

REMOTELY SENSING AND MODELING SEMI-ARID RANGELAND GRASS
BIODIVERSITY IN THE GREATER YELLOWSTONE ECOSYSTEM

by

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of the requirements for the degree

of

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in

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DEDICATION

I would not have the opportunity to shape my life around learning and science without the love and support of my parents, who intentionally nurtured my values and endlessly supported my journey in education and ecology. My mother ensured I spent my childhood outdoors, exploring the woods with dirt underneath my fingertips, and my father ignited my curiosity every morning as we drove into school.

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ABSTRACT

Western rangelands and their ecosystem services are integral to Montana's economy and culture. Researchers and land managers are increasingly relying on remote sensing techniques for monitoring and modeling ecosystems at scales far greater than possible when primarily relying on conventional field surveys. Despite growing academic interest in the value of rangelands and their ecosystem services, gaps remain regarding the degree to which remotely sensed products can assist in monitoring and modeling rangeland biotic communities. In this study, I examine two applications of remotely sensed data to study rangeland biodiversity, introduced in Chapter 1. In Chapter 2, I utilize EMIT imaging spectroscopy to capture signals of β -diversity in GYE rangelands outside of the growing season, detecting around half of the differences in plant community between sites based on differences in spectral variance from off-season images. While the degree to which this signal is driven by biotic and abiotic landscape features is unclear and warrants future interrogation, our findings suggest that imaging spectroscopy data can be valuable for understanding and monitoring rangeland biodiversity. In Chapter 3, I utilize remotely sensed environmental variables and rangeland grass species occupancy data from three separate studies/field seasons to develop species distribution models. These models are used to predict species occupancy across our study site and assess the degree to which internal model fit can be used to select models with reliable predictive accuracy. I also explore how this relationship between fit and predictive performance is impacted by the environmental variables used. I found significant correlations between model fit and assessments of model transferability, but these relationships are too weak to be useful for decision making. Additionally, predictive performance is highly dependent on the species being modeled and the environmental space within which predictions are being made. These two studies explore how remotely sensed products can be used to study biodiversity and species distribution at scales that are unrealistic when relying on traditional species surveys. In Chapter 4, I provide a synthesis and the conclusions that can be drawn from this research

CHAPTER ONE

INTRODUCTION TO THESIS

Grasslands cover between 26–40% of the Earth’s terrestrial surface (Zhao & Wu, 2020; Scholtz & Twidwell, 2022). They are vital biodiversity reservoirs, water supplies, and carbon sinks, and provide forage for over 300 billion kg of livestock annually, feeding one billion people (O’Mara, 2012; Bengtsson et al., 2019). The use of grasslands in cow-calf production is built upon the historic relationship between grazers and grasslands, tapping into native grasslands as a renewable source of nutrients for livestock production (Kleppel & Frank, 2022). The American West and, the State of Montana, in particular, strongly emphasizes sustainable cow-calf production on rangelands. Currently, Montana’s beef industry is dominated by commercial cow-calf production with over 1.5 million producing females (23% of all beef cows in the Western US), ranking Montana the 6th largest cow-calf producing state in the U.S. (USDA-NASS, 2022). Montana beef cattle production is heavily reliant on grazing rangeland agroecosystems, as over 70% of the land area is classified as rangelands.

Unlike other agricultural systems built around the large-scale maintenance of monocultures for producing a specific food or other products, rangelands are prime examples of socioecological systems where the ability to sustainably utilize the land relies on the maintenance of that land’s multiple ecosystem services. In the Greater Yellowstone Ecosystem (GYE), range managers rely on early ripening of cool-season grass-dominated rangelands and have historically been able to depend on grass production in the early spring to transition their cattle off costly winter feed and onto live forage (USDA-ERS, 2022). Changes in the climate threaten to alter grassland communities as well as forage timing and availability, a consequence

that is poorly understood and potentially costly for ranchers. Throughout the Northern Great Plains, there is a growing interest in understanding how changing environments and grazing management interact with plant community composition as well as nutrient and forage availability.

A thorough understanding of the variation in biotic communities across the landscape and the ability to reliably predict how species respond to environmental change requires robust monitoring and modeling strategies. However, field-based techniques for monitoring plant communities are time intensive and hard to scale to larger landscapes. Rangelands, by their nature, consist of large, difficult to access, and topographically diverse pastures, thus, researchers and land managers are increasingly relying on remote sensing techniques for monitoring and modeling rangeland systems at scales that would be impossible to capture using conventional field surveys.

In this thesis, we examine how remotely sensed data can be utilized to better understand plant species distribution and plant diversity across a GYE rangeland. In Chapter 2, we attempt to assess plant β -diversity outside of the growing season using EMIT (NASA's Earth Surface Mineral Dust Source Investigation, Green et al. 2021) imaging spectroscopy data. Imaging spectroscopy's high spectral resolution captures subtle differences in electromagnetic energy reflectance between different materials on Earth's surface, allowing us to detect differences in chemical composition and structure (Vane & Goetz 1988; Ustin et al. 2004). Past studies have found relationships between plant beta-diversity and spectral variance from airborne imagery, however these studies all take place in the growing season, and we are not aware of spaceborne imaging spectroscopy data used for this purpose (Wang et al., 2017; Gholizadeh et al., 2018;

Roccini et al., 2018; Laliberte et al., 2020; Schweiger & Laliberté, 2022). Our study uses off-season imagery and captures roughly half of the average variation in plant community composition among sites. Such findings suggest that the detection of rangeland plant diversity may not rely solely on differences among plant chemical traits which are most apparent during the growing season, but that differences in plant structural traits which remain detectable to some degree outside of the growing season may be important factors discriminating plant communities as well. Although more research is required, our results highlight the unique role imaging spectroscopy could play in large scale plant diversity monitoring.

In Chapter 3, we step back from detecting differences in plant communities using spectral measurements and instead utilize plant inventories and suite of remotely sensed variables for predicting species occurrence. We use inventory data to model species distributions and compare model performance. Species distribution models (SDMs) combine occupancy data with environmental data to predict occurrence across a landscape (Elith & Graham 2009; Miller, 2010). However, the factors that contribute to a model's ability to reliably predict occupancy in new spaces, also known as model transferability, are understudied (Sequeira et al., 2018; Charney et al., 2021). Sound estimates of transferability rely on validation data to predict the accuracy and dependability of a model outside of its training data, however, validation data is not always available. Internal model fit, i.e. how well a model describes its training data can be used for model choice, but it does not necessarily correlate with model transferability. We assess the degree to which internal model fit ($\Delta AICc$) and transferability (mean accuracy, precision, sensitivity, F1) are correlated when predicting species occupancy outside of the training conditions. We additionally look at how different predictors and classes of predictors contribute

to this relationship and to overall model transferability. Our study shows significant but impractical correlations between model fit and predictive accuracy, suggesting that model choice based on internal model fit does not automatically select the model with the best transferability. Model transferability was affected by the environmental variables used, but the relationships varied by species, supporting the notion that species distribution models are species specific.

In order to effectively manage rangelands at relevant scales, land managers need a detailed understanding of the distribution of their most ecologically and economically valuable plant species and how they may change due to grazing management and environmental change. Remote sensing shows promise in aiding our ability to assess rangeland biodiversity and species distributions in the future. These two studies show how remotely sensed can contribute to the study of plant diversity.

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CHAPTER TWO

EMIT SATELLITE-BASED IMAGING SPECTROSCOPY
DETECTS DORMANT-SEASON GRASSLAND β -DIVERSITYContributions of Authors and Co-Authors

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Abstract

Monitoring plant diversity is critical for ensuring the sustained resilience of ecosystem services. Remote sensing promises to offer large-scale data for monitoring and managing ecosystem health and biodiversity. Spectral variation calculated from imaging spectroscopy has been shown to correlate positively with plant species diversity. This relationship can be used to examine how plant communities vary across a landscape, also known as β -diversity, at scales that

would otherwise be impractical to sample by hand. The majority of research on the relationship between spectral variation and plant β -diversity has been conducted during the growing season. However, growing season data are not always available, especially in semi-arid grasslands with short growing seasons that are often obscured by smoke and clouds. In this study, we compare spectral variance, calculated from Earth Surface Mineral Dust Source Investigation (EMIT) imaging spectroscopy, and grassland beta diversity across three imaging spectroscopy data sets captured outside the growing season. We show that spectral β -diversity positively correlates with plant β -diversity outside the growing season, in a Greater Yellowstone Ecosystem grassland.

INTRODUCTION

Plant diversity is a critical buffer against disturbance and supports the long-term stability of ecosystems and their services (Hooper et al., 2012; Tilman et al. 1997; Tilman et al. 1998; Fargione et al. 2007; Cavendar-Bares et al., 2017). Biotic homogenization, due to loss of native species and establishment of exotic flora, increases a community's susceptibility to disturbance while limiting the ability of a site to perform necessary services (Reich et al. 2012; Tilman et al., 2014; Lefcheck et al. 2015; Mori et al., 2018). Traditional field-based methods for studying changes in biotic communities can struggle to efficiently assess the extent and rate of change over large areas, especially when climate change and changes in human use are affecting biotic communities at regional and global scales. Imaging spectroscopy has shown promise for detecting plant diversity across ecosystems, including grasslands (Wang et al., 2018a; Gholizadeh et al., 2018, 2020; Schweiger & Laliberté, 2022; Frye et al., 2022), and has potential to improve grassland monitoring.

Biodiversity can be defined hierarchically in terms of spatial or temporal scales. Gamma- (γ -) diversity measures the diversity of an entire study area and can be partitioned into beta- (β -) and alpha- (α -) diversity (Toumisto, 2010; Socolar et al., 2016). The α -diversity of an area describes the number or abundance of species within smaller subsections (*e.g.* plots, patches, microsites, or periods of time) (Anderson et al., 2011; Legendre & De Cáceres, 2013). Alpha diversity is associated with increased productivity, resistance, resilience, and multifunctionality (Isbell et al., 2015; Lefcheck et al., 2015). A loss in α -diversity can lead to plant communities being more susceptible to disturbance (Reich et al. 2012, Tilman et al., 2014; Mori et al., 2018). Since it measures diversity within a discrete area or timeframe, α -diversity can be estimated quickly and efficiently, but does not describe how communities vary over a landscape or time-period.

