

THESIS

LEVERAGING THE LANDSAT ARCHIVE TO CHARACTERIZE PLANT SPECIES
DIVERSITY AND POST-FIRE RECOVERY IN GREAT BASIN SHRUBLANDS

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ABSTRACT

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Great Basin shrublands in the United States are rapidly converting to annual grass-dominated ecosystems, driven primarily by increased wildfire activity. Post-fire vegetation recovery trajectories vary spatially and temporally and are influenced by the effects of topography, climate, soils, and pre-fire vegetation. Our study leverages spatially continuous Landsat data alongside spatial models of environmental drivers to account for variability across space to evaluate important drivers of post-fire vegetation recovery. We first tested the spectral heterogeneity hypothesis, which suggests that variation in spectral values relates to plant species diversity, which, in turn, is theorized to be an important predictor of resilience to disturbance and resistance to invasive species. Weak relationships from the spectral heterogeneity tests led us to explicitly model plant species richness using both Landsat spectral data and environmental predictor variables. To evaluate drivers and patterns of post-fire vegetation recovery, we assessed how the number of times a site burned, post-fire seeding, and a suite of environmental predictor variables (including pre-fire species richness) affected pre- and post-fire plant functional groups using Landsat models. We also applied the suite of predictors to model vegetation recovery (15-year post-fire functional group dominance) and used the model to predict recovery for a contemporary fire, the Saddle Draw Fire from 2014. Our model of species richness had robust validation and evaluation of variable importance elucidated key drivers. While species richness may be important for aspects of ecological functioning not addressed in this study, it was not found among the most important drivers of post-fire recovery within Great Basin shrublands.

However, the number of times burned affected post-fire recovery, which had a cumulative effect leading to increased annual herbaceous invasion and diminished perennial plant components. Meanwhile, on average post-fire seeding treatments had negligible influence upon post-fire perennial plant recovery. Post-fire recovery trajectories varied significantly across the fires evaluated in terms of both number of times burned and post-fire seeding. Models of post-fire recovery produced strong accuracy values when averaged across all fires and more tempered results when applied to new fires not included in model development. Spatially continuous analyses are important because they can account for variability in post-fire recovery of Great Basin shrublands. While such analyses have previously been hampered by data limitations, our results suggest that advances in data availabilities and cloud computing resources may be increasing opportunities for adopting spatial approaches for providing ecological insight and to inform post-fire management decision-making.

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CHAPTER 1: USING MACHINE LEARNING, REMOTE SENSING, AND ENVIRONMENTAL SPATIAL DATASETS TO MODEL PLANT SPECIES DIVERSITY IN GREAT BASIN SHRUBLANDS

Introduction

Plant species diversity has been established as an indicator of an ecosystem's capacity to sustain productivity, withstand stressors, and recover function following environmental shifts and disturbances (Folke et al., 2004; Isbell et al., 2015). Relationships among species diversity, ecological heterogeneity, and attributes of ecological stability and resilience are of fundamental interest in ecology (Folke et al., 2004; Grace et al., 2016; Isbell et al., 2015). Folke et al. (2004) presented evidence that losses of species and functional groups increases the risk of transitions to alternate stable states. Likewise, others have argued that species diversity (Schweiger et al. 2018) and species richness (Grace et al. 2016) are linked to net primary productivity. Diverse plant communities also support greater diversity of higher level taxa, such as herbivores and pollinators (Cardinale et al., 2006; Scherber et al., 2010).

The Great Basin shrublands of the Intermountain West of the United States have experienced dramatic changes to plant species assemblages and functional group composition compared to pre-settlement conditions—often transitioning to alternate stable states, which can have significant impacts to general ecosystem function (Stringham, Krueger, & Shaver, 2006; Chambers et al., 2014). Because of the broad scale and rapid pace of ecological changes, the resilience and resistance paradigm has gained significant traction in management and policy as agencies attempt to address this issue (Chambers, Pyke, et al., 2014). Specifically, resilience refers to maintenance of ecological function following stress and disturbance and resistance refers to resisting invasions by opportunistic non-native species (Maestas, Campbell, Chambers,

Pellant, & Miller, 2016).

Drivers of ecological change in the Great Basin include improper grazing, climate change, and the invasion of non-native, annual grasses (*Bromus tectorum* and others), which have subsequently contributed to increased fire frequencies and altered ecosystem structure and function (D'Antonio & Vitousek, 1992; Knapp, 1996). However, due to the diverse biophysical conditions in the region, the impacts of ecological drivers have not occurred uniformly across the landscape (Chambers, Bradley, et al., 2014). Rather, sites fall along a post-disturbance recovery continuum ranging between a) full recovery to ecological function in relatively short time intervals and b) transition to an alternate stable state with loss of function. Resilience and resistance concepts are useful for characterizing vegetation communities' positions on this continuum.

Plant species diversity has rarely been tested explicitly as a predictor of resilience and resistance in the Great Basin but species richness has been shown to have a negative relationship with cheatgrass (*Bromus tectorum*) cover (Shinneman & Baker, 2009). Given the theoretical relationships, spatially continuous estimates of plant species diversity may be important indicators of general plant community function. Additionally, these estimates of species diversity may help to predict post-fire recovery for shrubland plant systems of the Great Basin.

Detecting plant species diversity using remote sensing indicators

In the remote sensing literature, spectral heterogeneity has an established relationship with plant species diversity and ecological heterogeneity (Rocchini et al., 2010; Schweiger et al., 2018). This relationship has been formalized as the spectral heterogeneity hypothesis. Spectral heterogeneity can describe both the variance of pixel values across space and within-pixel heterogeneity between values of individual bands. The hypothesis has been tested using data at

spatial resolutions ranging from sub-meter to 500 m and with a variety of spectral resolutions ranging from visible light to multi-spectral to hyper-spectral imagery (Heumann, Hackett, & Monfils, 2015; Rocchini, 2007; Warren et al., 2014). At smaller spatial extents, relationships have been strong and statistically robust enough to predict species diversity across space and to monitor communities through time. Spatially continuous and temporally robust products from Landsat offer the potential to monitor species diversity across space and through time, which is patently unachievable using field-collected data alone. However, these multispectral remote sensing datasets are most powerful when used alongside field-collected ecological variables.

During the past two decades, the Bureau of Land Management (BLM) and Natural Resources Conservation Service (NRCS) have amassed large field-based datasets of methodologically-consistent plant community data that include species richness and evenness (Herrick et al., 2017). These datasets enable robust model training and validation using machine learning algorithms and can provide spatially continuous estimates of ecological characteristics, such as plant functional composition, plant heights, and bare ground (Jones et al., 2018; Rigge et al., 2019; Zhou, Okin, & Zhang, 2020). As of 2019, more than 11,000 field plots have been collected in the Great Basin and Snake River Plain since 2004. Here, we apply this dataset to assess relationships between Landsat-derived spectral heterogeneity indices and plant species diversity.

The Great Basin is a biophysically complex region with extreme topographic and climatic variability at multiple scales that confound spectral relationships (Rigge et al., 2019). Where spectral heterogeneity is elegant in its simplicity, applying a single measure across the entire region may have limited predictive power. There is some evidence that across broad geographies the spectral heterogeneity hypothesis has limited power (Rocchini et. al, 2014; Schmidtlein &

Fassnacht, 2017). Further, Rocchini et al. (2014) argued that at broad scales environmental variables can overtake spectral heterogeneity in terms of importance, owing to the importance of environmental variables in driving species distributions and, consequently, distributions of species richness values.

Modeling plant diversity using multispectral remote sensing indicators and environmental drivers

Beyond testing the spectral heterogeneity hypothesis, we aim to establish a modeling approach for characterizing species richness patterns more generally. If spectral heterogeneity relationships are weak, existing theory suggests that leveraging multispectral remote sensing variables alongside spatial datasets of environmental attributes, such as climate, soils, topography, and wildfire, would better predict species richness (Rocchini et al., 2014). Precipitation and aridity influence disturbance responses, invasion, net primary productivity, perennial vegetation cover, and species diversity in the Great Basin (Anderson & Inouye, 2001; Maurer, Hallmark, Brown, Sala, & Collins, 2020). Additionally, soil moisture and temperature regimes have been linked to ecological resilience and resistance. To the extent that species richness may predict resilience and resistance, soils properties, such as organic matter percentage, soil textures, θ_r (saturated soil water content), and θ_s (residual soil water content), may be important predictors of species diversity. Training machine learning algorithms for predicting species richness allows us to not only test the applicability of spectral heterogeneity and environmental predictors for characterizing species richness, but also to evaluate the importance of environmental variables as drivers of species diversity.

We tested the spectral heterogeneity hypothesis by developing and evaluating measures of spectral heterogeneity against field-collected plant species diversity measures. We then

applied a machine learning modeling approach to evaluate whether combining multiple spectral heterogeneity indices into a model explains more of the variance of the species diversity dataset than the individual measures on their own. We then trained an environmental model of species diversity, incorporating spectral heterogeneity measures and spectral indices indicative of vegetation health alongside environmental variables. Finally, we applied the environmental model across space and time to evaluate spatial and temporal variations in species diversity and identify important environmental drivers.

Methods

Study Area

The study area was comprised of shrublands in the Great Basin, here also including the Snake River Plain (Figure 1.1). The Great Basin is one of the most topographically variable regions in North America defined by north-south oriented mountain ranges and endorheic basins. Ecologically, shrublands primarily include salt desert shrub, tall sagebrush shrub, and low sagebrush systems historically co-dominated by perennial bunchgrasses (sagebrush steppe). Pinyon-juniper encroachment and annual grass invasion each exert competitive pressure on Great Basin shrubland communities, occasionally leading to ecological state changes as functional group dominance shifts. The project boundary is the union of the Central Great Basin, Northern Great Basin, and Snake River Plain level III ecoregions (Omernik, 1987). To exclude forested and woodland areas from our analyses, pixels were masked above a 20% tree cover threshold at an annual time-step using the Rangeland Analysis Platform dataset (Allred et al., 2020; Falkowski et al., 2017).



Figure 1.1: The Great Basin and Snake River Plain based on Level III Ecoregions of the United States.

Relationships between spectral heterogeneity and plant species richness

Spectral heterogeneity has been used as a proxy for species diversity in diverse regions (Figure 1.2) (Rocchini et al., 2010; Warren et al., 2014). To evaluate and establish relationships of spectral heterogeneity in the Great Basin, we used remotely sensed data from Landsat and field measurements of plant diversity from the BLM's Assessment, Inventory and Monitoring (AIM) and NRCS's Natural Resources Inventory (NRI) datasets, both of which apply comparable protocols (Herrick et al., 2017). Additionally, we supplemented the AIM and NRI datasets by collecting 43 post-fire field plots stratified by aerial and drill seeding (based on data from the Land Treatment Digital Library) and moderate and high fire severity (based on data from Monitoring Trends in Burn Severity) using methods from Herrick et al. (2017) to better account for wildfire as a driver of plant community composition. To avoid effects related to the species-area relationship, we excluded AIM plots that differed in area from the prevalent plot

size of 0.284 hectares. We evaluated both species cover (measured by line-point intercept) and species richness (measured in the species inventory) as species diversity response variables. While cover from line-point intercept enables calculation of species diversity indices like Shannon's H , statistical relationships between line-point intercept-derived species diversity and spectral heterogeneity variables were weaker than relationships between species richness derived from the species inventory data and spectral heterogeneity. Thus, we selected the species inventory dataset as our response variable, hereafter referred to as species richness.

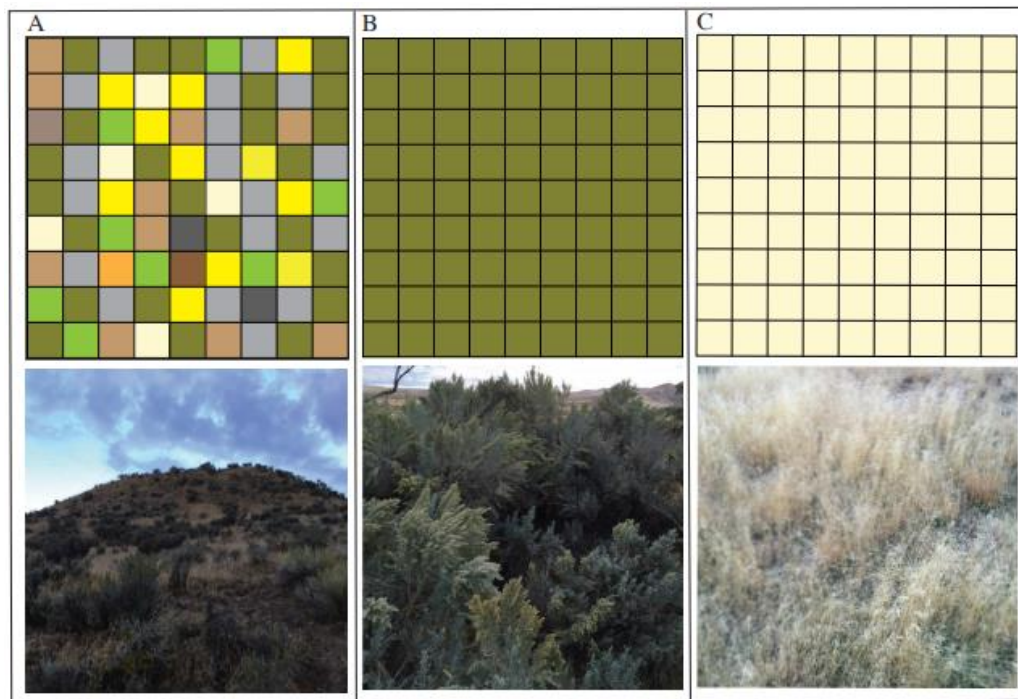


Figure 1.2: Conceptual relationship between spectral diversity and plant diversity in shrubland systems. Panel A is an intact ecosystem with high spectral and species diversity. Panel B is a sagebrush-dominated system with low species and spectral diversity. Panel C is a cheatgrass-dominated system with low species and spectral diversity.

Landsat data were accessed using Google Earth Engine's (GEE) Python API. We created annual composites of collection 1, tier 1 surface reflectance images using Landsat 5 Thematic Mapper (TM), Landsat 7 Enhanced Thematic Mapper (ETM), and Landsat 8 Operational Land Imagery (OLI) for each year of the Landsat archive from 1984–2019. We applied radiometric

harmonization coefficients to ensure comparability of OLI with TM and ETM (Roy et al., 2016). We then masked clouds (medium and high confidence), cloud shadows, water, and snow for TM and ETM using the quality assessment band provided with Landsat data. We applied similar masks to OLI but additionally applied the cirrus cloud and terrain occlusion masks unique to OLI. After applying harmonization and masking, the TM, ETM, and OLI images were considered comparable and subsequently merged into a single image collection for analysis. For each year, we produced a medoid composite from images captured between April 1–June 15, corresponding to the green-up period after winter and prior to summer senescence in the region.

For each annual medoid composite, we calculated a suite of spectral indices that are commonly applied for analyzing ecological characteristics. We calculated vegetation indices, including the normalized difference vegetation index (NDVI), soil-adjusted vegetation index (SAVI), soil-adjusted total vegetation index (SATVI), and the modified soil-adjusted vegetation index (MSAVI). Soil-adjusted indices are particularly useful in aridland systems in which bare ground is common in plant interspaces. For SATVI, SAVI, and MSAVI, we set the soil brightness correction factor L to 0.5. We also calculated the normalized burn ratio (NBR), normalized difference moisture index (NDMI), and tasseled cap indices for brightness (TCB), greenness (TCG), wetness (TCW), and the angle between greenness and brightness (TCA).

Equipped with a suite of ecologically-relevant multispectral remote sensing indices, we calculated spectral heterogeneity measures based on Warren et al. (2014). For each index, we calculated 100-meter radius focal grids of standard deviations and coefficients of variation. The 100-meter focal distance was selected based on a sensitivity analysis comparing relationships between spectral heterogeneity indices and plant diversity using 50-, 100-, and 150-meter focal grids of Landsat data. Additionally, for each index we divided the distribution of values into 20

bins and 40 bins and calculated 100-meter focal grids of binned richness (counts) and Shannon's H. Finally, we applied unsupervised classification to the Landsat multi-spectral data using the Weka K-means algorithm to produce 25-, 50-, 100-, 200-, and 500-class images (Sharma, Alam, & Rani, 2012). Unsupervised classification algorithms cluster similar pixels such that a higher number of unique classes within a geographic area indicate greater spectral heterogeneity. We applied a 100-meter focal grid to calculate Shannon's H and richness values for each unsupervised classification image. Because of the computational cost of the geographic and temporal scope of the project, we limited our analyses to the above spectral heterogeneity measures, which could be calculated using functions in GEE. The resulting 78 spectral heterogeneity measures are summarized in Table 1.1.

Table 1.1: Summary of the 78 spectral heterogeneity variables evaluated as predictors of plant species richness.

