

Identifying the Impact of Biotic Interactions on Meadow Species Distributions in Sagebrush and Bunchgrass Dominated Systems

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Abstract

Understanding drivers of species distributions is an important challenge for more accurately projecting ecological change under climate warming. Species distributions have often been modeled using solely environmental factors as predictors. However, there is much recent data supporting the hypothesis that biotic interactions strongly influence species distributions at both local and global scales. This study aims to provide data on how existing plant communities alter the realized ranges of other species. By comparing species distribution model (SDM) predictions with field observations, we analyzed the effects of two taxa of dominant plant cover, sagebrush and a Fescue bunchgrass, upon the distributions of ~20 different herbaceous meadow species in a subalpine valley in western Colorado. This data will add to our understanding of how plant community dynamics interact with observed distributions across scales.

Introduction

Predicting how plant communities will respond to climate change is a major challenge in Ecology. Climate models project environmental zones shifting over the next century (Burrows et al. 2011). Understanding how plant species ranges may track these changes is an important challenge for land managers and conservationists. Species Distribution Models (SDMs) are often created using abiotic environmental factors as major predictors, however there is growing evidence that biotic interactions play a large role in shaping distributions (Palacio and Girini, 2018, Staniczenko et al., 2018, Boulangeat et al., 2012), and that this is relevant at not only local but also global scales (Araújo and Luoto, 2007). Incorporating biotic interactions into these models can boost performance, but given the complexity of interspecific interactions, more data is required to better understand how they give rise to observed plant community assemblages at a landscape scale.

Much work has shown that both competition and facilitation occur in plants within subalpine to alpine meadows (Kikvidze et al., 2001, Wang et al., 2008, Dyer and Rice, 1999). Subalpine meadow communities often exhibit high plant diversity as well as a wide range of habitat heterogeneity. Plant community assemblages across these systems are often driven by abiotic environmental factors and influenced by patches associated with a dominant cover type (Langenheim, 1962). This patchwork of plant communities provides an ideal environment for testing hypotheses of how interspecific interactions may influence species ranges.

In this study, two taxa of dominant cover types were selected. These include sagebrush species of the genus *Artemisia*, and the bunchgrass *Festuca thurberi*. These taxa tend to dominate patches across the subalpine to alpine landscape of the East River valley, in Gunnison County, Colorado. Understanding the community ecology associated with sagebrush and bunchgrass is

important, as both sagebrush and bunchgrass are projected to expand their ranges in subalpine zones as the climate warms. Artificial warming experiments within the study area have shown a significant increase of sagebrush in warmed plots (Perfors, et al., 2003), and both taxa tend to dominate as soil moisture decreases (Berlow et al, 2002). These taxa provide a study system within which to compare the effects their populations have on surrounding meadow species.

In order to study these interactions, we selected 25 focal species of herbaceous plants common in subalpine meadows in the study region. We sampled throughout environments in the East River valley, in order to capture a range of environmental types. Using these as well as additional data collected in previous years, we developed SDMs for each of the focal species. The predictions from these models, taking into account only abiotic environmental variables, were then compared against field data collected in both sagebrush and bunchgrass dominated environments. We hypothesized that both sagebrush and bunchgrass abundance would be associated with decreased presence and abundance of the focal plant species, an effect possibly caused through a combination of below-ground resource competition and above ground shading/crowding.

Methods

Site Identification

Sites were selected throughout the extent of the East River valley along an elevational gradient. The selection process was developed to (i) maximize environmental heterogeneity to provide data for SDMs, and (ii), to provide data on community composition in sagebrush or bunchgrass dominated areas. Using geographic information systems (GIS) software, randomized points were created across the extent of the study area. From these, 20 points were chosen as “site” centroids. Within each site, 8 plots representing different environmental facets were chosen.

Environmental facets were identified using a methodology adapted from Beier and Brost (2010). A stack of raster datasets representing different environmental predictor variables were combined using raster addition, to create a raster with unique values for each unique combination of relevant environmental characteristics. Raster datasets utilized included elevation, slope, aspect, flow accumulation, land cover classification, and mean date of snow disappearance. This was then converted to a vector data set where a polygon represented each unique area (facet) of the environment. Within this, randomized points were created in each of the polygons, and selected to become study plots.

Sampling

At each site, each of the 8 facet points were sampled as a 4 m² plot. Each plot was orientated north-south and divided into four 1 m² subplots (southwest, northwest, northeast, and southeast). At these plots, we noted general site characteristics, and percent cover of canopy, herbs, shrub, grass, rock, moss, soil, wood, and litter. We then identified percent cover of each of the 25 focal species within each subplot. Percent cover was estimated based on the classes: none, trace – 5%, 6-25%, 26-50%, 51-75%, 75-95%, and 96-100%. The percent cover of sagebrush or bunchgrass were also noted. GPS coordinates were taken (at ~ 30-70 cm accuracy using a Trimble Geo7X

handheld GPS system) for each of the four corners of the plots for accurate georeferencing. In total, 137 plots were sampled, representing 18 different sites. These included 33 plots with $\geq 20\%$ cover of sagebrush, and 33 plots with $\geq 20\%$ cover of bunchgrass, which were held out of the modelling for later comparison (Fig 1).

Plots Surveyed in Study Area

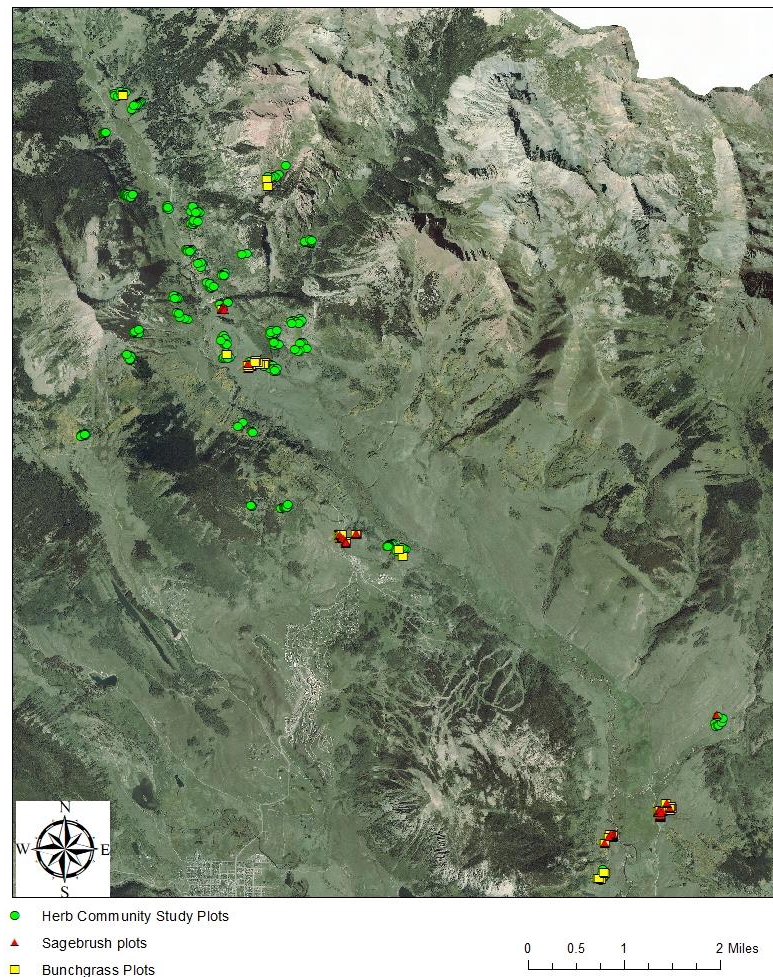


Figure 1: All plots surveyed in study area, including in sagebrush or bunchgrass dominated sites

Additional Data Collection

Data collected in previous years using similar methodology was also incorporated as additional training data for SDMs. 126 plots were incorporated from data collected in 2018 of percent cover data using the same cover classes and sampling methodology utilized in the present study. Another 128 field plots collected in 2018 in support of the NEON Airborne Observation Platform acquisition were incorporated as well. These plots used a slightly altered methodology in which percent cover was assessed in one 1 m² plot (as opposed to four 1 m² subplots per plot), and plant species presence was only noted if greater than 10% of the plot.

Species Distribution Modeling

Several model types were utilized to explore the predicted environmental niche space of the focal species. SDM model types included maximum entropy modeling (maxent) (Phillips et al, 2006), gradient boosting machines (Elith et al, 2008), and generalized additive modeling (Wood et al, 2014). The predictors for each model included the raster datasets on elevation, slope, solar irradiance, flow accumulation, land cover classification, and mean date of snow disappearance. Model outputs were combined, weighted by measures of model performance, in order to improve accuracy of predictions. The combination of models in SDM follows a technique known as ensemble forecasting, which can improve model performance, especially with small datasets (Araújo and New, 2007, Breiner et al., 2015).

Analysis

To test the hypothesis that sagebrush or bunchgrass dominated systems negatively impacted the distributions and abundances of the focal species, we analyzed predicted presences and abundance of each of the 25 focal species from the SDMs in comparison to field observations. For model predictions derived from presences/absences, a Generalized Linear Model (GLM) was fit, using predicted probability of presence as the independent, and observed presences as the dependent variables. A 1:1 linear model was fit as the null hypothesis, that the dominant species system had no effect on presence of the focal species. Findings were considered significant where the GLM deviated from the null model including 95% confidence intervals.

Results

Of the 25 species, 7 were excluded from the final analysis due to insufficient data. Figure 2 provides an example of the geographic output for the SDM, in this case for *Delphinium barbeyi*. 10 of the focal species showed a significantly reduced presence as compared to predictions in either or both sagebrush and bunchgrass dominated environments. Selected example plots showing decreased presences are shown in Figures 3-6, with the remaining plots listed in the appendix. Several of the species showed greater than expected presence in part of their range of environmental suitability predicted by the models, but this trend was only present in at some points, usually where SDMs predict low probability, and nonsignificant at higher probabilities (figures 7-9). Finally, figure 10 shows the overall findings on each of the focal species as which were found to be greater or lesser in their presence than predicted by SDMs in field sampling. This was assessed which species were consistently above or below the line of the null model, representing greater or lesser predicted presence. Comparisons of abundance vs models based on abundance data remain to be analyzed, as do the interactions between density of the cover types and presence of the focal species.