To describe how biodiversity varies over space or time, we measure β -diversity, which describes how communities vary over time, location, or environmental gradient (Toumisto 2010; Anderson et al., 2011; Legendre & De Cáceres, 2013; Socolar et al., 2016; Roccini et al., 2018). A landscape with high β -diversity is one in which the species composition varies across that landscape, increasing the potential for diverse habitats and ecosystem services (Mori et al., 2018). A system's β -diversity is generally assessed using dissimilarity matrices that compare species composition of different small sites (Anderson et al., 2011; Legendre & De Cáceres, 2013; Socolar et al., 2016). Biodiversity is also a function of geodiversity, which is the variation in the abiotic geochemical and environmental factors, including geology, topography and hydrology that affect plant community composition and distribution (Sebastiá, 2004; Record et al., 2020).

Biotic homogenization will be exacerbated by projected changes in climate over the next century (Bellard et al., 2012; Isbell et al. 2015; Socolar et al., 2016). In places like the Greater Yellowstone Ecosystems (GYE), for instance, such changes include shifting precipitation, higher temperatures, and increased weather severity (Bradley et al., 2010; Colautti et al., 2017; Whitlock et al., 2017). As environmental conditions become more unpredictable and change at increasing rates, the biotic communities react in turn, leading to quickening shifts in biodiversity. The effects of climate change occur at the regional and global scale, so the task of effectively monitoring such communities at such scales becomes far more challenging and impractical to capture using solely field based measurement. The costs of acquiring biodiversity data scale with the size, scope, and ecological complexity of the area being studied, and so it is difficult and expensive to inventory an entire landscape using traditional field techniques (Cavendar-Bares et al., 2022). Image-based remote sensing is quickly evolving as a tool for scaling up grassland biodiversity monitoring, enabling biodiversity assessments over large areas with minimal time and money invested (Dubovik et al., 2021; Seely & Asner, 2021). Multispectral imaging, which has been available for several decades e.g. through NASA's Landsat program (Ustin & Middleton, 2021), typically covers four-eight broad spectral bands (~300 nm ultraviolet to ~2400 nm shortwave-infrared regions of the electromagnetic spectrum). Metrics derived from the visible (400 – 700 nm) to near-infrared bands (700 – 1000 nm) of multispectral sensors—including the Normalized Difference Vegetation Index (NDVI), Soil Adjusted Vegetation Index (SAVI), and Enhanced Vegetation Index (EVI)—can offer valuable information about overall trends of productivity but struggle to offer the spectral detail needed for assessing plant species diversity or community

composition (Anderson, 2018; Sun et al., 2024). Imaging spectrometers, or ‘hyperspectral’ sensors with spectral resolutions consisting of hundreds of overlapping bands can detect subtle differences in the color and intensity of reflected light among species due to their ability to measure differences in plant chemistry and structure (Clark et al., 2005; Andrews & Ustin 2008; Ustin & Gamon, 2009; Féret & Asner 2012; Roth et al., 2015). The spectral resolutions offered by these sensors allow researchers to observe plant diversity by sensing extremely slight differences in reflectance (Schimel et al., 2011, 2013; Turner, 2013, Jetz et al., 2016; Cawse-Nicholson et al., 2021).

Not all imaging spectroscopy data are suited to study plant diversity at all scales. Assessing α -diversity, for instance, requires imaging data with pixels about the size of individual plants *e.g.* 1 cm² to 1 m² (Wang et al., 2018b; Gholizadeh et al., 2019, Schweiger & Laliberté, 2022). Therefore, remote sensing of α -diversity is often assessed using hand-held, scaffolded or UAV mounted imaging spectrometers (Wang et al. 2018b). While satellites can efficiently cover far larger spatial extents, imaging spectroscopy from space is limited to tens-of-meter resolutions (Cawse-Nicholson et al. 2021; Green et al. 2023) which struggle to assess α -diversity. However, satellite-based sensors can detect differences between plant communities contained within individual pixels, thus differences in reflectance among pixels may be used to calculate β -diversity (Roccini et al., 2018; Laliberte et al., 2020; Schweiger & Laliberté, 2022).

The spectral variation hypothesis (SVH) states that spectral heterogeneity of remotely sensed imagery is positively associated with biodiversity (Palmer 2002; Perrone, 2023; Torresani 2024), assuming that spectral variation captured by imaging spectroscopy sensors is impacted by plant diversity (Fassnacht et al., 2022). The SVH was expanded by Ustin

and Gamon (2010), who outline that plants can be categorized into ‘optical types’ based on their differences in reflectance, which is driven by functional differences in their chemistry and structure (Ustin & Gamon, 2010; Roth et al., 2016). The Spectral Species Hypothesis (SSH), posits that plant species or broader taxonomic groups cluster based on their spectral reflectance and can be estimated from imaging spectroscopy data (Ferét & Asner, 2014). Later, it was confirmed that the variation in species’ spectra is non-random but increases with species’ functional and phylogenetic distance (Schweiger et al. 2018). Thus, there is reason to believe that the spectral diversity of a landscape may be useful in sensing species β -diversity. Spectral diversity is not only driven by active phytochemicals and other pigments but also by geodiversity, encompassing a host of geochemical and geomorphic environmental factors including variations in geology, hydrology, snow cover, terrain and soil (Record et al. 2022). Many of these geochemical variables have unique spectral attributes that can be sensed both directly and indirectly due to their correlation with plant community variation. Therefore, if patterns of plant β -diversity are driven by geodiversity, then β -geodiversity may also be a sensible means of assessing community variation from space-based imaging spectrometers.

Because spectral variation can be driven by a combination of biotic and geochemical factors, some of which are retained outside of the growing season, we predict that plant β -diversity may be sensed with off-season EMIT imaging spectroscopy data, when plants are senesced and/or dormant, and when photosynthesis and phytochemical production are low or absent (Chadwick et al., 2025). A consistent challenge when working with air- or spaceborne remote sensing data is that overpasses may be infrequent and may coincide with clouds, wildfire smoke, snow, and other poor conditions, yet remotely sensed imagery collected outside of the

growing season has mostly been ignored. Our goal is to test how well spectral dissimilarity of NASA's Earth Surface Mineral Dust Source Investigation (EMIT) images can be used to assess plant β -diversity, or plant community dissimilarity outside of the growing season. The specific objectives of our study were 1) to determine to what degree spectral diversity calculated from off-season EMIT imagery relates to plant β -diversity in a grassland ecosystem located in the Greater Yellowstone Ecosystem (GYE), and 2) to explore abiotic and biotic factors driving this relationship.

METHODS

Study Site

Our study was conducted at Red Bluff Research Ranch in Madison County, Montana (48° 21' N 109° 30' W), a working year-round sheep and cattle ranch located in the GYE, owned and operated by Montana State University (MSU). Red Bluff Research Ranch is a semi-arid steppe, receiving an average annual precipitation of 406 mm, dominated by long-lived cool-season perennial grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Idaho fescue (*Festuca idahoensis* Elmer), and prairie junegrass (*Koeleria macrantha* (Ledeb.) Schultes). These bunchgrasses often grow at moderate densities and can leave a significant amount of inter-bunch space for other grasses, forbs, small shrubs, and lycophytes to occupy. Warm-season grasses like blue grama (*Bouteloua gracilis* (Willd. ex Kunth.) Lag. ex Griffiths), and to a lesser extent purple three-awn (*Aristida purpurea* Nutt.), are also present. Cacti (*Opuntia polyacantha* Haw., *Pelecypora missouriensis* (Sweet) DAquino & Dan.Sánchez.) and other arid adapted species also occur. Wetter microsites, mostly small ephemeral streams, host

basin wild rye (*Leymus cinereus* (Scribn. & Merr.) A. Löve), sedge (*Carex* sp.), and many forbs. Non-native grasses such as cheatgrass (*Bromus tectorum*), and to a lesser extent, crested wheatgrass (*Agropyron cristatum*, (L.) Gaertn.), and smooth brome (*Bromus inermis* Leyss.) are patchily abundant. These non-native grasses tend to grow in dense monocultures, while areas dominated by more native flora tend to feature a greater diversity of grasses and forbs. Soils are primarily developed in crystalline metamorphic rock that weathers to sandy textures with limited clay formation and wide variation in depth to bedrock and surface horizon thickness vertically and laterally across hillslopes, driving water storage and mirroring plant diversity patterns (NRCS, 2025).

Vegetation Data

We collected data from June-August 2023 at 21 newly created, crossed 100 x 100 m monitoring transects centered at a subset of 75 stakes marking historic transects established by George M. Van Dyne in the 1960's (Van Dyne, 1960). We placed a 1 m x 1 m quadrat every 10 m along each transect leg (Fig. 1. a-c), with 21 quadrats per transect (Fig. 1. d, e; 440 total, with one plot excluded for being outside the property boundary). One person (J. Honn) estimated basal percent cover for 10 focal species: bluebunch wheatgrass, Idaho fescue, blue grama, basin wildrye, needle-and-thread, prairie junegrass, western wheatgrass, smooth brome, and cheatgrass. All other species were recorded by functional group (perennial grass, annual grass, forb, shrub, perennial succulent). The remaining ground cover was recorded as bare soil, woody debris, leaf litter, feces, or stone.