Multispectral indices	Spectral heterogeneity measures
Normalized differenced vegetation index (NDVI) Normalized burn ratio (NBR) Normalized differenced moisture index (NDMI) Tasseled cap greenness (TCG) Tasseled cap wetness (TCW) Tasseled cap brightness (TCB) Soil-adjusted vegetation index (SAVI) Soil-adjusted total vegetation index (SATVI) Modified soil adjusted vegetation index (MSAVI2) Bands 1, 2, 3, 4, 5, and 7 (harmonized to Landsat TM and ETM+)	Standard deviations Coefficient of variation 20-bin richness 20-bin Shannon's H 40-bin richness 40-bin Shannon's H
Unsupervised classification	Spectral heterogeneity measures
25-class weka k-means 50-class weka k-means 100-class weka k-means 200-class weka k-means 500-class weka k-means	Richness Shannon's H

Once spectral heterogeneity measures were calculated, we evaluated relationships between the spectral predictors and species richness. We first extracted values for all spectral

heterogeneity measures at each of the 11,070 field plots by matching the year of the field plot to the corresponding year of spectral heterogeneity measures and exported them from GEE for further local processing and analyses within R statistical software. We removed plots with missing values, slightly reducing the number of plots in the analysis to 10,471. To evaluate relationships between spectral heterogeneity measures and species richness, we calculated Pearson correlation values and p-values. We also trained two Random Forest models of species richness - one using only spectral heterogeneity measures and the other including spectral means alongside the spectral heterogeneity measures. For the Random Forest models, we first removed multi-collinear variables and then further reduced model variables by evaluating ranked importance. We then trained the two models by tuning the *mtry* hyper parameter and setting *ntree* to 500. We evaluated model outputs in terms of variance-explained and the root mean square error (RMSE).

Environmental model of species richness

Modeling using machine learning algorithms provides a framework for ranking the importance of a large numbers of predictor variables and for generating predictive models. When applying machine learning toward highly dimensional ecological problems, such as biodiversity modeling, they can help scientists untangle complex relationships. Through the process of modeling species richness, we intended to 1) train and validate a model of species richness, 2) evaluate predictor variables that are most related to species richness, 3) apply models to predict species richness for each year between 1994–2017, and 4) use the annual species richness predictions to evaluate regional trends in plant species richness.

For each of the 10,471 AIM and NRI plots, we extracted and exported values for 220 predictor variables using GEE (Table 1.2). In addition to the spectral heterogeneity variables, we

also calculated 100-meter focal means for each of the individual Landsat bands and indices. Environmental covariates included climatic, soils, topographic, and wildfire variables. Climate variables were derived from Daymet V3 and were calculated based on those used by Rehfeldt (2006) both at an annual time-step and as 30-year averages (Thornton et al., 2016). Soil properties variables were from the POLARIS dataset from Chaney et al. (2019) and were downloaded in 1-degree tiles and mosaicked. Topographic variables were derived from the U.S. Geological Survey's National Elevation Dataset and the Ecologically Relevant Geomorphology dataset from Conservation Science Partners, which is also calculated from the National Elevation Dataset (Theobald et al., 2015). Wildfire data were acquired from the Monitoring Trends in Burn Severity Program (MTBS) as individual fire rasters and mosaicked into annual images of differenced normalized burn ratio (dNBR) and the relative differenced Normalized Burn Ratio (RdNBR) from which all other variables were derived (Eidenshink et al., 2007).

We used Random Forest modeling packages in R to perform variable selection, model training, and model validation. We first subset the AIM and NRI data into model training and validation set, leaving aside 15% of datapoints to validate the model. Using the remaining 85% for model training, we removed multi-collinear variables and then further reduced the number of variables in the model by evaluating variable importance and variance-explained outputs. Once we had selected the model variables, we tuned Random Forest hyperparameters using a tuning grid and selected the model with the highest reported variance-explained as the final model. We then applied the model to predict species richness on the validation set and calculated model accuracy statistics R^2 , RMSE, and mean absolute error (MAE).

We applied the final model to predict species richness across our study area for each year between 1994–2017. To produce annual maps, we downloaded raster layers corresponding to the

selected variables for the model. Many of the variables are constant through time, such as topography, 30-year climate averages, and soils. However, we downloaded data for each year for the multispectral remote sensing, annual climate, and fire variables. We then applied the model to produce spatiotemporal predictions of species richness and uploaded the final maps to GEE for time-series analysis. Our ability to produce maps before and after 1994–2017 was constrained by the availability of the MTBS data and the importance of the *years since fire* variable. To evaluate change through time, we produced a differenced image between the beginning and end of the time series. In an attempt to reduce some of the effects interannual variability, we subtracted a map of the mean values between 1994–1996 from a map of the mean values between 2015–2017, which produced a map of species richness gained and lost during that time period.

Table 1.2: Summary of the 220 environmental predictor variables applied in the environmental model of species richness.

Class	Dataset(s)	Spatial resolution	Variables
Multispectral Remote sensing	Landsat	30 meters	Spectral heterogeneity (Table 1.1) NDVI NDMI TCG TCW TCB TCA SAVI SATVI MSAVI2 Bands 1, 2, 3, 4, 5, and 7 (harmonized to Landsat TM and ETM+)
Climate	Daymet Note: Each variable was calculated as 30-year averages and annually.	1000 meters	Mean annual temperature Mean spring temperature Mean summer temperature Mean winter temperature Mean growing season temperature Mean summer maximum temperature Mean winter minimum temperature Summer-winter temperature difference Mean annual precipitation Mean spring precipitation Mean summer precipitation Mean winter precipitation Mean growing season precipitation Frost-free period Last freeze of spring First freeze of autumn Maximum snow-water equivalent 5-degree warming days 5-degree warming days during frost-free period 0-degree cooling days 0-degree cooling days from minimum temperature Annual dryness index Summer dryness index

Class	Dataset(s)	Spatial resolution	Variables
Topography	National Elevation Dataset (NED) Ecologically Relevant Geomorphology (ERGo)	1/3 arc-second	Elevation (NED) Aspect (NED) Northness (NED) Eastness (NED) Slope (degrees) (NED) Slope (percent) (NED) Slope northness (NED) Slope eastness (NED) Transformed aspect (NED) Topographic position index (ERGo) Continuous heat-load index (ERGo) Multiscale topographic position index (ERGo) Topographic diversity Landforms (ERGo) Physiographic diversity (ERGo)
Fire	Monitoring Trends in Burn severity	30 meters	Times burned Fire return interval Fire frequency Years since most recent fire dNBR of most recent fire RdNBR of most recent fire dNBR of most severe fire RdNBR of most severe fire
Soil	POLARIS Note: Each variable had four horizons (0–5 cm, 5–15 cm, 15–30 cm, and 30–60 cm)	30 meters	Percent sand Percent silt Percent clay Percent organic matter Bulk density pH θ_r (residual soil water content) θ_s (saturated soil water content)

Results

Relationships between spectral heterogeneity and plant species richness

Relationships between the 78 spectral heterogeneity predictors and plant species richness were generally highly significant but weak in terms of predictive potential (Figures 1.3 and 1.4). For most spectral heterogeneity predictors, the Pearson correlation (r) with species richness was

between 0.15 and 0.3 and given the sheer number of plots included, all variables above an r value of 0.06 were highly significant with p -values less than 0.000000001. The best performing spectral heterogeneity predictor was the Shannon's H index of NDVI binned at increments of 0.05 (40 bins) (Figure 1.4; Figure 1.5A). Of the Weka k -means unsupervised classification variables, class richness values generally had higher correlations with species richness than Shannon's H , and the 500-class classification had the highest correlation (Figure 3A). Of the standard deviations and coefficients of variation of the remote sensing indices, the standard deviations were uniformly the strongest predictors with the standard deviation of NDVI having the highest correlation (Figure 1.3B). Correlation values of the standard deviations and coefficients of variation for the Landsat bands were lower across the board than almost any other spectral heterogeneity measures, with band 7 having the highest correlation (Figure 1.3C). The binned remote sensing indices were the top performing spectral heterogeneity measures; NDVI with 40-bins was most correlated with species richness (Figure 1.4; Figure 1.5A). While the spectral heterogeneity predictors were highly significant, we decided to also compare them with the raw means of each of the indices and bands to test whether remote sensing indices on their own perform better or worse than the spectral heterogeneity measures (Figure 1.3D). Of the remote sensing index means, five of them had higher Pearson correlations than any of the spectral heterogeneity values with NDVI having the strongest relationship.

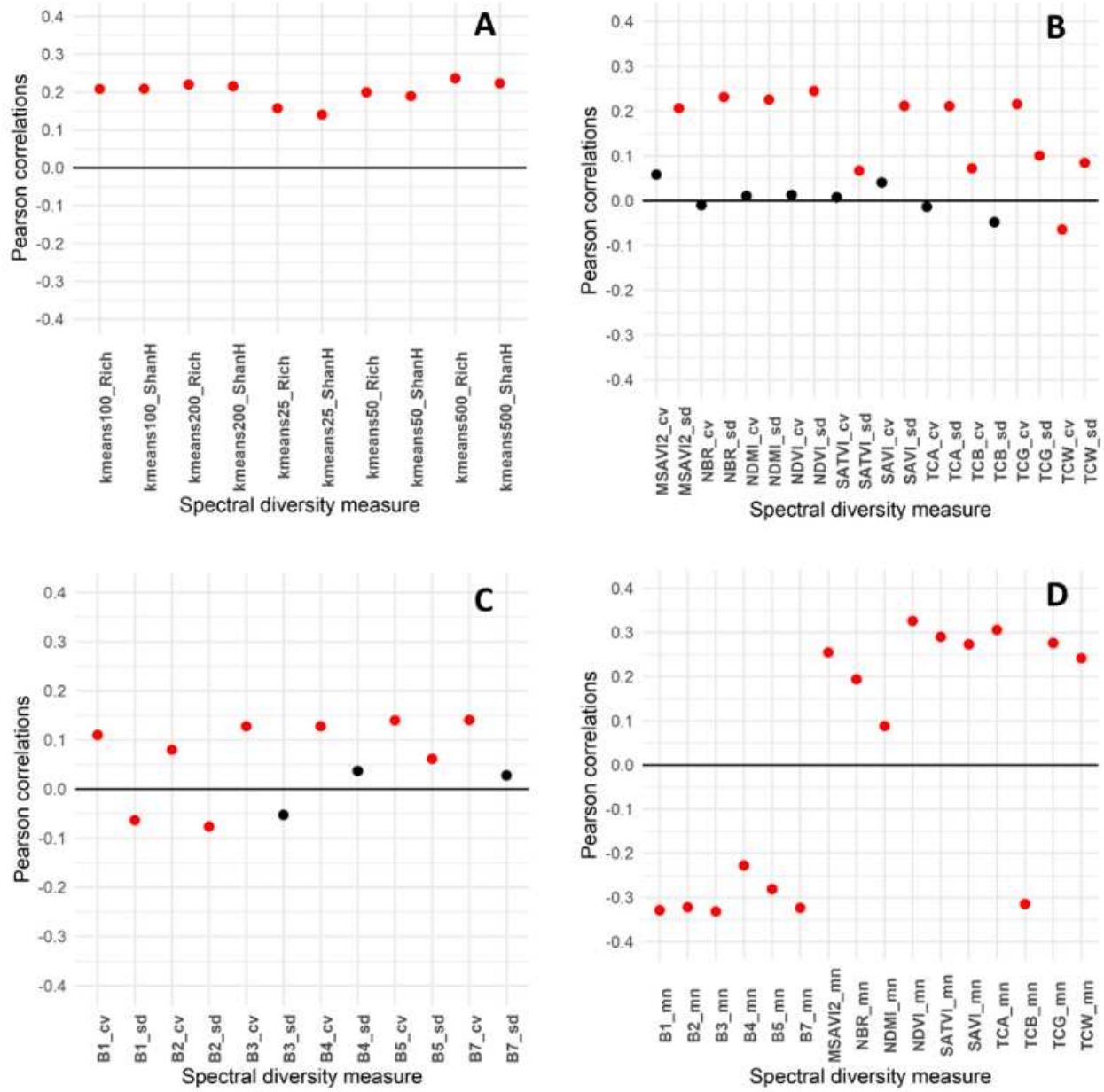


Figure 1.3: Pearson correlations with species richness for A) unsupervised classifications, B) standard deviations and coefficients of variation for remote sensing indices, c) standard deviations and coefficients of variation for Landsat bands binned indices, and D) Landsat means. Red dots indicate p -values < 0.00000001 .

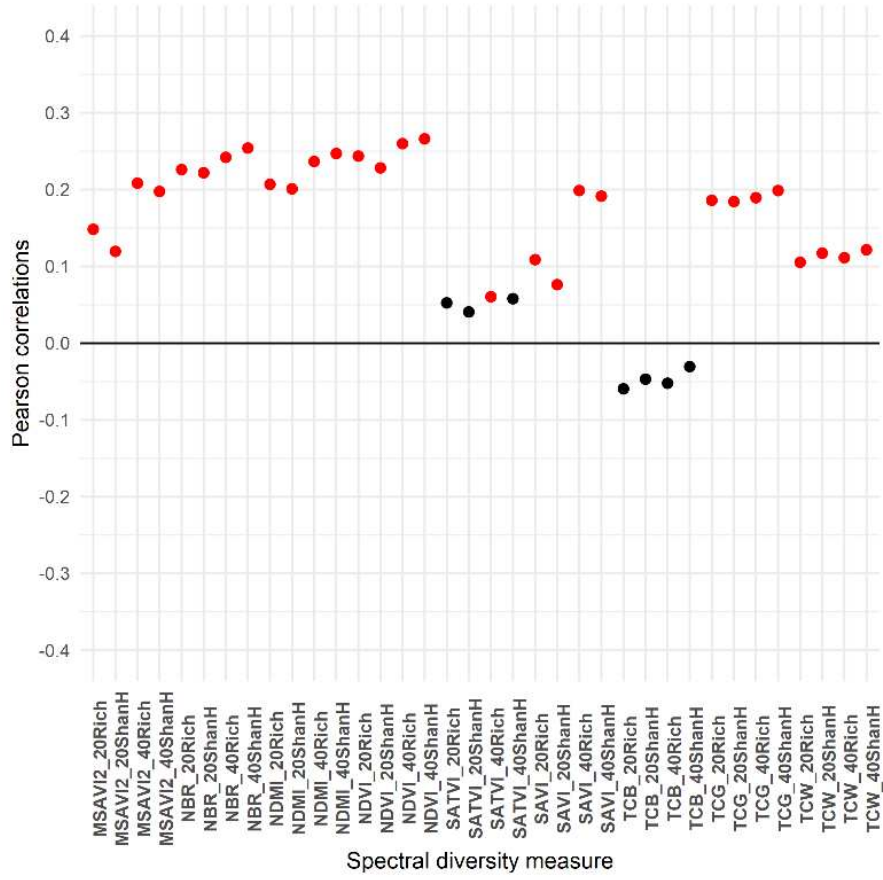


Figure 1.4: Pearson correlations with species richness for binned indices. Red dots indicate p -values < 0.000000001 .

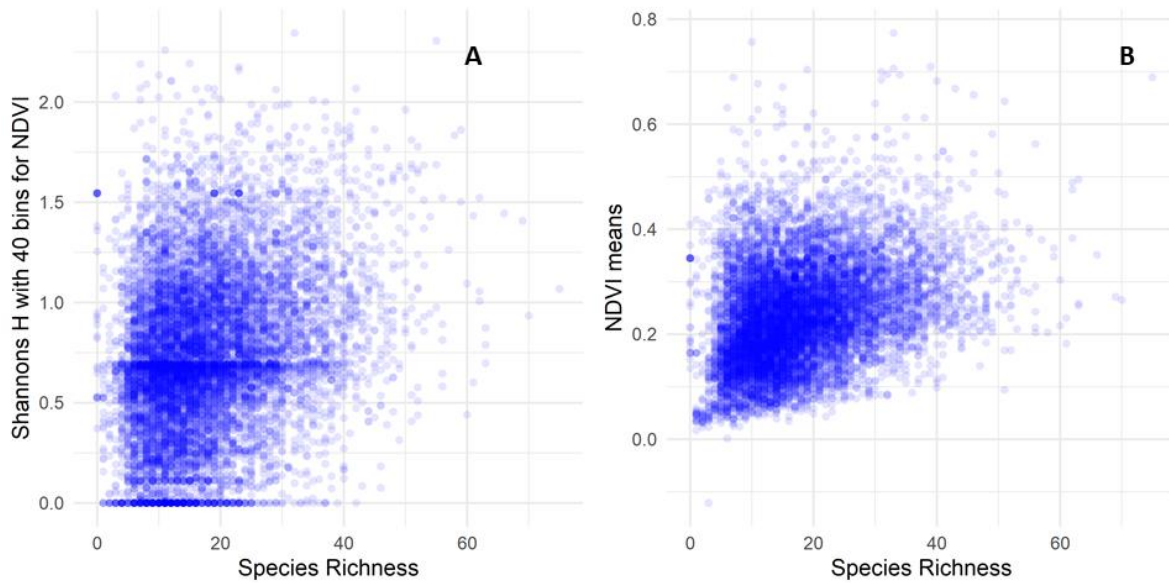


Figure 1.5: A) The top spectral heterogeneity predictor, Shannon's H with 40-bins for NDVI, and B) the top spectral predictor overall, mean NDVI.

