation decision-making that is transferable to other protected areas in the region.

Methods

Area of study

The John Day Fossil Beds National Monument is located in north-central Oregon, USA (Fig. 1), on the southern edge of the Columbia Plateau. The region is topographically heterogeneous, dominated by deeply eroded canyons of the John Day River and tributaries. The climate is semi-arid, with annual precipitation averaging $\sim$27 cm, although precipitation during the study period was consistently below the 30-year average. Snowpack is ephemeral and most precipitation falls as rainfall during October to June. The Monument itself consists of 3 disjunct management units: Clarno, Painted Hills, and Sheep Rock (Fig. 1). Sheep Rock also includes the disjunct Foree subunit that we treated as a distinct unit for purposes of our study. All units of the Monument were protected from intensive livestock grazing after establishment of the Monument in the late 1970s. In Clarno, a portion

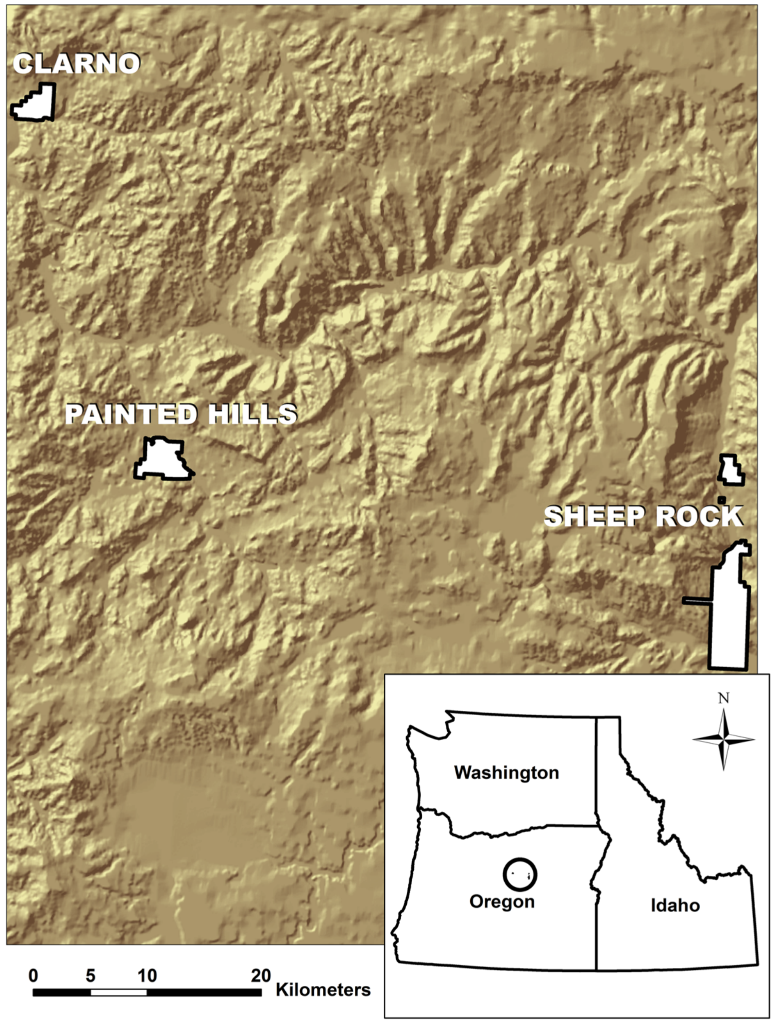

Fig. 1. A map of the John Day Fossil Beds National Monument study area, located in north-central Oregon, USA. The Monument consists of three widely separated units: Clarno, Painted Hills, and Sheep Rock. The Foree subunit is the northernmost portion of Sheep Rock.

of the unit remained in private ownership and was grazed until 2001.

The elevation range of the monument is from 421–1255 m asl. The US Department of Agriculture Natural Resources Conservation Service (NRCS) classified Monument soils as droughty, 9–12 inch ($\sim$22–30 cm) precipitation zone volcanic ash-derived clays and clay-loams, with aridic soil moisture and mesic temperature regimes (NRCS 2013). These abiotic conditions support a Wyoming big sagebrush ecosystem in the Monument (Erixson et al. 2011), a type of cold desert shrubland with a characteristic overstory of Wyoming big sagebrush (*A. t. wyomingensis*), a characteristic bunchgrass understory, and relatively low forb cover. This ecosystem type generally exhibits low resilience to disturbances like grazing and fire, and low resistance to invasion from Eurasian annual grasses (Chambers et al. 2014). Vegetation in the Monument during the study was dominated by bluebunch wheatgrass, the primary foundation species in the region, and other native perennial bunchgrasses (primarily Sandberg bluegrass [*Poa secunda*] and Thurber's needlegrass [*Achnatherum thurberiana*]), many annual grasses of Eurasian origin including cheatgrass and medusahead, and native shrubs including broom snakeweed

(*Gutierrezia sarothrae*) and Wyoming and basin big sagebrush (*A. t. tridentata*) (Yeo and Rodhouse 2012). Big sagebrush is not as extensive and dominant in the Monument and surrounding region as it is south of the Columbia Plateau in the Great Basin. Other important bunchgrass species common in the region, including Idaho fescue (*Festuca idahoensis*) and bottlebrush squirreltail (*Elymus elymoides*) associated with cooler and wetter mountain big sagebrush (*A. t. vaseyana*) habitats, and indian ricegrass (*Achnatherum hymenoides*) and sand dropseed (*Sporobolus cryptandrus*) associated with hotter and drier habitats, are rare in the Monument (Yeo and Rodhouse 2012). The NRCS reference site descriptions for the upland ecological sites types (sensu Society for Range Management 1995) that occur in the Monument show bluebunch wheatgrass, or in a few xeric site types, Thurber's needlegrass, yielding more than twice the amount of biomass than any other associated species, including big sagebrush (NRCS 2013). Sandberg bluegrass is a consistently present but much smaller and less productive species in all ecological site types, but it is known to be highly resilient to drought, grazing, and trampling and therefore of interest in the context of the current study.