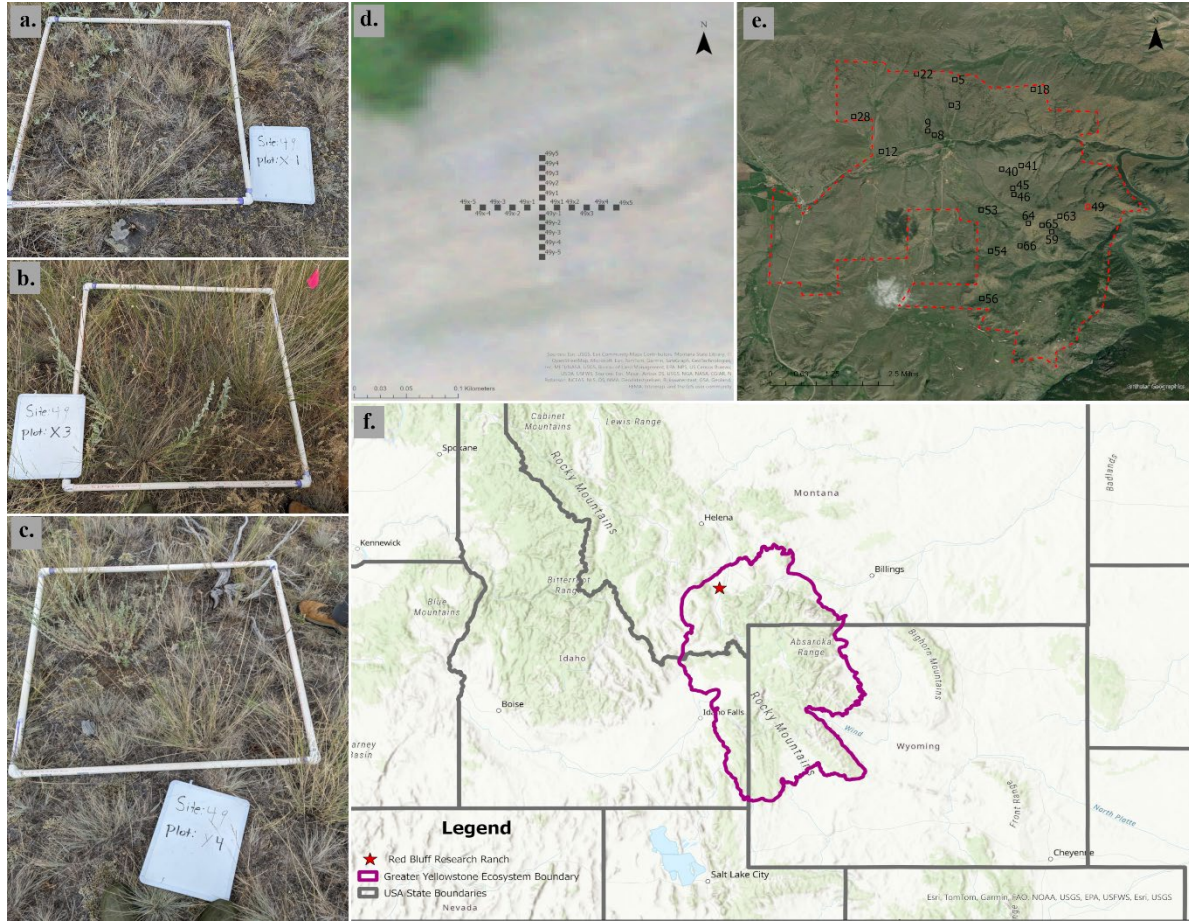


Fig. 1: Study location and inventory design: Example plots from site 49 (a-c). Sample sites were crossed 100 x 100 m transects (d). Red Bluff Research Ranch (red, e) is within the GYE (purple, f).

Imaging Spectroscopy Data

We used 285-band imaging spectroscopy data collected by EMIT on 04/15/23 (EMIT_L2A_RFL_001_20230415T204729_2310514_003), 10/07/24 (EMIT_L2A_RFL_001_20241007T174337_2428112_016), and 10/15/24 (EMIT_L2A_RFL_001_20241015T192403_2428913_018) under cloud-free conditions (Green et al., 2020). Launched in July of 2022 and hosted on the International Space Station (ISS), EMIT captures spectral reflectance data with a spatial resolution of 60 m, covering the spectral range between 380 – 2500 nm in 285 overlapping spectral bands (Green et al. 2020). The first image

(Fig. 2a), captured in April of 2023, represents a snow covered late-winter/early-spring landscape where most vegetation is still dormant although early growth is likely to have begun for some species. Some individual pixels are dominated by snow, and many show a mix of snow and dormant vegetation. The other two images (Fig. 2b, c) were captured in October of 2024 and represent a landscape after the growing season where plant material is visible but senescing and phytochemical production is low.

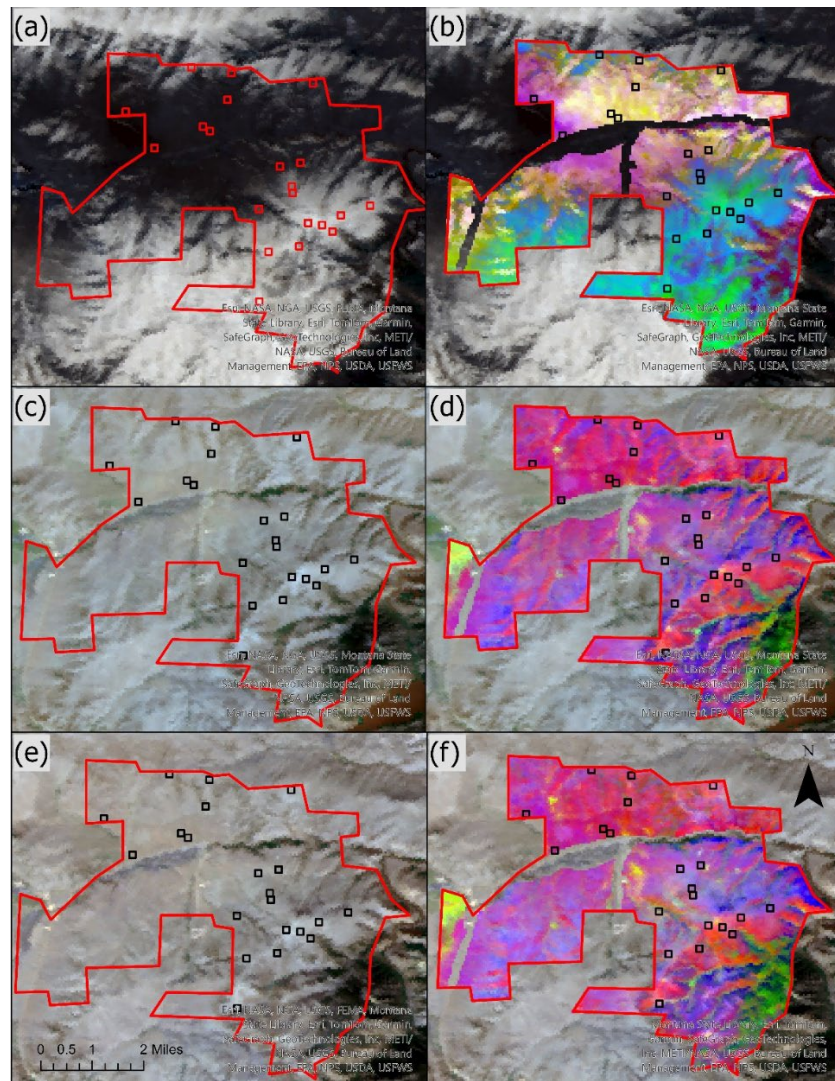


Fig. 2: Study site spectral diversity: True (left) and false (right) color EMIT images from 04-15-2023 (a-b), 10-07-2024 (c-d), and 10-15-2024 (e-f). False color shows the first three spectral components as Red, Green, Blue respectively. Squares indicate the 21 sampling sites, enlarged for clarity.

Topographic Variables

We assessed geodiversity using topographic variables (elevation, slope, aspect, mean curvature, topographic position index) derived from the 1 arc-second (~30 m) DEM collected by the Shuttle Radar Topography Mission (SRTM) in February 2000 (NASA, 2013) and averaged per site. Rainwater capture was estimated using topographic position index (TPI) averaged per site. We calculated aspect as northness and eastness for continuous distance measurements

$$\text{northness} = \left(\cos \left(\text{aspect} * \frac{\pi}{180} \right) \right) \quad \text{and} \quad \text{eastness} = \left(\sin \left(\text{aspect} * \frac{\pi}{180} \right) \right)$$

Snow Persistence

We estimated snow persistence using 4-band multispectral data with 3 m² ground resolution collected between November of 2023 and May of 2024 by Planet Labs' Dove sensor (Planet Labs PBC, 2024). The Dove sensor has a near daily return interval, and we selected all usable data with any visible snow present on the landscape, while also filtering out any images with over 10% cloud cover. For each day, a snow presence/absence classification model was applied across the study site. This model uses a variation of conventional normalized distribution of snow index (NDSI), utilizing the normalized ratio of red to blue bands based on the methodology of Burton-Johnson and Wyniaewaskyj in 2020, instead of relying on short-wave infrared bands as is traditionally used when generating snow classification models (Burton-Johnson and Wyniaewaskyj, 2020). While the RB-NDSI model, in their study, didn't outperform traditional NDSI methods, it was generally successful at differentiating snow from its surroundings depending on the presence/absence threshold applied to the model. We used RB-NDSI methods to classify snow pixels due to a lack of available high resolution (<10m² per pixel) data with both green and SWIR bands. Because we are interested in the local scale

relationship between microtopography, snow, and plant communities, the increased granularity gained with the RB-NDSI model outweighed the benefits of using traditional methods.

$$\text{NDSI} = (\text{Green} - \text{SWIR}) / (\text{Green} + \text{SWIR})$$

$$\text{RB-NDSI} = (\text{Blue} - \text{Red}) / (\text{Blue} + \text{Red})$$

When applied to Red Bluff spectral data, the RB-NDSI model was able to adequately identify snow from non-snow when an appropriate threshold was applied to each image. However, no single threshold appeared to sufficiently identify snow pixels in both mixed and full snow landscapes. The final snow persistence model utilizes variable thresholds for different snow cover intensities based on the methodology of Thaler et al., 2023, where the overall distribution of blue wavelength range intensity across the landscape was used to classify winter images based on the level of landscape snow cover (Thaler et al., 2023). Images where the average blue-band brightness across the landscape was above 6000 are classified as full snow, and an RB-NDSI threshold of (-0.05) is applied. If the average blue reflectance is below the 6000 threshold, the landscape is classified as mixed-snow, and an RB-NDSI threshold of (-0.09) is applied. Pixels with RB-NDSI values greater than the threshold for their landscape are classified as snow. Multispectral reflectance data were collected from 20 mixed and full snow landscapes, captured by planet lab's 4-band multispectral sensor between November 2023 and May 2024. Relative snow persistence was calculated as the average snow pixel presence divided by total days analyzed.