While individual spectral measures were highly significant, no single index accounted for enough of the variance to create spatial predictions of species richness patterns across the study area on their own. Thus, to account for variable interactions, we created two Random Forest models which incorporated multiple spectral heterogeneity measures and multispectral remote sensing indices. After variable reduction procedures, the first model for species richness using only the spectral heterogeneity predictor variables included a total of 24 predictor variables and reported a variance-explained (pseudo- R^2) of 17.65% and an RMSE of 75.86. The top predictor variables in the model were TCA coefficient of variation, TCA standard deviation, and TCG coefficient of variation, which differed significantly from the rankings in the single-variable correlation analyses. The model for species richness using all spectral variables included a total of 28 variables for the final model and reported a percent variance-explained of 22.58% and an RMSE of 71.52 (Figure 1.6). The top predictor variables in this second model were Landsat band 1, band 3, and band 2 means, which also differed significantly from the correlation analysis. Altogether, the spectral variables in the Random Forest models were still limited in regards to how much of the variance of species richness was explained.

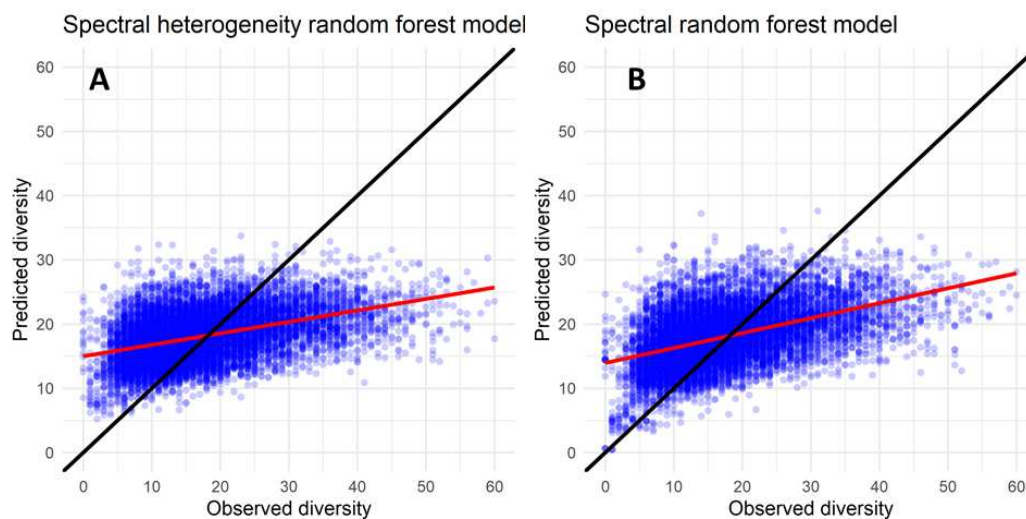


Figure 1.6: Plots of model predictions against observed species richness for A) the spectral heterogeneity model and B) the model using all spectral variables. A 1:1 line is displayed in black and a linear regression fit is displayed in red.

Environmental model of species richness

The environmental model explained more variance of species richness than the multispectral remote sensing models but tended to over-predict species richness values at the lower extreme and under-predict values at the higher extremes (Figure 1.7). After applying the multicollinearity test and reducing variables by evaluating variable importance metrics, we produced a final model of species richness including 21 predictor variables. Based on predictions upon the validation dataset of 1,561 field plots, the R^2 value for the model was 0.524 with an RMSE of 6.69 and mean absolute error (MAE) of 5.03. Model predictions cluster closely with observed data (Figure 1.7) and the coefficients for the linear regression fit were a slope of 0.466 and an intercept of 9.76.

Variable importance ranking revealed that many of the top predictors were related to precipitation and aridity, but that a variety of variables (climate, topography, multispectral remote sensing, and fire) were important drivers of species richness (Table 1.3). In general, variables that indicated higher precipitation or lower aridity had a positive relationship with species richness, with 11 of the 21 selected variables being either measures of seasonal or annual precipitation or aridity. Interestingly, spectral remote sensing variables were relatively unimportant once environmental variables were included. Mean TCA and mean NDVI both had positive relationships with species richness and ranked 12th and 14th, respectively in terms of variable importance. Among the original Landsat bands, band 1 (blue) and band 3 (red) were both selected for the model and had negative relationships with species richness. The negative relationship between species richness and band 3 was unsurprising as red reflectance indicates plant stress (Tucker, 1979). Many of the relationships between predictors and species richness were non-linear. Random Forest is robust to non-linear relationships which may help to explain why variables with complex relationships were selected. One example is 0-degree cooling

days—a measure of accumulation of cold outside of the frost-free period. Sites with relatively low and relatively high values for 0-degree cooling days each had low species richness, while sites with moderate values of 0-degree cooling days had higher species richness. None of the 78 spectral heterogeneity predictors were selected for the final model because of low variable importance scores. This underscores that while those relationships were highly significant, they were not appropriate for predicting plant species richness in the Great Basin.

Table 1.3: Variables selected for the environmental model of species richness, their variable importance, and the direction of the relationship.

Rank	Variable	Importance (%IncMSE)	Direction
1	Mean annual dryness index	16.72	↓
2	Mean annual precipitation	15.42	↑
3	Annual winter precipitation	13.23	↑
4	Slope percent	12.20	↑
5	Mean snow water equivalent	11.40	↑
6	Annual 5-degree warming days	11.21	↓
7	Annual annual dryness index	11.17	↓
8	Landsat band 1 mean	9.63	↓
9	Mean summer precipitation	9.47	↑
10	Topographic diversity	9.18	↑
11	Mean spring precipitation	9.17	↑
12	Mean TCA	8.98	↑
13	Elevation	8.92	↑
14	Mean NDVI	8.86	↑
15	Mean minimum temperature 0-degree cooling days	8.71	↑
16	Years since fire	8.60	↓
17	Annual precipitation	8.28	↑
18	Annual snow water equivalent	8.01	↑
19	Annual winter minimum temperature	7.85	↑
20	Landsat band 3 mean	7.22	↓
21	Annual summer precipitation	6.59	↑

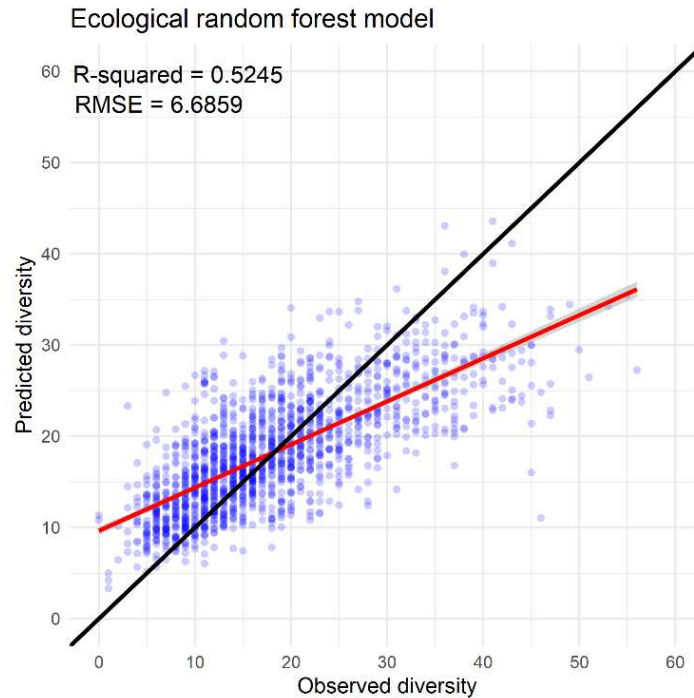


Figure 1.7: Model predictions from the environmental model of species richness plotted against observed species richness counts from AIM and NRI plots. The 1:1 line is displayed in black and a linear regression fit is displayed in red.

We applied the final model of species richness to produce annual maps across our study area for each year between 1994–2017. When examining 2017, there were distinct spatial patterns of species richness particularly along elevational and latitudinal gradients (Figure 1.8). Species richness was generally predicted to be higher in the north and in more mountainous sites, while playas had low predicted values of species richness. At a more local level, models captured general patterns of species richness but struggled to capture the variance in the reference field dataset. For example, although the lowest and highest values in the species richness field dataset appeared to match the lowest and highest values in the mapped predictions (Figure 1.8, right), the mapped predictions fail to capture the extremes in the field-collected dataset (Figure 1.8, left). Thus, while the model represents general landscape patterns in species richness, it is likely under-predicting both low and high values at local scales.

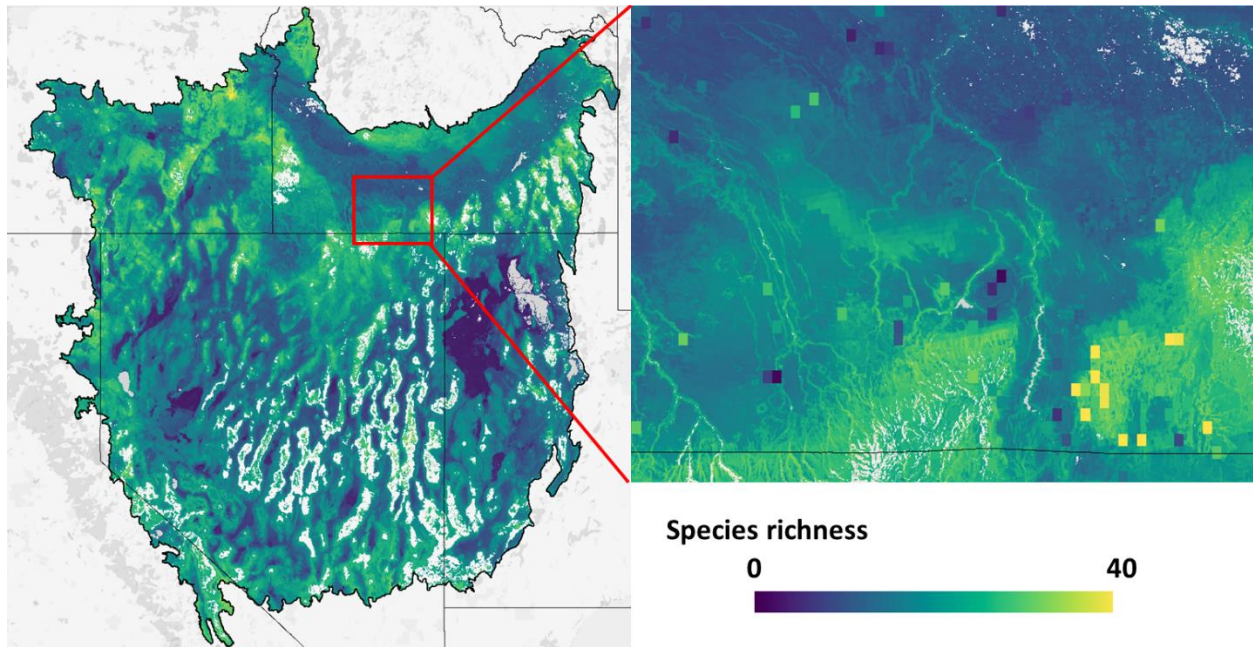


Figure 1.8: Predicted species richness values for the Great Basin for 2017 (left) and spatially continuous model predictions overlaid with field collected values of species richness from AIM and NRI (right).

Differencing predictions across two temporal windows (1994–1996 and 2015–2017) revealed both losses and gains in species richness (Figure 1.9). We chose to create a mean image for each of those date ranges to reduce the influence of the interannual variability. In general, species richness decreased in the west central portion and is increasing in the southern portion of the Great Basin. Locations that were modeled to have decreasing species richness also closely match sites modeled to have high annual herbaceous cover, which are often noxious species (Figure 1.10) (Allred et al., 2020). Species richness tended to be relatively stable within valley locations.

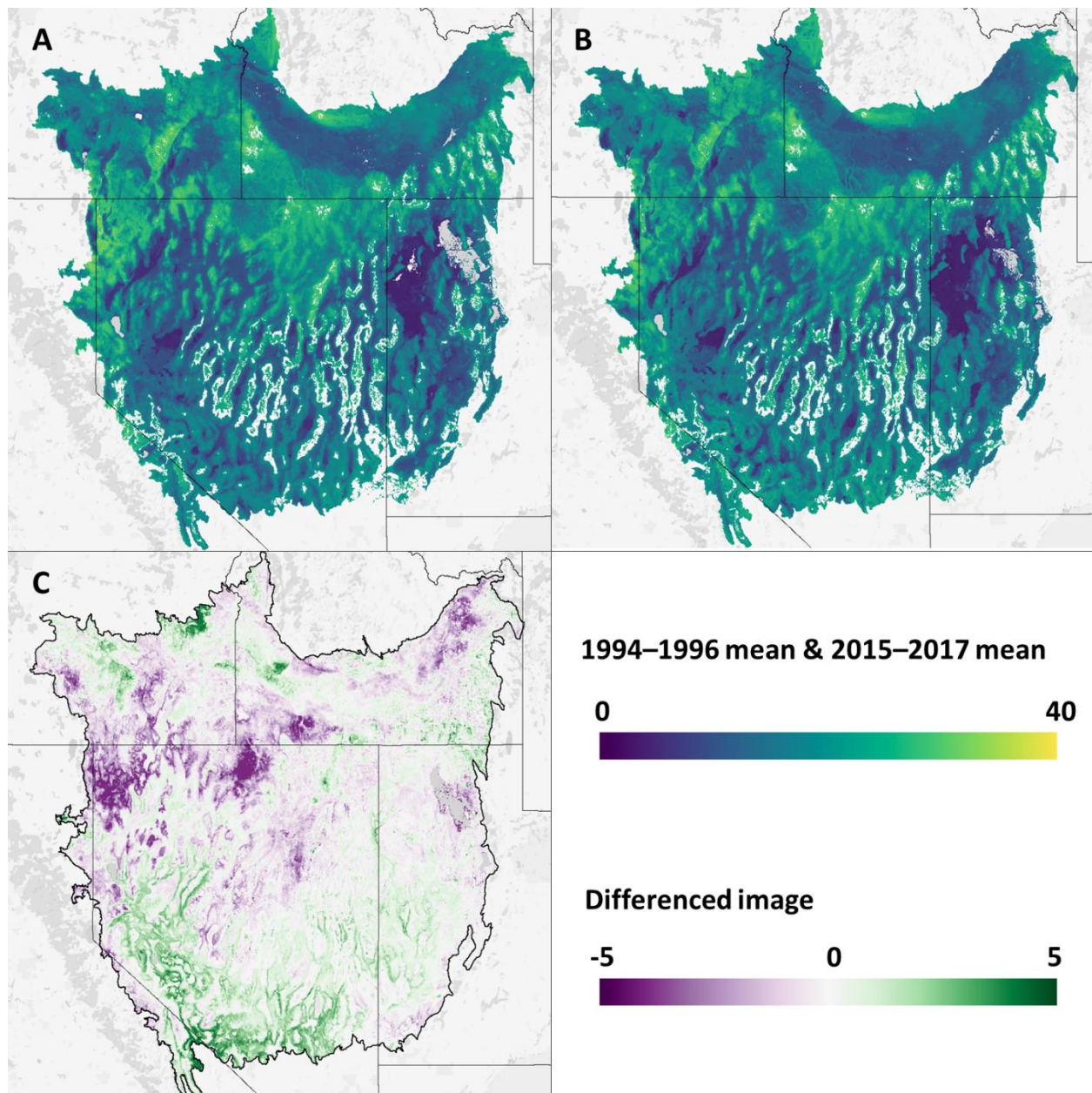


Figure 1.9: Mean images of species richness between 1994–1996 (A) and 2015–2017 (B). The map of species richness change through time (C) shows increases in the southern Great Basin species richness and declines across much of the northern Great Basin.

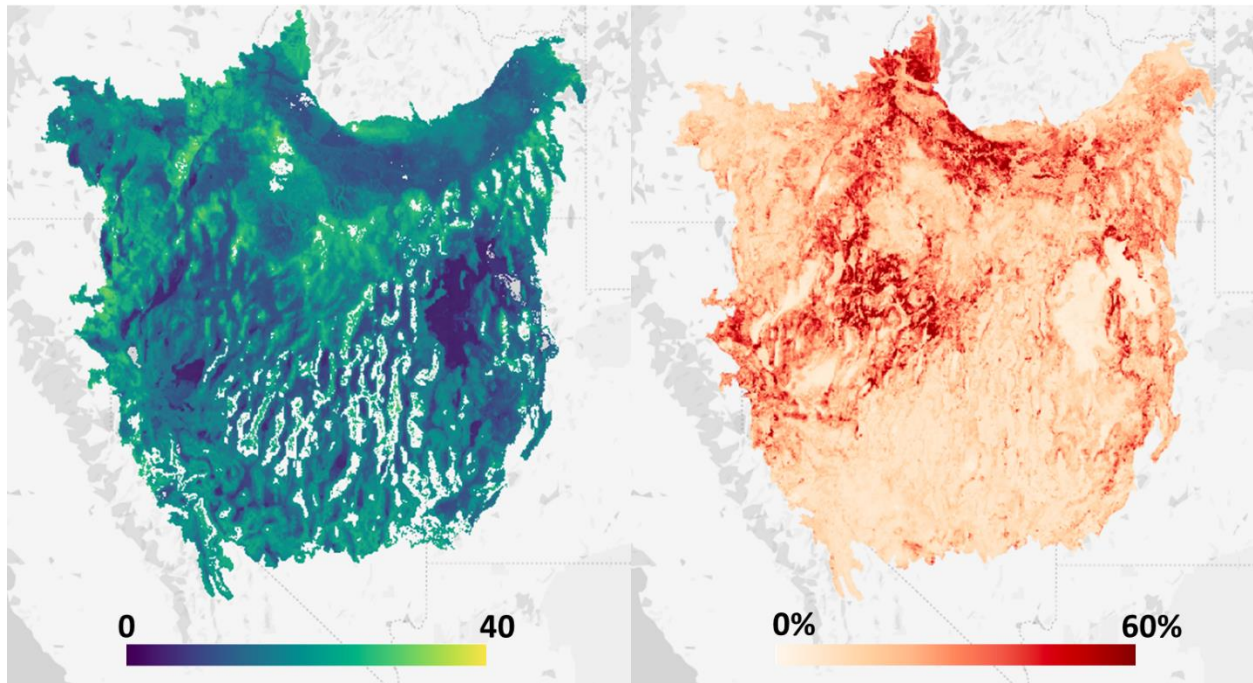


Figure 1.10: Comparison of spatial patterns of modeled species richness (left) and modeled annual forb and grass cover (right) (Allred, et al. 2020). Each map is comprised of mean pixel values averaged over images between 2015–2017.