Data collection

Plot-based categorical estimates of foliar cover, by species, were obtained through monitoring as part of the National Park Service Vital Signs Monitoring Program (Fancy et al. 2009) during June 2009 and June 2011 (Rodhouse 2010, Yeo and Rodhouse 2012). Following the rapid-assessment methods developed by Yeo et al. (2009), plots were 1-m^2 quadrats placed on the ground at UTM coordinates generated with a spatially-balanced Generalized Random Tessellation Stratified (GRTS) random sampling algorithm (Stevens and Olsen 2004). This sampling design provided robust statistical scope of inference across defined sampling frames that covered >60% of the uplands of the Monument, excluding unsafe cliffs and barren ashbeds (Yeo et al. 2009). Plant cover, by species, was then estimated using ocular estimation and recorded in the following Daubenmire (1959) cover classes: 0%, >0–5%, >5–25%, >25–50%, >50–75%, >75–95%, and >95%. A total of 1169 plot observations of grass cover were obtained from these two surveys and utilized in modeling.

Data analysis

We used proportional-odds logistic regression (i.e., ordinal regression) (Agresti 2010) to predict the abundances, in cover classes, of bluebunch wheatgrass, Thurber's needlegrass, and Sandberg bluegrass across the four units of the Monument along gradients of topography, disturbance, cheatgrass abundance, and medusahead occurrence. Medusahead is still relatively rare in some portions of the landscape, yielding sparse data in the upper cover classes, so we chose to collapse the ordinal cover class observations for this species into a binary presence-absence classification for purposes of modeling. We randomly allocated 75% of the dataset (877 plot observations) for use as a training dataset in model fitting and estimating predictor coefficients. We used the remaining 25% holdout (292 plot observations) as a validation dataset to evaluate model predictive performance. In this way, observations were only used to either fit or test models, but were never used simultaneously for both purposes, which would lead to overestimated measures of predictive performance (Shmueli 2010).

Predictor variables

We assembled a suite of predictor variables for regression along gradients that was chosen to reflect working hypotheses about the most important influences on the region's bunchgrass steppe ecological resilience to disturbance and resistance to weed invasion. These predictors were constructed as raster datasets with 10-m resolution in a GIS. Plot locations were overlaid on raster layers and assigned values associated with underlying 10-m pixels. We focused on topographic proxies for effective soil moisture because sagebrush steppe communities on wetter, cooler sites have been found to be more resistant to cheatgrass invasion. This is thought to reflect differences in resource availability, productivity, and timing of resource utilization between invasive annuals and native perennial grasses along topographic-soil moisture gradients (i.e., the fluctuating resource hypothesis) (Chambers et al. 2007, Condon et al. 2011, Davies et al. 2012, Reisner et al. 2013, Chambers et al.

2014). Given the ruggedness of the Monument landscape we expected topography to exert strong influence in models. We used a 10-m digital elevation model (DEM) for the Monument provided by the US Geological Survey National Elevation Dataset to provide a measure of elevation. We used the DEM to calculate sin(slope) $\times$ cos(aspect), which we refer to as topography, that provided an integrated measure of insolation or "northness". This variable ranges from -1 to 1, with steeper south-facing slopes being close to -1, and steep north-facing slopes being close to 1. We also estimated flow accumulation with the DEM and a GIS tool to provide a measure of drainage and elevated soil moisture in which raster pixels were assigned values based on the sum of upstream pixels. Additionally, we included crop-year precipitation, the sum total of precipitation from the months of September to May prior to the survey (e.g., beginning in September 2008 for 2009 plot records). Monthly precipitation estimates across the entire study area were provided by the PRISM Climate Group's 800-m resolution data products (Daly et al. 2008). These datasets were resampled to match the 10 m resolution of the DEM-derived raster layers.

Because human and livestock travel corridors are known to serve as vectors of annual grass invasion and facilitate increased invasive weed propagule pressure (Gelbard and Belnap 2003, Davies et al. 2013), we calculated the distance of each 10-m raster pixel to the nearest road and Monument boundary.

Fire has emerged as a major influence on steppe invasibility (Miller et al. 2013). Whereas intact bunchgrass stands may be relatively resilient to fires, ruderal annual grasses often respond vigorously to fire because of increased resource availability and reduced uptake of resources from slowly recovering native species (Miller et al. 2013). This is particularly apparent in Wyoming big sagebrush ecosystems (Chambers et al. 2014). Although details of the Monument's fire history are incomplete, fire perimeters are available for all wildfires that occurred in Clarno and for all prescribed fires that occurred in the other units beginning in 1994. No prescribed fires occurred in Clarno, and no wildfires occurred in the other units over the same time period. We constructed a 10-m raster in which pixels within known fire perimeters were assigned a value of 1 and pixels outside of perimeters were assigned a value of 0 in order to approximate this disturbance history.

Finally, we included the observed abundances (cover classes) of cheatgrass and the observed occurrences (presence-absence) of medusahead as additional predictors. We developed predictive raster surfaces for cheatgrass cover class and medusahead occurrence across the entire Monument by fitting a separate ordinal regression model to the cheatgrass cover class data and by fitting the more familiar logistic regression model to the medusahead occurrence data.

