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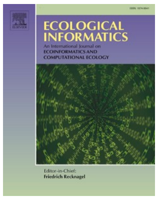

Predicting fine-scale forage distribution to inform ungulate nutrition

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ABSTRACT

The quantity and nutritional quality of forage are key drivers for ungulate populations, including mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*), in the western U.S., but current vegetation maps are too coarse spatially and temporally to effectively characterize fine-scale habitat. To address some of these gaps, we tested a novel approach using existing vegetation surveys, maps, and remotely sensed data to develop fine-scale forage species distribution models (SDMs) across Idaho, USA. We modelled 20 forage species that are suitable for mule deer and Rocky Mountain elk. Climatic, topographic, soil, vegetation, and disturbance variables were attributed to approximately 44.3 million habitat patches generated using multi-scale object-oriented image analysis. Lasso logistic regression was implemented to produce predictive SDMs. We evaluated if the inclusion of distal environmental variables (i.e., indirect effects) improved model performance beyond the inclusion of proximal variables (i.e., direct physiological effect) only. Our results showed that all models provided higher predictive accuracy than chance, with an average AUC across the 20 forage species of 0.84 for distal and proximal variables and 0.81 for proximal variables only. This indicated that the addition of distal variables improved model performance. We validated the models using two independent datasets from two regions of Idaho. We found that predicted forage species occurrence was on average within 10% of observed occurrence at both sites. However, predicted occurrences had much less variability between habitat patches than the validation data, implying that the models did not fully capture fine-scale heterogeneity. We suggest that future efforts will benefit from additional fine resolution (i.e., less than 30 m) environmental predictor variables and greater accounting of environmental disturbances (i.e., wildfire, grazing) in the training data. Our approach was novel both in methodology and spatial scale (i.e., resolution and extent). Our models can inform ungulate nutrition by predicting the occurrence of forage species and aide habitat management strategies to improve nutritional quality.

1. Introduction

The nutritional quantity and quality of forage is an important population driver of ungulates in the western U.S., including mule deer (*Odocoileus hemionus*; Hurley et al., 2017; Tollefson et al., 2011; Tollefson et al., 2010), Rocky Mountain elk (*Cervus elaphus nelson*; Cook et al., 2016; Cook et al., 2004; White et al., 2010), bighorn sheep (*Ovis canadensis*; Enk et al., 2001), and moose (*Alces alces*; Monteith et al., 2015; Schrempp et al., 2019). With habitat changes related to climate and declines in ungulate populations in the western U.S., the nutritional content and productivity of ungulate forage is becoming increasingly important to understand (Monteith et al., 2015; Schrempp et al., 2019; White et al., 2010). Recent research has suggested that managing summer and winter ranges to increase forage productivity (e.g., quantity and quality) could increase recruitment in ungulate populations (Lukacs et al., 2018; Proffitt et al., 2016). Furthermore, higher productivity of forage has been shown to partially compensate for other environmental drivers, such as predation, harvest, and weather conditions (Lukacs et al., 2018; Melis et al., 2009; Monteith et al., 2015).

Many ungulate species, including mule deer and Rocky Mountain

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elk, are highly sought-after game species that are economically important to state wildlife agencies and local communities (Arnett and Southwick, 2015). Ensuring the long-term persistence of ungulate populations is a management priority for state wildlife agencies particularly when recent declines in populations have been observed (White et al., 2010). Habitat management and restoration aimed at improving the nutritional quality and quantity of forage is a common population management tool used by state wildlife agencies (Cook et al., 2016; Schrempp et al., 2019). Additionally, the ability to quantify the heterogeneity of forage across broad landscapes is useful for researchers demonstrating mechanistic links between forage nutrition and ungulate populations (Schrempp et al., 2019).

Understanding ungulate nutrition can be informed by predicting the relative abundance, biomass, or nutritional quality of important forage species. However, a critical first step in determining the distribution of forage conditions across the landscape is predicting the occurrence of those forage species, thereby providing wildlife managers with the initial pieces of fine-scale information needed to improve habitats and in turn populations. National mapping efforts such as LANDFIRE (www.landfire.gov), the USGS Gap Analysis Project (http://gapanalysis.usgs.gov/), and the National Land Cover Database (www.mrlc.gov) have mapped vegetation across large spatial scales but lack information on individual forage species distributions. Additionally, the fine scale vegetation assessments needed to evaluate the distribution of forage species across a broad landscape are limited. Alternatively, species distribution models (SDMs) can be used to make predictions of individual forage species occurrence at any scale of interest. SDMs may use a number of statistical approaches including generalized linear models, Bayesian hierarchies, maximum entropy models (MaxEnt), classification and regression trees, Random Forest, and logistic regression (e.g., Hegel et al., 2010; Merow et al., 2014).

In SDMs, environmental variables can be described by their relationship with the species being predicted. These variables can be considered either proximal, in that they exert direct physiological effects on forage species, or distal, which influence forage indirectly. For instance, mean minimum temperature and depth to soil restrictive layer, which have direct effects on cellular and root growth respectively, would be considered proximal environmental variables (Prentice et al., 1992). Water uptake by forage species is directly affected by 30-year normal minimum precipitation, total annual precipitation, and available water supply in the soil (Austin and Van Niel, 2011; Nippert and Knapp, 2007). These variables would also be considered proximal. Distal environmental variables, including elevation, slope and aspect, influence plant processes indirectly and are often used as surrogates for proximal variables (Austin, 2002; Austin and Van Niel, 2011), but this can lead to inaccurate representations of species-environment relationships (Austin and Van Niel, 2011; Merow et al., 2014). A growing consensus in the ecological literature suggests the incorporation of variables based on their functional scale will yield more robust models, provide stronger predictions, and provide more reliable inferences of ecological relationships (McGarigal et al., 2016; Miller et al., 2015; Store and Jokimäki, 2003; Weaver et al., 2012). Whether the inclusion of distal variables improve the functional scale of SDMs beyond proximal variables alone is relatively unknown across broad landscapes. To effectively inform ungulate nutrition using fine-scale predicted distributions of forage, we used a novel combination of habitat patches derived from object-oriented segmentation of high-resolution (1 m) imagery and percent probability of select plant species occurrence based on logistic regression with the least absolute shrinkage and selection operator (lasso), which handles multi-collinearity and reduces model complexity without the need for advanced parameter tuning (Dormann et al., 2013; Hastie et al., 2017; Tibshirani, 1996). Our objectives were (1) to predict forage species occurrence across Idaho, USA at a fine-scale (i.e., habitat patches), and (2) to assess if the inclusion of distal variables improved model performance beyond proximal variables only. We focused on 20 forage species in Idaho, divided across four life forms (grass, forb, shrub, and tree), that are suitable forage for mule deer or Rocky Mountain elk. The combined range of mule deer and Rocky Mountain elk are spread across the state and both species are closely monitored and managed within Idaho. Even though we focused on these two ungulate species, our approach can be used to predict the distribution of forage species that are nutritionally important to other wildlife species (i.e., Schrempp et al., 2019).

2. Methods

2.1. Study area

Idaho (216,440 km^2) is ecologically diverse due to vast topographical and climatic gradients, resulting in a range of habitat types including: dry canyon grasslands, xeric shrublands and steppe, dunes, deciduous forests and shrublands, non-native herbaceous lands, arable land, Palouse prairie, wetlands, riparian woodlands, dry and mesic coniferous forests, subalpine forests, and rocklands Idaho Department of Fish and Game (IDFG), 2017. East-west mountain ranges and the Salmon River naturally divide the state into two regions with different climactic, topographic, and biotic characteristics; northern Idaho (i.e., the Panhandle) and southern Idaho.