Discussion

While spectral heterogeneity measures proved to be weak predictors of plant species richness in Great Basin shrublands, environmental variables explained much of the variability in species richness across the region. Here, we demonstrated an approach for quantifying spatial patterns and drivers of plant species diversity at a regional scale. If theoretical relationships between plant species richness and general attributes of ecological resilience and resistance hold for this region, then our findings would be of value for spatial analyses of post-disturbance recovery.

Spectral heterogeneity is weakly related to species richness

In practice, the spectral heterogeneity hypothesis has been a valuable tool for monitoring plant species diversity in many parts of the world. However, across shrubland communities within the Great Basin the relationships were highly significant but weak. Warren et al. (2014)

found that of the 168 spectral heterogeneity variables tested in Germany, several had correlation coefficient values greater than 0.6. Those data were collected over a 16 km² area using 4-meter IKONOS data. Similarly, in a study at a 6 km² nature preserve in Italy, Rocchini (2007) tested sensors of varying spatial resolution ranging from 2.8 meters (QuickBird) to 60 meters (resampled Landsat ETM+) and found that Quickbird, Landsat ETM+ (native resolution), and Landsat ETM+ (resampled to 60 meters) all had correlation coefficients greater than 0.65 in relation to plant species richness. That study demonstrated that relatively coarse spatial resolution does not necessarily reduce statistical relationships (Duccio Rocchini, 2007). Similar results are not uncommon in the literature (Féret & Asner, 2014; Gillespie, 2005; Hernández-Stefanoni et al., 2012). However, in our analysis, the top performing spectral heterogeneity predictors did not approach the strength of any of aforementioned studies.

There are likely several reasons that the spectral heterogeneity relationships were relatively weak in our analysis. Schmidtlein & Fassnacht (2017) noted that little attention had been paid to whether relationships hold across space and time during the development of the spectral heterogeneity hypothesis. Using 500-meter resolution MODIS data, they found that in some regions spectral heterogeneity relationships were strong, while in other regions relationships were weak and varied by season. In our analysis, our Landsat data was from the period of April 1–June 15 to roughly coincide with the green-up period. However, the green-up period varies significantly across latitudinal and elevational and from year-to-year, which likely complicates statistical relationships. Further, Rocchini et al. (2014) asserted that at broad spatial scales, the geographic variability of spectral data may wash out relationships of heterogeneity in species diversity. They suggested that at regional and continental scales, environmental parameters like temperature, topography, and insolation primarily drive biodiversity (Rocchini et

al., 2014). Our results seem to support the conclusions of Rocchini et al. (2014) in that our environmental model, which incorporated climatic, topographic, and other variables, performed better than our spectral models. Another confounding factor of multispectral remote sensing in the Great Basin is soil reflectance. Where most spectral heterogeneity studies have been applied in systems in which vegetation cover is more-or-less continuous, in Great Basin shrublands bare ground cover is often 20% or more. Soil reflectance is variable based on moisture conditions, parent material, and organic matter content and may influence spectral heterogeneity without directly relating to plant community characteristics. Each of these factors likely contributes to weak spectral heterogeneity relationships. For those reasons, a more environmentally-driven approach was required within our study region.

Environmental spatial variables and multispectral remote sensing predict species richness

Our environmental model of species richness included 21 final variables—three topographic, six 30-year climate means, seven climate annuals, four multispectral remote sensing, and one fire regime characteristic. Many of these predictors match prevailing theory related to Great Basin ecosystems and distributions of species richness. For instance, precipitation and aridity were most important in prediction species richness and have similarly been found important in other studies, especially for perennial grasses (Anderson & Inouye, 2001). Similarly, precipitation is closely linked to net primary production in North American dryland ecosystems, which in turn is related to species richness (Maurer et al., 2020). Interannual variability in precipitation relates to interannual variability in species richness, particularly in relation to annual forbs.

The negative relationship of *years since fire* with species richness contradicts related studies. Repeated fires often push Great Basin shrubland systems beyond environmental

thresholds into annual dominated states that reduce species richness (Chambers, Pyke, et al., 2014; Shinneman & Baker, 2009). However, in ponderosa pine forests, fire produced higher species richness of forbs in burned landscapes when compared with unburned landscapes (Burkle, Myers, & Belote, 2015). As in our study, that result contradicted the prevailing theory. It is possible that the post-fire reduction of the less diverse shrub component reduces competition on annual and perennial forbs and enables higher species richness counts overall. Thus, while our finding of a negative relationship between years since fire and species richness conflicts with regional theory, the relationship is likely complex and variable across space such that sites that are less susceptible to cheatgrass invasion may gain species richness while sites that are more susceptible to invasion lose species richness.

Aspect rather than topographic slope is commonly considered an important driver of shrubland health (Kulpa, Leger, Espeland, & Goergen, 2012). However, the theory of midpoint attraction may help explain the importance of slope (Colwell et al., 2016). Theoretically, temperature and precipitation drive net primary production, which is related to species richness. In the Great Basin, temperature and precipitation are most extreme at low and high elevations; however, species richness typically peaks at intermediate elevations (Rahbek, 1995, 2005). Intermediate elevations are inherently relative and vary in terms of meters above sea level across the region. However, intermediate elevations are likely to be on mountainsides and, hence, to have relatively steep slopes. Thus, more sloped sites may support more species richness than flatter sites.

The spatial landscape patterns of species richness predicted by the model are supported by other studies that have found negative relationships between annual herbaceous cover and species richness. One of the few studies that evaluated species richness as a predictor for

ecological condition in the Great Basin found that species richness was negatively correlated with cheatgrass cover (Shinneman & Baker, 2009). Thus, we would expect to see lower values of modeled species richness in sites with higher annual herbaceous cover (Anderson & Inouye, 2001). When comparing our models of species richness and the Allred et al., 2020 models of annual forb and grass cover, sites mapped as having high annual grass cover also had lower predicted species richness and vis-a-versa, particularly in the northern Great Basin. Similarly, many sites predicted to have lost species richness over time also gained annual forb and grass cover during the same period, suggesting that annual forbs and grasses are outcompeting native species and reducing species richness.

Our final environmental model explained more than 50% of the variance of species richness, however we are aware of limitations of our analysis. One significant limitation is that, while our spectral data are from spring, phenology varies significantly across the region. It is likely that some sites in our study area reach peak greenness after the end of our window during cooler years. An additional limitation is that, while Burkle et al. (2015) lends some support to the fire relationships that we found, the model may not properly be modeling post-fire condition in other cases. For example, the model often predicts higher species richness within fire polygons in the year following fire than the year prior to the fire. While increased plant species richness immediately following fire is certainly possible, it would be unexpected. Finally, we know that the models have lower variance than the field data, likely an artifact of the Random Forest algorithm.

Implications and applications

Plant species diversity is important to land and resource managers from a conservation perspective. In the Great Basin, there are many rare and endemic species native to the region.

The spatial predictions of species richness from our study could be used to identify priority areas for conservation. Additionally, evaluating sites that are losing or gaining species richness through time can help managers better make decisions about sites that may be most at risk of degradation. For botanists and field monitoring efforts, the species richness maps could be used to identify sites for sampling, which could help prioritize field sampling resources for managers to improve understanding of spatial distributions of biotic resources.

Trends in Great Basin plant species diversity almost certainly affect biodiversity of higher-level taxa, such as insects and birds. Auto-correlation models of bird assemblages in the Great Basin found that bird diversity was closely related to plant taxonomic composition, even more so than vegetation structure or primary productivity (Fleishman & Mac Nally, 2006). Few studies have evaluated the effects of plants diversity on higher trophic levels in the Great Basin; however, relationships are well established elsewhere (Cardinale et al., 2006; Scherber et al., 2010). Future Great Basin biodiversity monitoring efforts could sample for higher-level taxa associated with plant communities.

Building on the general utility of modeling species richness, the use of this approach would be amplified if plant diversity, indeed, predicts post-fire recovery. In practice, sites with a greater number of pre-fire species may have a more diverse ruderal seed source from which to recover post-fire perennial species than sites with fewer species. Given the pressure from annual herbaceous plants on shrubland communities, if species richness contributes to vegetation recovery following fire, then pre-fire species richness maps could be used as a decision-support layer for post-fire restoration—prioritizing sites that are less likely to recover. Further studies should examine the relationship of pre-fire plant species diversity to post-fire recovery trajectories of Great Basin perennial plant communities.

Conclusions

Our results indicate that spectral heterogeneity measures are likely inappropriate for monitoring plant species diversity at the broad scale of the Great Basin. Confounding factors, such as soil reflectance and topographic and latitudinal gradients that influence plant phenology, as well as the general breakdown of spectral heterogeneity relationships across regional extents may contribute to this conclusion. Some of these factors may indicate that spectral heterogeneity will have limited utility as a proxy for species diversity across aridlands systems without carefully controlling for these confounding factors. However, while spectral diversity relationships may not be strong enough to predict species richness on their own, they are highly significant and may contribute valuable information to future multivariate analysis, especially at smaller spatial extents.

Multivariate Random Forest models produced predictions of species richness that are statistically defensible and that match prevailing theory of plant systems in the Great Basin. More sophisticated machine learning algorithms incorporating additional spatial environmental variables, such as deep neural networks, may produce further gains in terms of performance. Additionally, NRI and AIM datasets enable robust training and validation of models of species richness across the broad extent of the western United States (Allred et al., 2020; Rigge et al., 2019). These multivariate models are appropriate for accounting for complex and non-linear relationships between predictor variables. In particular, a strength of models incorporating environmental predictors alongside multispectral remote sensing variables is that accounting for climate variables may enable predictions of changes to species richness under various climate futures.

Snyder et al. (2019) suggested that recent climate records have indicated increased temperatures, and thus aridity, for the Great Basin in recent years. The trend of increased aridity

is expected to continue in coming decades as a result of the influence of climate change.

Droughts are likely to be more frequent and longer in duration, which will apply another pressure on perennial shrublands (Snyder et al., 2019). Based on our findings of strong negative relationships between aridity and species richness, it seems likely that plant species richness would also decrease under warmer climates in the future. These trends underscore the importance of data-driven approaches to natural resources management and conservation in the Great Basin, as they can help inform increasingly strategic management and conservation actions. Thus, these models represent a leap forward for informing plant species diversity conservation and, to our knowledge, a first step in spatially continuous and temporally-robust characterization of plant species diversity in the Great Basin.

CHAPTER 2: SPATIAL DRIVERS, MODELS, AND PREDICTIONS OF POST-FIRE VEGETATION RECOVERY AND RESILIENCE AND RESISTANCE IN GREAT BASIN SHRUBLANDS

Introduction

Concepts of Resilience and Resistance

Disturbance is ubiquitous across ecological communities globally and includes events that occur at varying spatial and temporal extents and frequencies (Delcourt & Delcourt, 1988). Importantly, these disturbance events drive structure and heterogeneity in plant communities, but repeated or severe events can push communities beyond ecological thresholds, leading to often irreversible changes in ecological function (Briske, Fuhlendorf, & Smeins, 2005; Stringham et al., 2006). Ecological resilience describes the capacity to which ecological communities are able to absorb disturbance and maintain function following disturbance (Folke et al., 2010; Holling, 1973). In the Great Basin region of the southwestern United States (Figure 2.1), resilience concepts are typically accompanied by the concept of ecological resistance, which refers to the capacity of ecological communities to withstand and limit invasion by noxious species (Elton, 1958; Chambers, Pyke, et al., 2014). These concepts of resilience and resistance have become prevalent in the literature and in resource management decision-making due to plant invasions and altered fire regimes in recent decades.

Fire is a fundamental driver in Great Basin shrublands and continues to become more prevalent through time. During the past 20 years, the ten-year average for annual acres burned has increased from 478,000 acres to 963,000 acres according to data from the Monitoring Trends in Burn Severity (MTBS) program. Additionally, MTBS polygons suggest that many areas, particularly in the north central Great Basin, have burned more than five times between 1984 and 2017 (Figure 2.2). More frequent fires have largely been driven by increases in fine fuels from

annual grasses, especially cheatgrass (*Bromus tectorum*), which competes with native grasses and shrubs (Pilliod, Welty, & Arkle, 2017). Fires were up to four times more likely to occur in cheatgrass dominated-systems than native plant-dominated systems in the Great Basin (Balch, Bradley, D'Antonio, & Gómez-Dans, 2013)



Figure 2.1: The Great Basin and Snake River Plain based on Level III Ecoregions of the United States

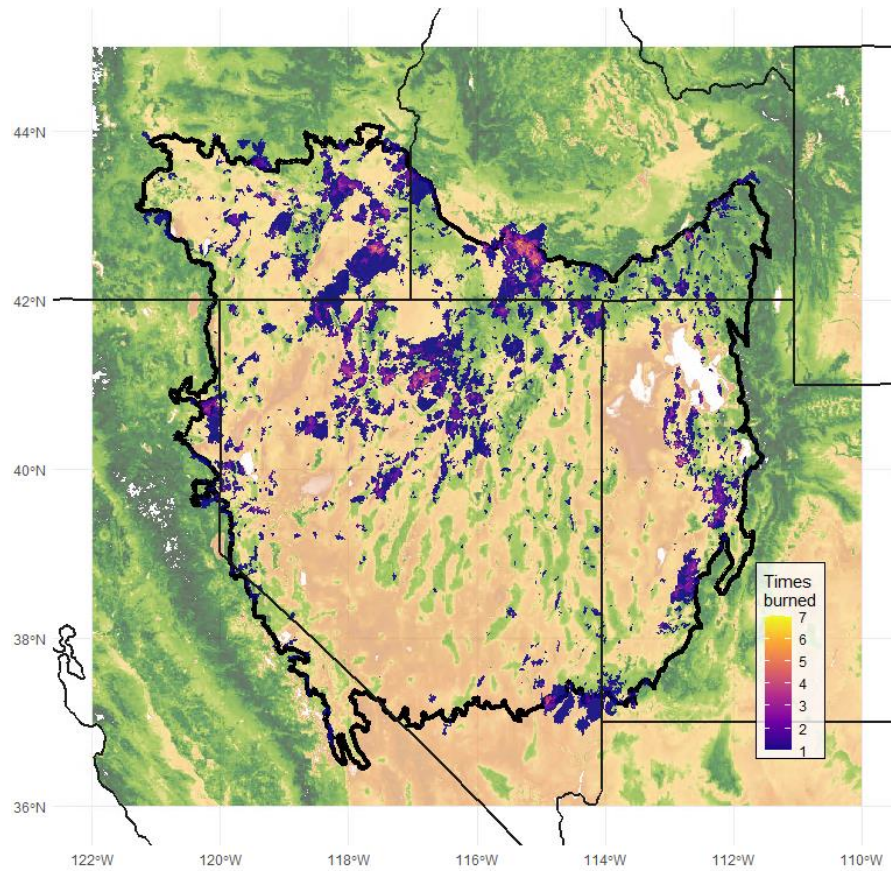


Figure 2.2: Number of times burned between 1984–2017 based on *Monitoring Trends in Burn Severity* data. Pixels have burned between 0 and 7 times.

Mitigating ecological state transitions

These ecosystem traits of high fire frequency and annual grass dominance define an alternative stable state (McIver et al., 2010). Concurrently, sagebrush (*Artemisia spp.*) has been estimated to have lost 45% of its historic distribution, often through transitions to annual-dominated states or conifer encroachment (Miller et.al. 2011). Additionally, climate analysis suggests that for each 1°C increase in temperature, 87,000 km² of existing sagebrush habitat will be lost (Neilson et al., 2005, Miller et.al. 2011). Areas that have transitioned to alternative states are costly and resource-intensive to return to their pre-fire state. It is suggested that areas with high resilience and resistance need less post-fire management intervention, whereas areas with low resilience and resistance will require greater restoration efforts. Therefore, strategic

application of post-fire restoration resources and methods is imperative.