Model fitting

Ordinal regression provides a parsimonious method for obtaining estimates of the cumulative probabilities of each species' cover in each of the seven ordered cover class categories for each of the 877 plot observations used in the training dataset. Formally, for a multinomial ordinal response $\boldsymbol{y}_i = (y_{i1}, y_{i2}, \ldots, y_{i,J})$, with $j = 1, \ldots, J$ categories, observations are coded as $y_{ij} = 1$ when in cover class j, and $y_{ij} = 0$ otherwise in each plot i from 1, ..., n. We model the cumulative probabilities using a logit link function $\text{logit}(P[Y_i \leq j|\text{x}]) = \alpha_j - \boldsymbol{\beta}'\mathbf{x_i}$, $j = 1, \ldots, J-1$, for the $\mathbf{x}$ predictors and associated $\boldsymbol{\beta}$ parameters. The intercepts α_j are the "cutpoints" of the latent (unobserved) continuous cover scale on the logistic distribution (Agresti 2010, Irvine and Rodhouse 2010). Cumulative probabilities sum to 1 and are estimated by $P(Y_i \leq j) = \exp(\alpha_j - \boldsymbol{\beta}'\mathbf{x})/1 + \exp(\alpha_j - \boldsymbol{\beta}'\mathbf{x})$; the interpretation of regression coefficients are made in terms of an increase in the probability of being in a higher cover class for each 1-unit increase in predictor values. We accepted the proportionality assumption inherent in this model structure in which the estimated effect size of each predictor is the same for each cover class (Agresti 2010). Cover class predictions to unobserved portions of the monument were assigned to the category with the highest predicted probability (i.e., the fitted values). We also predicted the cumulative probabilities for bunchgrass cover >25% (i.e., $1 - P[Y_i \leq 3]$).

We developed separate models for foundation bunchgrass species and for invasive annual grass species. We used the following vector of covariates to create predictive surfaces for cheatgrass abundance and medusahead occurrence: $\boldsymbol{\beta}$ = [park unit, topography, topography^2, elevation, distance to park unit boundary, distance to nearest road, crop year precipitation, fire perimeter, fire perimeter $\times$ topography, flow accumulation]. Park unit refers to the inclusion of indicator variables for each unit, which allowed for predicted probabilities to be adjusted for each unit as an additional fixed effect (i.e., separate intercepts). For bunchgrass models we used the same vector of predictor variables as used in the annual grass models, but also included inputs from the plot-based cheatgrass cover class and medusahead occurrence observations. Park unit and fire perimeter were constructed as indicator variables and all other variables were standardized so that model intercepts could be interpreted as mean probabilities at mean input values, and regression coefficients interpreted in terms of a 1-SD change in those inputs. A quadratic term was included for topography because we anticipated an increasing (non-linear) influence of topography on occurrence and abundance patterns on steeper slopes. We also included an interaction term for topography and fire perimeter, anticipating that the influence of fire on abundance and occurrence patterns would vary along the topographic gradient.

Landscape prioritization

We prioritized the landscape for implementation of the EBIPM decision-support tool. We were particularly interested in areas predicted to have high foundation species abundance, following recommendations by Sheley et al. (2006), Chambers et al. (2014) and others (Chambers and Wisdom 2009, Davies et al. 2011, Davies and Sheley 2011), in which the emphasis for Wyoming big sagebrush ecosystems is increasingly on protection of intact stands of native vegetation rather than on expensive and often unsuccessful active restoration of heavily degraded sites. Our primary focus was on bluebunch wheatgrass because of its ecological dominance and iconic status in the Monument. Bluebunch wheatgrass is widely used in sagebrush steppe restoration (St. Clair et al. 2013) and is widely understood to confer ecological resilience and invasion resistance to steppe communities (Miller et al. 2013). Also, the Monument provides an important historic interpretive theme to visitors involving settlement-era (circa 1890s) ranching culture, during which time it is thought that robust stands of bluebunch wheatgrass were the dominant feature of the landscape (Beckham and Lentz 2000). This iconic role provided a natural bridge between contemporary natural resource management and visitor experience in the Monument that increased the likelihood that our findings and recommendations could be incorporated into Monument management planning and successfully guide implementation of EBIPM. Areas predicted to currently support $\geq$25% cover of bluebunch wheatgrass were classified as priority 1 for protective efforts. Areas with $\geq$5% to 25% were ranked as priority 2 for control efforts, and areas with $<$5% cover were classified as priority 3, where restoration of focal areas such as accessible oldfields visible to Monument visitors might be pursued.

Model evaluation

For each model we estimated Nagelkerke's R^2 to provide a measure of variance explained by the model fitted with training data. We evaluated the predictive performance of models by comparing model predictions with field observations for the 292 plots in the validation holdout dataset. We estimated the area under the curve (AUC) of the plot of true positive and false positive rates (the receiver operating characteristic). We further evaluated the success of the three prioritization classifications of the bluebunch wheatgrass model with estimates of AUC for each of the three classes. AUC is widely used to evaluate predictive models (Fielding and Bell 1997, Agresti 2010) and ranges from 0.5 to 1, with 0.5 indicating that model predictions were no better than random chance, and 1 indicating that the model predicted perfectly (no false positives and no false negatives). AUC $>$ 0.7 is generally regarded as indicating acceptable predictive performance (Fielding and Bell 1997). We also provided another measure of performance, Somers' *D*, a rank-based correlation coefficient measuring association between two variables (in this case, between observed and predicted classifications) that ranges from -1 to 1. Somers' *D* is a commonly reported measure for binary and ordinal predictive models that complements the information provided by AUC (Agresti 2010).