ANALYSIS

We calculated β -diversity as site-to-site Euclidian dissimilarity in species composition, spectral composition, and abiotic variables (Anderson et al., 2011; Legendre & Fortin, 2010, 2013; Roccini et al., 2015). All variables were scaled between 0 and 1 using the *decostand* function in the R package *vegan* (Oksanen et al., 2025), before calculating Euclidean distances using the *dist* function. We extracted spectral data for all pixels within the Red Bluff boundary with paved roads and riparian areas removed (Fig. 2) and performed separate principal component analyses (PCAs) for each date using R package *psych* (Revelle, 2025). We extracted the first 10 principal components (PCs) per plot and averaged the component values for each of our 21 sites measuring 100 x 100 m. Since spectral PCs that explain only small amounts of the total spectral variation can be important for differentiating plant species and communities (Kothari and Schweiger, 2022), we explored how the number of PCs used to calculate spectral β -diversity affected our analyses.

We generated 10 different spectral dissimilarity matrices with the numbers of components ranging from 1 (only the first PC) to 10 (the first 10 PCs). We calculated plant β -diversity as inter-site community dissimilarity, based on the relative abundances of our focal grass species (Anderson et al., 2011; Legendre and De Caceres, 2013). Similarly, we calculated β -geodiversity (*i.e.*, how abiotic conditions vary across sites) based on the inter-site dissimilarity in aspect, elevation (m), slope (degrees), TPI (m), snow persistence (days), and bare-ground cover (%). Because we hypothesized that snow was a major driver in both biodiversity and spectral diversity, especially in the spring image, we calculated a third dissimilarity matrix based only on snow persistence β -diversity (*i.e.*, how plots varied among one another in snow persistence).

We used the Mantel test to test correlations between spectral β -diversity and plant β -diversity, β -geodiversity, and snow persistence β -diversity. Each of the 10 spectral dissimilarity matrices were analyzed for correlations with the plant β -diversity matrix (10 spectral-plant Mantel correlations), with the geodiversity matrix (10 spectral-geodiversity Mantel correlations), and with the snow persistence diversity matrix (10 spectral-snow persistence Mantel correlations).

Finally, we correlated geodiversity and plant diversity (one plant-geodiversity correlation and one plant-snow correlation) All analyses were performed in R version 4.5 (R Core Team, 2025), using GGplot2 for data visualization (Wickham, 2016) and “tidyverse” packages for data manipulation (Wickham et al., 2019).

RESULTS

Spectral β -diversity correlated with plant β -diversity for all three EMIT images acquired during the off-season, although the strength of the correlation varied by date and number of spectral PCs included in the analyses. For the spring imagery (Fig. 4, a), spectral β -diversity calculated using two PCs captured 52.7% of plant β -diversity, while for the two fall images (Fig. 4, b, c) seven PCs were needed for spectral β -diversity to capture 43.9% and 54.4% of plant β -diversity, respectively (Fig. 3). Spectral β -diversity based on one PC captured 37.7% of the variation in geodiversity in the spring, while capturing 35.1% and 28.9% in the first and second fall images using two PCs.

On average, Mantel correlations were higher between spectral β -diversity and plant β -diversity than between spectral β -diversity and β -geodiversity. We found no significant correlation (Mantel test, $R = 0.075$, $p = 0.273$) between geodiversity and plant diversity. The spectral/snow correlations tended to be higher than the spectral/geodiversity correlations under

most model conditions (i.e. number of spectral PCs and time-of-year). Because snow was a component of geodiversity, this suggests that addition of other geodiversity parameters did not necessarily add important information to the models beyond that already captured by snow persistence. This trend was strongest in the spring but also occurred in fall images. Spectral β -diversity, calculated using the spring imagery and two PCs, captured 44.4% of the variation in snow persistence, and when using the fall imagery based on seven and eight PCs 43.2% and 40.4% of variation snow persistence, respectively. In addition, the variation in snow persistence among sites explained 38.9% of plant β -diversity.

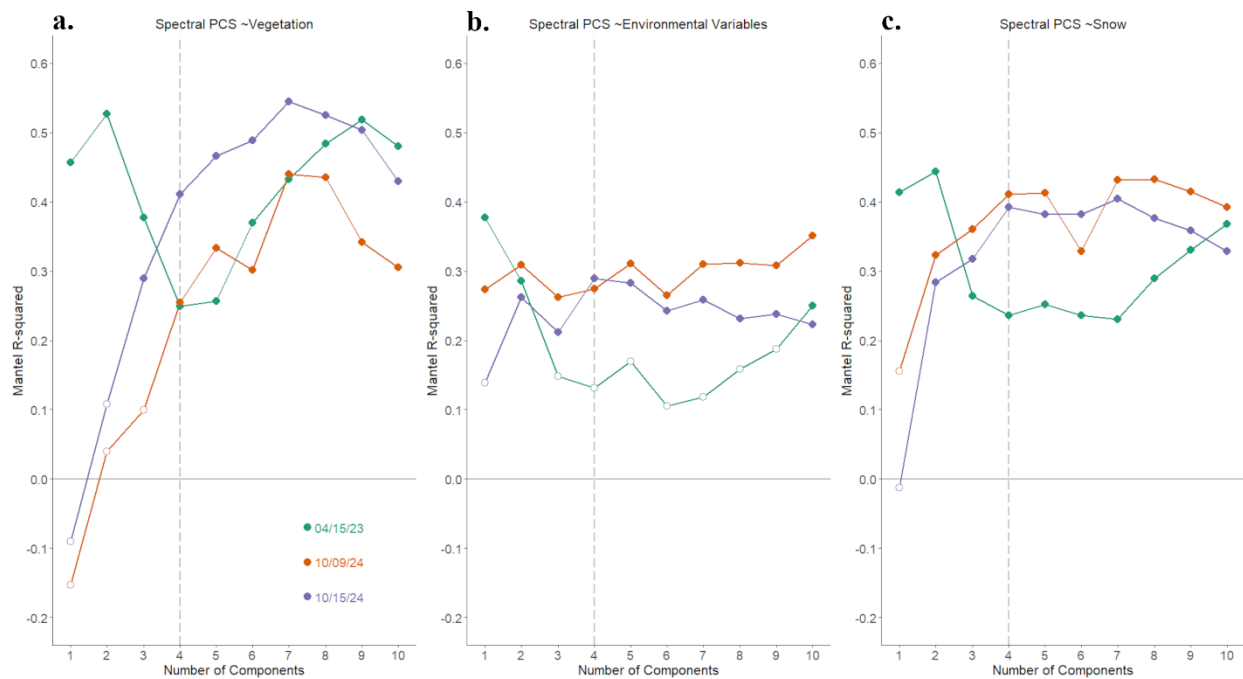


Fig. 3: Mantel Correlations: Correlation between plant diversity (a), geodiversity (b) and snow diversity (c) and spectral variation with 1-10 spectral components. Color indicates date (green: 04/15/23, orange: 10/07/24, purple: 10/15/24). Symbols show statistical significance (open: $p > .05$, closed: $p < 0.05$).

DISCUSSION

Our results support the hypothesis that imaging spectroscopy data can detect differences in grassland community composition in GYE rangelands, even outside the growing season. Spectral and species β -diversity were positively correlated in all data sets analyzed, with 43–54% of the total variation in plant community composition explained by spectral dissimilarity during the off-season (Fig. 4). This relationship could be directly driven by the reflectance properties of the geodiversity, the vegetation, or a combination of the two. Although our we cannot identify the precise spectral signals that relate to plant diversity at each date, we can, given the timing of our image acquisitions, assume that phytochemical production and composition may not be the primary drivers of spectral variation in the dormant season.

The strength of the correlation between spectral and vegetational β -diversity (Fig. 3) depended upon the number of spectral component variables used. In April, just two spectral component variables achieved the highest observed correlation between spectral and vegetational diversity. In October, seven components were needed. Seemingly, in the fall, a large number of sensible abiotic and biotic signals reflect differences in plant diversity, even though many of these signals contribute vanishingly little to the total spectral variation at a site; thus, there may be tremendous information hidden in the smallest components of spectral variation of a senesced grassland. In the spring, on the other hand, the majority of variation was captured by just two spectral components, which we interpret as describing variation in spring snow cover. If true, the spring imagery may have provided a more indirect detection of vegetation diversity (*i.e.* one based on environmental conditions) than the fall imagery, which is more likely to have directly captured variation in species reflectance.