2.2. Data

Vegetation survey data were collected by the Bureau of Land Management (BLM) and IDFG between 2012 and 2016 (Table A.1). Surveys consisted of 1,525 50 or 100 m transects sampled every 0.5 or 1 m using the line-point intercept method (Canfield, 1941; Herrick et al., 2005). This method limits observer subjectivity by dropping a pin at each point and recording all intersected forage species as well as interceptions with rock, litter, duff, bare ground, lichen, and moss. The data sources we used mitigated location bias through stratified sampling; however, the line-point intercept transects could be biased due to site accessibility and invisible factors such as soil condition (Canfield, 1941). Additionally, with each line-point on a transect, the observations are not spatially independent. Point thinning could be used to further decrease spatial dependence among the sampling points but would also result in data loss for modelling (Araújo and Guisan, 2006). With any method, including line-point intercept, rare species are likely to be missed (Vittoz and Guisan, 2007). Greater sample size can be used to overcome the problem of independent sampling and species rarity (Everson et al., 1990), therefore we chose to keep all line-point observations to prevent loss of precision in occurrence estimates for less common species.

We initially identified all forage species that are suitable for either mule deer or Rocky Mountain elk as potential modelling candidates (Alldredge et al., 2002; Cook, 2002; Cox et al., 2009; Frisina et al., 2008; Hayden et al., 2008). From these, 20 forage species were selected based on the number of occurrences in the vegetation surveys, representing a variety of life forms (i.e., grass, shrub, forb, and tree). Occurrences for the 20 selected forage species ranged from 97 to 11,481, with grasses being the most abundant and trees the least (Table 1). The total number of sampled points was 84,971. Some forage species were difficult to distinguish within a genus (i.e., sedge (*Carex* spp.), lupine (*Lupinus* spp.), and willow (*Salix* spp.)), thus were grouped by genus for modelling purposes. We modelled forage species presence statewide because the combined range of mule deer and Rocky Mountain elk cover Idaho and because forage species occurrence was of interest to wildlife managers for informing habitat management to improve nutritional quantity and quality of other wildlife species.

To model forage presence statewide, we first utilized multi-scale object-oriented image analysis, which identifies natural boundaries and patches in the landscape based on color and shape to create relatively homogenous polygons (i.e., habitat patches). This approach provides better characterization of landscape patterns than a conventional per-pixel approach (Burnett and Blaschke, 2003; Lobo, 1997) and

Table 1
Forage species selected for distribution modelling and the number of times observed in the field data (out of 84,971 points). Scientific name, common name, and life form are included.

Scientific name	Common name	Life form	Number of points
Pseudoroegneria spicata	Bluebunch wheatgrass	Grass	11,481
Poa secunda	Sandberg bluegrass	Grass	7.067
Festuca idahoensis	Idaho fescue	Grass	5.818
Calamagrostis rubescens	Pinegrass	Grass	3.052
Carex spp.	Sedge spp.	Grass	2.134
Lupinus spp.	Lupine spp.	Forb	3.554
Balsamorhiza sagittata	Arrowleaf balsamroot	Forb	1.323
Achillea millefolium	Common yarrow	Forb	1.133
Geranium viscosissimum	Sticky purple geranium	Forb	373
Mahonia repens	Creeping Oregon grape	Shrub	1.103
Artemisia tridentata ssp. vaseyana	Mountain big sagebrush	Shrub	6.571
Purshia tridentata	Antelope bitterbrush	Shrub	3.317
Symphoricarpos albus	Common snowberry	Shrub	2.746
Amelanchier alnifolia	Saskatoon serviceberry	Shrub	721
Physocarpus malvaceus	Mallow ninebark	Shrub	386
Populus tremuloides	Quaking aspen	Tree	581
Prunus virginiana	Chokecherry	Tree	594
Pseudotsuga menziesii	Douglas-fir	Tree	413
Salix spp.	Willow spp.	Tree	699
Pinus contorta	Lodgepole pine	Tree	97

provided us with a more meaningful fine-scale unit of analysis. Using eCognition Developer 9.2 (Trimble Inc., Westminster, CO), 1 m resolution National Agriculture Imagery Program imagery (NAIP 2015; http://www.insideidaho.org) was segmented into polygons based on blue, green, red, and near infrared (NIR) spectral values. NAIP from 2011 was substituted in a few instances where areas were obscured by snow or clouds. Following testing, a shape value of 0.1 and a compactness value of 0.3 were selected within eCognition, producing polygons defined more by color and smoothness rather than shape and compactness. This helped minimize variation in vegetation characteristics within polygons and capture variation between polygons. Approximately 44.3 million polygons were delineated across Idaho from our segmentation procedure.

Next, we attributed the segmented polygons with 28 environmental variables using the ArcPy Python site package in ArcGIS 10.4 (ESRI, Redlands, CA) with climate, topography, soil, vegetation, and disturbance using the mean for continuous variables and mode for indexed variables. We identified 12 environmental variables as proximal, which we believe have direct physiological effects on forage and 14 distal environmental variables, which have indirect effects on forage (Table A.2). For our modelling comparison, we generated separate model sets using only the 12 proximal variables and using all 28 distal and proximal (distal-proximal) variables. Climatic variables included 30-year normal temperature (°C) and precipitation (mm) values from PRISM climate data 1981–2010 (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 2015), downscaled to a 250 m resolution using cubic convolution for precipitation and an empirical algorithm for temperature (Holden et al., 2011). Topographic variables included elevation (m), slope (deg), aspect (deg), topographic wetness index (determines hydrologic influence; Moore et al., 1993), slope position index (classifies hilltops, valley bottoms, exposed ridges, and flat plains), landscape curvature index (indicates if surface is convex or concave), and solar radiation index were generated from a 10 m digital elevation model (DEM; http://www.insideidaho.org). Aspect was transformed into index values to measure northness (i.e., cosine of aspect in radians) and eastness (i.e., sine of aspect in radians). The solar radiation index was calculated separately for each degree of latitude across Idaho using average radiation through the main growing season (15 May through 31 August 2015) using equations from Fu and Rich (2002) implemented in ArcGIS 10.4.

Soil characteristic variables were generated by stitching together the Natural Resource Conservation Service's (NRCS) Soil Survey Geographic (SSURGO) and State Soil Geographic (STATSGO) 1901–2015 surveys across Idaho. Variables included soil available water supply (cm), percent clay, percent sand, percent silt, percent organic matter, percent calcium carbonate, pH, cation-exchange capacity (mEq/100 g), and depth to restrictive layer (cm) (Natural Resource Conservation Service, http://websoilsurvey.nrcs.usda.gov/). Vegetation variables at 30 m resolution included percent canopy cover of trees from the 2011 National Land Cover Database (NLCD; Holmer et al., 2015) and percent canopy cover of shrubs (LANDFIRE 1.1.0, https://landfire.gov/). Disturbance variables included time since most recent wildfire (years) and wildfire frequency (years) between 1984 and 2014 derived from 30 m Monitoring Trends in Burn Severity data (MTBS; Eidenshink et al., 2007). The centroid latitude and longitude of each polygon were also included to examine locational influences. To limit focus on areas of natural vegetation we used 30 m USDA National Agricultural Statistics Service (NASS; www.nass.usda.gov) data to omit agricultural areas, barren land, and perennial snow and ice from the analysis and results. NLCD data was used to omit developed areas.