We used the *rms* package (Harrell 2013) in the

Table 1. Performance measures and parameter estimates and standard errors (in parentheses; asterisks indicate statistical significance at $\alpha = 0.05$) from ordinal regression models of cheatgrass (*Bromus tectorum*), bluebunch wheatgrass (*Pseudoroegneria spicata*), Thurber's needlegrass (*Achnatherum thurberianum*), and Sandberg bluegrass (*Poa secunda*) abundance, and a logistic regression model of medusahead (*Taeniatherum caput-medusae*), for the John Day Fossil Beds National Monument, Oregon, USA.

Metric	Cheatgrass	Medusahead	Bluebunch wheatgrass	Thurber's needlegrass	Sandberg bluegrass
Performance measures					
Nagelkerke's R^2	0.24	0.30	0.35	0.20	0.26
AUC	0.75	0.84	0.78	0.68	0.51
Parameter estimates (SE)					
Topography	−2.3 (0.7)*	0.6 (2.7)	3.2 (0.9)*	−3.0 (1.4)*	3.6 (0.9)*
Topography^2	−7.4 (1.7)*	−16.5 (4.4)*	9.8 (2.1)*	−1.7 (3.1)	−8.6 (2.4)*
Elevation	−0.2 (0.1)*	−0.2 (0.2)	1.0 (0.1)*	0.1 (0.2)	0.8 (0.1)*
Flow accumulation	0.0 (0.1)	−0.6 (0.5)	−0.2 (0.1)	0.1 (0.1)	0.0 (0.1)
Crop year precipitation	−0.6 (0.1)*	−0.1 (0.4)	−0.3 (0.2)*	0.0 (0.2)	−1.0 (0.1)*
Fire	0.5 (0.2)*	1.2 (0.4)*	−0.2 (0.2)	0.0 (0.3)	0.1 (0.2)
Fire × topography	1.1 (0.9)	−0.6 (2.7)	−0.2 (1.0)	0.2 (1.5)	0.3 (1.0)
Distance to boundary	0.1 (0.1)	0.0 (0.1)	0.3 (0.1)*	−0.1 (0.1)	0.1 (0.1)
Distance to road	0.0 (0.1)	0.4 (0.2)*	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)
Medusahead presence	NA	NA	−1.3 (0.3)*	−1.0 (0.3)*	−1.0 (0.2)*
Cheatgrass cover					
1–5%	NA	NA	0.02 (0.3)	0.1 (0.5)	0.4 (0.3)
5–25%	NA	NA	−0.1 (0.3)	0.5 (0.5)	0.0 (0.3)
25–50%	NA	NA	−0.5 (0.3)	0.8 (0.5)	−0.2 (0.3)
50–75%	NA	NA	−1.7 (0.4)*	1.0 (0.5)	−0.7 (0.3)*
75–95%	NA	NA	−2.7 (0.5)*	−1.0 (0.7)	−1.3 (0.4)*
> 95%	NA	NA	−9.4 (23.0)	−6.2 (21.0)	−2.0 (0.6)*

R statistical programming environment (R Development Core Team 2011) to fit and evaluate models. Predictions mapped across the study area were made with the *raster* package (Hijmans and van Etten 2012). Maps were assembled in the project GIS, with predictive rasters overlain with other relevant information, including the park vegetation map (Erixson et al. 2011) and base cartography (e.g., roads and trails). The assembled GIS was then queried and mapped for display during meetings with stakeholders.

Results

Cheatgrass, medusahead, and bluebunch wheatgrass were the most frequent and abundant species in plots. Thirteen percent of plots were estimated to have near-monocultures of annual grasses in excess of 75% cover. Sixteen percent of plots were estimated to have bluebunch wheatgrass cover >25%, and, in particularly robust stands, 4% of plots were estimated to have bluebunch wheatgrass cover >50%. In contrast, Thurber's needlegrass and Sandberg bluegrass cover rarely (~1%) exceeded 25% and never exceeded 50%. This resulted in predicted probabilities for these two species occurring with >25% cover always less than 50%. Variance explained and predictive performance of models, as indicated by R^2 and AUC, reflected these abundance patterns. In general, R^2 values were modest and similar for all species, although highest for bluebunch wheatgrass (Table 1). AUC values were high for cheatgrass, medusahead, and bluebunch wheatgrass, moderate for Thurber's needlegrass, and low for Sandberg bluegrass. Predictive performance of the three bluebunch wheatgrass prioritization classes was also high, particularly for priority 1 and priority 3 classes (Table 2).

Table 2. Predictive performance of the bluebunch wheatgrass (*Pseudoroegneria spicata*) ordinal regression model used to prioritize the study area for management and restoration decision-making into 3 priority classes (see text for prioritization details).

Measure	Priority 1	Priority 2	Priority 3
AUC	0.84	0.74	0.87
Somers' *D*	0.68	0.48	0.75

There was evident niche differentiation among all 5 grass species along the topographic (northness) gradient (Fig. 2A). Overall, topography exerted the strongest influence in models, partic-