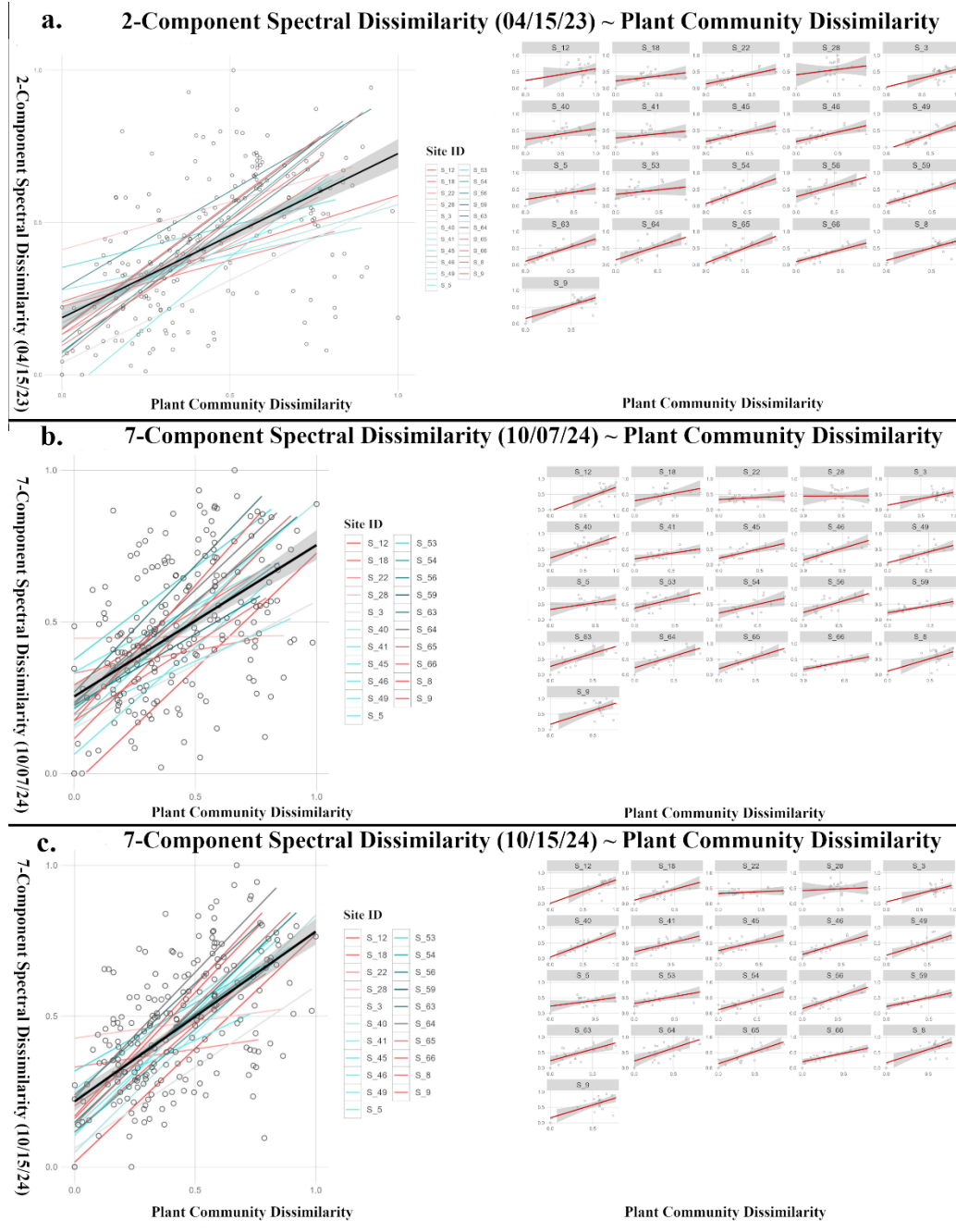


Fig. 4: Spectral β -diversity predicts plant β -diversity: Top correlations between spectral β -diversity and plant diversity for each date (a: 04/15/23, b: 10/07/24, c: 10/15/24). Correlations for all sites are shown on the left and for individual sites on the right.

We achieved similar maximum Mantel correlations from all time periods, suggesting that information quality is not necessarily gained or lost as the season progresses, and we shift from

indirect to direct spectral information sources. We hypothesize that much of the signal for β -diversity captured by EMIT and other imaging spectroscopy sensors is driven by a combination of biotic characteristics like variation in species, structure, density, and phenology as well as abiotic site features like topography, soil structure, exposure, moisture, snow persistence, *etc.*, which both determine plant community diversity and have unique reflective properties.

The strength of the correlation between spectral β -diversity and geodiversity may have been due to uninformative variables obscuring more informative correlations. While determining the individual contributions of each variables to spectral variation is beyond the scope of this project and requires further study, we analyzed snow persistence separately from the other abiotic variables and found that it yielded stronger spectral correlations alone than when all abiotic variables were considered together, indicating that some of the other environmental metrics we used may have been much less informative. We hypothesize that snow persistence both directly and indirectly drives plant community variation by altering subsurface soil moisture in this semi-arid grassland biome, while also interacting with the topographic variation that indirectly drives plant community composition. In April, the landscape was partly snow-covered, and individual pixels represent a mix of snow and exposed vegetation and/or bare ground (Fig. 2, a). Most of the variation in species composition described by April spectra are captured by the first two component variables, which we attribute to the degree of snow cover (*i.e.* full-snow vs. varied pixels). Not coincidentally, diversity in snow persistence correlated strongly with diversity of the top two spectral components in the spring (Fig. 3, a, c). Variation in snow persistence explained 38.9% of variation in species between sites in April and was able to capture 40.4-43.2% of spectral variation even from snow-free October landscapes. We believe that snow may

have been a useful signal of biodiversity both because snow persistence was readily sensed in April and because snow itself is a major determinant of plant community composition in the study area. Moreover, snow accumulation and persistence reflect topography and vegetation patterns in this arid, windy environment. The strong spectral and ecological connection makes snow a useful information source even when plants themselves are dormant and/or cannot be directly observed.

CONCLUSION

While these analyses cannot identify causal relationships between spectra, environmental variables, and species composition, we do find that off-season analysis of imaging spectroscopy data can detect β -diversity in rangeland prairies. Our results hint that a vast amount of informative spectral variation exists in senesced grasslands throughout the year, both indirectly *via* environmental variables like snow and topography and directly *via* reflectance of senesced plants. Most remote sensing studies on plant biodiversity are based on growing-season data, yet many ecological systems have short and variable growing seasons, resulting in unusable, sparse, or non-existent growing-season data for analysis. However, shoulder season data may contain useful information for monitoring biodiversity. Furthermore, these data may be valuable even when direct detection of vegetation is impossible, *i.e.* due to partial snow cover. Off-season imagery may serve as a valuable stopgap if growing-season imagery is unavailable or may itself contribute important information that should not be ignored when sensing grassland biodiversity.

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CHAPTER THREE

ASSESSING TRANSFERABILITY OF LOCAL-SCALE
SPECIES DISTRIBUTION MODELS IN GYE RANGELANDSContributions of Authors and Co-Authors

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Abstract

Grasses are foundational to the ecology of western rangelands, and in a changing world it's imperative that we have the appropriate tools for monitoring and managing our grassland communities. Species distribution models (SDMs) are frequently used to predict the distribution of ecologically and economically valuable species, however we still largely lack a framework for assessing the generality of such models outside of their training space. For SDMs to be useful,

they must be reliably predictive, and the primary way to assess predictive power is utilizing validation data. When validation data are absent, researchers may rely on internal information quality, calibration, and/or fit metrics to assess model transferability. In this study, we assessed if a common information quality metric (AICc) relates to model transfer and if models with the best fit also perform best when predicting occupancy based on data from subsequent surveys within the same study site. Although our plant inventories were collected in the same general areas, albeit with focus on different landscape features, we only found weak correlations between fit and transferability, and metrics varied across validation data, target species and the set of environmental predictors, supporting the consensus that SDM transfer performance is highly species and environment specific.

INTRODUCTION

To manage and conserve ecosystems globally, we need a detailed understanding of the distribution of species and how their survival and occupancy are shaped by their environment (Grinnell, 1917, 1924; Wiens & Graham, 2005; Soberón, 2007; Addison et al., 2013; Evans et al., 2015; Sequeria et al., 2017). However, due to the logistic and financial constraints involved with manually surveying species, we often lack adequate knowledge, data, and tools needed to make informed management decisions based on species distributions (Raymond et al., 2013; Addison et al., 2013). Species distribution models (SDMs), also known as habitat suitability/occupancy models or ecological niche models, offer a potential solution by allowing us to estimate a species' potential distribution and to understand the relationship between environmental conditions and occupancy. While techniques vary, in general, all SDMs attempt to predict a species' distribution based on known

occupancy and environmental data (Soberón, 2007; Miller, 2010; Werkowska et al., 2016; Elith and Franklin 2017).

Species distribution models are powerful tools for conservation and restoration, giving researchers and managers the ability to model current and potential future distributions of imperiled or ecologically/economically valuable species. In addition to following species trajectories over time, SDMs are also frequently used to predict a species' potential occurrence in different areas (Charney et al., 2021; Yates et al., 2018). We refer to the ability of a model to accurately predict occurrences outside of the environmental and geographic space within which the model was trained as 'transferability' (Elith and Lethwick, 2009; Werkowska et al 2016; Yates et al., 2021). If a model can sufficiently transfer and make accurate predictions, it can then be used to inform management decision making, conservation efforts, or restoration (Pinto-Ledezma and Cavendar-Bares, 2021). Ecologists and land managers are increasingly utilizing SDM predictions for decision making, thus there is an increasing need for a methodological framework for assessing their transferability (Andrew and Ustin, 2009; Elith and Graham, 2009; Elith and Leathwick, 2009; Miller, 2010; Sequeira et al., 2018).

Transferability Challenges and Model Specification

Transferability is regarded as a major challenge in predictive use of SDMs (Wenger and Olden, 2012; Sequeira et al., 2017; Yates et al., 2018). For example, the predictive accuracy of SDMs is known to degrade, often severely, as geographic distance and differences in environmental conditions increase, yet this shortcoming undermines the most desired function of SDMs—to predict how species will respond to translocation or environmental change (Petitpierre et al., 2016; Sequeira et al., 2018, Charney et al., 2021; Rousseau and Betts,

2022). In addition, as model complexity increases, transferability tends to decrease in response (Merow et al., 2014; Charney et al., 2021). Parsimonious statistical models like GLMs and GAM and/or models with limited predictors often outperform overparameterized or inherently complex models like those produced by some machine learning techniques (Heikkinen et al., 2012; Merow et al., 2014; Werkowska et al., 2016; Petitpierre et al., 2017).