Delphinium barbeyi Species Distribution Model

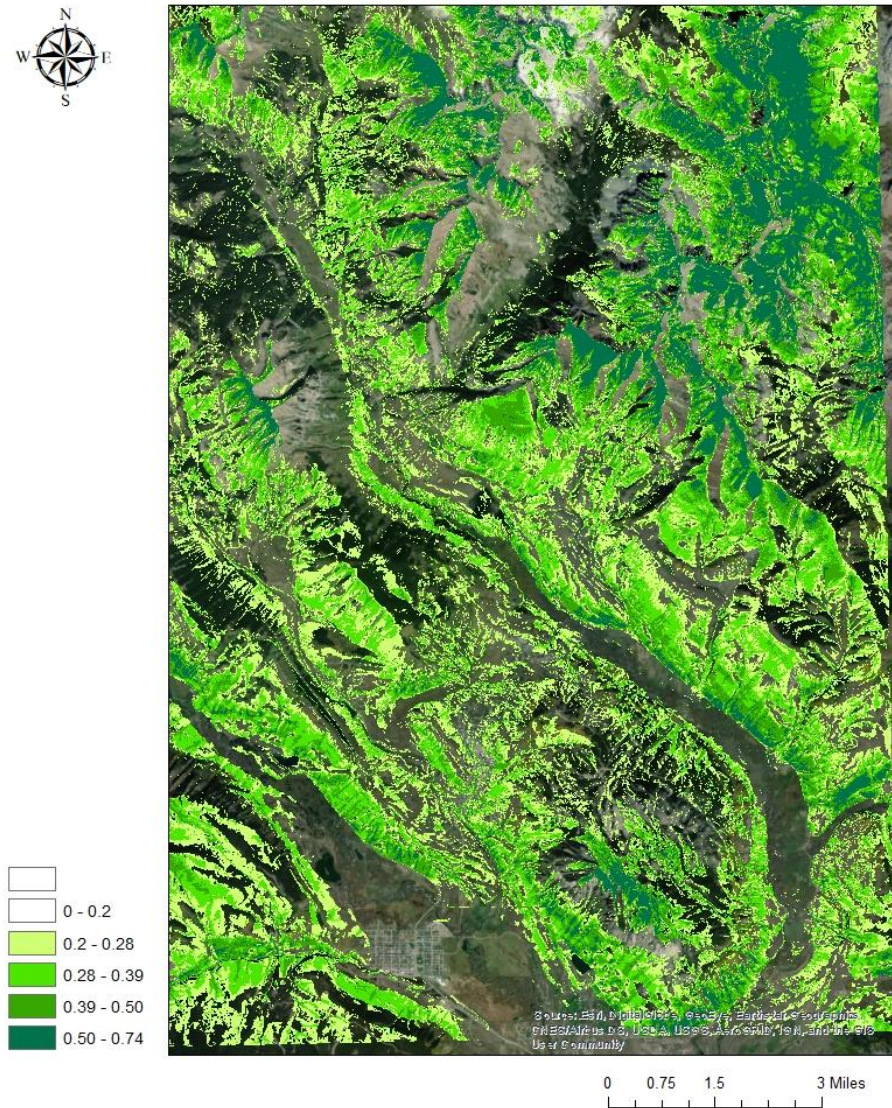


Figure 2: Species Distribution Model of *Delphinium barbeyi*

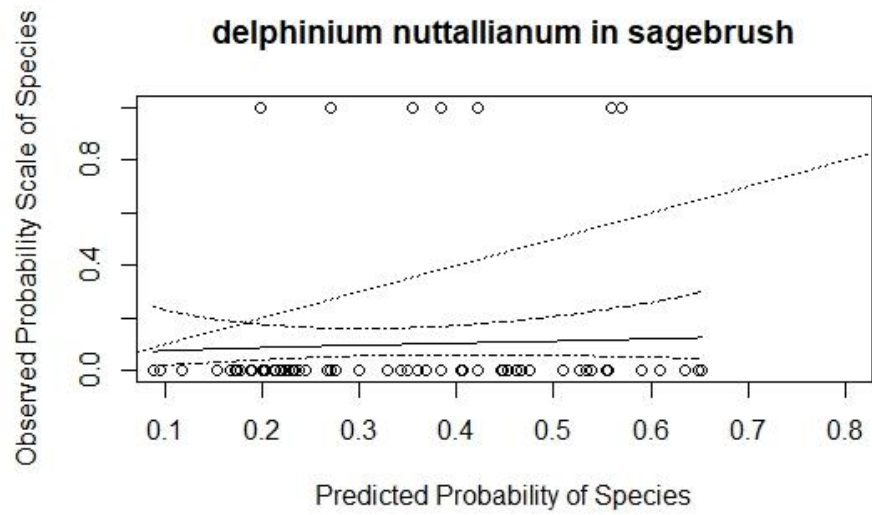


Figure 3: *Delphinium nuttallianum* predicted probability vs observed presence in sagebrush, with 1:1 null model line, showing lesser than expected presence

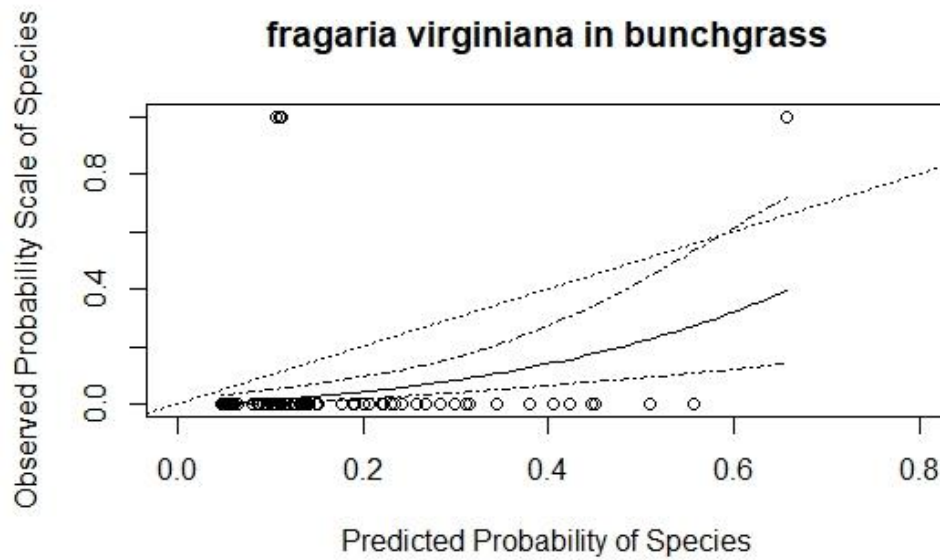


Figure 4: *Fragaria virginiana* predicted probability vs observed presence in bunchgrass, with 1:1 null model line, showing lesser than expected presence

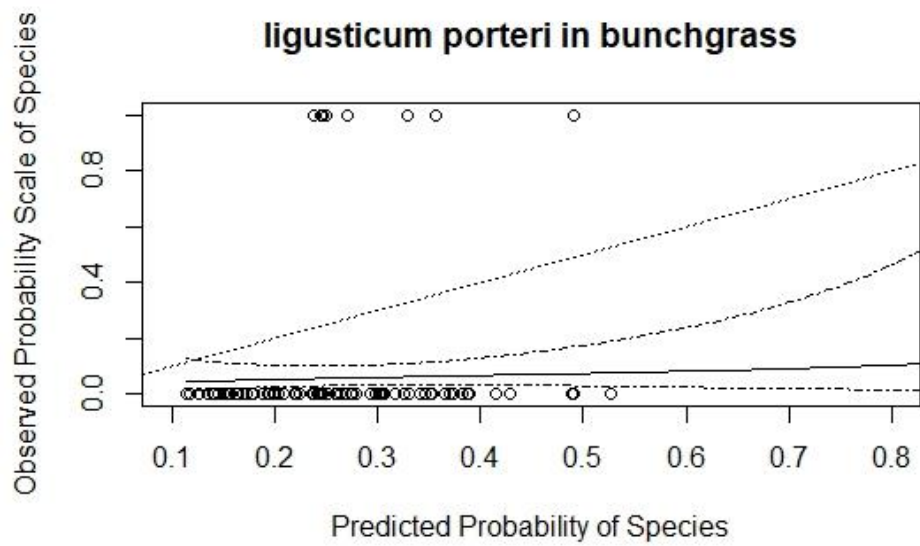


Figure 5: *Ligusticum porteri* predicted probability vs observed presence in bunchgrass, with 1:1 null model line, showing lesser than expected presence

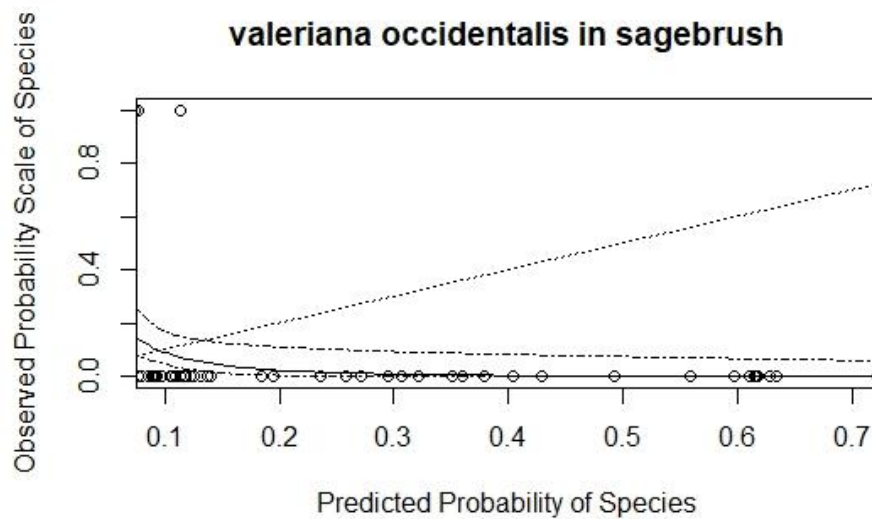


Figure 6: *Valeriana occidentalis* predicted probability vs observed presence in sagebrush, with 1:1 null model line, showing lesser than expected presence

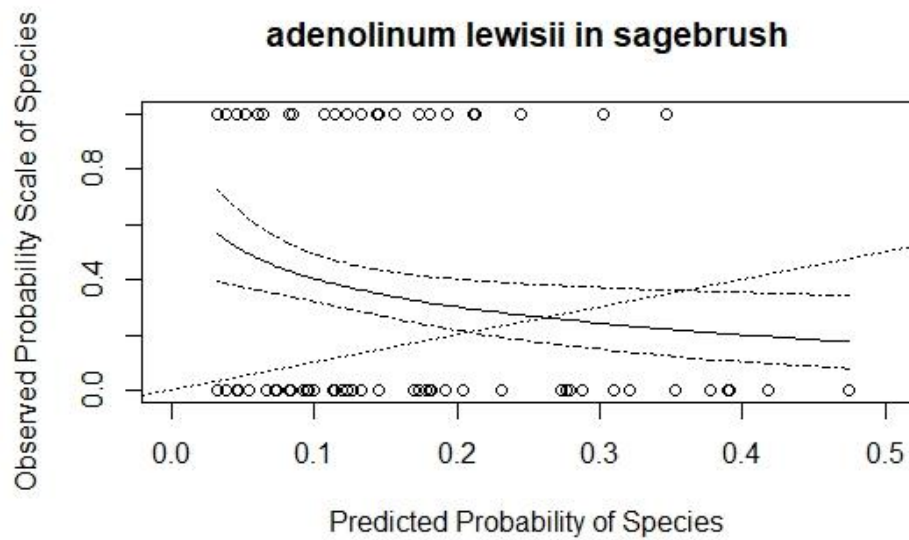


Figure 7: *Adenolinum lewisii* predicted probability vs observed presence in sagebrush with 1:1 null model line, showing higher than expected presence at low predicted habitat suitability but lower than expected presence at higher predicted habitat suitability