2.3. Modelling

SDMs are widely used for predicting species occurrence, but each method has strengths and weaknesses. MaxEnt has emerged in the ecological literature as one of the most popular approaches (Merow et al., 2013; Phillips et al., 2017). However, the use of MaxEnt requires a considerable number of decisions regarding appropriate data inputs and software settings (Merow et al., 2013). Standard logistic regression uses presence and absence data, which has been shown to be better suited for fine-scale datasets than presence-only approaches such as MaxEnt (Huang and Frimpong, 2015). However, standard logistic regression has also been shown to overfit models (Gastón and García-Viñas, 2011). In contrast, lasso logistic regression performs equally well or better than MaxEnt (Gastón and García-Viñas, 2011; Huang and Frimpong, 2015). Additionally, Huang and Frimpong (2015) demonstrated that lasso logistic regression, which uses presence and absence data, was better suited for fine-scale datasets than presence-only approaches such as MaxEnt.

We employed lasso logistic regression (Tibshirani, 1996) via the 'glmnet' package in R (Friedman et al., 2010) to predict the probability of forage species presence within polygons. The lasso logistic regression applies a penalty term to the maximum likelihood function which forces variable coefficients to become zero if no improvement in model performance is observed (Hastie et al., 2017; Tibshirani, 1996). This effectively eliminates weak predictors from the model, providing a pragmatic approach for variable selection (Hastie et al., 2017; Tibshirani, 1996).

Vegetation survey data was used to produce a ratio of presence/absence for each selected forage species at each of the 3,150 unique polygons used for modelling. Presence counts were determined by the number of times a forage species was intercepted along transects at each polygon. Absence counts were calculated as the total number of transect points in a polygon minus the number of forage species interceptions. Separate models were generated for each of the 20 forage species using distal-proximal and proximal variables as explanatory inputs (i.e., two species models were created per forage species). We selected variable coefficients from the model where mean cross-validated error was minimized and used those coefficients to make predictions statewide. To visualize the predictions, the probability of occurrence for each forage species was predicted from the models within each polygon in Idaho. Polygons were then rasterized to a 30 m grid for the purpose of coarse-scale visibility.

2.4. Validation

Model predictive accuracy was validated using k-fold cross validation (k = 10) and the area under the curve (AUC) of the receiver-operating characteristic (ROC) curve (Hanley and McNeil, 1982). For each forage species model, we generated a cross validation curve, which included the number of variables that were selected by the lasso logistic regression and an average AUC at each penalty. Training data could not be obtained uniformly across the state, leading to geographic bias and uncertainty about the predictive power of the models in unsampled areas. This warranted additional validation to test how accurately the models were extrapolated statewide.

Vegetation survey data for model validation were acquired from two independent areas. Validation-focused field sampling on nine target polygons was conducted in 2019 at the Taylor Ranch Wilderness Research Station (TWRS), located within the Frank Church River of No Return Wilderness in central Idaho and approximately 60 km from the nearest field sites used for model training. Vegetation survey data were also collected at Rinker Rock Creek Ranch (RRCR) Biological Research Station, southwest of Hailey, Idaho and approximately 20 km from the nearest training data. At TWRS, forage species were identified along 50 m transects at every 0.5 m using line-point-intercept for nine segmented polygons. At RRCR pre-existing line-point intercept data were acquired from 2018 and 2019. For these data three 25 m transects were sampled every 0.5 m at each site location. Line-point intercept data were also collected in 2020 at polygons randomly stratified by elevation, latitude, and longitude to fill in gaps on RRCR from the 2018 and 2019 data. One or more 50 m line-point intercept transect was sampled at each target polygon, with point spacing of 0.5 m. The final RRCR dataset had 183 polygons containing at least 100 sampled points each.

Sampling density for the training data averaged 27 points per polygon, while average points per polygons of the validation datasets were 439 at TWRS and 188 at RRCR. The greater number of observations in the validation datasets increased the likelihood of accurately characterizing each polygon and detecting rare forage species (Everson et al., 1990). For both validation datasets, percent observed forage species occurrence was calculated from the number of forage species points divided by the total number of points in the polygon. This number was compared to percent probability of occurrence predicted from the model. We compared average observed and predicted occurrence for all 20 forage species to assess how well the models extrapolated species occurrence to other parts of Idaho.

3. Results

Models using distal-proximal and proximal environmental variables were produced for the 20 forage species, applied to all habitat patches (i.e., polygons; Fig. 1), and mapped across the state (Figs. 2 and 3). Most predicted probabilities were under 10%, so the results were displayed in log scale. Many forage species were predicted to occur nearly statewide, particularly most grass and forb species. However, some forage species were predicted only for certain regions. Sticky purple geranium

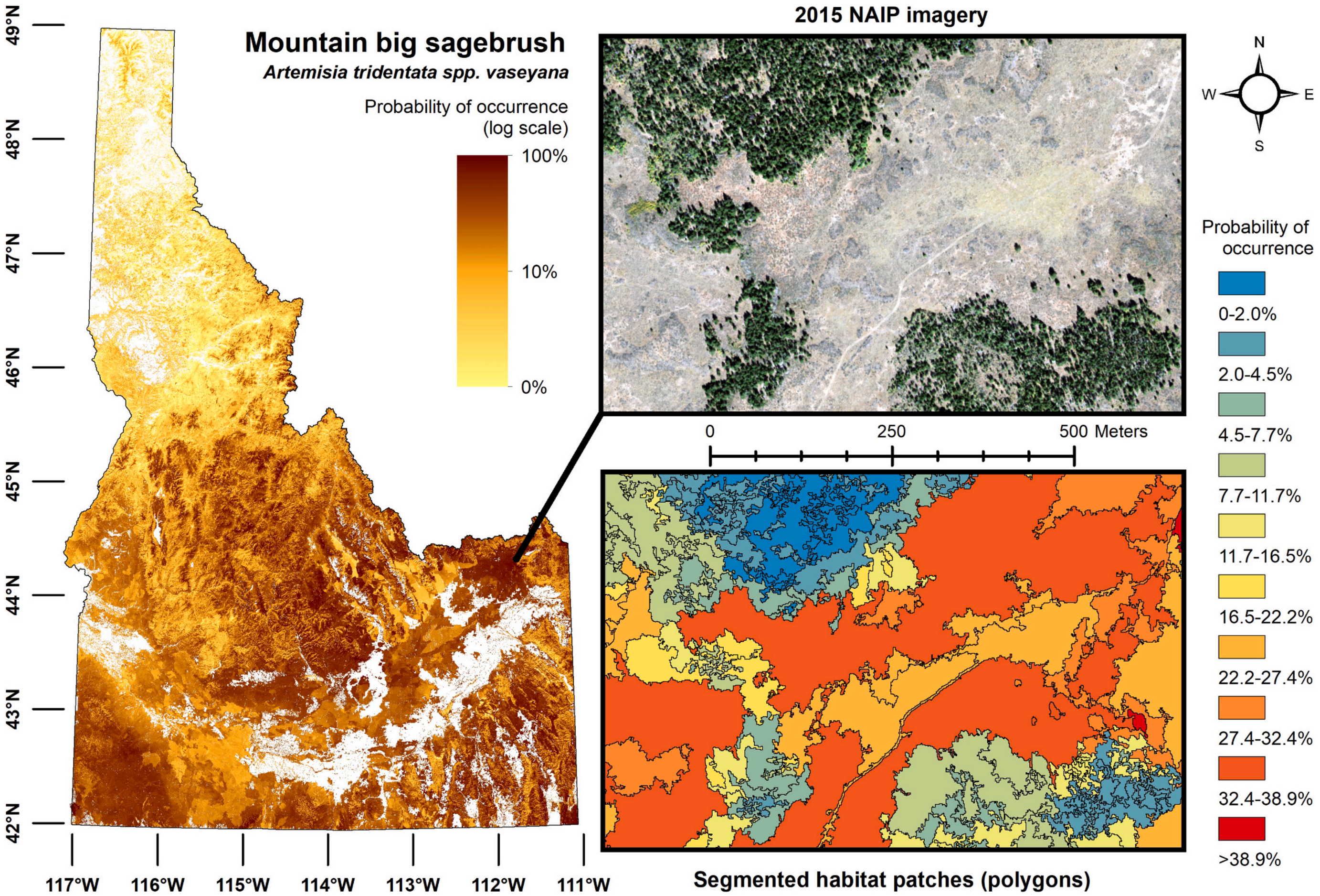

Fig. 1. Habitat patches (i.e., polygons) developed from NAIP imagery and attributed with percent probability occurrence of mountain big sagebrush using a model containing distal and proximal (distal-proximal) environmental variables. Statewide values are mapped using a natural log scale and aggregated to 30 m resolution. The inset example is from the Caribou-Targhee National Forest in eastern Idaho.