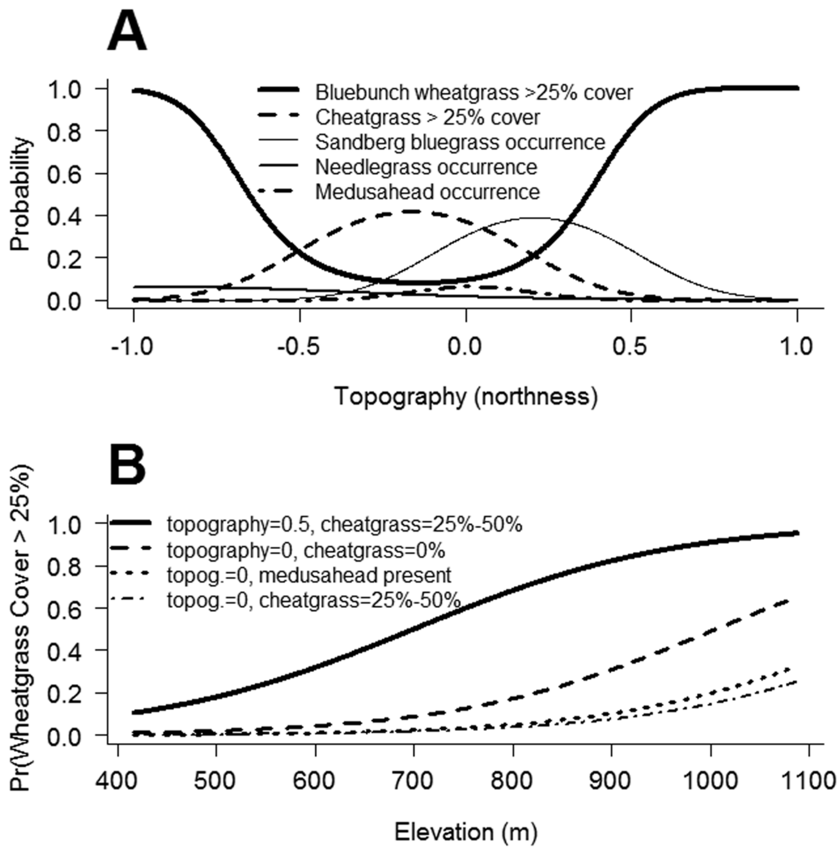

Fig. 2. (A) Predicted probabilities for bluebunch wheatgrass (*Pseudoroegneria spicata*) and cheatgrass (*Bromus tectorum*) cover >25% and for medusahead (*Taeniatherum caput-medusae*), Thurber's needlegrass (*Achnatherum thurberianum*), and Sandberg bluegrass (*Poa secunda*) occurrence along the topographic gradient in the Monument study area. Topography or "northness", was measured as sin(slope) × cos(aspect), yielding a range of possible values from −1 (steep south-facing) to 1 (steep north-facing). (B) Predicted probability of bluebunch wheatgrass >25% cover along the elevation gradient for combinations of cheatgrass and medusahead abundance and topography.

ularly for wheatgrass, bluegrass, and cheatgrass (Fig. 2A and Table 1). Wheatgrass was most strongly associated with north-facing slopes, but a strong positive quadratic effect of topography was also apparent for this species that manifested high probabilities for cover >25% on very steep south-facing slopes as well (Fig. 2A and Table 1). Bluegrass occurrence (>0% cover) was also associated with north-facing slopes. Conversely, cheatgrass and, to a lesser extent, needlegrass were associated with south-facing slopes. The topographic effect on medusahead was small, but very strongly negatively quadratic, indicating the species was most likely to be found on flat ground (Fig. 2A and Table 1).

Other abiotic predictors were much less consistently influential than topography. The annual grass species were both weakly associated with lower elevations in the Monument, whereas wheatgrass and bluegrass were moderately associated with higher elevations (Fig. 2B and Table 1). Wheatgrass probabilities for cover >25% increased sharply along the elevation gradient on steep north-facing slopes (i.e., topography >0.5) (Fig. 2B). Elevation was not estimated to influence needlegrass abundance. Flow accumulation had a weak negative influence with medusahead and wheatgrass but not with the other three species. Crop year precipitation had a small negative effect, most notably with cheatgrass,wheatgrass, and bluegrass(Table 1).

Environmental disturbance as measured with burn perimeter and proximity to roads and Monument boundary influenced abundance patterns for some species. The influence of fire was notable for the annual grasses. Areas within burn perimeters were 1.6 times more likely to be in a higher cheatgrass cover class (i.e., $e^{0.5}$) (Table 1). Similarly, the odds of medusahead occurrence were estimated to increase by three times in burned areas. The estimated direct influence of fire on bunchgrass abundance was negligible, as were the estimated interactions between topography and burn perimeter (Table 1). Proximity to roads and park boundary appeared to be mostly inconsequential to abundance patterns. There was some evidence that wheatgrass abundance increased away from the Monument boundary and, counterintuitively, the probability of medusahead occurrence apparently increased away from roads (Table 1).

As expected, the abundance of cheatgrass and medusahead strongly influenced bunchgrass abundance (Table 1 and Fig. 2B). The probability of wheatgrass cover being in the next highest cover class declined by 73% in plots with medusahead (Table 1). Similar strong negative relationships were also seen between medusahead and needlegrass and bluegrass. Probabilities of increasing wheatgrass and bluegrass cover also declined strongly as the abundance of cheatgrass in plots increased (Table 1). There was a notable non-linear increase in the magnitude of estimated effect sizes as cheatgrass cover class increased, with an inflection point when cheatgrass cover exceeded 25% (Table 1). Fig. 2b illustrates these patterns of change in the probability of wheatgrass cover >25% when medusahead is present and when cheatgrass cover is 25–50% on flat slopes (topography = 0) and on moderate, north-facing slopes (topography = 0.5). Surprisingly, there was a positive association between cheatgrass and needlegrass, even when cheatgrass cover was 50–75%. This relationship became strongly negative when cheatgrass cover exceeded 75%.