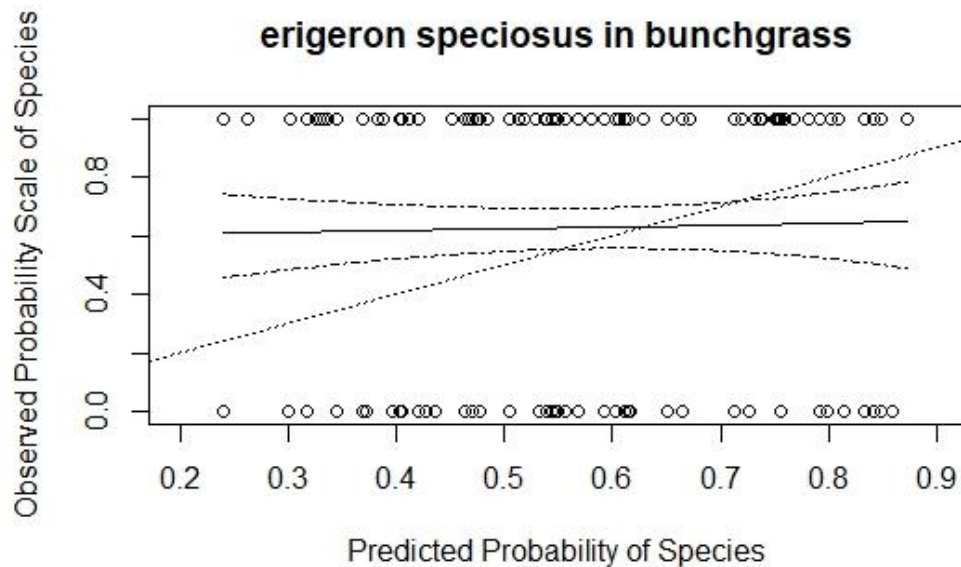


Figure 8: *Adenolinum lewisii* predicted probability vs observed presence in sagebrush with 1:1 null model line, showing higher than expected presence at low predicted habitat suitability but lower than expected presence at higher predicted habitat suitability

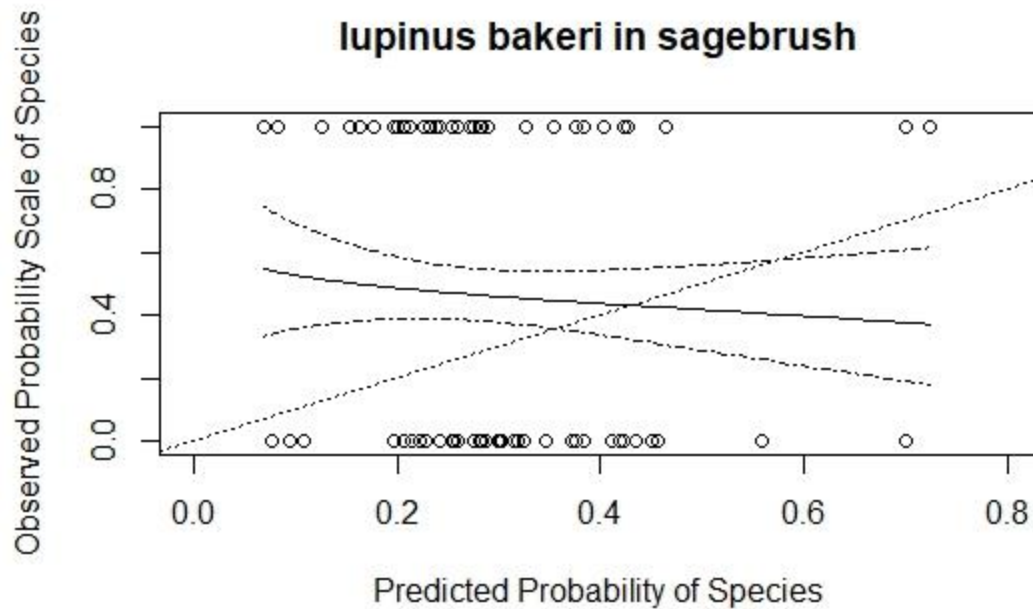


Figure 9: *Adenolinum lewisii* predicted probability vs observed presence in sagebrush with 1:1 null model line, showing higher than expected presence at low predicted habitat suitability but lower than expected presence at higher predicted habitat suitability

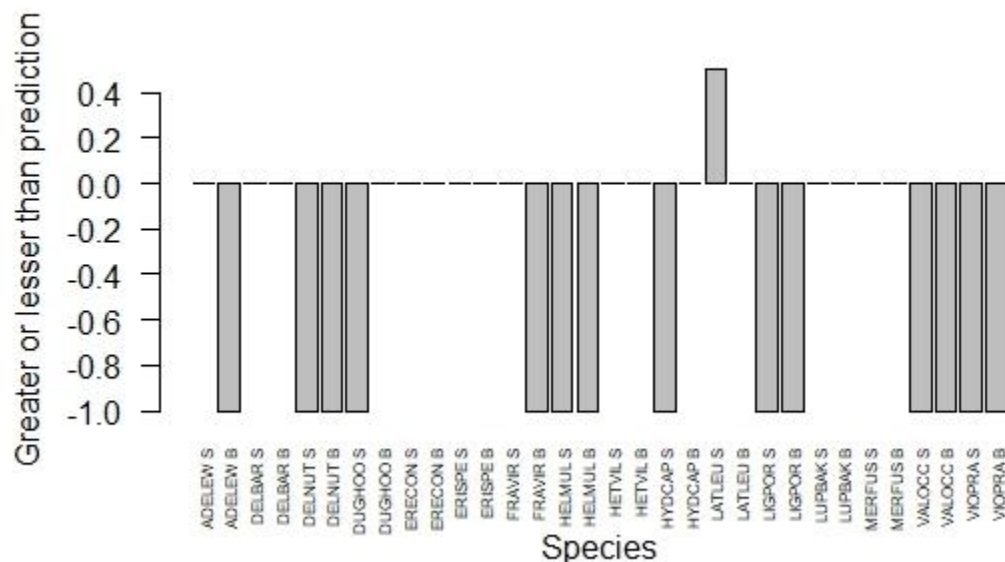


Figure 10: An overview of which species were consistently above or below (1, -1) expected values in both sagebrush and bunchgrass habitats, the only positive value is *Lathyrus leucanthus* which was only partially (not fully) above predicted values across the range of predictions

Discussion

Our analyses show that it is possible to relate SDM predictions based on abiotic environmental factors to observations in the presence of other species and identify where discrepancies may occur. However, much work remains to be done in our analysis, as well as in determining if this is a method to incorporate biotic interactions into models or develop hypotheses about how community dynamics affect species ranges at different scales. In continuing this analysis, SDMs will continue to be refined in order to more accurately reflect suitable abiotic environments. Models based on abundance will be further developed to compare directly against observed abundances, which may provide additional information to models missed by presence and absence data alone. Modeling the responses of both presence and abundance to changes in density of the cover types assessed will also be carried out, in order to determine how this factor affects the patterns observed in the existing data. Future directions for this area of study include modelling distributions in the presence of different types of cover, different environments, and larger spatial scales. Incorporating as much empirical data as possible to answer the question of what role biotic interactions play in shaping patterns of distribution will continue to be an important challenge.

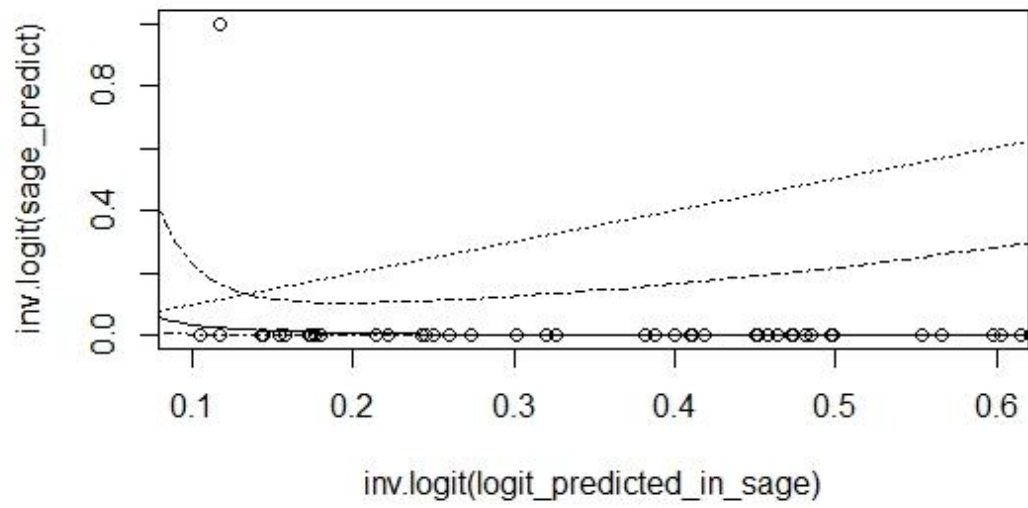
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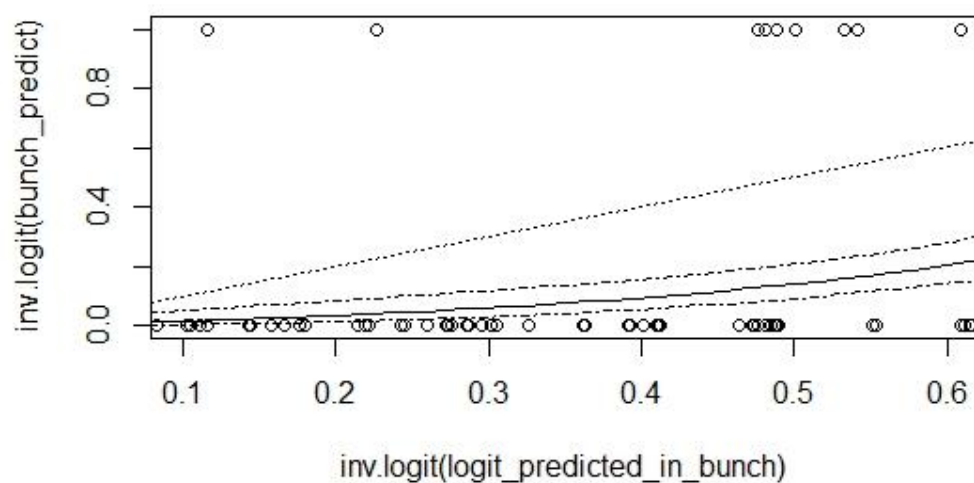
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Appendix