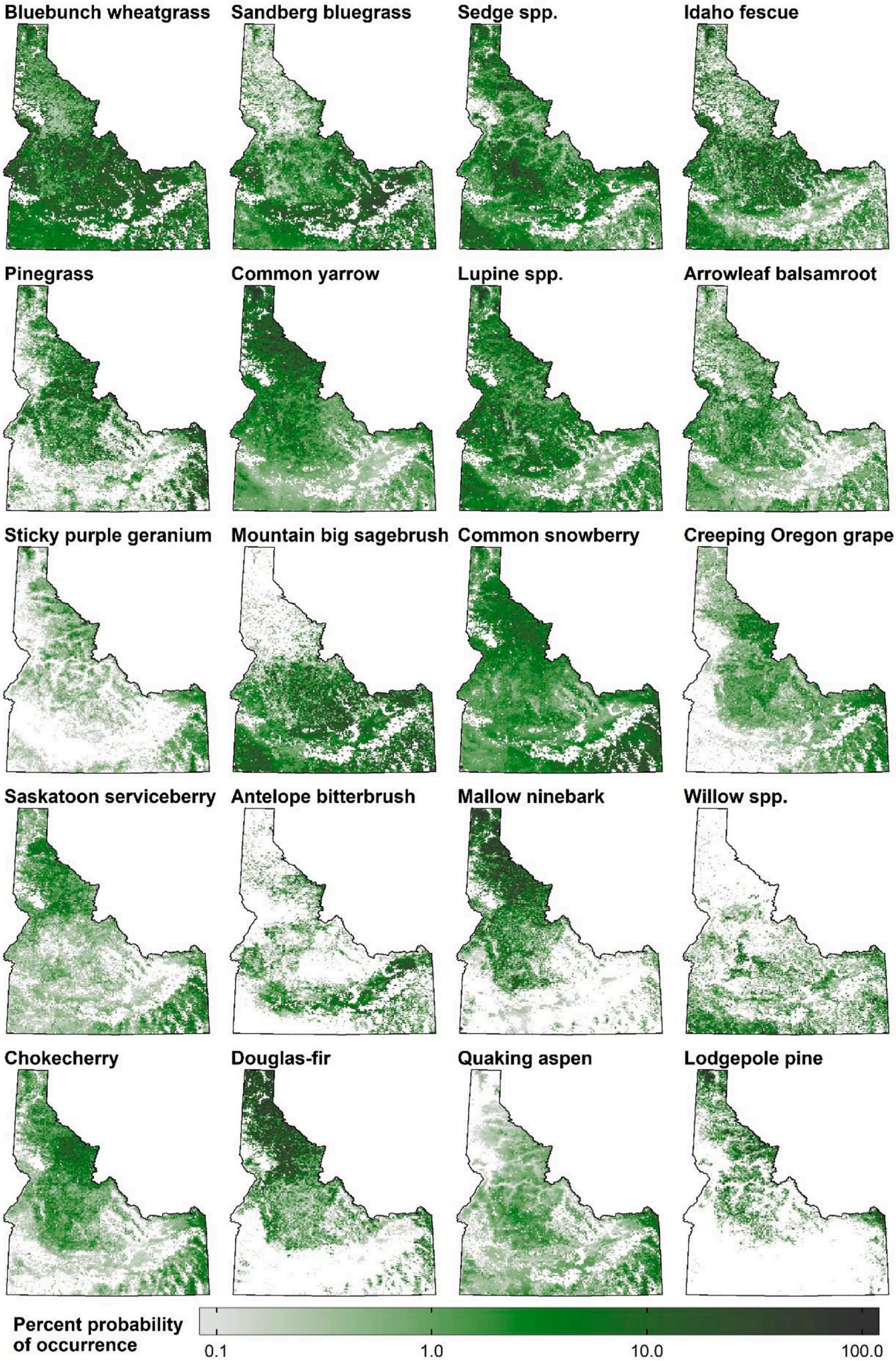

Fig. 2. Percent predicted occurrence (log-scale) for 20 forage species using both distal and proximal (distal-proximal) environmental variables. See Table 1 for forage species scientific names.