The choice of environmental predictor variables can significantly impact a model's transferability. In theory, the most transferable models are built on the predictor variables that directly relate to a species' core physiological needs, because these variables most accurately reflect the environmental drivers of a species' distribution (e.g., solar energy input, temperature, moisture, or nutrient resources; Petitpierre et al., 2017; Wang et al., 2024; Merow et al., 2014; Evans et al., 2015; Petitpierre et al., 2017; Yates et al., 2018). Other variables, which are not functional drivers of a species' distribution, may correlate with occurrence in some locations but not others (Wenger and Olden, 2012; Werkowska et al., 2016). For example, if soil water is a functional driving variable, occurrences may correlate with topographic curvature in water-limited regions of the species' distribution, where local concavities promote increased local soil moisture. However, in areas with increased water availability, a species may be found outside of concavities. A model trained on soil moisture would make accurate predictions, and a model trained on topographic curvature would not. Suboptimal variable selection can also result in overfitting, which occurs when a model mistakes correlations due to unaccounted for patterns or stochasticity from real correlations with underlying model predictors, also known as spurious correlations. This can result in non-functional variables being included in a model, further degrading transferability when the model is projected into areas where the overfit variables no

longer correlate with presence (Wegner and Olden, 2012; Yates et al., 2018). Such errors can also occur when a predictor variable is correlated with the response variable under local conditions but not across the species' full distribution.

It is unclear how to best identify the functional variables that drive species distributions, and these data may not be easily measured (He et al., 2015). Because of these limitations, SDMs are typically based on publicly-available earth observation data such as precipitation, temperature, land cover, and soil classification on large spatial scales, and topography on smaller scales, all of which are assumed to correlate with functional drivers if they are not the driving variables themselves (Andrew et al., 2009; He et al., 2015; Deblauwe et al., 2016). Such predictors, while accessible, may not be functional drivers, may not represent the time frame being studied, and rarely cover all relevant environmental variation important for occupancy, especially at local scales (Manzoor et al., 2018; Sillero & Barbosa, 2021).

Modern, high-resolution, remote sensing systems represent a new potential data source for SDMs, as unpiloted aerial vehicle- (UAV) airborne, and satellite-based sensors can provide direct, up-to-date ecosystem measurements with up to centimeter-scale spatial resolution. These can result in improved topographic measurements, such as the 1 arc-second (30 m²) global digital elevation model (DEM) produced by the Shuttle Radar Topography Mission (NASA JPL, 2013; He et al., 2015). In addition, multispectral images captured by satellites and campaigns like Landsat and the Moderate Resolution Imaging Spectrometer (MODIS) can be used to calculate ecologically relevant variables such as the NDVI (Normalized Difference Vegetation Index), which can be correlated with plant health, phenology, and productivity because it captures vegetation greenness (Feilhauer et al., 2012; He et al.,

2015; Wan et al., 2015; EROS, 2021). Another potential advantage of reflectance data is that they make direct observation of the vegetation and/or soil and may therefore enable detection of more proximate functional drivers than landscape and climate variables. As earth observation continues to evolve, so too will the data available for SDMs, raising the possibility of improving SDM transferability with improved predictors.

Species-specificity

Model transferability is highly species-specific and can be influenced by a species' life-history, ecology, and interspecific relationships, as well as the regional or environmental conditions (Wisz et al., 2013; Petitpierre et al., 2017; Charney et al., 2021). Additionally, the format of the occupancy data impacts the predictive accuracy of the model produced. For instance, SDMs based on presence only and presence/pseudoabsence data generally perform worse than those based on presence/absence data, which perform worse than SDMs trained on abundance data (Waldock et al., 2021). While historic distribution data can be valuable for building SDMs, such data may have differences in methodology, metadata, or geographic information, and as a result may be difficult to compare to contemporary data sources (Wang et al., 2024).

Evaluating transferability

Useful predictive models must transfer with a high degree of accuracy, precision, and sensitivity (Elith & Leathwick, 2009; Yates et al., 2018); however, assessment of model transferability is impossible without subsequent, independent validation from newly collected data, belying the need to transfer models into times and places for which no data exist. A framework for developing generalizable SDMs could, for example, allow practitioners to reliably

make their own choices when selecting sites or species for restoration, conservation, or management. However, predictive use of SDMs requires that we fully understand the degree to which local-scale SDMs can be dependably applied to a new target ecosystem. In the absence of such a framework, land managers and researchers may rely on a common metric like model fit, which is a notoriously unreliable predictor of transferability (Guillera-Arroita et al., 2015; Sillero & Barbosa 2021).

The primary objective of this study is to explore the degree to which internal best fit metrics (Akaike Information Criterion corrected, AICc) of species distribution models can be used to select variables or models with improved accuracy when predicting species occupancy. We also explore whether optical remote sensing data can improve model transferability compared to models using only abiotic terrain variables, and we assess the impact of each predictor on model transferability. We leverage existing vegetation monitoring data for three common grassland species collected at Red Bluff Research Ranch in Norris, MT, to address the following questions:

1. Can model transferability across time at a rangeland study site be assessed using internal best fit metrics prior to occupancy predictions?
2. How does the life history of a species relate to the transferability of its models?
3. Does the use of terrain-based vs. reflectance-based variables affect model transferability?
4. How does environmental similarity between the training and target environments relate to model transferability?
5. Do individual environmental variables vary in their ability to improve transferability, and are their effects consistent across validation datasets and species?

METHODS

Study site

Our study was conducted at Red Bluff Research Ranch in Madison County, Montana (48° 21' N 109° 30' W), a working sheep and cattle ranch located in the Greater Yellowstone Ecosystem, owned and operated by Montana State University (MSU). Red Bluff Research Ranch is a semi-arid steppe, receiving an average annual precipitation of 406 mm (PRISM Climate Group, 2026). Soils are primarily developed from crystalline metamorphic rock that weathers to sandy textures with limited clay formation. Soils vary in depth to bedrock and surface horizon thickness vertically and laterally across hillslopes, driving water storage and mirroring plant diversity patterns (NRCS, 2025). Long-lived cool-season perennial bunchgrasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Idaho fescue (*Festuca idahoensis* Elmer), and prairie junegrass (*Koeleria macrantha* (Ledeb.) Schultes) are abundant, with other grasses, forbs, small shrubs, and lycophytes occurring at lower densities. Warm-season grasses, including blue grama (*Bouteloua gracilis* (Willd. ex Kunth.) Lag. ex Griffiths) and, to a lesser extent, purple three-awn (*Aristida purpurea* Nutt.) are also present, but tend to occupy warmer well-drained microsites. Similarly, cacti (*Opuntia polyacantha* Haw., *Pelecypora missouriensis* (Sweet) DAquino & Dan.Sánchez.) and other arid adapted species also occur intermittently across the landscape. Wetter, more productive microsites, mostly small ephemeral streams and hollows, basin wildrye (*Leymus cinerus* (Scribn. & Merr.) A. Löve), sedges (*Carex* sp.), and many forbs. Non-native grasses such as cheatgrass (*Bromus tectorum* (L.)), crested wheatgrass (*Agropyron cristatum*, (L.) Gaertn.),₂ and smooth brome (*Bromus*

inermis Leyss.) occur in low-diversity patches, likely from past intentional seeding, while areas dominated by native flora feature a greater diversity of grasses and forbs.

We collected vegetation community data over the course of three summers between 2023–2025. In 2023, we collected vegetation community data from June–August, at 21 crossed 100 x 100 m transects centered, based on existing historic transect locations (Van Dyne, 1960). These crossed transects were roughly aligned with the cardinal directions (North, South, East, West), with 10 1 m x 1m sampling plots extending out in each direction resulting in 21 quadrats per transect (440 total, with one quadrat excluded for being outside the property boundary). One person (J. Honn) estimated basal percent cover (%) for 10 focal species: bluebunch wheatgrass, Idaho fescue, blue grama, basin wildrye, needle-and-thread, prairie junegrass, Western wheatgrass, smooth brome, and cheatgrass. All other species were recorded by functional group (perennial grass, annual grass, forb, shrub, perennial succulent). The remaining ground cover was recorded as bare soil, woody debris, leaf litter, feces, or stone. Of the 440 plots, 70% were randomly assigned to be used for the calibration of our distribution models, while the remaining 30% were set aside for calibration. Data from the 2023 effort were chosen as ‘training’ data for the SDMs, which were then transferred to predict occupancy in the monitoring plots established in 2024 and 2025, as described below.

Topographic variables

Topographic variables were derived from the 1/3 arc-second (~10 m) DEM provided by USGS as part of the USGS 3D Elevation Program (3DEP), collected between 2000 and 2015 (United States Geological Survey, 2021). The DEM ground resolution closely matches the 10 m sampling protocol, which allowed us to capture environmental gradients within our

transects at relevant scales. From the DEM we calculated slope, aspect, terrain ruggedness index (TRI), roughness, and topographic position index (TPI) using the package Terra (Hijmans, 2025) in R (R Core Team, 2025). We converted aspect to a 4-class categorical variable, since a continuous measurement of aspect does not consider the similarity between extreme values just west and east of true north.

Soil Data

We used a soil map provided by the U.S. Department of Agriculture, National Resources Conservation Service's Web Soil Survey (Web Soil Survey, 2024). Map units are delineated as areas dominated by one or more soil components based on soil taxonomic classification (Soil Survey Staff, 2025). Map units are broad categorizations which will to some degree fail to capture the true variability in soil conditions within and between sites, however, the true heterogeneity of the soil characteristics across microsites is not reliably mapped. As a result, we opted to rely on these broader delineations to capture main differences in soil across our landscape.