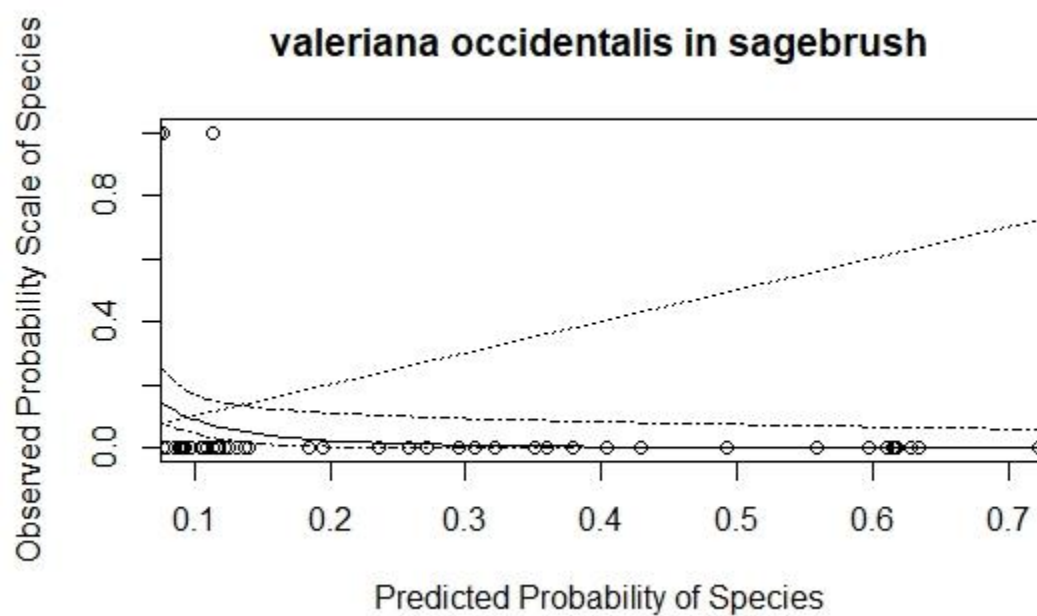
viola praemorsa in sagebrush



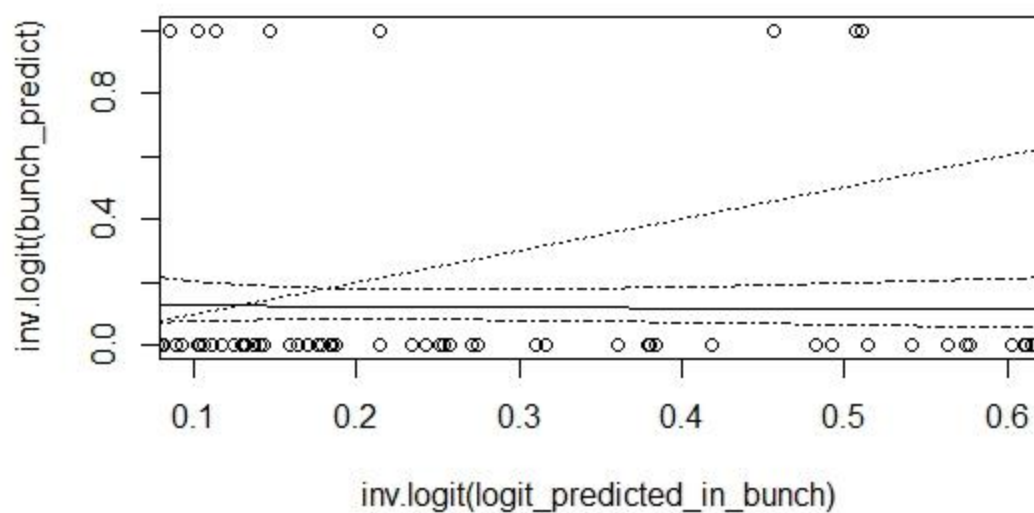
viola praemorsa in bunchgrass



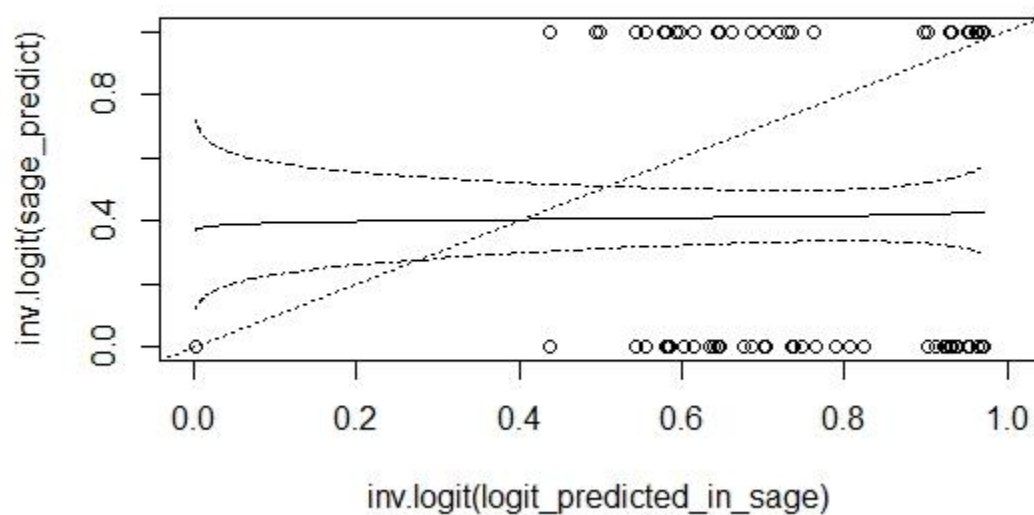
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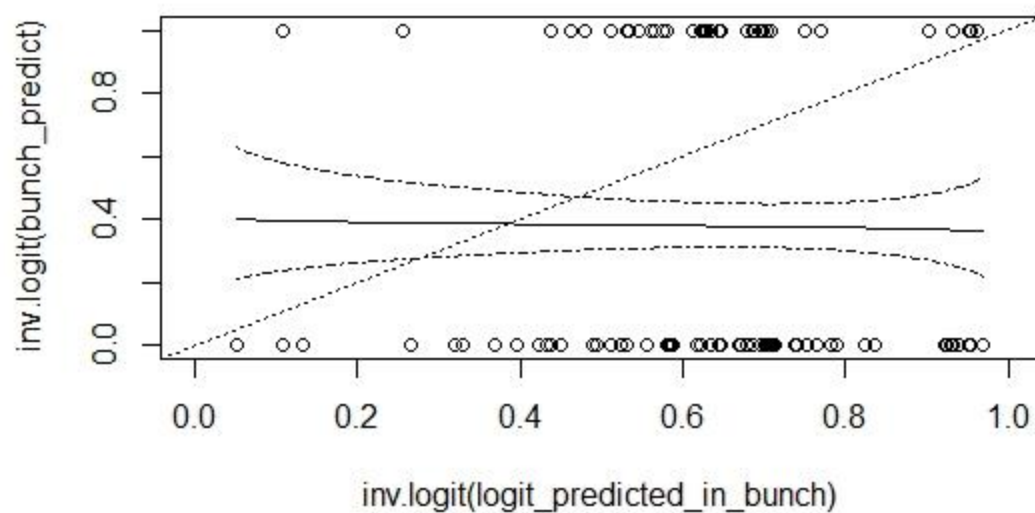
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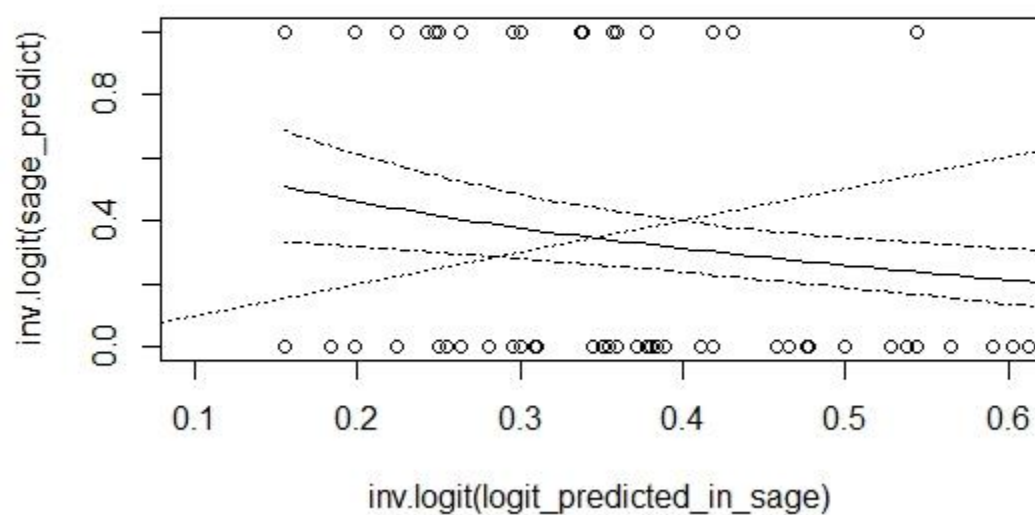
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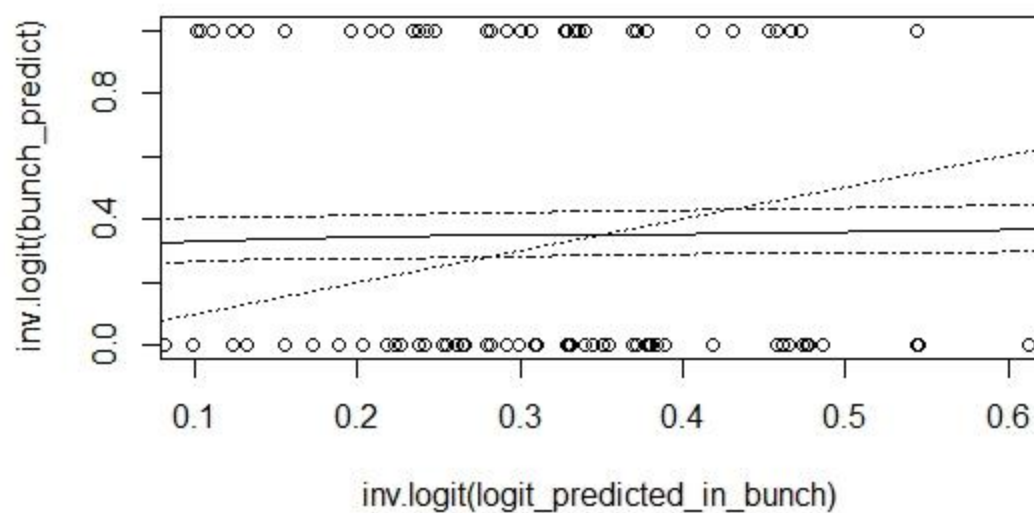
potentilla pulcherrima in bunchgrass