Based on these results, we created prioritization maps from the predicted probabilities of wheatgrass cover that described landscapes dominated by priority 3 areas (wheatgrass cover ≤5%) (Fig. 3). Only 25% of the Monument's 5800 ha were predicted to contain priority 1 conditions with bluebunch wheatgrass cover >25%. Large contiguous areas of priority 1 conditions were particularly rare in the smaller units of the Monument (Fig. 3). However, even within these priority 1 areas there was substantial variation in the predicted probabilities of bluebunch wheatgrass cover >25% (Fig. 4). Probabilities averaged only 50–60% and were as low as 30% in some areas. We identified several important locations warranting urgent protection activities where the probability of priority 1 conditions were very high (e.g., >90%) and where priority 1 conditions predicted to occur with probability >50% occurred contiguous to roads and trails frequented by Monument visitors (e.g., areas A and B encircled on Fig. 3). We also identified several flat, accessible priority 3 areas where active restoration could be pursued with the decision-support tools of EBIPM.

Discussion

In this study we utilized a spatially extensive plot-based monitoring dataset for biogeographic modeling of foundation bunchgrasses and invasive annual grasses in a rugged protected-area landscape in order to increase our understanding of the specific conditions associated with bunchgrass abundance. We used these models to predict and map abundance patterns of a particularly important species, bluebunch wheatgrass, for prioritizing conservation activities, including implementation of the EBIPM decision-support tool. Predictive performance of our models for invasive annual grasses and for bluebunch wheatgrass was high. Our predictions of the three wheatgrass abundance classes used for prioritization were particularly successful. Predictive performance for two other subdominant bunchgrass species was low, reflecting the community status and ecological characteristics of these species. We found abiotic factors, namely topography, to be the strongest predictor of abundance patterns for the five modeled species. The Monument is entirely within the Wyoming big sagebrush ecosystem zone, which is generally understood to exhibit low resilience to disturbances like fire and low resistance to weed invasion (Miller et al. 2013, Chambers et al. 2014). However, our models provided compel-