Multispectral Vegetation Indices

Trends in vegetation productivity were captured using 4-band multispectral imagery with 3 m² pixel resolution collected by Planet Labs' Dove sensor (Planet Labs PBC, 2024). Reflectance data were used to calculate optical indices related to productivity, including NDVI (Rouse et al. 1974), Soil Adjusted Vegetation Index (SAVI; Huete, 1988), and Modified Soil Adjusted Vegetation Index 2 (MSAVI2; Rondeaux et al., 1996). Both SAVI and MSAVI2 are modified versions of NDVI and may be more appropriate for rangeland analysis since they account for differences in soil variation and soil exposure. We calculated 10 x

10 m raster layers representing the mean, maximum, and standard deviation for each index using Planet data collected between March and September 2024. All 12 metrics were used as candidate variables in our distribution models.

Thermal Indices

Thermal indices (mean spring, summer, and fall land surface temperature) were calculated at 1 arc-second (30 m) resolution using Landsat 8 and 9 data collected at 30 m resolution. We selected data with less than 10% cloud cover and no smoke obscuring at the study site, then averaged them across 4 years for each of three target months: May, July, and September. These three surface temperature rasters were bilinearly interpolated to match the 10 x 10 m spatial resolution of our other environmental data layers.

Snow Persistence

We estimated snow persistence per pixel as the number of days with snow divided by the total number of days using 4-band multispectral data with 3 m² pixel resolution collected between November 2023 and May 2024 by Planet Labs' Dove sensor (Planet Labs PBC, 2024; details in Chapter 2). We used all available data between these dates with less than 10% cloud cover and no smoke obscuring the study site.

Environmental Similarity

We visualize the difference in environmental space occupied by sites across our three field seasons by using a principal component analysis (PCA) to reduce the dimensionality of our environmental predictors into principal components. The PCA was performed using all continuous environmental predictors, except NDVI and SAVI to reduce redundancy (R Core

Team, 2025). Soil map unit was not included due to it not being a continuous variable. We compared the first and second principal components for each sampling quadrat across our three seasons and then fit a convex hull around the space occupied by quadrats from each season, offering us a general visualization of the environmental space occupied by each set of occupancy data, as well as the general degree of overlap between datasets. The scatterplot and convex hull were produced using GGplot2 for data visualization (Wickham, 2016) and “tidyverse” packages for data manipulation (Wickham et al., 2019).

Transferability Testing Data

Models trained on 2023 surveys were projected onto vegetation plots measured at Red Bluff Research Ranch for two separate research projects to determine which factors affected SDM transferability to other sites in the same area. The 2024 study was a soil moisture monitoring study which targeted 10 sites (60 plots) within a delineated soil map unit. The 2025 study explored effects of microtopography on plants and soils, with 12 transects (180 plots) laid across swales. Target species varied among studies, but three species had % cover records in all years: bluebunch wheatgrass (*P. spicata*), Idaho fescue (*F. idahoensis*) and Western wheatgrass (*P. smithii*). Bluebunch wheatgrass and Idaho fescue are the two most abundant forage species within Red Bluff Research Ranch as well as much of the Greater Yellowstone Ecosystem (Lesica et al., 2022). Both species are long-lived, cool season perennial bunchgrasses which depend on early season meltwater as a moisture source (Lesica et al., 2022). In contrast to bluebunch wheatgrass and Idaho fescue, western wheatgrass is a shorter-lived rhizomatous species, often more disturbed sites.

ANALYSIS

Environmental Predictor Classes

The third objective of this study was to compare whether models fit on terrain vs. optical data vary in their transferability. To address this goal, we fit models using three different sets of environmental data. One set of models, which we call the terrain model set, was trained solely on abiotic terrain variables: slope, aspect, elevation, roughness, topographic ruggedness index, topographic position index and soil data. We also included interaction terms for elevation on aspect, elevation on slope, and aspect on slope. The next set of models, which we call the optical model set, was trained solely on variables derived from remotely sensed reflectance data, including surface temperature, multi-spectral vegetation indices (NDVI, SAVI, MSAVI2), and snow persistence data. The third set of models, which we call the combined model set, was trained on all terrain and reflectance variables. All these three model sets were trained for each of our three focal grass species.

Models

We generated generalized linear models for each species, containing all allowed variable combinations for each of the environmental predictors within a set (terrain, optical, or combined). We excluded covarying predictor variables ($r > 0.6$) in any one model. This resulted in 48 candidate models for the optical model set, 669 for the terrain model set, and 9758 for the combined model set, which we limited to the top 1000 models for computational efficiency. All models were specified as generalized linear models with a binomial link function, trained using a random subset of 70% of the presence/absence data collected in 2023. The remaining 30% from that year was set aside as hold-out or external validation data. Models were ranked according

to Akaike Information Criterion (AICc) using the MuMIn package (Bartoń, 2025) in R (R Core Team, 2025).

Measuring Transferability

We used the SDMs trained on 2023 survey data to predict species' occupancy for the hold-out plots from 2023, as well as for the 2024 and 2025 datasets. A plot was "occupied" if the predicted probability for species occurrence was greater than 60%. Model transferability was assessed using confusion matrices, which compare actual and predicted occupancy for each plot. Our primary metric for assessing transferability was the accuracy of each model. Accuracy, referred to here as mean accuracy, is defined as the overall proportion of correct classifications, true positives (Tp) and true negatives (Tn), relative to all observations, including false positives (Fp) and false negatives (Fn) (1).

$$(1) \text{ Accuracy} = \frac{Tp+Tn}{Tp+Tn+Fp+Fn}$$

However, mean accuracy alone does not indicate how well models predict true occurrences, which is particularly problematic in unbalanced data sets where detection probability is low and species are rare. For instance, a model with very high rates of true negatives can have high accuracy even when failing to identify true positives. When assessing model performance in terms of true occurrences, the probability of detection (recall/sensitivity) (2) and the correct positive prediction rate (precision) (3) are more useful metrics. Sensitivity describes the proportion of true positives out of all observations that should be classified as positives and is a useful metric when trying to minimize missed detections (Fn). Precision on the other hand describes the rate of true positive predictions relative to all positive classifications and is useful when trying to minimize false positives.

$$(2) \text{ Sensitivity} = \frac{Tp}{Tp + Fn}$$

$$(3) \text{ Precision} = \frac{Tp}{Tp + Fp}$$

Sensitivity and precision tend to be inversely proportional to each other, because as false positives increase, false negatives inversely decrease. When producing models, where the goal is to both limit the rate of missed detection and limit the rate of false detection, one can consider F1 scores, which represent the harmonic mean of precision and sensitivity. F1 is useful for identifying models that adequately limit missed and false detection while prioritizing true detection (4). For assessing the overall transferability of models, we consider both accuracy and F1 scores.

$$(4) \text{ F1 score} = \frac{2 * (\text{precision} * \text{sensitivity})}{\text{precision} + \text{sensitivity}}$$

For each model set (terrain, optical, and combined), each focal species (bluebunch wheatgrass, Idaho fescue, and western wheatgrass), and each transfer scenario (2023 training to 2023 testing; 2023 training to 2024; and 2023 training to 2025) we calculated accuracy, sensitivity, precision, and F1 score as external validation metrics, and assessed their relationships with model fit ($\Delta AICc$).

Assessing the Impact of Individual Predictors on Transferability

To test the impact of individual predictor variables on the relationship between $\Delta AICc$ and transferability, we fit another set of generalized linear models with each of our validation metrics as the response variable, and $\Delta AICc$ and each environmental variable (encoded as present or absent) and their interaction as predictors.

Example model format:

$$\text{External Validation Metric} \sim \text{Predictor Presence}(0,1) * \Delta AICc$$

These models enabled us to explore how model transferability covaried with model fit metrics, and whether the inclusion of certain predictors contributed positively to model transferability. A positive effect of model fit, indicated by low ΔAICc , on transferability would mean that models with better fit also transferred better. Positive effects of any given predictor would mean that transferability was improved when that variable was included in a model. A negative “ $\Delta\text{AICc} \times \text{variable presence}$ ” interaction term would mean that fit provided better information about transferability when that variable was present in a model than when that variable was absent. For contrast coding, zero was used as the reference value for ΔAICc (0) and variable presence (1) was the reference value for variable inclusion effects.

RESULTS

The relationship between model fit and transferability metrics varied across species, models, and the validation data used. For all three species, models were able to produce accurate predictions (mean accuracy $> .75$), and increases in model fit were associated with increases in mean accuracy, however only a small fraction of the total variation in ΔAICc was explained by this relationship (Fig. 1). However, predictive performance differed across species when considering precision and sensitivity (Appendix A, Figs. A1, A2). While a number of western wheatgrass models were highly accurate (mean accuracy $> .75\%$), many entirely failed to capture true positive classification. This lack of detection for western wheatgrass also results in models with lower precision scores compared to other species (Appendix A, Fig. A1)