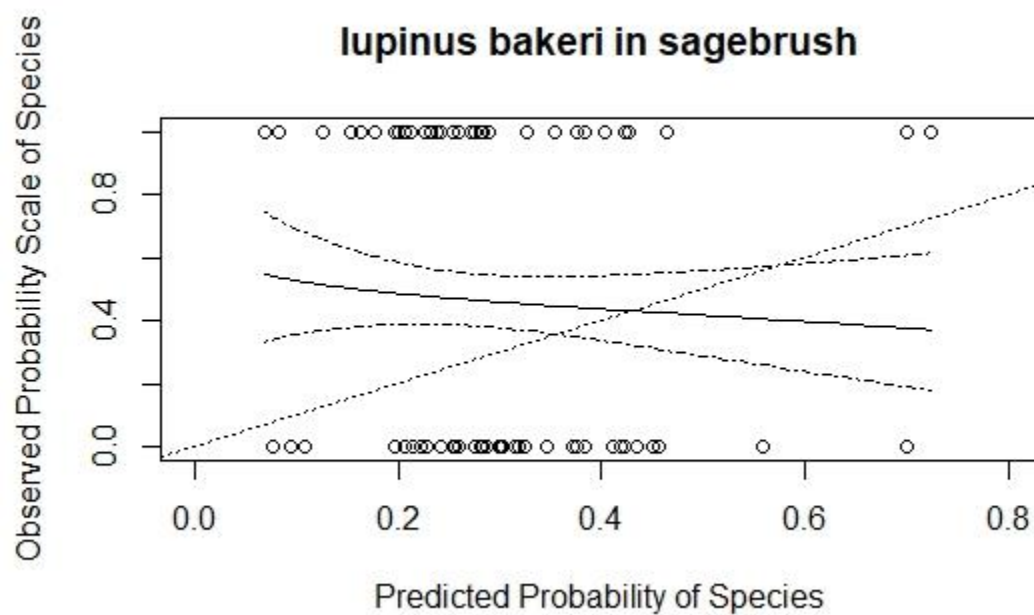
mertensia fusiformis in sagebrush



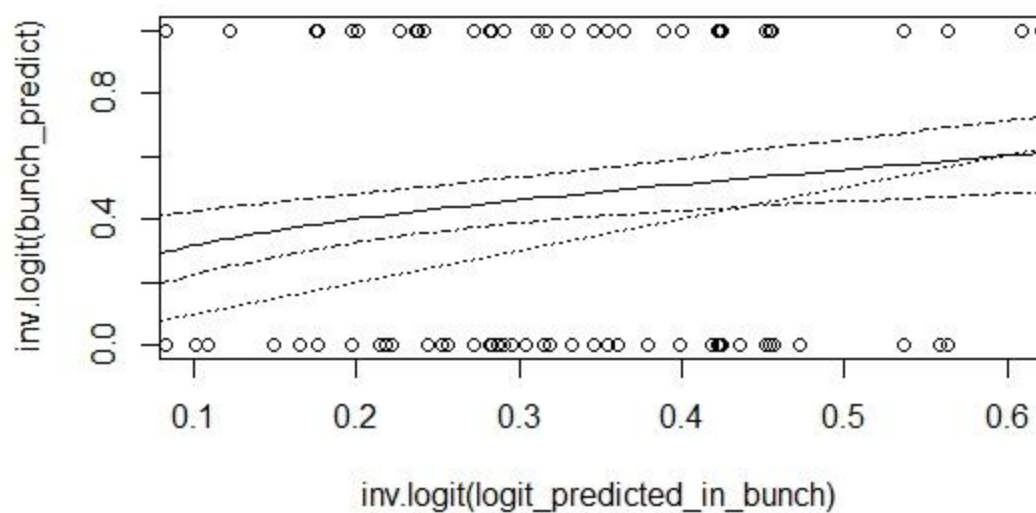
mertensia fusiformis in bunchgrass



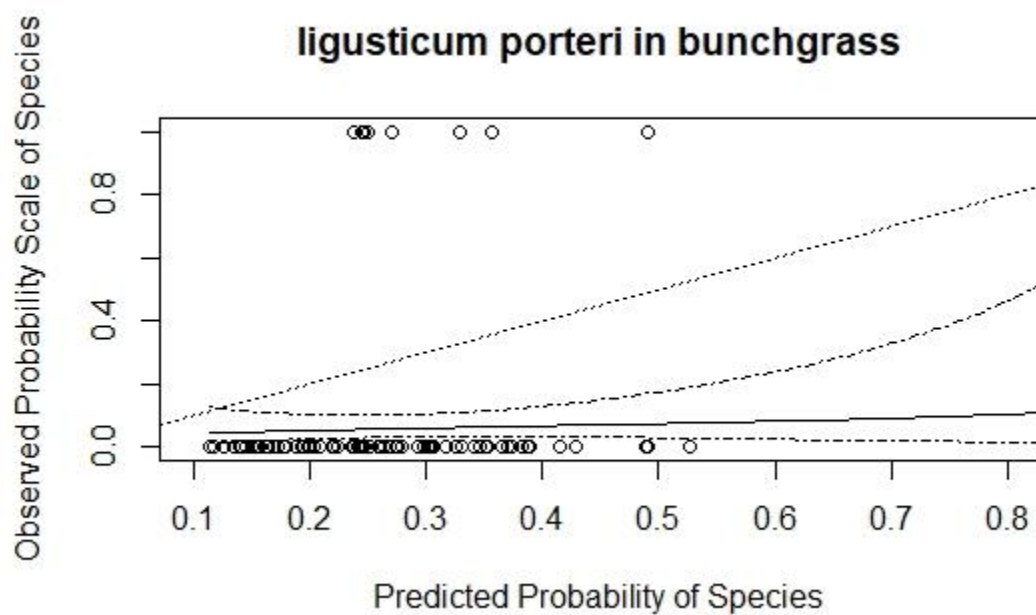
lupinus bakeri in sagebrush



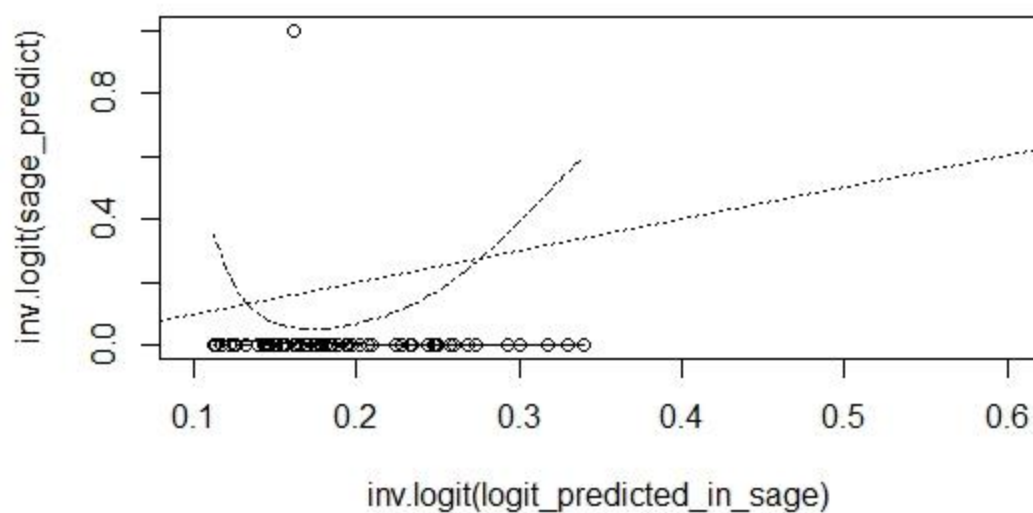
***lupinus bakeri* in bunchgrass**



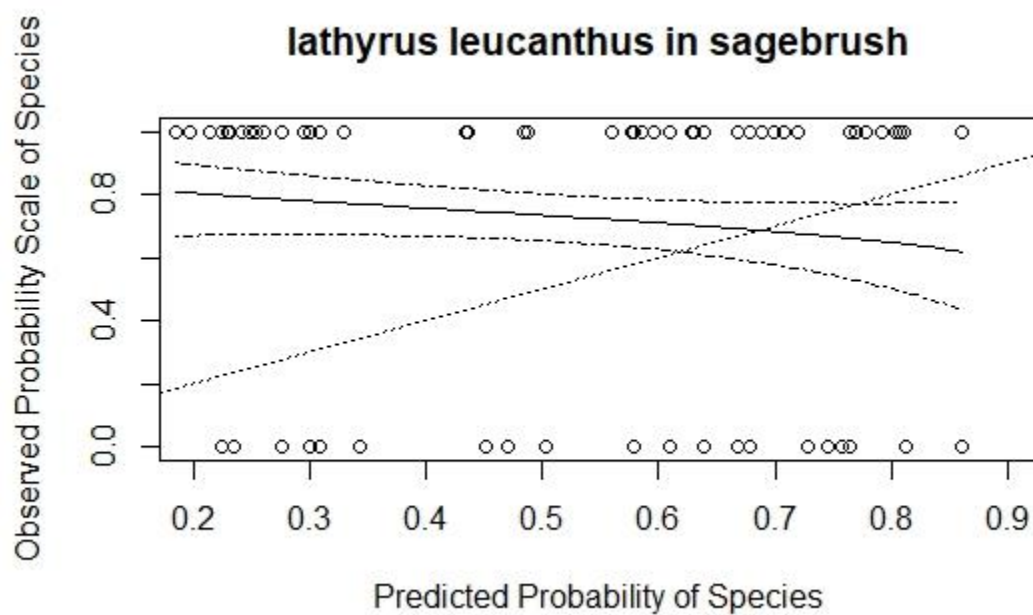
***ligusticum porteri* in bunchgrass**

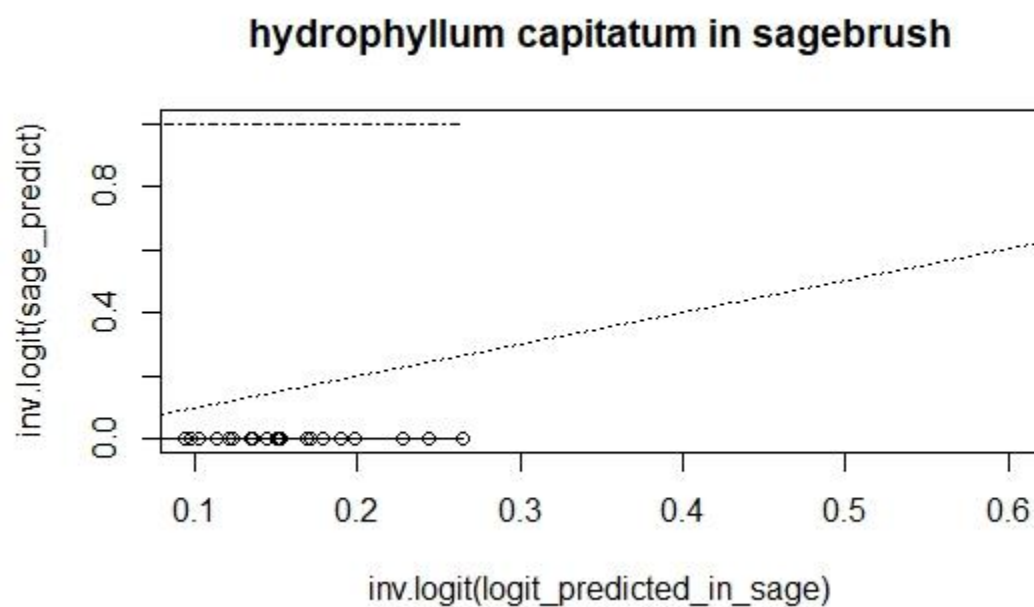
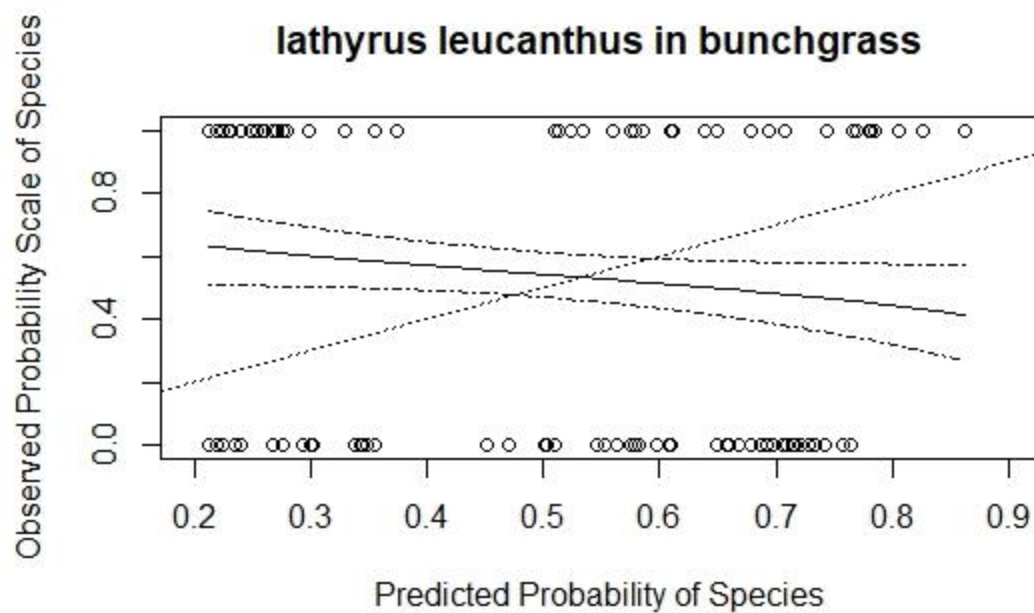