In attempts to mitigate the impacts of fire and promote the recovery of native perennial communities to Great Basin shrublands, the Bureau of Land Management (BLM) commonly applies drill and aerial seeding following fire. In many cases, seeding efforts are spatially extensive (Arkle et al., 2014). However, despite ambitious efforts, the outcomes have had mixed results with successes and failures often occurring across environmental gradients, such as topography and climate (Arkle et al., 2014; Knutson et al., 2014). Meanwhile, the Land Treatment Digital Library has catalogued over 75 years of post-fire treatments in the western United States and can be used as a spatial dataset of seeding treatments for analysis (Pilliod, Welty, & Toevs, 2017).

Spatially continuous approaches

Developing understanding of drivers and spatial patterns of resilience and resistance is of fundamental and applied interest to researchers. Plot-based studies of resilience and resistance in Great Basin shrublands have found that climate, soils, and topographic variables are all important for influencing post-fire recovery. In particular, soil moisture and temperature regimes have been linked to resilience and resistance — with increased growing season moisture promoting growth of native perennials and generally cooler soil temperatures inhibiting cheatgrass (Chambers, et. al 2014). Additionally, climatic factors, such as wetter winters and early springs, promote growth of perennial forbs and grasses (Roundy et al., 2018). Elevation is also an important variable for habitat recovery but is closely related to climatic variable such as precipitation and temperature (Arkle et al., 2014). Additionally, plant species richness may relate to ecological resilience and resistance in the region though the relationship has never been tested directly (Arkle et al., 2014; Folke et al., 2004; Shinneman & Baker, 2009). While plot-based

approaches have been useful in elucidating ecological drivers, spatially continuous approaches that leverage these relationships have a greater potential to steer management.

The Great Basin is heterogeneous at a variety of scales in terms of climate, topography, and ecology. As a result, inference drawn from plot-based time-series studies and monitoring programs, while insightful, can be limited. To abate the spatial limitations of plot-based designs, researchers frequently leverage time-series spectral remote sensing datasets, particularly those from the Landsat program (Bright, Hudak, Kennedy, Braaten, & Khalyani, 2019; Kennedy, Yang, & Cohen, 2010; Kennedy et al., 2018). While these approaches have been gainfully applied particularly in forested systems of the western United States, the relationships in shrubland systems are complex and confounded by weak vegetation signals, high bare ground, and high interannual phenological variability (Rigge et al., 2019). As a result, spatially continuous modeling of post-fire vegetation recovery has remained elusive in Great Basin shrublands.

In recent years, however, a confluence of advancements in natural resources monitoring and computing have enabled time-series analysis using remote sensing based modeled spatial products (Gorelick et al., 2017). The development of methodologically-consistent monitoring protocols adopted by the NRCS on private lands and BLM on public rangelands has produced over 11,000 field plots in the Great Basin (Herrick et al., 2017). Those datasets have become powerful training points for using machine learning algorithms to produce spatial predictions of ecological characteristics, such as functional group fractional cover, bare ground cover, primary production, and species richness—each mapped at an annual timestep (Allred et al., 2020; Jones et al., 2018; Rigge et al., 2019; Jensen, Chapter 1). These models represent the fusion of remote sensing and field-based approaches, leveraging time-series data from Landsat and trained on in

situ ecological measurements. By applying spatial time-series analysis techniques, we can further refine understanding of resilience and resistance in the Great Basin.

Modeling post-fire recovery trajectories addresses issues of fundamental and applied interest in ecology. Fundamentally, models of recovery can address community ecology questions of variables governing resilience and resistance; from an applied perspective, they can provide decision support tools to managers and decision-makers to help guide the allocation of limited post-fire restoration resources. To address knowledge gaps related to impacts of fire on post-fire plant community trajectories in Great Basin shrublands, we identified three objectives: 1) analyze the impact of the number of times burned on post-fire vegetation recovery trajectories, 2) assess the effectiveness of post-fire seeding on vegetation recovery trajectories, and 3) use machine learning algorithms to model post-fire recovery using environmental predictor variables.

Methods

Study Area

Seven fires were selected for analysis (Table 2.1) based on criteria of: 1) having burned between 1995–2003, 2) a significant portion of the fire having not burned since 2003 to allow for a period of recovery assessment, 3) the burned areas primarily being shrubland systems such as sagebrush shrub and salt desert shrub, 4) fires were spatially distributed across the Great Basin and Snake River Plain, and 5) fires having had significant aerial and/or drill seeding applied following fire, as well as unseeded areas that serve as a control. Our spatial domain was the extent of fire polygons derived from the MTBS and our temporal domain was the period between 1984–2017 (Table 2.1).

We used ArcGIS Pro version 2.X to produce spatial polygons that burned-once, burned-more-than-once, and were unburned (Figure 2.3), according to the MTBS record. Polygons in

the burned-more-than-once layer burned between two and four times. To produce unburned polygons, we buffered each fire polygon by five kilometers and applied the Erase tool to remove any areas that intersected with MTBS fire perimeters. While the MTBS dataset provides reliable information about fires that have burned since 1984, we acknowledge that our analyses and summary of times burned do not take into account fire histories prior to that.

Table 2.1: Summary of fires analyzed. Adjoining fires burned in the same year as the fire of interest and were within the 5-kilometer buffer.

Fire name	Year	Acres burned	Adjoining fires
Tuana Complex	1995	80,638	Three Creek (1995)
Shirttail	1999	11,976	New Pass Complex (1999)
Sadler Complex	1999	183,908	Mineral, Railroad Pass, Dido Complex (1999)
Sombrero	1999	128,143	Dun Glenn Complex (1999)
Bilk Creek Complex	2000	69,694	N/A
West Basin	2000	56,396	Choke Cherry (2000)
Big Juniper	2001	95,148	N/A

Spatial polygons of aerial and drill seeding were compiled from the Land Treatment Digital Library (<https://ltdl.wr.usgs.gov>). Seeding polygons were clipped to the burned-once boundaries to control for number of times burned within our seeding treatment specific analyses (Pilliod, Welty, & Toevs, 2017). Additionally, seeding polygons were only included in the analysis if they occurred during the year following the fire of interest to focus on the impact of immediate post-fire restoration activities.

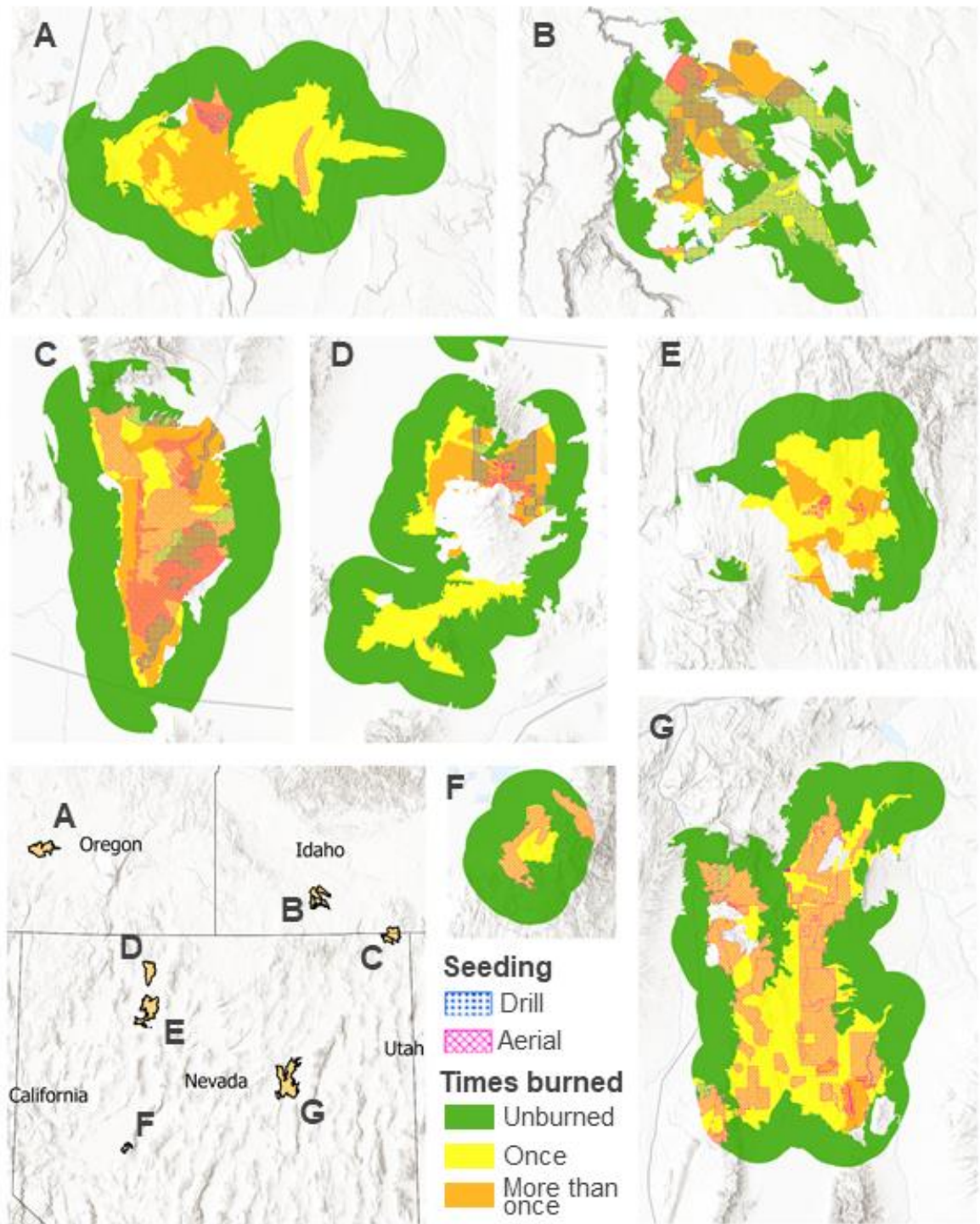


Figure 2.3: Strata of numbers of times burned and post-fire seeding (drill or aerial) for each fire. A) Big Juniper (2001), B) Tuana Complex (1995), C) Bilk Creek (2000), D) Sombrero (1999), E) West Basin (2000), F) Shirttail (1999), G) Sadler Complex (2000). The areas that are not represented by a polygon either fell outside of the buffered area or have burned since the fire of interest.

The normalized differenced perennial dominance index

Ecological modeling is most powerful when the response variable represents ecologically-important traits, is succinct, and where interpretations of results have the potential to provide management relevant information. Many vegetation modeling studies in the Great Basin use shrub or other plant functional group percent cover as a response variable (Barnard et al., 2019; Rigge et al., 2019). However, percent cover varies across systems and thus can be a biased indicator. Here, we introduce an alternative metric, the normalized differenced perennial dominance index (NDPDI). Inspired by the normalized differenced vegetation index (Tucker, 1979), this index differences percent cover of perennial plants (shrubs, forbs, and grasses) against annual plants (grasses and forbs) (eq. 1).

$$NDPDI = \frac{Perennial \% - Annual \%}{Perennial \% + Annual \%} + 1 \quad [\text{eq. 1}]$$

The NDPDI is bound from 0–2 and is easily interpretable, with values of less than 1 being dominated by annual plants and values greater than 1 being dominated by perennial plants. One of the advantages of such an approach is that it is unbiased for low or high vegetation cover systems. For example, high elevation mountain sagebrush systems naturally have much higher cover than valley salt desert shrub. It is also sensitive to relatively minor shifts in dominance. One notable limitation of NDPDI is that it treats all perennial functional groups the same which can wash over important distinctions. Yet, in many portions of the region simply establishing perennial plants in the post-fire environment is viewed as a restoration success. Thus, we propose the index as a scalable modeling variable indicative of perennial plant dominance.

Time-series analysis of multiple times burned on post-fire recovery

To investigate the effect of the number of times burned on post-fire vegetation trajectories, we conducted a time-series analysis of pixels within polygons that were unburned,

burned once, burned twice, burned three times, and burned four times. We first removed pixels that had ever been classified as agriculture or developed using the National Land Cover Database (Jin et al., 2019). Then, we used Google Earth Engine (GEE) to extract values of fractional cover of annual forbs and grasses (AFGC), perennial forbs and grasses (PFGC), shrubs (SHR), and bare ground (BG) from the Rangeland Analysis Platform (RAP) (Allred et al., 2020). We also calculated an image for NDPDI by summing the PFGC and SHR to represent perennial cover percentage and using AFGC as the annual cover percentage. We exported mean values of each vegetation variable across the times-burned strata at an annual time-step for each fire.

We imported and analyzed the time-series data in R—producing time-series plots and extracting post-fire linear regression coefficients (R Core Team, 2018; Wickham et al., 2019). Our time-series plots visualize important facets of the pre-fire and post-fire trajectories. For each times-burned stratum, we produced plots of AFGC, BG, and NDPDI. Each plot visualizes the mean of the data, as well as linear regressions fit through the pre-fire and post-fire period. We then used the linear regressions to plot residuals through time to evaluate interannual variability—an indicator of ecological instability. Our plots also visualized the pre-fire envelope for the mean values for each variable to identify departures from pre-fire condition. For each stratum and each fire, we extracted the post-fire linear regression slopes and 15-year intercepts (condition fifteen years following fire) of NDPDI to enable quantitative comparison of recovery trajectories.

Influence of post-fire seeding on post-fire recovery

To assess the efficacy of seeding on post-fire vegetation recovery, we evaluated locations that were drill seeded, aerial seeded, and unseeded following fire (Pilliod, Welty, & Toevs, 2017). We focused on areas that burned only once to reduce variability introduced by multiple

times burned following the approach of Knutson et al. (2014). We extracted values for AFGC, PFGC, SHR, BG, and NDPDI from the RAP using GEE at an annual time-step for drill, aerial, and unseeded polygons and exported them as CSVs (Allred et al., 2020). Then, we imported the CSVs into R and used a similar approach as described above to produced time-series plots and extract post-fire linear regression slopes and 15-year intercepts of NDPDI (R Core Team, 2018; Wickham et al., 2019).

Modeling post-fire recovery trajectories using environmental, fire, and management variables

Modeling using machine learning algorithms provides a framework for ranking the importance of a large numbers of predictor variables and for producing predictive models. Applied toward highly dimensional ecological problems, machine learning analysis can help scientists to untangle complex relationships. We had three sub-objectives for modeling post-fire recovery: 1) train and validate a model of 15-year post-fire NDPDI, 2) evaluate predictor variables that are most related to 15-year post-fire NDPDI, and 3) apply models to predict recovery for the Saddle Draw Fire (2014). To train the model we generated 1,500 random points per fire for a total of 10,500 points.

For each of the generated points, we extracted and exported values for 106 climatic, soils, topographic, fire, and pre-fire vegetation predictor variables and our response variable using GEE (Table 2.2). Climate variables were derived from Daymet V3 and were calculated based on those used by Rehfeldt (2006) for the post-fire period (3-year average following fire) and as 30-year averages (Thornton et al., 2016). Soil variables were from the POLARIS Soil Properties dataset from Chaney et al. (2019) and were downloaded in 1-degree tiles and mosaicked. Topographic variables were derived from the U.S. Geological Survey's National Elevation Dataset and the Ecologically Relevant Geomorphology dataset from Conservation Science

Partners, which is also calculated from the National Elevation Dataset (Theobald et al., 2015).

Fire data were acquired from the Monitoring Trends in Burn Severity Program (MTBS) as individual fire rasters and mosaicked into annual images of differenced normalized burn ratio (dNBR) and the relative differenced Normalized Burn Ratio (RdNBR) from which all other variables were derived (Eidenshink et al., 2007). Pre-fire vegetation and the response variable were derived from the Rangeland Analysis Platform and from the models described in the first chapter (Allred et al., 2020; Jensen, chapter 1).

Table 2.2: Summary of the 106 predictor variables applied in the model of post-fire recovery.

Class	Dataset(s)	Spatial resolution	Variables
Climate	Daymet Note: Each variable was calculated as 30-year averages and as post-fire averages	1000 meters	Mean annual temperature Mean spring temperature Mean summer temperature Mean winter temperature Mean growing season temperature Mean summer maximum temperature Mean winter minimum temperature Summer-winter temperature difference Mean annual precipitation Mean spring precipitation Mean summer precipitation Mean winter precipitation Mean growing season precipitation Frost-free period Last freeze of spring First freeze of autumn Maximum snow-water equivalent 5-degree warming days 5-degree warming days during frost-free period 0-degree cooling days 0-degree cooling days from minimum temperature Annual dryness index Summer dryness index
Topography	National Elevation Dataset (NED)	1/3 arc-second	Elevation (NED) Aspect (NED) Northness (NED) Eastness (NED)

Topography, cont.	Ecologically Relevant Geo- morphology (ERGo)		Slope (degrees) (NED) Slope (percent) (NED) Slope northness (NED) Slope eastness (NED) Transformed aspect (NED) Topographic position index (ERGo) Continuous heat-load index (ERGo) Multiscale topographic position index (ERGo) Topographic diversity Landforms (ERGo) Physiographic diversity (ERGo)
Fire	Monitoring Trends in Burn severity	30 meters	Times burned dNBR of most recent fire RdNBR of most recent fire
Pre-fire vegetation	Rangeland Analysis Platform (RAP) Jensen, Chapter 1	30 meters	NDPDI (RAP) Pre-fire percent cover AFGC (RAP) Pre-fire percent cover PFGC (RAP) Pre-fire percent cover SHR (RAP) Pre-fire percent cover BG (RAP) Pre-fire Species richness (Jensen)
Soil	POLARIS Note: Each variable had four horizons (0–5 cm, 5–15 cm, 15–30 cm, and 30–60 cm)	30 meters	Percent sand Percent silt Percent clay Percent organic matter Bulk density pH θ_r (residual soil water content) θ_s (saturated soil water content)
Management	Land Treatment Digital Library	Polygons	Aerial seeding Drill seeding

We conducted modeling within R using the randomForest package (Liaw & Wiener, 2007; R Core Team, 2018). Prior to modeling, we removed multi-collinear variables and then further reduced the number of predictors using a variable selection function. We selected an optimal number of variables for the final model using variable importance plots and variance-explained values. We withheld 20% of the 10,500 points (2,100 points) for model validation, calculating R^2 and root mean square error (RMSE) values for predictions applied to the validation data set. To account for spatial autocorrelation, we also applied a leave-one-fire-out

model validation approach, where we trained 7 separate models leaving one fire out within each model iteration. We then applied each model to produce predictions for the fire that had been left out of training. The leave-one-out approach may better reflect the accuracy that we would expect when producing predictive recovery maps for contemporary fires. Using the final model, we then evaluated variable importance and direction of relationships, enabling us to evaluate drivers of post-fire recovery.