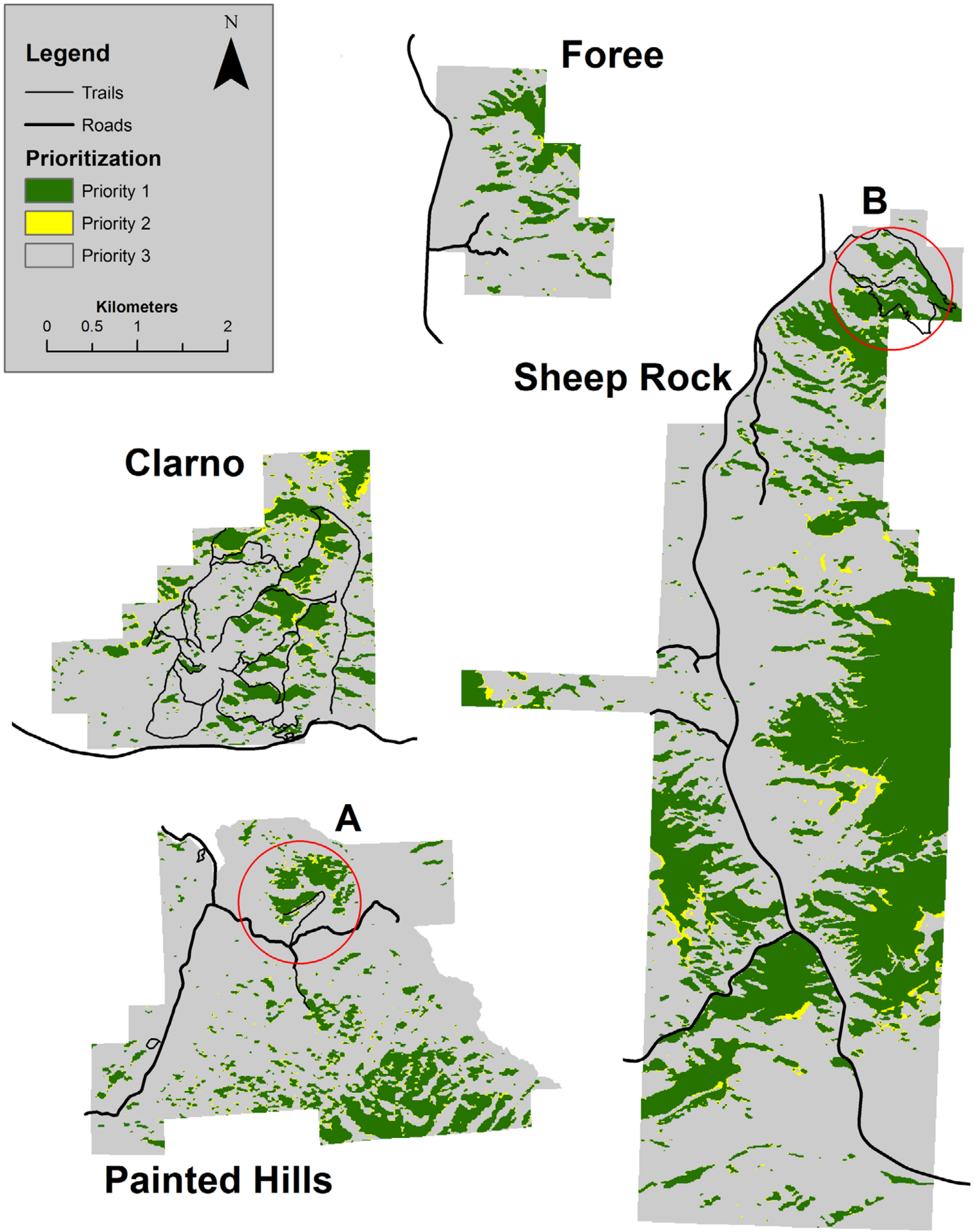

Fig. 3. The prioritization maps for each of the John Day Fossil Beds management units included in the study. Priority 1 areas were predicted to contain bluebunch wheatgrass (*Pseudoroegneria spicata*) in abundance >25% foliar cover. Priority 2 areas were predicted to contain bluebunch wheatgrass in abundance ≥5% cover but <25% cover. Priority 3 areas were predicted to contain no bluebunch wheatgrass, or bluebunch wheatgrass in abundance <5% cover. The abundance of cheatgrass (*Bromus tectorum*) and the presence of medusahead (*Taeniatherum caput-medusae*), two aggressive invasive annual grasses, was incorporated into predictive models along with a suite of environmental attributes. Thurber's needlegrass (*Achnatherum thurberianum*), another tall-stature native bunchgrass species, was considered for use in the prioritization but did not occur in sufficient abundance in the Monument. Areas circled in red and labeled A and B were two of several areas identified that contained intact stands of steppe vegetation dominated by bluebunch wheatgrass adjacent to roads and trails. These two areas were considered to be in urgent need of protection and prevention efforts.

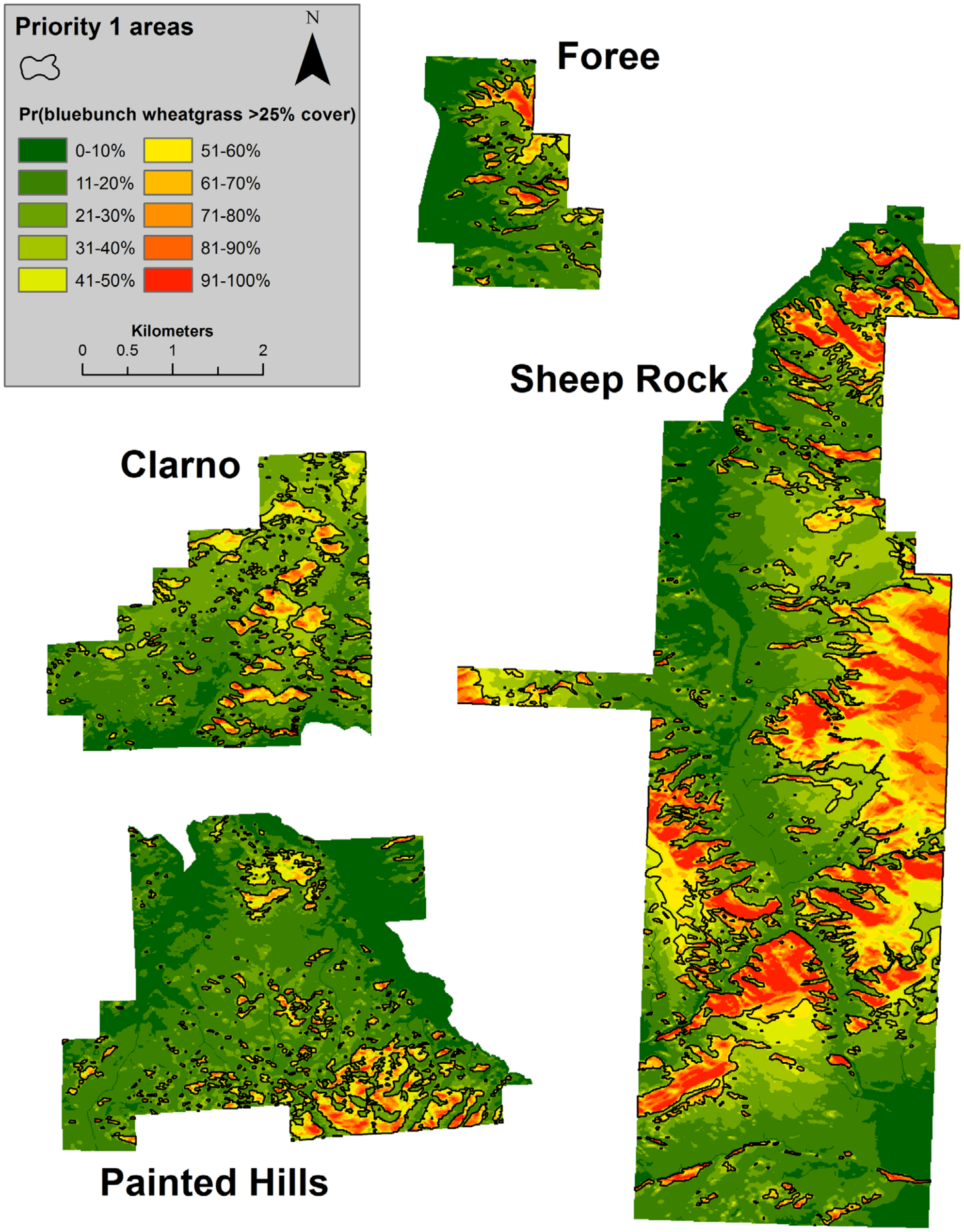

Fig. 4. Predicted probabilities for bluebunch wheatgrass occurring in abundance >25% foliar cover, with boundaries of priority 1 areas also shown.

ling evidence for important variation in resilience and resistance along the topographic-soil moisture gradient within this zone. The most robust stands of bunchgrass, characterized by high cover of bluebunch wheatgrass, were most likely to occur on steep north-facing slopes at higher and more remote portions of the Monument. In these cool, mesic sites, productivity is higher, allowing for bluebunch wheatgrass to effectively out-compete invasive annual grasses (Condon et al. 2011, Davies et al. 2012, Chambers et al. 2014). Historic grazing pressure in the landscape prior to Monument establishment was also likely to have been less intense on these steeper slopes.