ligusticum porteri in sagebrush

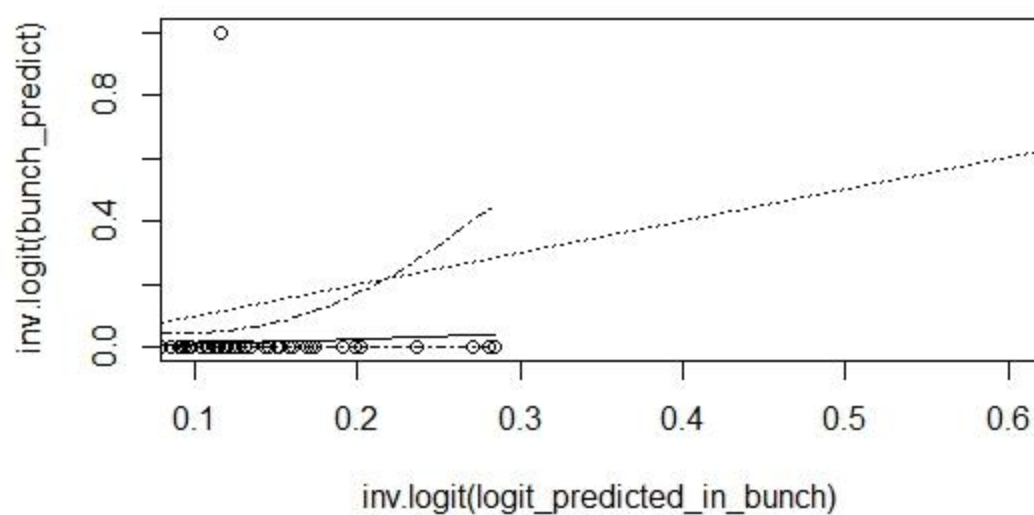


lathyrus leucanthus in sagebrush

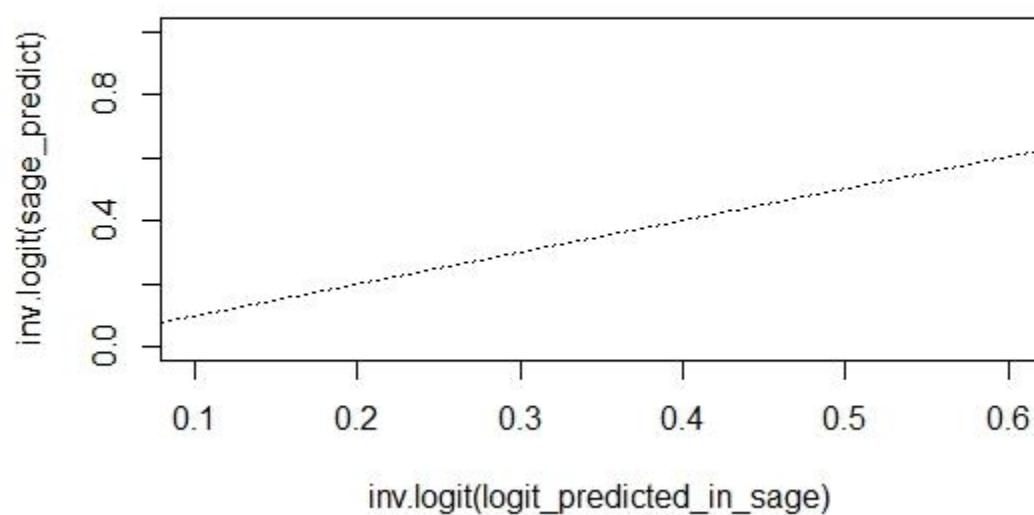




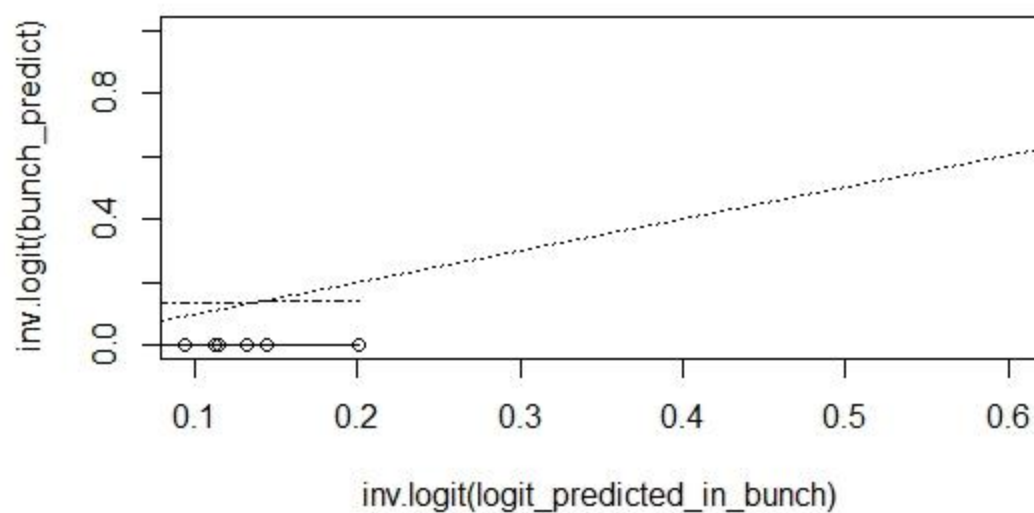
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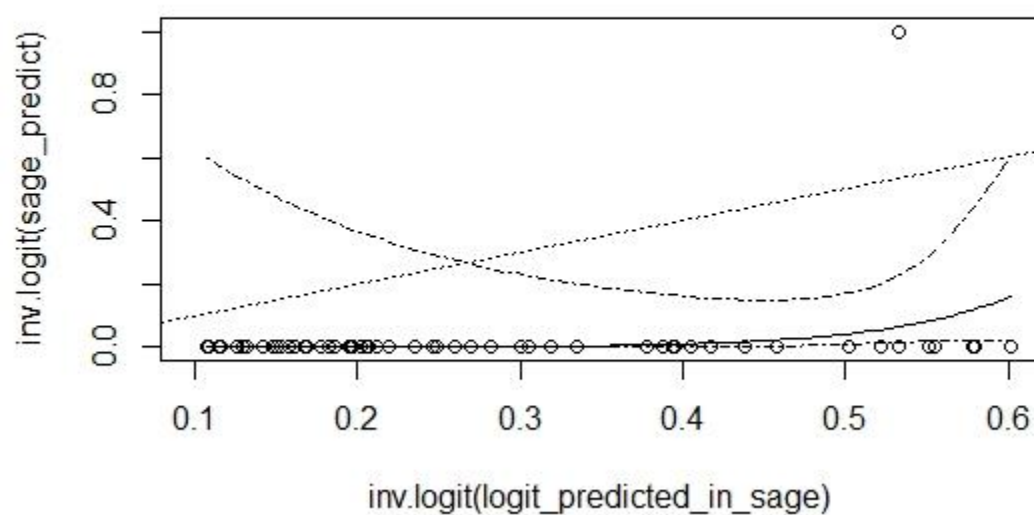
heterotheca villosa in sagebrush



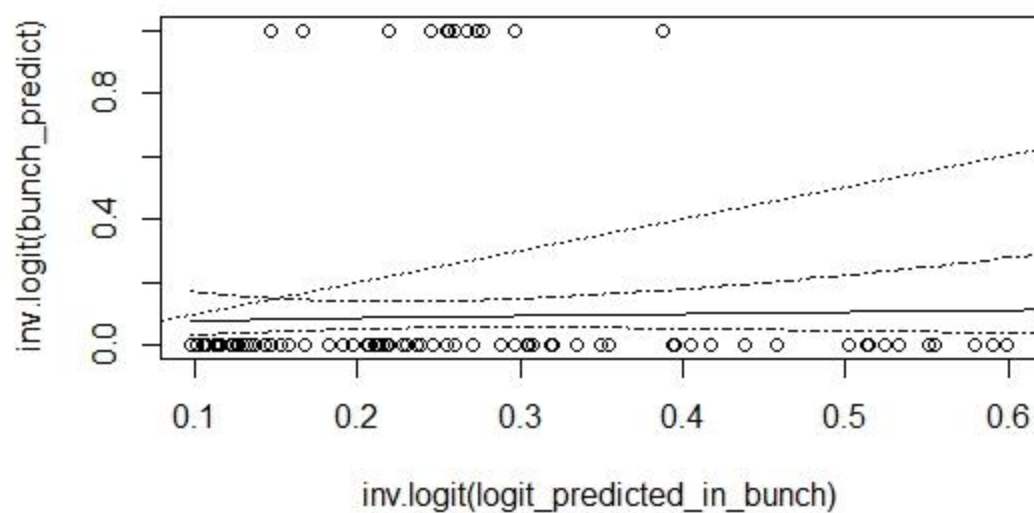
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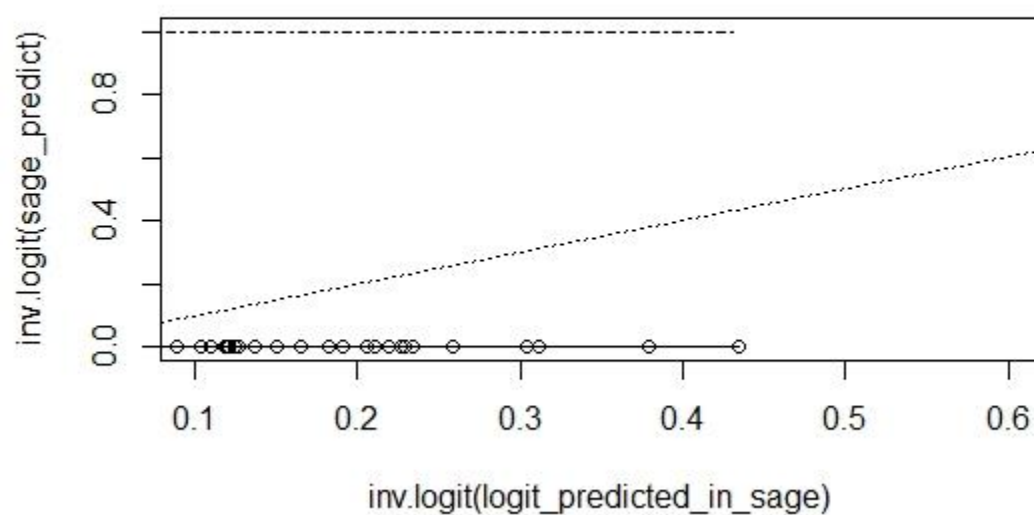
heliomeris multiflora in sagebrush