We concluded by applying the final model of 15-year post-fire condition to produce a predictive map of post-fire recovery for the Saddle Draw Fire—which burned 284,065 acres in Oregon in 2014. To produce the map, we downloaded 30-meter images from GEE for each of the selected predictor variables for the Saddle Draw Fire geography and time-period. Images that were coarser than 30-meters were resampled using the nearest neighbor approach and images that were finer were resampled using bilinear interpolation. In R, we applied the Random Forest model to the Saddle Draw Fire images to predict condition for 15-years following the fire—in this case, relating to the year 2029—continuously across the fire geography.

Results

Time-series analysis of multiple times burned on post-fire recovery

Number of times that burned negatively affected post-fire trajectories of NDPDI, AFGC, and BG (Figure 2.4). Notably, even the baseline trajectories of NDPDI for unburned pixels had negative slopes and increases in residuals—indicating an increased prevalence of annual herbaceous plants and decreased stability through time. While areas that burned once had similar pre-fire trajectories to those that were unburned, immediately following fire burned-once areas had a steep decline in NDPDI and increase in AFGC, as well as increased residuals; after the initial drop, though, post-fire regression slopes were similar for unburned and burned-once areas in terms of both AFGC cover and NDPDI. For areas that burned multiple times, those with

higher numbers of times burned had progressively higher AFGC cover and lower NDPDI with each successive fire; these patterns are especially evident in the 15-year post-fire intercepts (Table 2.3). Although there were steep declines in NDPDI for each multiple times burned strata throughout the fire period (Figure 2.4), post-fire slopes were largely flat. This suggests relative stability through time without a marked trend toward recovery or decline for areas that burned more than once. BG is visualized to evaluate to what extent AFGC may be infilling bare ground as it becomes more dominant, as opposed to displacing perennial plants. For each strata, BG declines throughout the time-series, suggesting that some of the increase in AFGC can be attributable to infilling. Notably, 1984–1986 AFGC values were highest for areas that burned most frequently over the period of analysis. Elevated AFGC cover values suggest that areas that burned multiple times between 1984–2019 may have also burned more frequently even prior to 1984.

Table 2.3: Post-fire slopes and intercepts of NDPDI for number of times burned averaged across all fires.

	Unburned	One time	Two times	Three times	Four times
Post-fire slope	-0.009	-0.009	0.000	0.000	0.000
0-intercept	1.67	1.38	1.30	1.11	0.46
15-intercept	1.55	1.24	1.30	1.11	0.49

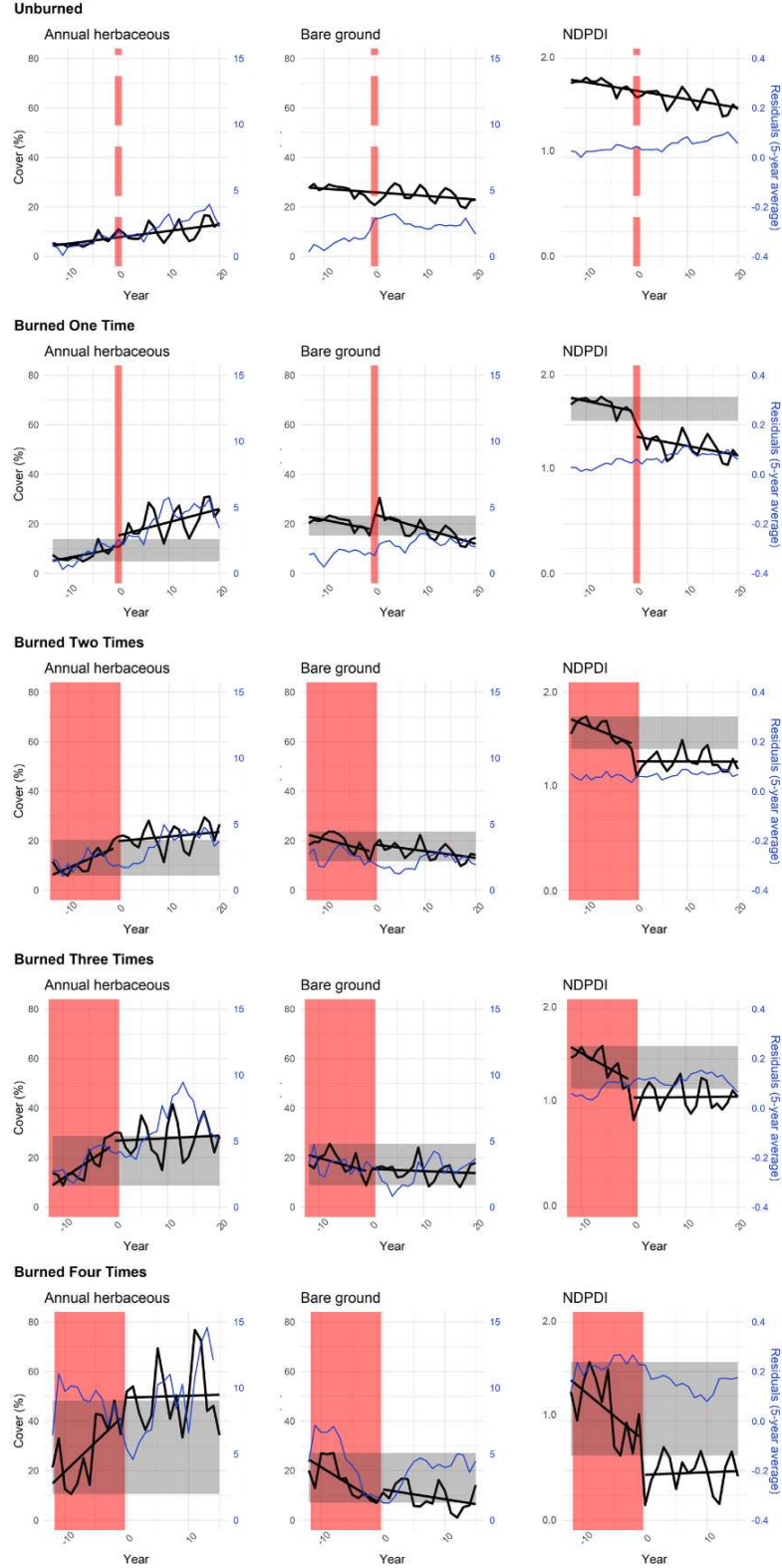


Figure 2.4: Time-series plots for pixels that were unburned, burned once, burned twice, burned three times, and burned four times. Red bars depict the year of the fire of interest and are dashed for unburned. For areas that burned multiple times the entire period of fire is depicted in red. Grey boxes represent the pre-fire envelope for each variable.

Post-fire recovery trends varied across the fires studied in relation to the number of times burned (Figure 2.5; Table 2.4). Among areas that burned once, those within the West Basin fire had a 15-year post-fire intercept NDPDI value of 1.82 (high perennial dominance), whereas those within the Shirttail, Sombrero, and Bilk Creek fires all had values <1 (annual herbaceous dominance). In general, the West Basin fire recovered anomalously well regardless of the number of times burned; even areas that burned three times had a 15-year post-fire intercept NDPDI value of 1.77. The Bilk Creek and Sombrero fires are in close spatial proximity to one another and had similar trajectories across every times-burned class. Both of those fires had 15-year post-fire NDPDI intercepts <1 for all areas that had burned, indicating degradation. Additionally, residuals in AFGC and NDPDI both saw sharp increases following these two fires. The Big Juniper fire in the northwestern portion of the Great Basin had moderate annual grass invasion during the post-fire period evidenced by some increase in AFGC and decrease in NDPDI. However, Big Juniper areas that burned were still generally dominated by perennial plants based on 15-year intercepts, as indicated by NDPDI values of around 1.5.

Table 2.4: Post-fire linear regression slopes and 15-year intercepts of NDPDI for each fire for the number of times burned.

	Unburned		One time		Two times		Three times		Four times	
Fire	Slope	15-int	Slope	15-int	Slope	15-int	Slope	15-int	Slope	15-int
Big Juniper	-0.001	1.76	-0.002	1.52	0.015	1.51	N/A	N/A	N/A	N/A
Bilk Creek	-0.008	1.50	-0.011	0.97	0.005	0.83	0.000	0.62	0.002	0.49
Sadler	-0.004	1.69	-0.003	1.42	0.013	1.46	N/A	N/A	N/A	N/A
Shirttail	-0.011	1.32	-0.020	0.85	N/A	N/A	N/A	N/A	N/A	N/A
Sombrero	-0.012	1.34	-0.005	0.92	0.011	0.89	N/A	N/A	N/A	N/A
Tuana	-0.009	1.62	0.001	1.53	-0.002	1.34	0.001	1.33	N/A	N/A
West Basin	-0.003	1.82	0.008	1.82	0.007	1.77	0.011	1.77	N/A	N/A

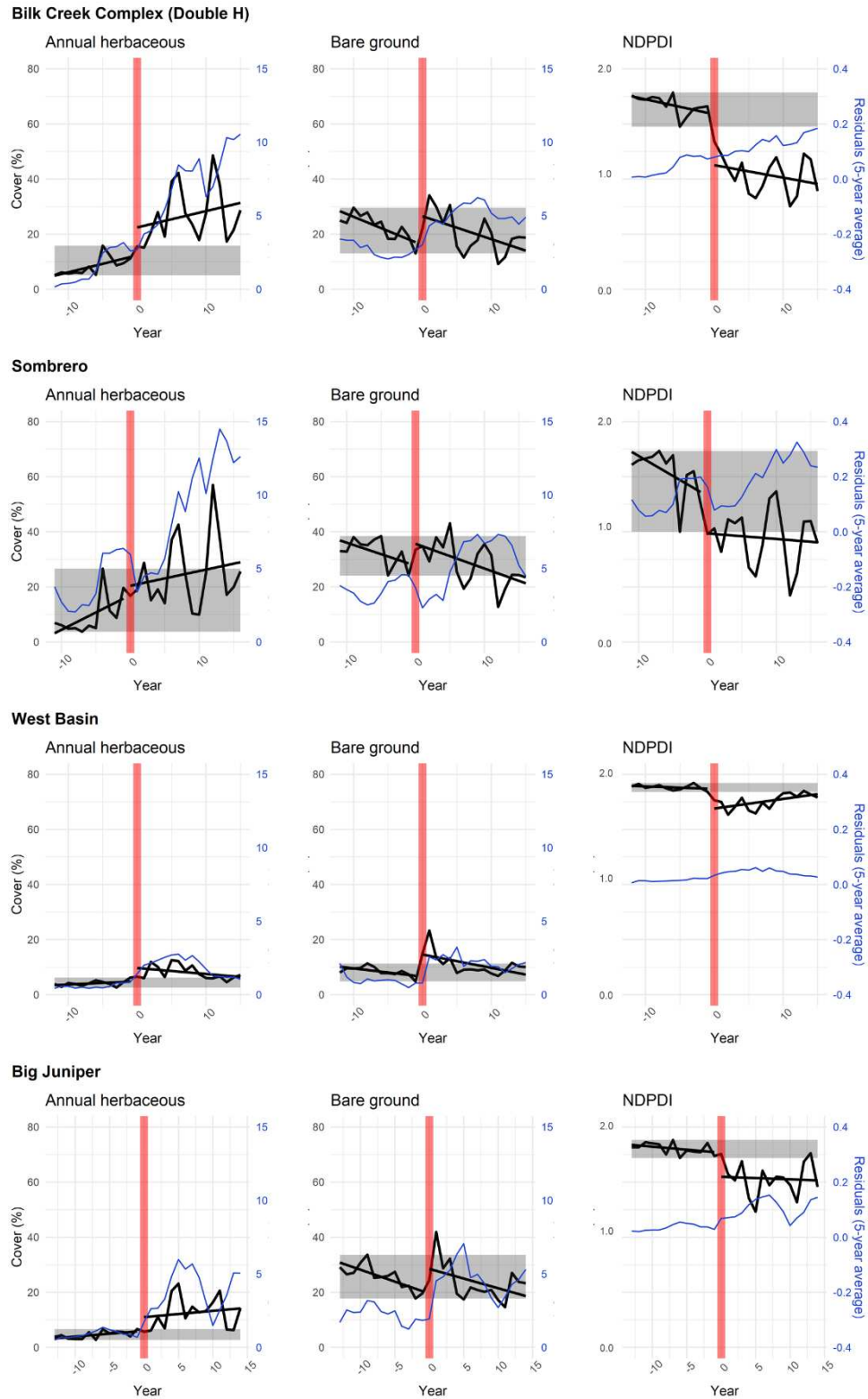


Figure 2.5: Time-series plots for pixels in four of the seven fires of interest. Fires were selected for plotting based on their location to depict some of the variability in recovery trajectories. Red bars depict the year of the fire of interest. For areas that burned multiple times the entire period of fire is depicted in red. Grey boxes represent the pre-fire envelope for each variable.

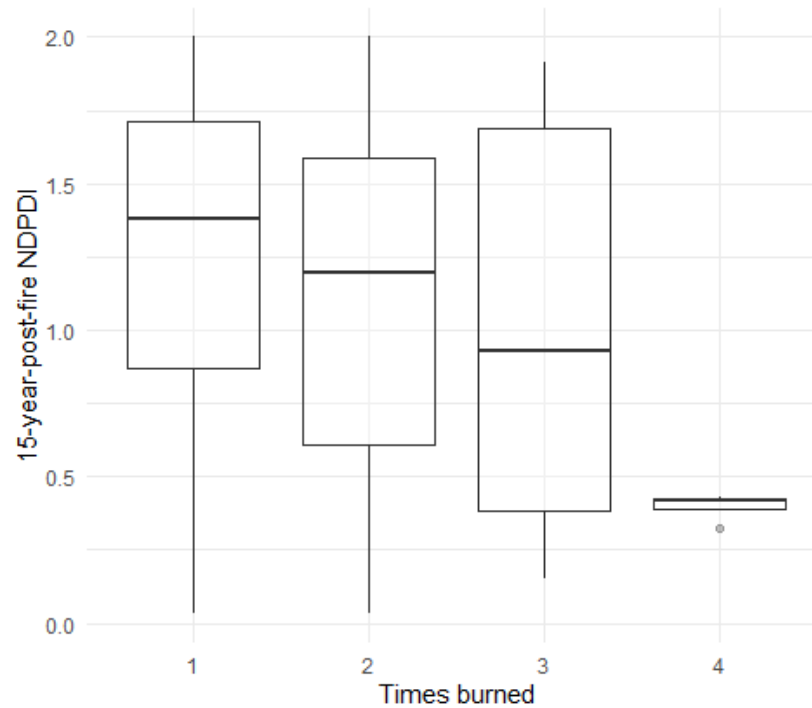


Figure 2.6: The relationship between number of times burned and 15-year post-fire NDPDI. The box-and whisker shows the mean value, upper and lower quantile and minimum and maximum values.

Influence of post-fire seeding on post-fire recovery

When looking across all fires, seeding had little impact on post-fire recovery for the fires evaluated (Figure 2.7; Table 2.5). The differences in the post-fire trajectories were minor among drill seeded, aerial seeded, and unseeded locations with similar post-fire trends in terms of regression slopes, 15-year intercepts, and residuals. Post-fire recovery slopes of NDPDI were most steeply negative for unseeded pixels, but the intercepts (0-intercept: 1.41; 15-intercept: 1.27) were also higher than seeded pixels, suggesting that the unseeded areas maintained their perennial component better than those that were seeded. Aerial seeding resulted in relatively moderate NDPDI intercepts (0-intercept: 1.33; 15-intercept: 1.20) and the slopes were only slightly less steep than unseeded. Drill seeding had the lowest post-fire NDPDI intercepts (0-intercept: 1.21; 15-intercept: 1.20) but also had the flattest slopes suggesting more stability

through time. During the post-fire period, residuals of AFGC were somewhat higher for the drill seeded than either aerial seeded or unseeded locations, suggesting that drill seeded areas may be less stable than even those that were not seeded.