Another native bunchgrass, Thurber's needlegrass, was most abundant on south-facing xeric sites, but in positive association with cheatgrass. Needlegrass is a tall-stature perennial bunchgrass like bluebunch wheatgrass that may also confer invasion resistance (e.g., Davies 2008). However, in our study system it rarely occurs in high abundance, perhaps because of cheatgrass competition, past grazing pressure, and the inherently lower fire resilience of xeric sites (Uresk et al. 1976, Condon et al. 2011). The co-association of needlegrass with cheatgrass on these slopes was striking and is consistent with recent studies (Chambers et al. 2007, Condon et al. 2011, Davies et al. 2012) that have also demonstrated cheatgrass to occur with greater abundance on xeric sites, interpreted to reflect its competitive advantage in such settings.

Our models described a landscape overwhelmed by annual grasses. Only 25% of the landscape met priority 1 conditions, and even less had convincingly high probabilities of these conditions (Fig. 4). The role of fire in influencing these patterns was clear: both cheatgrass and medusahead occur in greater abundance in burned areas of the Monument. While bluebunch wheatgrass may be relatively resilient to fire (Table 1; Miller et al. 2013), cheatgrass and medusahead exploit post-fire conditions and rapidly infest into previously intact areas, particularly if bluebunch wheatgrass fire-induced mortality is high (Mata-Gonzalez et al. 2008, Davies et al. 2009). The Monument study area is very rugged and the erosion of intact bunchgrass stands from fire, weeds, and historic grazing appears to be strongly buffered by topography (Fig. 2). This pattern provides an important foothold for managers, with the many steep north-facing slopes and canyons and draws still supporting relatively intact bunchgrass stands. Protecting the largest of these presents both an opportunity and a challenge for managers, but it is likely the best long-term strategy for success at the landscape scale.

Notably, invasion dynamics were not clearly tied to proximity to roads and Monument boundary. Roads are thought to be a vector in some areas (Gelbard and Belnap 2003, Davies et al. 2013). Protected-area boundaries might also be expected to provide some insularity from outside-in patterns of invasion. However, the probability of medusahead occurrence was actually estimated to increase away from roads (Table 1). Bluebunch wheatgrass abundance probabilities increased away from park boundary, suggesting a possible effect of insularity. However, with a relatively small effect size (Table 1) and many large priority 1 areas mapped along the boundary (Fig. 3) it is not clear how meaningful this pattern is. The apparent lack of insularity likely reflects a much older invasion process that began during the era of intense livestock grazing before the Monument was established, and is alarming given how little of the sagebrush steppe biome is contained within the conservation reserve system (Caicco et al. 1995, Storms et al. 1998). Noss et al. (1995) reported that sagebrush steppe was one of the most imperiled ecosystem types in the USA. Given that the size and establishment dates of many of the protected areas in the region are similar to the Monument study area (Storms et al. 1998) and the insularity of even the largest ones compromised (e.g., Bangert and Huntly 2010), our study would suggest that the conservation reserve system contributes much less to ameliorate this imperilment than has been previously recognized.

We present our case study as a motivation for others to follow in the North American sagebrush biome and elsewhere. We expect that a model-based focus on mapping foundation species distributions and abundances, with an explicit link to monitoring and decision-support tools like EBIPM, will be a broadly useful strategy, particularly in protected-area contexts. The applicability of our approach to other systems will be predicated on the existence of similar kinds of well-established ecological relationships between foundation species and community processes such as invasion resistance. An active, spatially extensive monitoring program is required for modeling and periodic evaluation of restoration and management actions. We drew upon a rapid-assessment protocol currently used in NPS units across the Columbia and Wyoming Basins that allows for large datasets to be developed with a small field crew in a relatively short period of time (e.g., 4 weeks). Model validation is a critical step, and also dependent upon large samples which can be obtained through this type of monitoring program. Furthermore, we note that our models articulate working hypotheses of resilience and resistance that can be tested over time with this monitoring approach. Remotely sensed data will be useful for monitoring readily observable taxa (which foundation species typically are), but we emphasize the importance of having repeat measurements on a time scale appropriate to the dynamics of the given system; reliance on prohibitively costly measures (e.g., LiDAR) that cannot be repeated will hamper the process.

Our approach differs from invasive species management and mapping strategies that emphasize weed mapping by focusing on a community attribute, the abundance patterns of a foundation species, thought to confer ecological resilience and invasion resistance. It complements the "positive" interventions paradigm in modern restoration ecology (Gomez-Aparicio 2009) and is particularly compatible with the EBIPM decision-support framework developed for rangelands in the western USA. The hallmark of EBIPM is its emphasis on the identification of tools and strategies that managers can use to alter successional processes and allow plant communities to change in a favorable direction (James et al. 2010). Because of the facilitative role of foundation species in plant communities, knowing where intact stands are most likely to occur offers a tremendous advantage to land managers and restoration practitioners, particularly when confronted with large, rugged landscapes. Prioritization maps based on foundation species can be used in the EBIPM framework not only to identify high priority areas warranting protection and prevention efforts but also to help identify where rangeland health assessments should be conducted in advance of specific decisions about the ecological processes in need of repair and the tools needed to repair them. Also, our predicted probability map could be used to target early-detection weed surveillance activities around the perimeters of high priority areas (e.g., areas A and B in Fig. 3), a strategy known as sampling with probability proportional to predictions (Ringvall and Kruys 2005). In the specific setting of sagebrush steppe, both the extent of degradation (Chambers and Wisdom 2009, Davies et al. 2011) and the relative paucity of healthy sagebrush steppe in the existing conservation reserve system (Caicco et al. 1995, Storms et al. 1998) underscores the importance of trying new approaches of prioritization and evidence-based decision-making (Chambers and Wisdom 2009, Chambers et al. 2014).

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