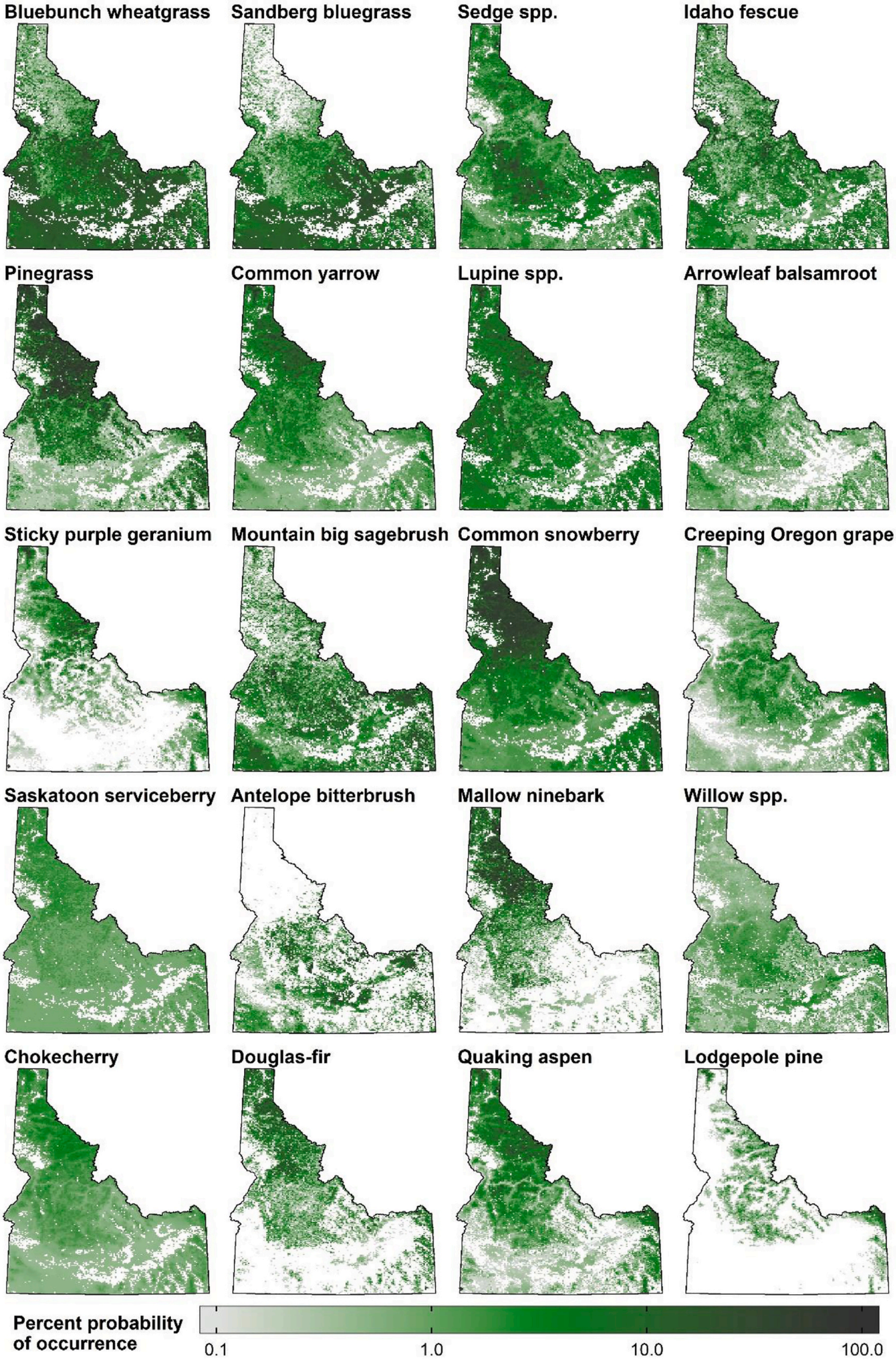

Fig. 3. Percent predicted occurrence (log-scale) for 20 forage species using proximal environmental variables. See Table 1 for forage species scientific names.

(*Geranium viscosissimum*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) were predicted only in mountainous and mesic parts of Idaho. Meanwhile mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) and willow were predicted mainly in southern Idaho using distal-proximal variables, while antelope bitterbrush (*Purshia tridentata*) was predicted mainly in southern Idaho using proximal variables.

3.1. Model accuracy and environmental variables

All models provided higher predictive accuracy than chance, as demonstrated by the cross-validation curves (Figs. 4 and 5). The inclusion of distal variables broadly resulted in higher accuracy as measured by AUC. Models containing distal-proximal variables had AUC values that ranged from 0.68–0.97 with a mean value of 0.84, selecting between 11 and 28 variables (Table A.3). Whereas models containing only proximal variables had AUC values ranging from 0.67–0.96 with a mean value of 0.81, selecting between 1 and 12 variables (Table A.4).

Pinegrass (*Calamagrostis rubescens*), mallow ninebark (*Physocarpus malvaceus*), and lodgepole pine had models with the highest predictive accuracies (at or above AUC: 0.94) using both proximal and distal-proximal variables (Tables A.3 and A.4). The model for common yarrow (*Achillea millefolium*) had the lowest predictive accuracy for distal-proximal (AUC: 0.68) and proximal (AUC: 0.67) variables. Notably, even though the proximal model for saskatoon serviceberry (*Amelanchier alnifolia*) had a relatively high accuracy (AUC: 0.84), it selected only percent tree cover as a predictor. Also, the models for willow and chokecherry (*Prunus virginiana*) had less agreement in cross-validation as indicated by the wide confidence ribbons (Figs. 4 and 5).

Tables of the model coefficients were produced to assess how the lasso logistic regression treated individual environmental variables (Tables A.3 and A.4). For models including the distal-proximal variables (Table A.3), the lasso logistic regression did not appear to preferentially select either proximal or distal variables. Percent organic matter and

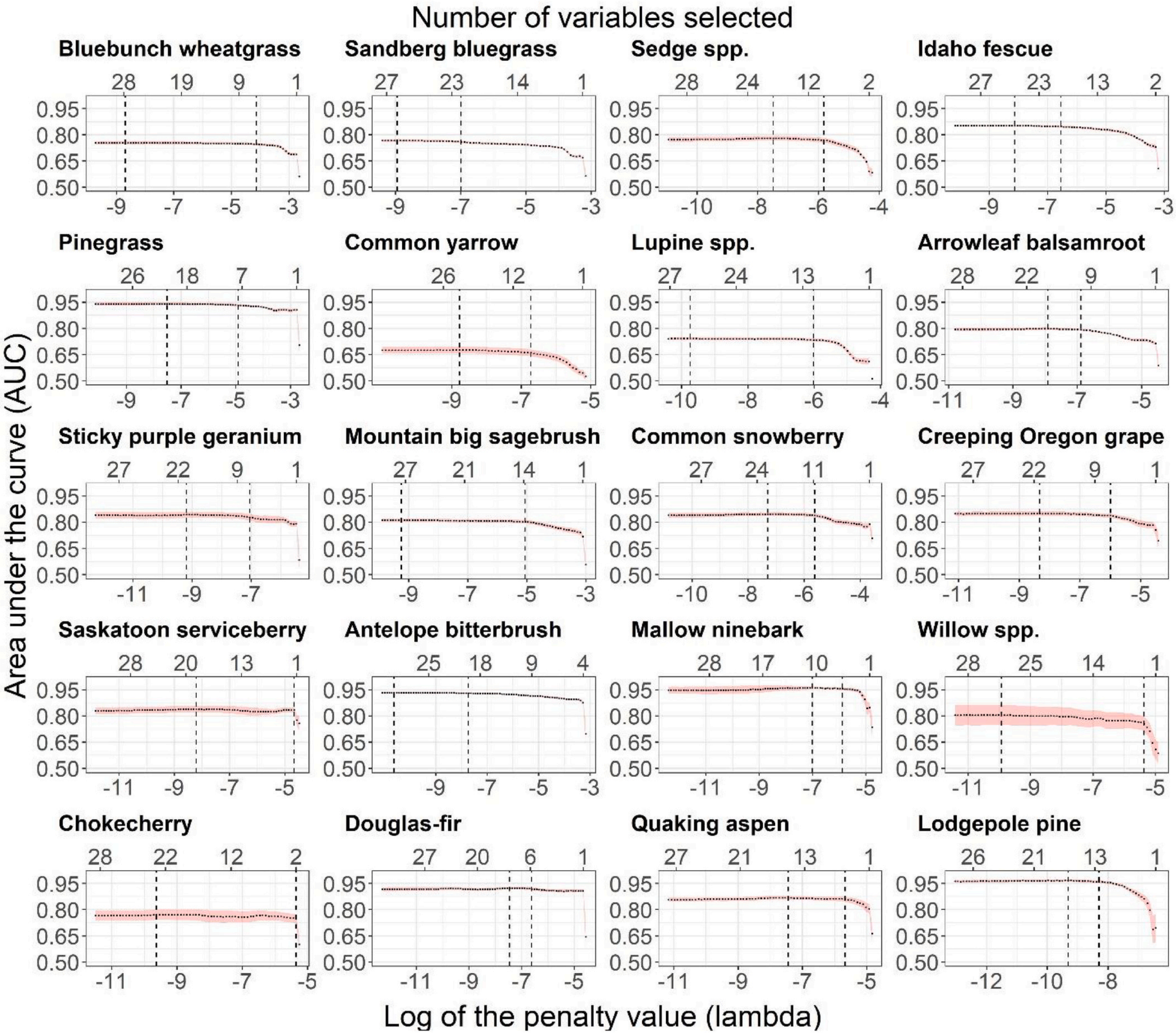

Fig. 4. Cross validation curves for all forage species distribution models containing both distal and proximal (distal-proximal) environmental variables with confidence interval ribbon shown in red. Vertical dashed lines indicate the penalty value (bottom x-axis) and number of environmental variables selected (top x-axis) for the highest predictive accuracy (left dashed line) and one standard error from the highest predictive accuracy (right dashed line). See Table 1 for forage species scientific names. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