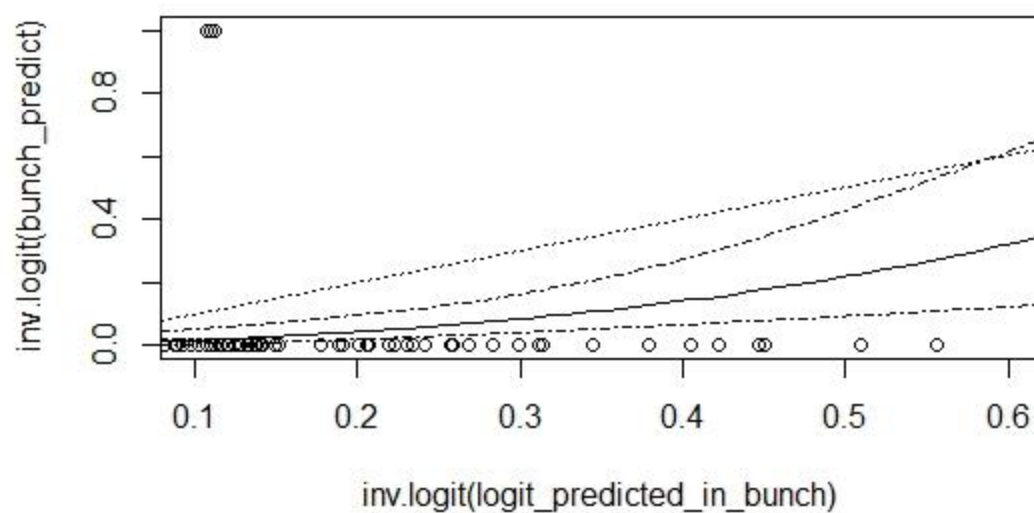
heliomeris multiflora in bunchgrass



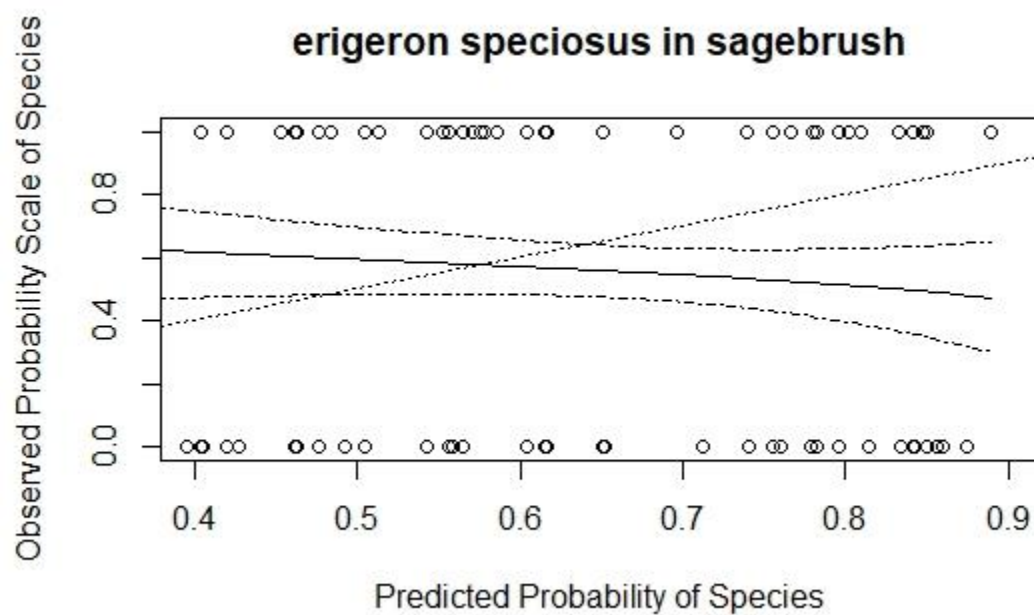
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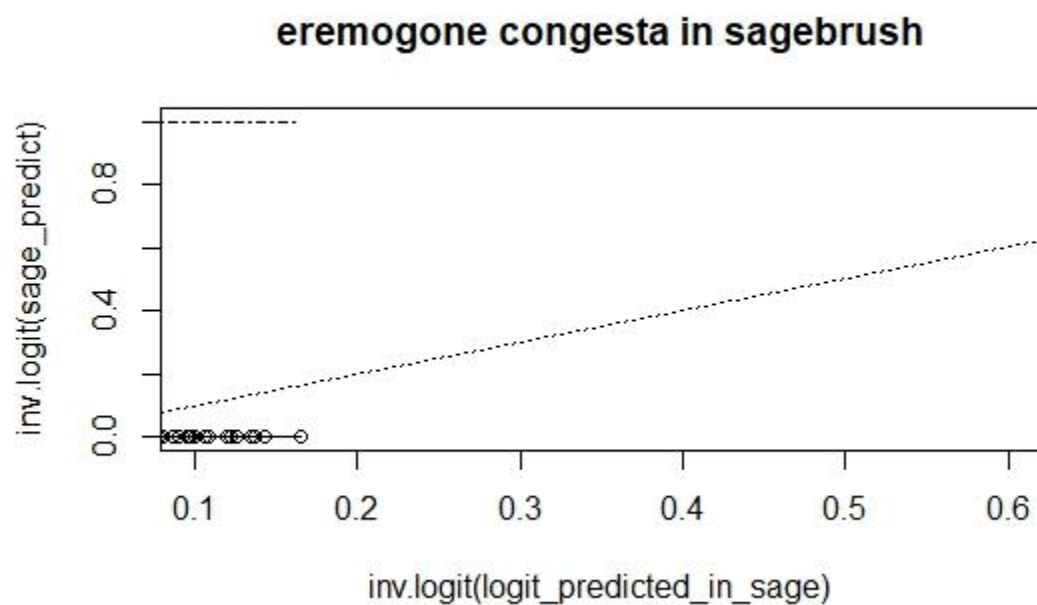
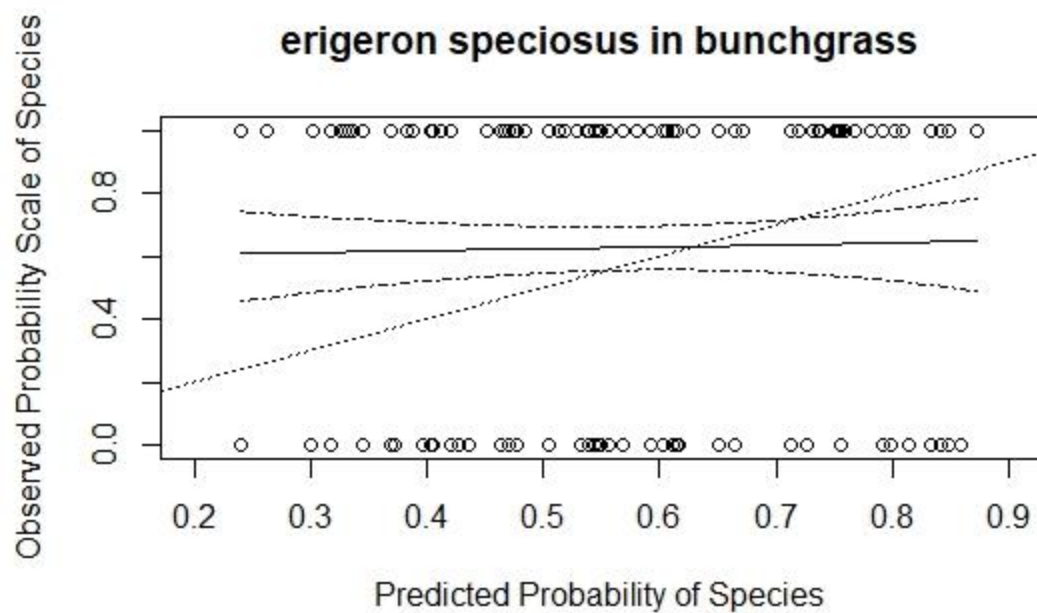