While post-fire trajectories were similar for areas that received seeding treatments and those that were unseeded when averaged across all fires, there were important distinctions when fires were viewed individually. Most unseeded areas had higher 15-year regression intercepts for NDPDI than did either aerial or drill seeded when treatments were evaluated within each fire separately (Table 2.6). The only exception to that pattern was the Tuana Complex, which had >0.1 increase in 15-year intercept of NDPDI for both aerial and drill seeded when compared with unseeded. However, multiple fires had positive post-fire slopes for seeded areas despite negative slopes in unseeded areas. For example, drill seeded areas in the Sombrero, Sadler, and Tuana fires all had positive slopes of NDPDI. The only fire with a positive slope following aerial seeding was the West Basin fire with all other fires registering negative post-fire slopes.

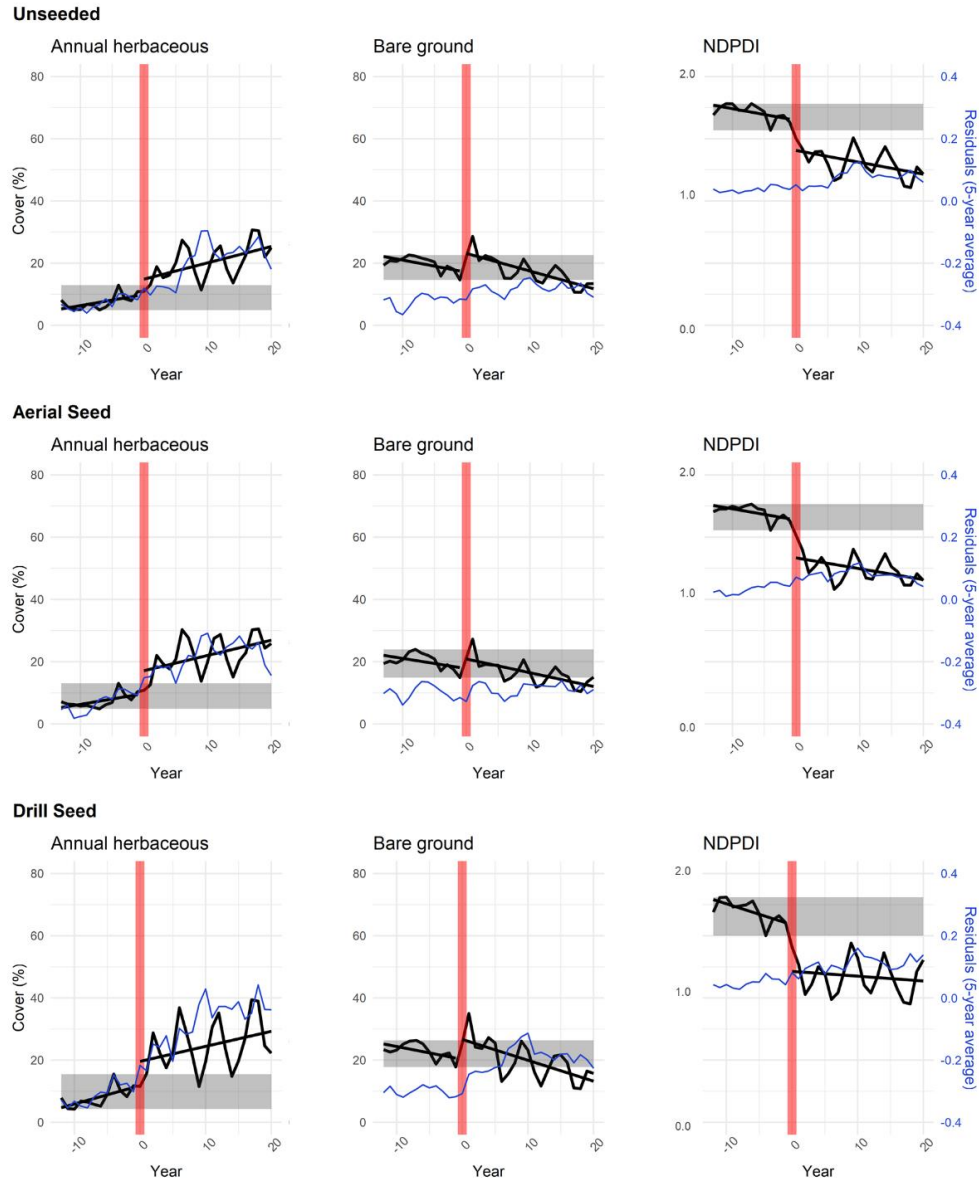


Figure 2.7: Time-series graphs of post-fire recovery trajectories based on seeding strata for unseeded, aerial seeded, and drill seeded areas averaged across all fires. Red bars depict the year of the fire of interest. For areas that burned multiple times the entire period of fire is depicted in red. Grey boxes represent the pre-fire envelope for each variable.

Table 2.5: Summary of post-fire linear regression slopes and intercepts of NDPDI across seeding strata averaged across all areas that burned once.

	Unseeded	Drill seed	Aerial seed
Post-fire slope	-0.010	-0.004	-.0009
0-intercept	1.41	1.21	1.33
15-intercept	1.27	1.16	1.20

Table 2.6: Post-fire linear regression slopes and 15-year intercepts of NDPDI for each fire for each seeding strata.

	Unseeded		Drill		Aerial	
Fire	Slope	15-int	Slope	15-int	Slope	15-int
Big Juniper	-0.002	1.52	N/A	N/A	-0.001	1.38
Bilk Creek	-0.010	1.02	-0.019	0.94	-0.010	0.94
Sadler	-0.004	1.46	0.007	1.34	-0.002	1.39
Shirttail	-0.017	1.03	N/A	N/A	-0.022	0.77
Sombrero	-0.005	0.92	0.005	0.89	-0.008	0.82
Tuana	0.000	1.45	0.001	1.56	-0.010	1.59
West Basin	0.008	1.81	N/A	N/A	0.010	1.74

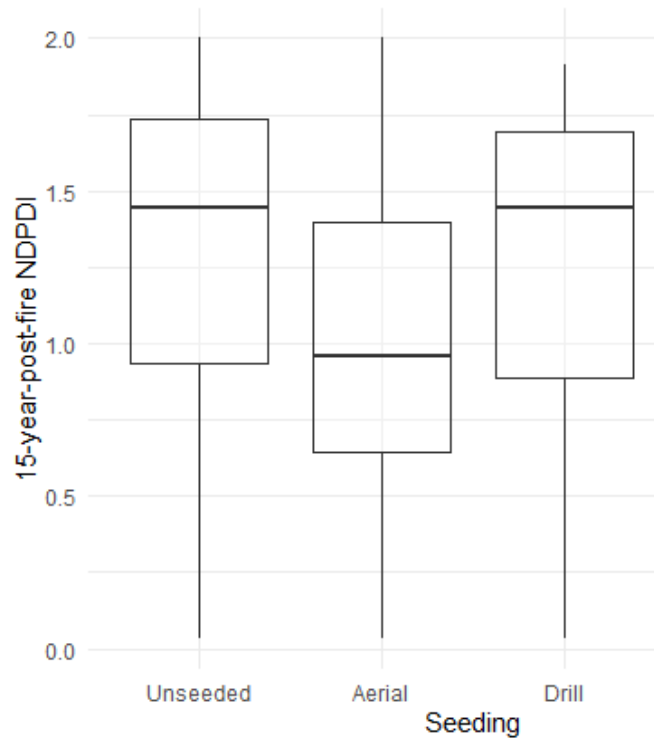


Figure 2.8: Relationships between seeding types and 15-year post-fire NDPDI. The box-and-whisker shows the mean value, upper and lower quantile and minimum and maximum values.

Modeling post-fire recovery trajectories using environmental, fire, and management variables

Our Random Forest model of 15-year post-fire NDPDI reported strong accuracy statistics. The final model had 17 predictor variables and reported an R^2 of 0.830, RMSE of 0.208, and mean absolute error of 0.158. A scatterplot of model predictions vs. observed responses are displayed in Figure 2.9. The slope of the linear regression fit was 0.790, indicating that model predictions are approaching the desired 1:1 line of predicted vs. observed. Leave-one-fire-out model validation reported an R^2 of 0.338 with an RMSE of 0.370, suggesting that the model generalizes somewhat well when predicting for fires that it is not trained on, but that the overall R^2 of the model is likely too optimistic (Table 2.7; Figure 2.10). This suggests that localized relationships drive post-fire recovery and that the spatial variability of the fires, and thus lack of local analogues, limits model predictions on new fires. The model generalized best to the Shirttail Fire, possibly because it shared similar post-fire trajectories with the Bilk Creek and Sombrero Fires. However, it performed most poorly for predicting the West Basin Fire, likely because of the West Basin fire's anomalously strong post-fire recovery.

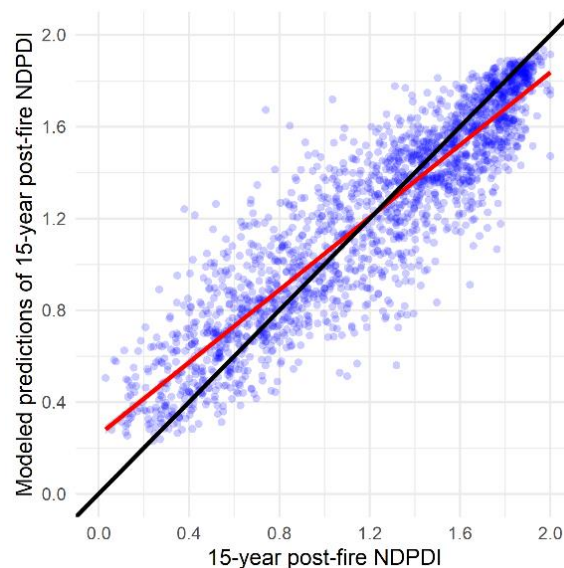


Figure 2.9: Model predictions plotted against the validation set for 15-years after fire. The red line indicates the linear regression fit through the datapoints and the black line is the 1:1 line.

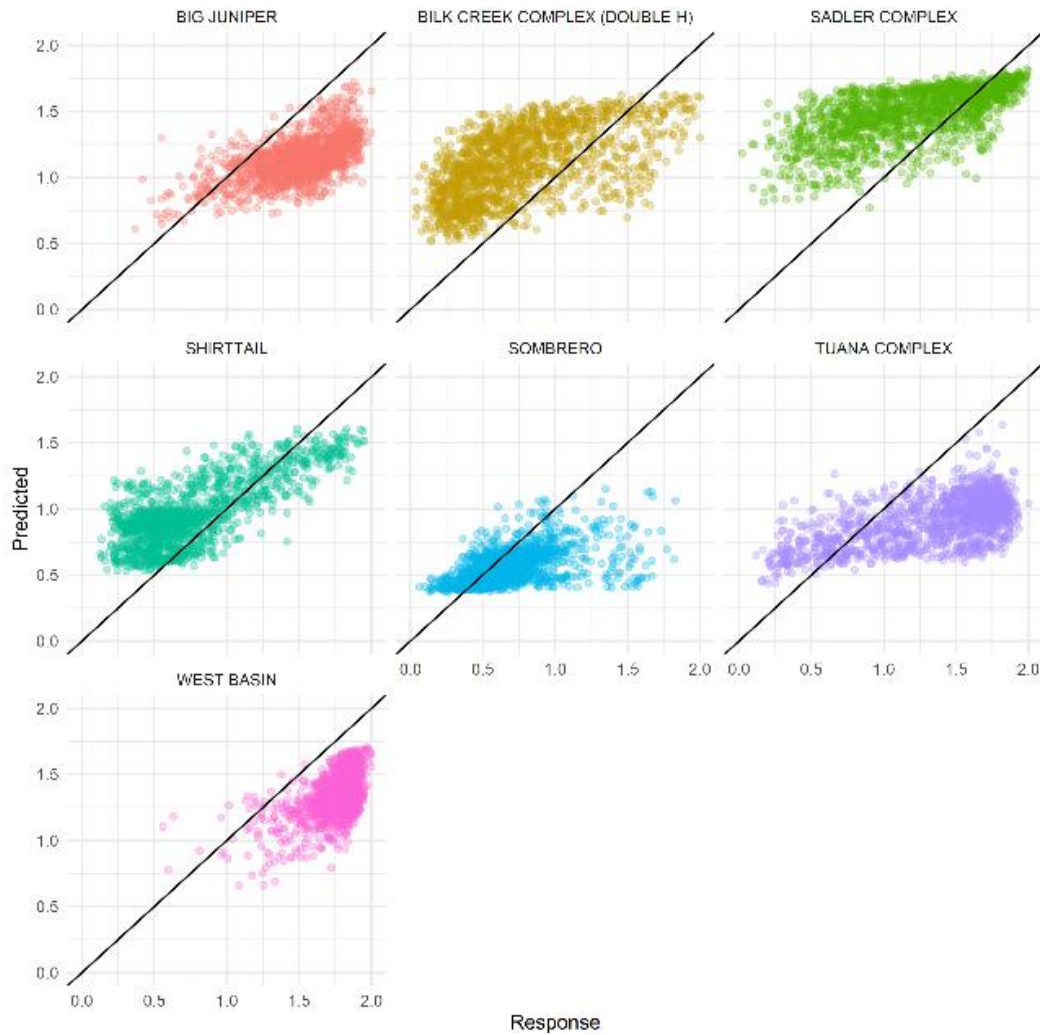


Figure 2.10: Predicted vs. observed plots from leave-one-out model validation from Random Forest regression models

Table 2.7: Leave-one-out validation statistics for the model of post-fire recovery. The name of the fire in the table represents the fire that was left out of the model training and the subsequent validation of predictions upon the fire. Validation statistics are reported as the coefficient of determination (R^2 and root mean square error (RMSE)

Fire	R^2	RMSE
Big Juniper	0.286	0.331
Bilk Creek Complex	0.401	0.490
Sadler Complex	0.373	0.384
Shirrtail	0.458	0.305
Sombrero	0.340	0.309
Tuana Complex	0.278	0.381
West Basin	0.234	0.386
Total	0.338	0.370

Predictor variables included in the final model of post-fire recovery included climatic, topographic, pre-fire vegetation, and fire predictors (Table 2.8). Pre-fire vegetation variables of NDPDI (Figure 2.11A) and AFGC were both found to be important drivers of recovery. A variety of summer aridity/precipitation measures were also highly ranked, including post-fire summer precipitation (Figure 2.11B), post-fire summer dryness index, and average 5-degree warming degree days (a measure of heat accumulation throughout a season). Relatedly, heat-load index and slope northness (calculated as the slope percentage multiplied by the cosine of the aspect) are both related to potential evapotranspiration deficits, with northern slopes being correlated with higher post-fire NDPDI values. Interestingly, elevation was not retained within the final model, possibly because precipitation and temperature variables already captured ecologically important aspects of elevation. Both measures of fire severity were included, albeit with opposite directionality. Here, we calculated directionality using simple linear regression slopes; because Random Forest handles non-linear relationships, it is likely that the model was finding more nuanced relationships in the data. Notably, species richness was not selected as an important variable in the final model, contrary to expectations based on existing literature (Figure 2.11C).