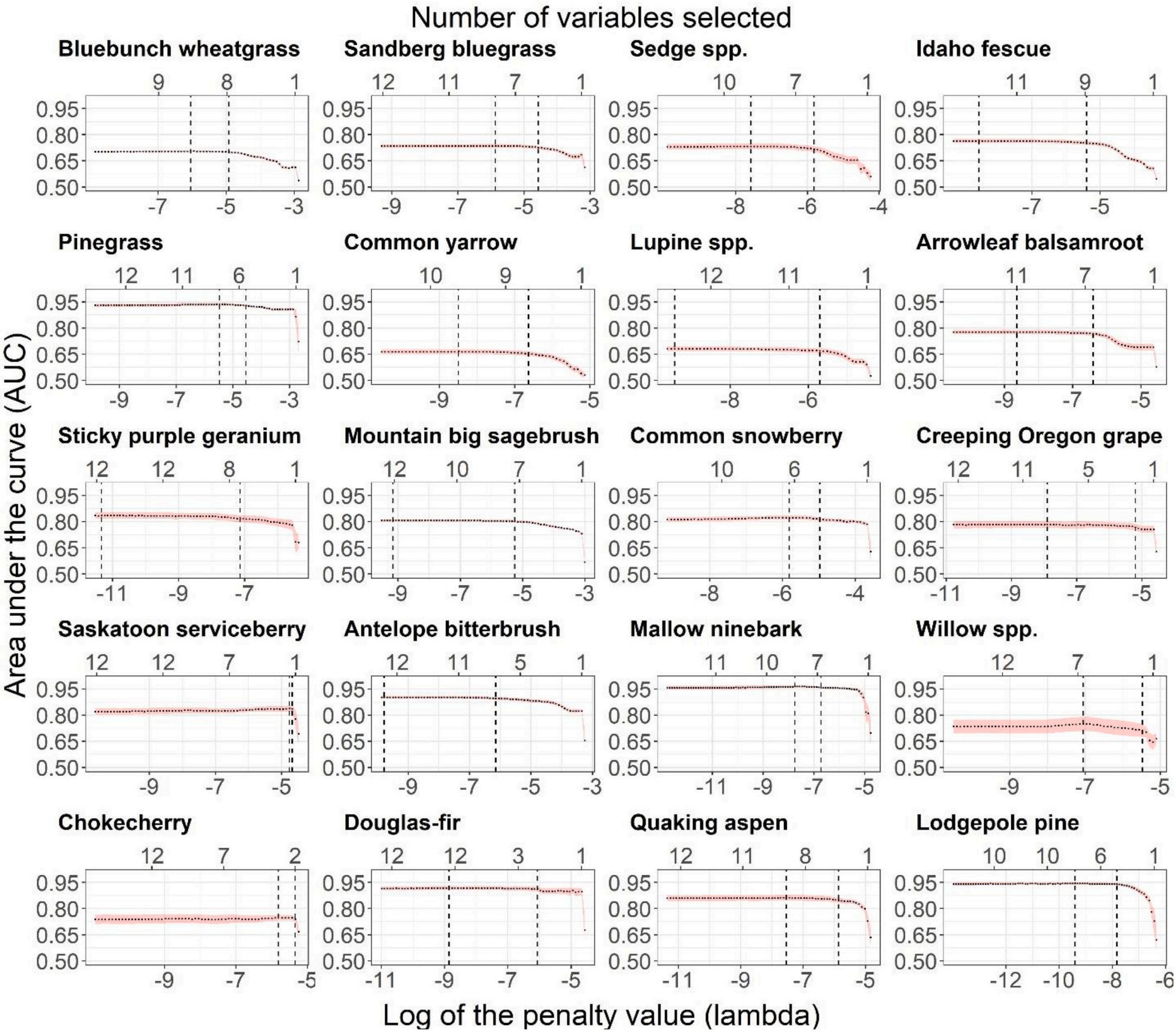

Fig. 5. Cross validation curves for all forage species models containing proximal environmental variables with confidence interval ribbon shown in red. Vertical dashed lines indicate the penalty value (bottom x-axis) and number of environmental variables selected (top x-axis) for the highest predictive accuracy (left dashed line) and one standard error from the highest predictive accuracy (right dashed line). See Table 1 for forage species scientific names. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

percent tree cover, which we defined as proximal, were both selected across all forage species. Other commonly selected environmental variables (for ≥17 species models) were evenly divided between distal and proximal, including: slope, northness (i.e., cosine of aspect in radians), topographic wetness index, 30-year normal minimum precipitation, 30-year normal minimum temperature, soil percent calcium carbonate, shrub cover, and latitude. Elevation was the variable most penalized by the lasso process (for nine of the species models), indicating it was one of the least valuable predictor variables.

For the models using proximal variables only (Table A.4), percent tree cover was selected for all forage species models, although most forage species models (≥17) also selected 30-year normal minimum precipitation and 30-year normal minimum temperature. Fire frequency and time since the last fire were penalized the most (at least half the species models) by the lasso process.

3.2. *Model validation*

3.2.1. *TWRS*

The validation field survey at TWRS recorded between 0 and 473 occurrences for the 20 forage species within the nine target polygons (Table 2). Bluebunch wheatgrass (*Pseudoroegneria spicata*) and common snowberry (*Symphoricarpos albus*) were the most abundant forage species observed, having average occurrences of 16.3% and 10.1% respectively. Sticky purple geranium, mountain big sagebrush, antelope bitterbrush, chokecherry, quaking aspen (*Populus tremuloides*), and lodgepole pine were not observed at all in the target polygons. Among forage species that were observed, average predicted occurrence was within 8.3% of observed using distal-proximal variables, and 7.8% of observed using only proximal variables. In both cases, common snowberry was under-predicted and had the greatest difference between predicted and observed.

Observed occurrences displayed much higher variance between

Table 2

Statistics for all forage species in the Taylor Ranch Wilderness Research Station (TWRS) validation polygons ($n = 9$), including number of observed occurrences, mean percent observed occurrence plus/minus the standard deviation, and mean probability of occurrence plus/minus the standard deviation for the models containing distal and proximal environmental variables and proximal only. See Table 2 for forage species scientific names.

Forage species	Number of observed occurrences	Observed occurrence (%)	Probability of occurrence (%) (Distal-Proximal)	Probability of occurrence (%) (Proximal-only)
Grasses				
Bluebunch wheatgrass	473	16.3 ± 19.93	19.5 ± 11.91	17.8 ± 5.74
Sandberg bluegrass	117	3.3 ± 4.47	3.4 ± 1.43	6.6 ± 2.59
Sedge spp.	11	0.3 ± 0.57	1.1 ± 0.60	0.9 ± 0.31
Idaho fescue	89	3.2 ± 5.57	1.9 ± 1.45	7.6 ± 4.00
Pinegrass	168	2.9 ± 6.45	0.3 ± 0.22	1.3 ± 0.97
Forbs				
Common yarrow	101	2.8 ± 2.84	0.7 ± 0.19	1.0 ± 0.33
Lupine spp.	14	0.4 ± 0.88	0.7 ± 0.27	1.8 ± 0.36
Arrowleaf balsamroot	57	2.2 ± 4.33	1.9 ± 1.55	1.1 ± 0.40
Sticky purple geranium	0		0.0 ± 0.02	0.0 ± 0.01
Shrubs				
Mountain big sagebrush	0		1.4 ± 1.19	1.7 ± 1.61
Common snowberry	419	10.1 ± 10.54	1.8 ± 0.57	2.3 ± 0.55
Creeping Oregon grape	181	4.8 ± 6.88	0.7 ± 0.36	0.8 ± 0.24
Saskatoon serviceberry	15	0.3 ± 0.46	0.3 ± 0.13	0.8 ± 0.08
Antelope bitterbrush	0		1.2 ± 1.30	2.4 ± 3.15
Mallow ninebark	173	2.9 ± 8.70	0.3 ± 0.25	0.2 ± 0.14
Trees				
Willow spp.	2	0.0 ± 0.11	0.1 ± 0.11	0.6 ± 0.46
Chokecherry	0		0.9 ± 0.49	0.6 ± 0.03
Douglas-fir	9	0.6 ± 1.68	0.2 ± 0.07	0.2 ± 0.15
Quaking aspen	0		0.1 ± 0.10	0.2 ± 0.17
Lodgepole pine	0		0.0 ± 0.003	0.0 ± 0.005

habitat patches than the predicted occurrences for both distal-proximal and proximal models (Table 2). In most cases there was overlap between observed and predicted occurrence comparing the average occurrence plus or minus the standard deviation. Only the predictions for lupine and willow using proximal variables were outside the range (mean ± s.d.) of observed occurrences, but these forage species were also rarely observed.