fragaria virginiana in bunchgrass

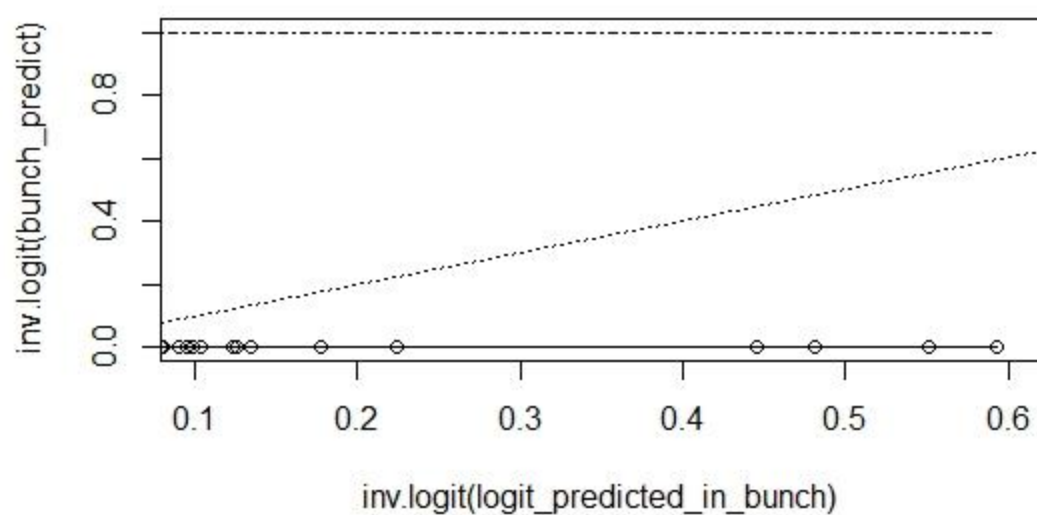


erigeron speciosus in sagebrush

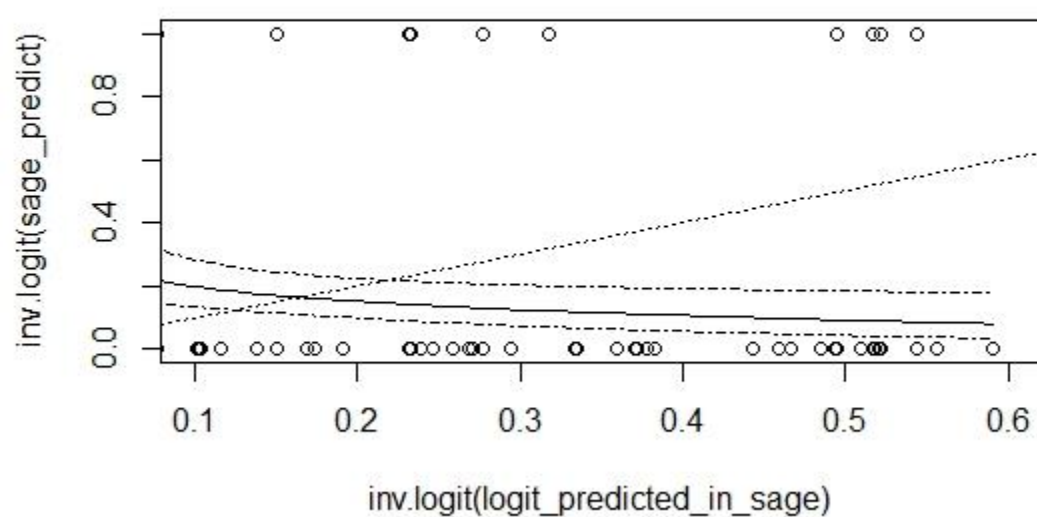




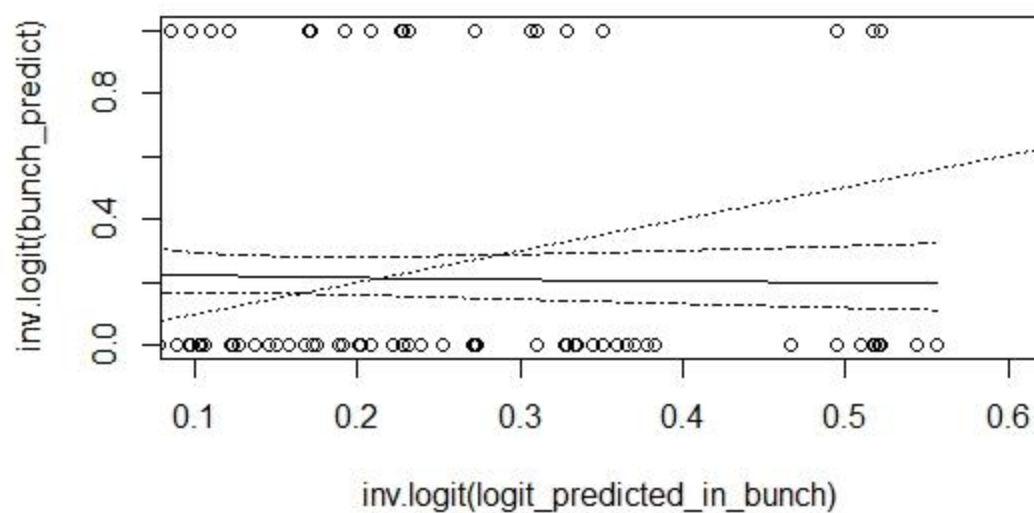
eremogone congesta in bunchgrass



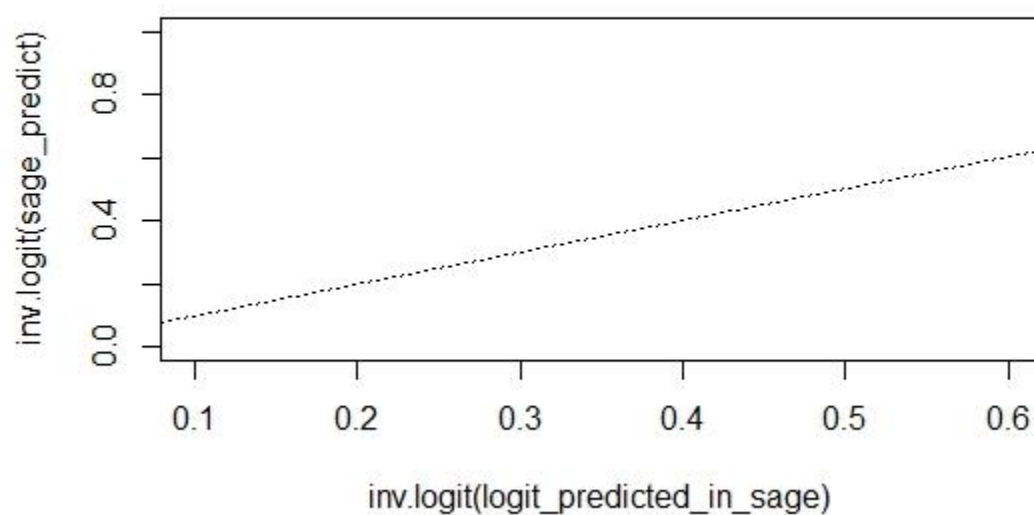
dugaldia hoopesii in sagebrush



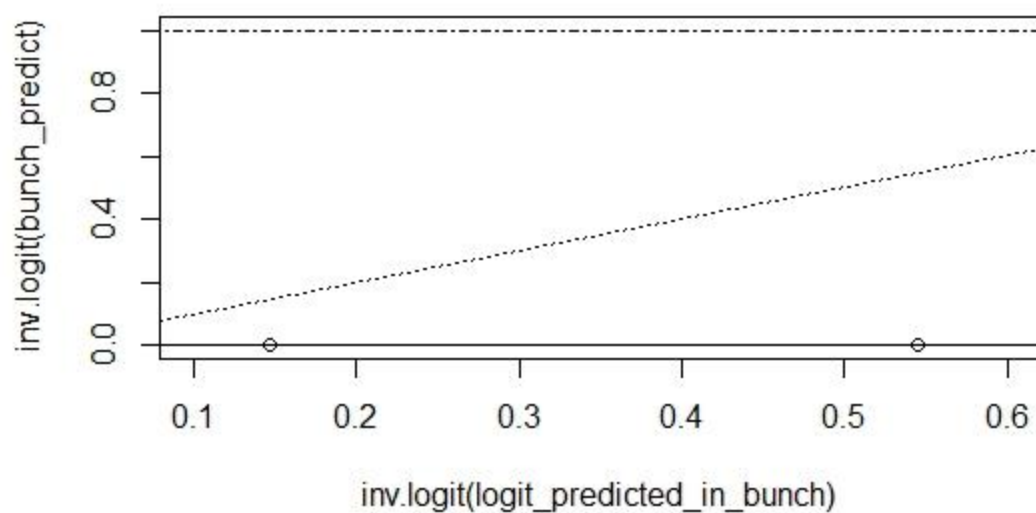
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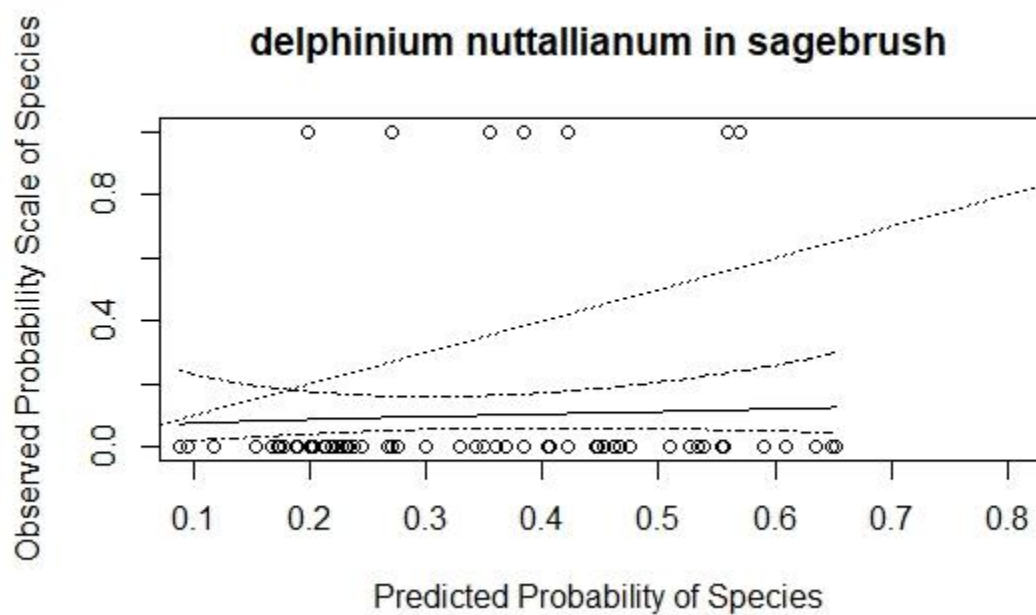
draba aurea in sagebrush

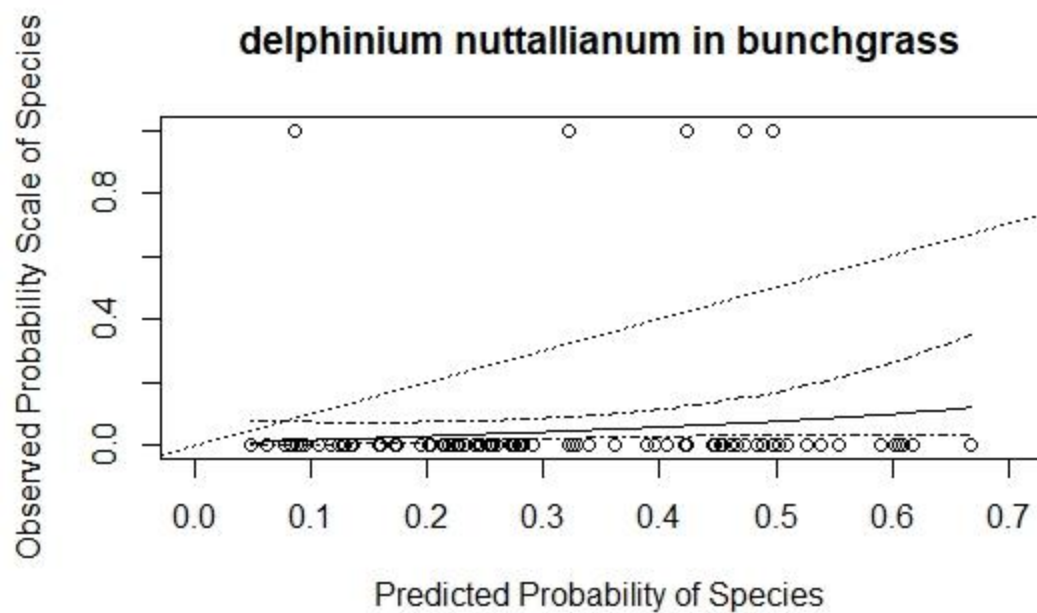


draba aurea in bunchgrass

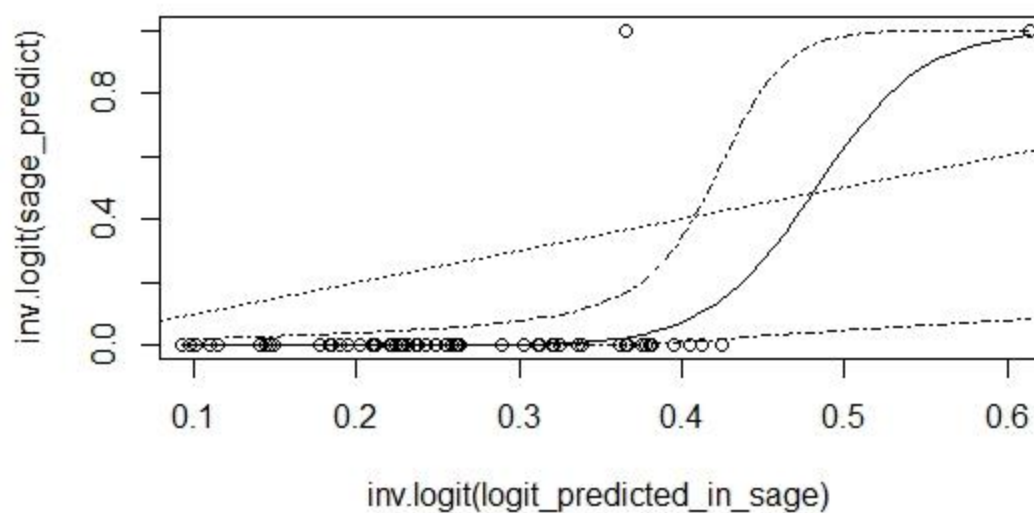


delphinium nuttallianum in sagebrush





delphinium barbeyi in sagebrush



delphinium barbeyi in bunchgrass