Table 2.8: Variable importance rankings and directionality for all variables in the model of 15-year post-fire NDPDI

Rank	Variable	Importance (%IncMSE)	Direction
1	Pre-fire NDPDI	320.24	↑
2	Post-fire summer precipitation	298.31	↑
3	Post-fire summer dryness index	247.05	↓
4	Average summer precipitation	168.22	↑
5	Pre-fire AFGC	160.44	↓
6	Slope northness	133.02	↑
7	Average cooling 0-degree-days	93.46	↑
8	Average winter temperature	88.68	↓
9	Average spring precipitation	77.29	↑
10	Heat load index	75.94	↓
11	RdNBR	72.82	↓
12	dNBR	63.63	↑
13	Average warming 5-degree-days	58.50	↓
14	Post-fire snow water equivalent	56.39	↑
15	Average winter precipitation	48.90	↑
16	Average annual dryness index	48.60	↓
17	Post-fire mean annual precipitation	46.36	↑

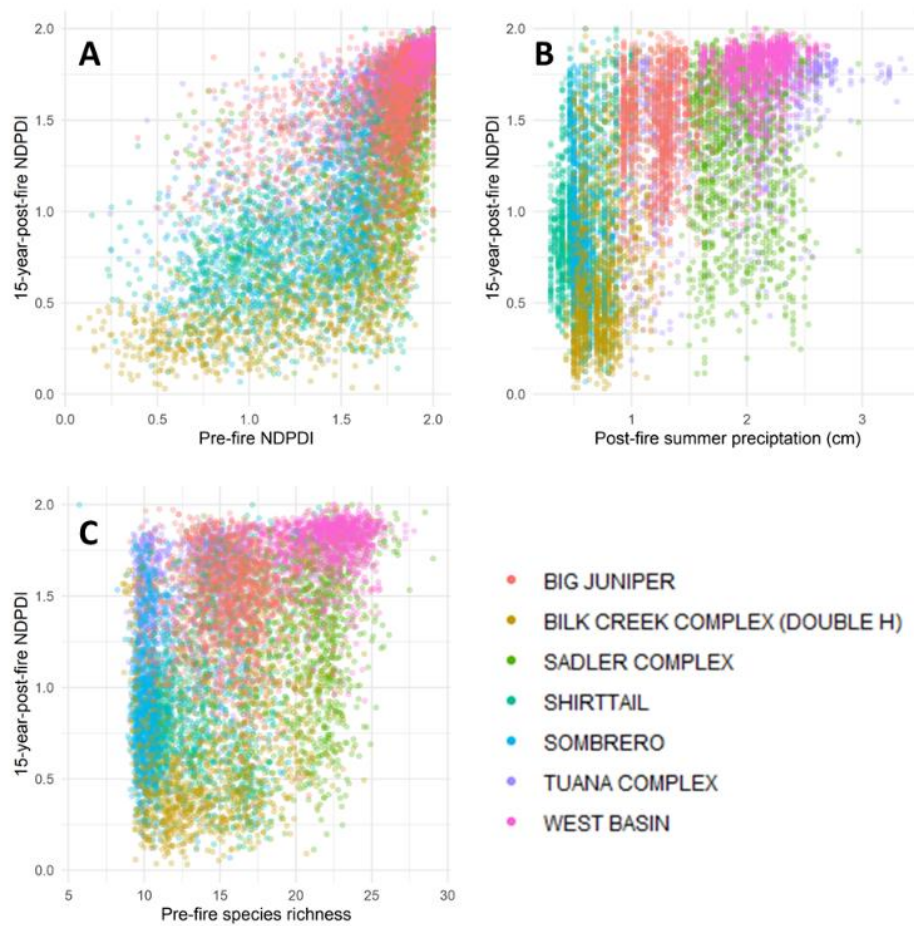


Figure 2.11: Univariate relationships between 15-year post-fire NDPDI and A) pre-fire NDPDI, B) post-fire summer precipitation, and C) pre-fire species richness

Our strong validation statistics for the model of 15-year post-fire NDPDI led us to continue with assessing the utility for predicting post-fire recovery for a more recent fire event, the Saddle Draw Fire (2014). Based on our modeling approach, these mapped results can be considered predictions for the year 2029. Mapped predictions revealed that, while diminished NDPDI can be expected across the fire, it will not be uniform (Figure 2.12). In particular, the model suggests that southern aspects and locations that had relatively high pre-fire NDPDI may have the most significant decreases in NDPDI following fire. The model also suggests that some areas may see increased NDPDI following fire. While some post-fire increases in NDPDI are for

pixels that had very low pre-fire NDPDI, for which the model may not be fully capturing the variance in the response, at other locations predicted increases in NDPDI may indicate areas that would be more likely recover without restoration.

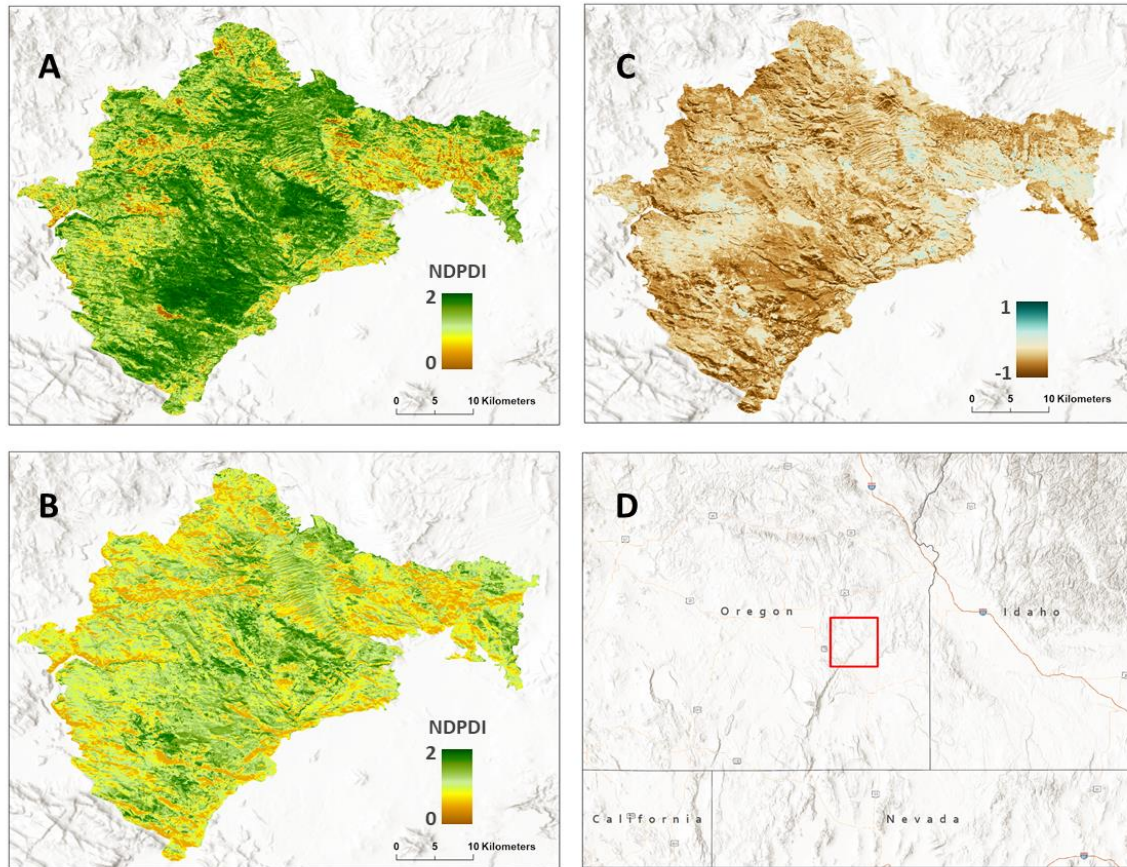


Figure 2.12: Maps of NDPDI for the Saddle Draw Fire. A) Pre-fire NDPDI (median of NDPDI between 2011–2013), B) modeled predictions of 15-year post-fire NDPDI corresponding to the year 2029, and C) differenced image of B – A.

Discussion

The cheatgrass-fire cycle is a primary driver in Great Basin shrubland systems, often inhibiting post-fire recovery of native perennial plant communities. However, sites vary in their susceptibility to fire and invasive annual plants. Our analysis leverages Landsat-derived data that captures the variability in shrubland communities because of its comprehensive spatial coverage. Our findings revealed that the number of times burned affects post-fire trajectories, seeding did

not produce appreciably better results than not seeding, and spatial modeling elucidated drivers and produced spatially continuous predictions of post-fire condition.

Repeated fire degrades Great Basin shrubland plant communities

We found that for each successive time burned there was an increasingly negative response in the postfire vegetation trajectories—AFGC increased and NDPDI decreased and post-fire slopes often showed little recovery (Figure 2.6). Supporting our findings, Mahood & Balch (2019) found that in their study in north-central Nevada where they evaluated areas that had burned between 0–3 times, repeatedly burned locations had successively lower alpha-diversity and native perennial cover percentage. They found that community composition fundamentally changed after one fire, converting shrub-dominated systems to ones dominated by annual grasses which then persist for decades (Mahood & Balch, 2019). Consequently, areas with >15% annual grass cover have been found to be twice as likely to burn and four times as likely to burn multiple times over a fifteen year period (Bradley et al., 2018). Lending support to those studies, we found that areas that burned multiple times also had elevated cover of AFGC *prior* to the fires we analyzed, indicating that AFGC is both a driver and response to fire. Similar patterns apply in salt desert shrub communities as well, which have been found to have 5 times higher non-native cover in locations that burned than those that were (Haubensak, D’Antonio, & Wixon, 2009). While it is well-established that fire degrades shrublands in the Great Basin, no studies have evaluated the impact of repeated burning in a spatially distributed manner in the Great Basin.

The effects of repeated burning on post-fire trajectories in Great Basin shrublands varied widely across different parts of the region. The Bilk Creek and Sombrero fires both burned geographically near the study area evaluated by Mahood & Balch (2019) and our findings for

those fires closely matched theirs—the first fire dramatically increased AFGC and each subsequent fire incrementally led to slightly more dominance by AFGC. However, trajectories were much different for some other fires, especially in the northern and eastern portions of the Great Basin. In fact, the Big Juniper, Sadler, Tuana, and West Basin fires all maintained perennial dominance even burning as many as three times. There has not been a spatial analysis of post-fire recovery in the Great Basin, however maps of resilience and resistance based on soil temperature and moisture suggest that locations in the northern Great Basin would be expected to have stronger post-fire recovery than in the central Great Basin (Maestas, Campbell, Chambers, Pellant, & Miller, 2016). While the soil-based resilience and resistance maps are coarse, our results support the general patterns.

Post-fire seeding does not appreciably improve post-fire recovery

Post-fire aerial and drill seeding did not improve recovery 15 years following fire, and in some cases had worse outcomes (Figure 2.8). In a similar study of post-fire aerial and drill seeding between 1990–2003, Knutson et al. (2014) also found that native perennial grass cover did not increase on seeded sites except in instances of drill seeding competitive non-native perennial grasses. Rather, precipitation and elevation were more important drivers of recovery than seeding. In any event, the documented effectiveness of drill seeding non-native perennial grass cultivars may help to explain why our results showed that drill seeding was more effective than aerial seeding. Similarly to Knutson et al. (2014), a study of 313 plots seeded after fire in greater sage-grouse (*Centrocercus urophasianus*) habitat found that none of the plots met all sagebrush guidelines for breeding habitat, although 50% met understory habitat requirements. However, some aerial and drill seeded plots in that study had relatively high probabilities of sage-grouse occupancy based on their models (Arkle et al., 2014). Environmental variables are

often important in supporting post-fire recovery of seeded sites, particularly climate and topography (Kulpa et al., 2012; Svejcar, Boyd, Davies, Hamerlynck, & Svejcar, 2017). Thus, while seeding has some demonstrated impact on post-fire recovery, just as often the projects have no better outcomes than those left unseeded. Generally, recovery trajectories are primarily driven by environmental variables.

It is likely that our finding that seeding had little positive influence on post-fire trajectories is partially related to the incentive that managers apply seeding to areas that most severely burned. There are known limitations of the MTBS dataset in the Great Basin, particularly the inclusion of unburned islands and fingers within the fire perimeters with commission errors as high as 15% (Sparks et al., 2015). Thus, while the MTBS fire perimeters likely include some component of unburned areas and additional low burn severity areas, post-fire managers are unlikely to apply seeding to those areas. This is evident in our results, as there is no reason that applying aerial seeding would cause worse outcomes than applying no seeding at all. Nonetheless, our finding that many aerial seeded areas are dominated by AFGC 15 years following fire suggests that there is much room for improvement in post-fire seeding treatments.

Machine learning models predict post-fire vegetation recovery outcomes

Our models of post-fire vegetation recovery generated robust validation statistics and generalized to fires for which there was not post-fire data reasonably well. A similar machine learning approach was applied to predict post-fire restoration outcomes in terms of sagebrush cover for 2,171 plots three years following the Soda Fire (Barnard et al., 2019). That study included geospatial predictors as well as field-collected data as predictor variables and reported model R^2 values of 0.58–0.79 across 33 models. There have been other efforts to map resilience and resistance explicitly, typically using single-variable relationships such as soil moisture and

temperature regime (Maestas, Campbell, Chambers, Pellant, & Miller, 2016). Other studies have outlined frameworks for developing spatially explicit maps of resilience and resistance, but have not directly incorporated them into mapping efforts (Chambers, Allen, & Cushman, 2019; Ricca & Coates, 2020). While we decided not to take the additional leap of modeling resilience and resistance explicitly, our validation statistics lend confidence that our approach may be able to be extended to produce spatially explicit resilience and resistance models. Lending further confidence to our approach is that many of the predictor variables selected for our model match with previous studies and ecological theory.

Climatic, topographic, pre-fire vegetation, and fire predictors were all found to be important drivers of post-fire recovery. Arkle et al. (2014) similarly found that latitude, climatic and topographic variables affected the probability of post-fire vegetation communities meeting greater sage grouse brood-rearing habitat, especially sites that were further north and that accumulated less warmth throughout the summer. However, our findings contradict their finding that summer precipitation was negatively correlated with post-fire recovery (Arkle et al., 2014). Multiple studies have also found that wetter winter and early springs are related to post-fire perennial vegetation cover, which our results support (Arkle et al., 2014; Barnard et al., 2019; Roundy et al., 2018). Previous studies have identified soil properties as important drivers of post-fire recovery, especially the soil moisture and temperature regimes (Maestas et al., 2016; Roundy et al., 2018). Our models did not find any soils variables to be important, possibly because of the elevated error common in spatial soil modeling (Chaney et al., 2019). Pre-fire vegetation plays a driving role in Great Basin post-fire communities particularly pre-fire functional group composition. Sites with high cover of perennial native grasses and forbs tend to better recover their perennial grasses and forbs components following fire (Barker, Pilliod, Rigge, & Homer,

2019; R. F. Miller, Chambers, Pyke, Pierson, & Williams, 2013; Rhodes, Bates, Sharp, & Davies, 2010). For sites with few perennial native species prior to fire, the converse is true (Chambers, et al. 2007; Barnard et al., 2019). Likewise, pre-fire NDPDI and AFGC were two of the most important variables in our models. Our results agreed with Shinneman and Baker's (2009) that species richness is negatively correlated with cheatgrass cover, but ultimately we did not find species richness to be an especially important variable in our models.

Our post-fire vegetation recovery model predictions for the Saddle Draw Fire suggest that post-fire trajectories are spatially variable and governed by ecological drivers. Southern aspects in the Saddle Draw Fire were generally predicted to have elevated negative departures from pre-fire NDPDI, likely driven by several of the most important variables in the model. Meanwhile, some of the sites that had the highest NDPDI values pre-fire were projected to maintain relatively high NDPDI fifteen years following fire. However, while using machine learning to evaluate drivers of post-fire recovery is valuable, mapping post-fire condition should be considered novel. Similar studies have, as yet, not gone as far as spatially explicit predictions of post-fire recovery (Barnard et al., 2019). However, we believe that improvements in vegetation time-series mapping from Landsat and improved modeling of ecologically important predictor variables make this type of modeling increasingly defensible and, indeed, an imperative of 21st century restoration planning (Allred et al., 2020; Jones et al., 2020).

Conclusions

Recent advancements in spatially-continuous time-series modeling of vegetation condition can enable detection of ecological state transitions (Allred et al., 2020; Jones et al., 2020; Rigge et al., 2019). Two of the most common state-transitions in Great Basin shrublands result from repeated fire and annual grass invasion, analyzed here, and incursion of conifers. The NDPDI leverages spatial vegetation models to monitor shifts in dominance between perennial

plants and annual plants; thus, it may aid in identifying transitions to annual-dominated ecological states, supported by relatively flat recovery slopes of NDPDI following fire. Additionally, the NDPDI could be extended into a tree-dominance index, with trees differenced against native shrubland composition to detect shifts in dominance between shrubland and woodland condition. Further analysis will need to be completed to establish thresholds of dominance that relate to ecological state tipping points, however this approach may help to develop and validate spatially-explicit state-and-transition models (Steele, Bestelmeyer, Burkett, Smith, & Yanoff, 2012).

Post-fire seeding is currently the most important management intervention for maintaining perennial shrublands and mitigating ecological state transitions in the Great Basin. While our results suggested limited effectiveness, there have been significant advancements in restoration techniques and strategies in the twenty years since the treatments analyzed here were applied (Davies, Boyd, Madsen, Kerby, & Hulet, 2017; Fisk, Apostol, Ross-Davis, Cahoy, & Davis, 2018; Shock, Feibert, Shaw, Shock, & Saunders, 2015). Our results suggest that, on top of current challenges, climate change will present further limitations to establishment of native perennial plants following fire in the Great Basin. Climatic aridity variables and topographic variables related to heat load were negatively associated with post-fire recovery in our analysis. Meanwhile, most climate models suggest warmer summer temperatures and are ambivalent regarding precipitation, which would result in more severe drought and summer aridity in the future (Snyder et al., 2019). Nonetheless, these patterns of post-fire stress and recovery will be spatially variable, underscoring the importance of recovery models that account for spatial heterogeneity.

Spatial approaches will play a fundamental role in characterizing resilience and resistance

in the Great Basin in the coming decades (Jeanne C. Chambers et al., 2019; Ricca & Coates, 2020). While preliminary efforts to map resilience and resistance leverage established relationships between soil and post-fire recovery, future maps will be increasingly data-driven—built upon multi-variate relationships between environmental predictors and models of post-fire recovery (Maestas et al., 2016). More comprehensive models of post-fire recovery than those established here might analyze all fires that burned in the Great Basin between 1994–2005, would include robust validation, and determine thresholds of post-fire recovery to produce maps of low, medium, and high resilience and resistance to align with the current paradigm (J.C. Chambers et al., 2017). Developing data-driven maps of resilience and resistance will present challenges, especially communicating the uncertainty implicit in model outputs. However, despite the hurdles, data driven approaches, as demonstrated here, are increasingly attainable by analysts and may present a new path forward for identifying at-risk sites and informing post-fire decision making.

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