Table 3

Statistics for all forage species in the Rinker Rock Creek Ranch (RRCR) Biological Research Station validation polygons ($n = 183$), including number of observed occurrences, mean percent observed occurrence plus/minus the standard deviation, and mean probability of occurrence plus/minus the standard deviation for the models containing distal and proximal environmental variables and proximal only. See Table 2 for forage species scientific names.

Forage species	Number of observed occurrences	Observed occurrence (%)	Probability of occurrence (%) (Distal-Proximal)	Probability of occurrence (%) (Proximal-only)
Grasses				
Bluebunch wheatgrass	1741	5.2 ± 6.19	11.2 ± 4.35	9.2 ± 1.44
Sandberg bluegrass	3673	11.2 ± 9.50	8.3 ± 3.50	11.5 ± 3.17
Sedge spp.	910	2.5 ± 8.58	4.9 ± 4.07	5.0 ± 2.57
Idaho fescue	877	2.7 ± 6.58	2.2 ± 2.20	1.6 ± 0.96
Pinegrass	0		0.3 ± 0.35	0.3 ± 0.31
Forbs				
Common yarrow	142	0.4 ± 1.04	0.7 ± 0.18	0.7 ± 0.16
Lupine spp.	1020	3.1 ± 3.99	2.7 ± 1.42	2.2 ± 0.72
Arrowleaf balsamroot	478	1.4 ± 2.54	0.6 ± 0.32	0.5 ± 0.23
Sticky purple geranium	30	0.1 ± 0.42	0.1 ± 0.03	0.0 ± 0.04
Shrubs				
Mountain big sagebrush	4614	13.7 ± 13.89	11.3 ± 4.32	7.9 ± 2.75
Common snowberry	148	0.5 ± 3.07	1.0 ± 0.38	0.9 ± 0.19
Creeping Oregon grape	23	0.1 ± 0.60	0.4 ± 0.22	0.9 ± 0.27
Saskatoon serviceberry	3	0.0 ± 0.15	0.1 ± 0.08	0.7 ± 0.03
Antelope bitterbrush	1105	3.1 ± 5.44	1.6 ± 1.25	13.2 ± 8.15
Mallow ninebark	0		0.4 ± 0.22	0.1 ± 0.07
Trees				
Willow spp.	1087	2.9 ± 12.38	0.2 ± 0.42	0.8 ± 0.76
Chokecherry	228	0.7 ± 4.07	0.3 ± 0.12	0.5 ± 0.02
Douglas-fir	0		0.1 ± 0.04	0.1 ± 0.06
Quaking aspen	105	0.3 ± 2.41	0.3 ± 0.21	0.2 ± 0.18
Lodgepole pine	0		0.0 ± 0.01	0.0 ± 0.01

3.2.2. RRCR

The validation at RRCR recorded between 0 and 4,614 occurrences for the 20 forage species of interest (Table 3). The most common forage species and their average observed occurrence were mountain big sagebrush (13.7%), sandberg bluegrass (*Poa secunda*; 11.2%), bluebunch wheatgrass (5.2%), antelope bitterbrush (3.1%), willow (2.9%), and lupine (3.1%). Pinegrass, mallow ninebark, Douglas-fir, and lodgepole pine were not observed at all in the RRCR sampling. The biggest difference between predicted and observed average occurrence was 5.9% for bluebunch wheatgrass, which was over-predicted using distal-proximal variables, and 10.0% for antelope bitterbrush, which was over-predicted using proximal variables.

Like TWRS, the observed occurrences at RRCR displayed much higher variance between habitat patches than the predictions for either model. (Table 3). Only predictions for saskatoon serviceberry using the proximal model were outside the range (mean ± s.d.) of observed occurrences, but this forage species was rarely observed.

4. Discussion

Using a novel approach that combines fine-scale habitat patches derived from object-oriented segmentation and lasso logistic regression, we predicted forage species occurrence across Idaho at a fine-scale (i.e., habitat patches) for 20 forage species suitable for mule deer and Rocky Mountain elk. We also assessed if the inclusion of distal variables improved model performance beyond proximal variables only. We observed that all models provided higher predictive accuracy than chance, with an average AUC of 0.84 for distal-proximal variables and an AUC of 0.81 for proximal variables. The inclusion of distal variables produced slightly higher overall AUC values, demonstrating the value of including environmental variables in SDMs that have indirect effects on forage.

4.1. Model accuracy and environmental variables

While predictive accuracies were only slightly higher for models using distal-proximal variables, in some cases they generated drastically different statewide patterns. We compared our predicted occurrence maps to the USDA NRCS plant guide (https://plants.sc.egov.usda.gov/), which provides coarse (county level) species distribution maps. Visual comparisons suggest the distal-proximal models better represented statewide distribution, although there were some exceptions. For example, neither mountain big sagebrush nor antelope bitterbrush are commonly found in northern Idaho (Patterson et al., 1985), which suggests that the distal-proximal model performed better for mountain big sagebrush in that region, while the proximal model performed better for antelope bitterbrush (Figs. 3 and 4). Additionally, the proximal model predicted willow occurrence throughout the state, while the distal-proximal model was limited to southern Idaho, in contrast with the findings of Schrempp et al. (2019). This suggests that variables beyond those with proximal effects are useful for SDMs on a species by species basis. In some cases, proximal variables alone may be suitable and have the advantage of containing fewer inputs (i.e., greater parsimony).

In addition to demonstrating overall good predictive properties, our models revealed key species-environment relationships that can be supported by ecological theory. For example, pinegrass is predominately a forest species and exhibits increased growth in years with higher precipitation and/or cooler temperatures (Matthews, 2000; Parish et al., 1996). Respectively, our model exhibited positive correlations with percent tree canopy cover and 30-year normal minimum precipitation, and negative correlations with percent shrub canopy cover and 30-year normal minimum temperature. Pinegrass also has high soil water usage during its rapid early-season growth and acts as an aggressor for soil moisture which may explain the positive correlation observed with soil available water supply (Matthews, 2000). Our model also had a negative correlation with depth to soil restrictive layer which may be explained by pinegrass' sod-forming root system and occupancy of shallower sites (Agee, 1993; Matthews, 2000). Furthermore, our models indicated a strong positive effect from fire frequency, which is reasonable given that pinegrass is often present following high-severity wildfire events (Johnson, 1998; Matthews, 2000). Such inferences are needed to better examine forage distributions, quantity, and timing, and we were able to pick out similar results for all the forage species models. Therefore, our results should be useful in informing decisions related to habitat restoration aimed at improving nutritional conditions for ungulates, for example when prioritizing specific areas for restoration. Our models could help identify locations that maximize suitability for restoring multiple forage species, and if used in conjunction with disturbance severity information (e.g., wildfire severity, or livestock grazing management), could inform how disturbance regimes might be harnessed to help manage ungulate habitat.

There are some notable limitations with some of the environmental variables, although they were included because they represent an integration of the best available data in remote sensing, landscape fire and succession modelling, and predictive landscape mapping available for the entire state. For example, only fires larger than 404 ha (1,000 ac) are included in MTBS for Idaho (Eidenshink et al., 2007). Additionally, MTBS generates wildfire layers using entire fire perimeters meaning unburned or low severity areas within perimeters are not accounted for separately and may result in commission errors (Sparks et al., 2015). The soil data we used varied in spatial resolution across the state. Areas with prime agricultural land were mapped at fine-scale, but many large remote areas of the state such as wilderness areas were attributed with a single value for each soil variable. This issue raises questions about the effectiveness of the models using currently available soil datasets in remote areas. A potential solution for future studies is use of the probabilistic remapping of SSURGO (POLARIS; Chaney et al., 2016), which models missing values such as those observed in remote areas of Idaho. Lastly, some variables were shown to be less important by the lasso selection process. For instance, elevation, a distal variable, was eliminated for 9 of 20 distal-proximal models, suggesting its impact might be captured by proximal variables. Fire frequency and time since last fire were not selected from at least half of the proximal models. Fire is known to be an important driver in vegetation occurrence (Agee, 1993), but the rarity with which it occurs compared to the area of Idaho gave us few reference points for the training data.

Ideally, our analysis would have included all temporal stages of disturbance and succession. Adequately capturing each successional stage following an event like wildfire would benefit the models by providing reference observations for any given point in time. To better capture disturbance and successional state, two areas of improvement could be made to strengthen the models. First, additional training data that captures successional states for both wildfire and other disturbances not accounted for here (e.g., drought, insects and disease, grazing) would improve the range of reference conditions in the models. Second, we suggest other variables might be considered, such as: shrub cover at finer resolutions (i.e., less than 30 m), tree structural layers, seasonal effects of temperature and precipitation (e.g. growing season precipitation), influences of interactions with other plant species, and disturbance severity, including wildfire or herbivory.

4.2. Model validation

Model validation was performed in two ways. Cross validation, which allows for validation of the model by holding back a portion of the training data during each iteration, was used to generate a more robust model. The resulting AUC values indicated that the models performed well across the training regions. However, because training data was unevenly distributed across the state, additional validations were conducted to assess the model's predictive power in two areas. The validation at TWRS was limited (i.e., only nine polygons were tested), but it provided an opportunity for validation of some forage species not detected at RRCR. Furthermore, even with a limited sample, predictions for all forage species were on average within 8.3% of observed, suggesting functional accuracy at the landscape level. Commission errors were minimal for most forage species, meaning that forage species not observed were also modelled at nearly 0% probability (Table 2).

The validation at RRCR provided a larger sample than TWRS. Average predictions at RRCR were within 10% for proximal models and within only 5.9% for distal-proximal models (Table 3). Commission errors were also small. This supports the results at TWRS showing that the models accurately represented average forage species occurrence across the landscape. However, for both validations the observed occurrences were more variable than the predicted occurrences, suggesting the models were not able to capture the heterogeneity at the level of the habitat patches. This may have been due to the scale of the environmental variables, which was coarser than many of the segmented polygons and would have therefore not sufficiently differentiated adjacent habitat patches.

Our results are encouraging for wildlife managers making decisions regarding habitat management to address nutritional quantity and quality for ungulates across large areas, such as Idaho. The validation suggests that the average probability of occurrence for both models is within 10% of observed. However, at the scale of habitat patches, the models are underfit such that the observed occurrence of a forage species within a habitat patch might be quite different. At the extreme, we observed one polygon at RRCR with a distal-proximal model prediction for willow that was 77.4% lower than the observed value, and a proximal model prediction that was 76.8% lower. Such drastic underpredictions were outliers, but they show how errors for individual habitat patches can be significant.

4.3. Modelling approach

Our use of the lasso logistic regression to achieve model optimization, variable selection, and coefficient estimation for forage distribution modelling has been implemented infrequently in ecological research (Gastón and García-Viñas, 2011; Huang and Frimpong, 2015; Schrempp et al., 2019). One of the greatest challenges in SDMs is selecting appropriate candidate variables (Araújo and Guisan, 2006; Elith and Leathwick, 2009), and the lasso process provides a reasonable solution. It restrains the effects of the coefficients to identify variables that contribute little to the explanation of the response and removes those variables from the model. Consequently, the lasso process treats issues with multi-collinearity and reduces model complexity (Dormann et al., 2013; Hastie et al., 2017; Tibshirani, 1996). This approach is useful in situations like ours, where the information about numerous environmental variables and their relative influence on multiple forage species is limited.

Ideally, expert knowledge regarding the underlying mechanisms, interactions, and complex relationships between forage species and environmental variables, and between variables themselves should be incorporated in SDMs (Austin, 2002; Evans et al., 2011). This was supported by our finding that simply using proximal or distal-proximal variables did not improve models for all forage species. However, determining known interactions requires better a priori knowledge about the forage species being modelled and more careful sampling design than what was available for our study (Wisz et al., 2013). Our approach was a necessary simplification of the ecological processes that limits where forage occurs to create models that can predict forage occurrence across broad scales.

A non-parametric algorithmic approach like MaxEnt could have been used to explore non-intuitive relationships (Evans et al., 2011). However, MaxEnt previously required complex refinements of software settings, while the process for fitting lasso logistic regression was simple and widely re-producible. Phillips and Dudik (2008) found with specific parameter tuning, MaxEnt was effective in modelling distributions of 226 plant species from 6 regions, but this kind of detailed parameter tuning requires good statistical knowledge and their findings suggest more regularization may be needed if the number of environmental variables exceeds 11–13. The release of open-source MaxEnt software (Phillips et al., 2017) resolves the issues of model transparency and methods for regularization, which should broaden its appeal. Still, our expectations were to estimate the relative effects of environmental variables on forage species occurrence, and extrapolate this information to predict distributions statewide, which is not as straight forward with non-parametric methods (Phillips and Dudik, 2008; Whitley and Ball, 2002). Additionally, others have shown that lasso logistic regression performs better than MaxEnt at finer resolutions (Huang and Frimpong, 2015), which was a critical aspect of our study. There are other approaches, such as nearest-neighbor imputation, which can capture the complex variance-covariance structure of unknown relationships (Henderson et al., 2014). Further research toward leveraging the relationships between plant species in SDMs is worthwhile but beyond the scope of our study. Additionally, the need for fine-resolution environmental variables will be an issue for any SDM and should be considered a priority for future efforts.

5. Conclusions

Our novel approach demonstrates an effective method for estimating probabilities of forage species occurrence at fine spatial resolutions across broad landscapes to inform nutritional quantity and quality of ungulate habitat. Our models can be tailored by wildlife resource managers to assess the nutritional conditions of habitat for other individual herbivore species, including species of conservation interest such as greater sage-grouse, depending on forage preference and nutritional need. Furthermore, distal environmental variables, which exert indirect effects on forage, can help improve model accuracy beyond proximal (direct) variables alone. The validations at TWRS and RRCR indicate that model errors can be high for individual habitat patches, but average errors across larger areas are small. Additionally, we suggest that variables such as shrub cover at finer resolutions (i.e., less than 30 m), tree structural layers, and more detailed disturbance history may improve future iterations of the models. Finally, our models can be a management tool to predict the presence of forage species across Idaho to inform habitat management and restoration that improves nutritional quality and quantity of ungulate habitat and in turn ensures the long-term persistence of ungulate populations.

Declaration of Competing Interest

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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