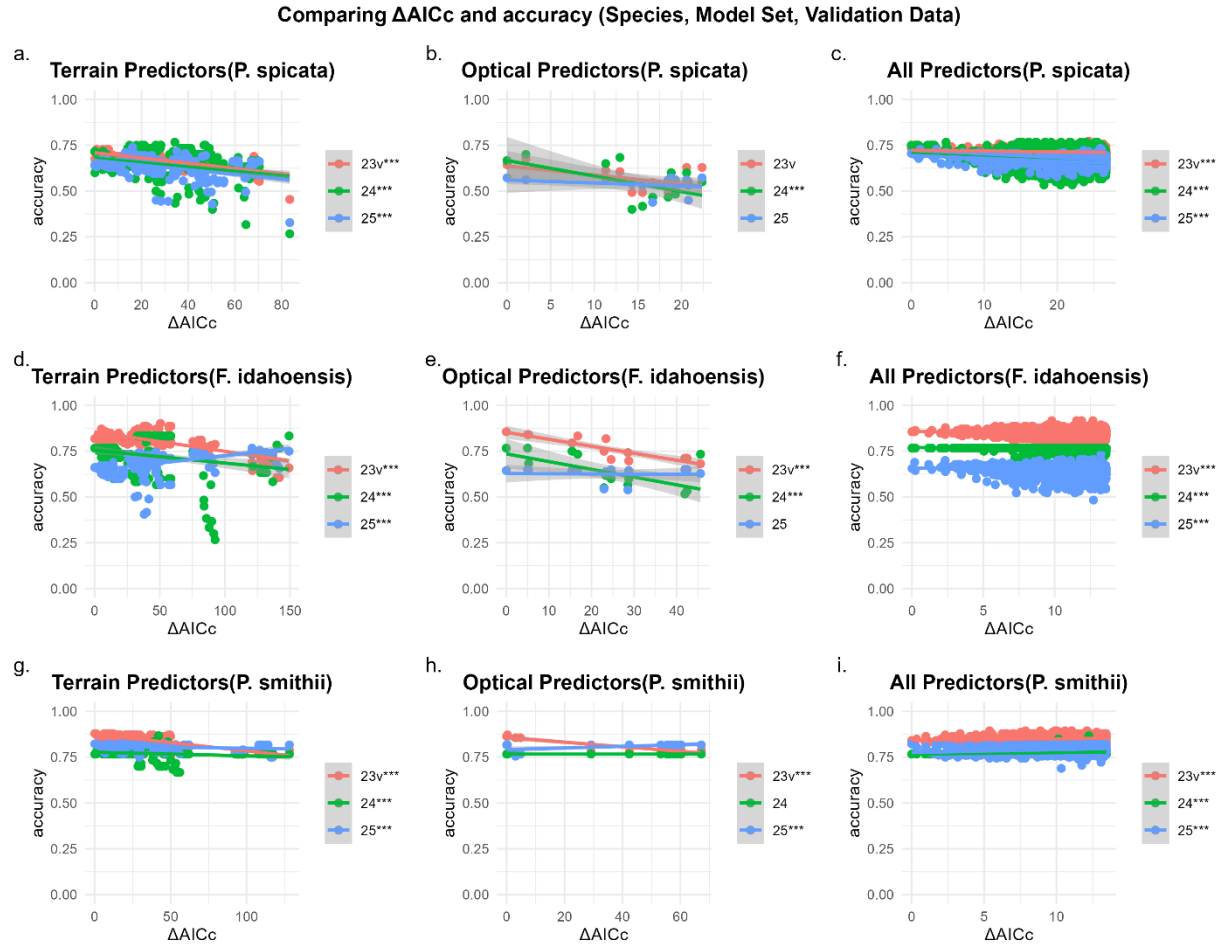


Fig. 1: Relationships between model accuracy and $\Delta AICc$ across three sets of models (terrain, optical, global) and three years of validation data, for each focal grass species (*P. spicata* (Bluebunch wheatgrass), *F. idahoensis* (Idaho fescue), *P. smithii* (Western wheatgrass)). 23v represents the 30% holdout data set from 2023, 24 represents occupancy data collected in 2024, and 25 represents occupancy data collected in 2025. Significant relationship between predictor and response are denoted with “***”.

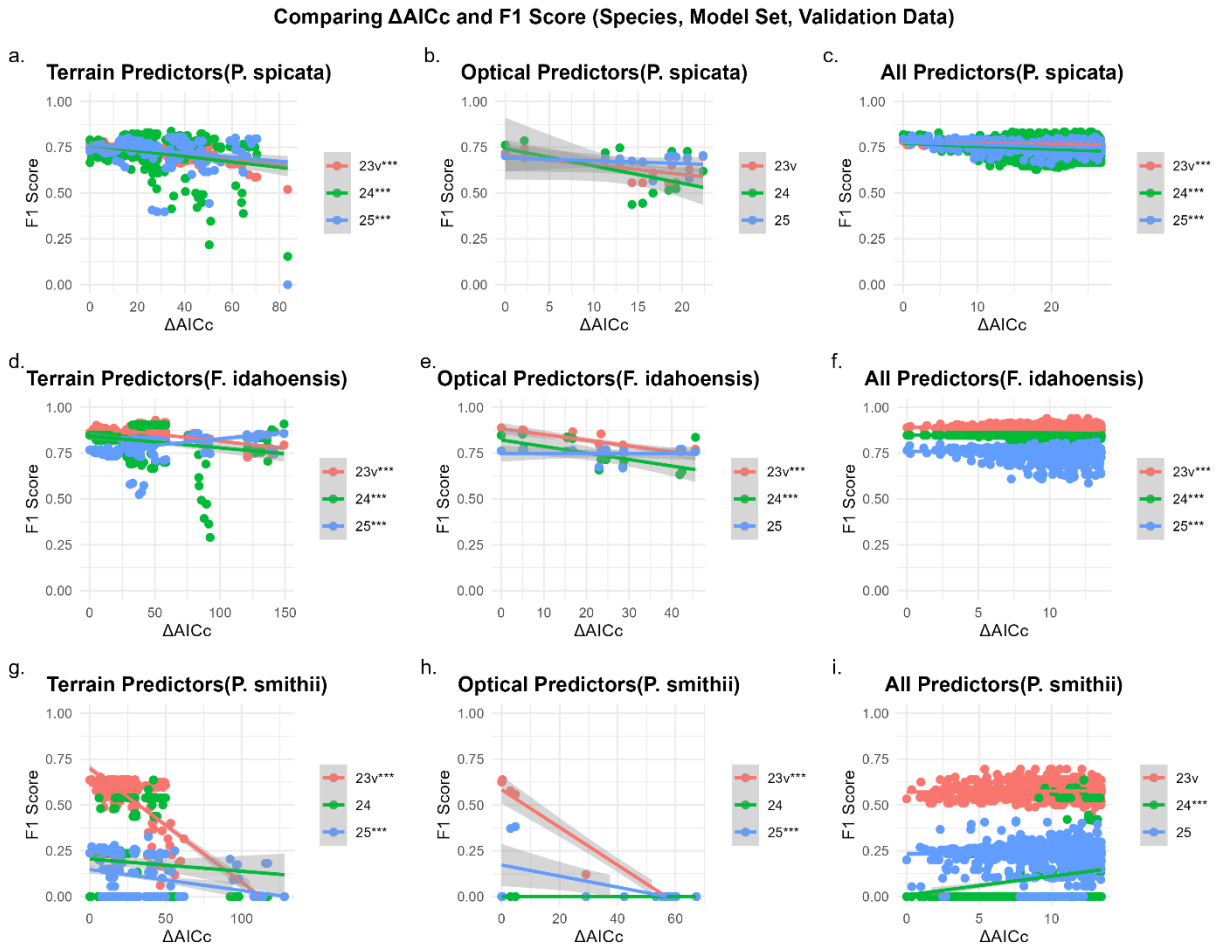


Fig. 2: Relationships between F1 scores and $\Delta AICc$ across three sets of models (terrain, optical, global) and three years of validation data, for each focal grass species (*P. spicata* (Bluebunch wheatgrass), *F. idahoensis* (Idaho fescue), *P. smithii* (Western wheatgrass)). 23v represents the 30% holdout data set from 2023, 24 represents occupancy data collected in 2024, and 25 represents occupancy data collected in 2025. Significant relationship between predictor and response are denoted with “***”.

When we compared model fit indicated by $\Delta AICc$ versus F1 score, the differences in predictive performance across species became especially evident, as the western wheatgrass models were penalized for failing to identify true positives (Fig. 2 g, h, i). In comparison, bluebunch wheatgrass (Fig. 2 a, b, c) and Idaho fescue models (Fig. 2 d, e, f) were able to effectively identify true positives while limiting false positive and false negative rates, resulting in a greater rate of acceptable F1 scores ($F1 > .75$) across all predictor class sets. Using the

combined predictor variable set, 37.8% of the bluebunch models (Fig. 2 c) and 85% of the Idaho fescue models (Fig. 2 f) scored an F1 greater than .75, while no western wheatgrass models reached that threshold (Fig. 2 i).

Environmental similarity

The three validation datasets largely overlapped in their environmental similarity. When comparing the first and second principal components for all of our plots, we can see that the 2023 data covered the greatest amount of environmental space (Fig. 3). For all species, model accuracy using the combined set of predictor variables was highest when using the 2023 validation data set (Fig. 4 iii, vi, ix; all $p < .001$). While we found no significant difference in the accuracy between 2024 and 2025 ($p = 0.57$) for bluebunch wheatgrass, model accuracy differed significantly across all years using the combined predictor set for both Idaho fescue and western wheatgrass (Tukey HSD, $p < 0.001$ for both comparisons, Fig. 4 vi, ix). These differences in model accuracy across sets were mirrored the results when comparing F1 across validation sets. (Fig. 5 iii, vi, ix).

Predictor Class

For models containing only terrain variables, accuracy and $\Delta AICc$ were weakly but significantly negatively correlated across all three species and years (Fig. 1 a, d, g), with the exception of 2025 Idaho fescue models which had a positive relationship between fit and accuracy (Fig. 1 d). Similarly, F1 scores and $\Delta AICc$ were weakly but significantly negatively correlated across all three species and years (Fig. 2 a, d, g), except for the 2024 western wheatgrass models, where the relation was insignificant (Fig. 2 g) and for the 2025

Idaho fescue models, where the relationship between F1 scores and ΔAICc was significant but positive (Fig. 2 d).

Average F1 scores for terrain models across all three validation data sets were moderate to high for bluebunch wheatgrass (Mean = 0.746, SE = 0.0008, Fig. 5 i) and Idaho fescue (Mean = 0.822, SE = 0.0010, Fig. 5 iv). In comparison, western wheatgrass models performed very poorly (Mean = 0.296, SE = 0.0037, Fig. 5 vii), especially for the 2024 and 2025 validation data (combined mean = 0.165, SE = 0.0027, Fig. 5 vii).

For the optical model set, the relationship between F1 score and ΔAICc was inconsistent, with significant correlations found only for the Idaho fescue models predicting occupancy for the 2023 and 2024 validation data (Fig. 2 e), and for western wheatgrass models predicting occupancy for 2023 and 2025 validation data (Fig. 2 h). The lack of correlation might be due to a smaller number of total models and an overall lower range of ΔAICc scores in the optical compared to the terrain models. Average F1 scores for optical models across all three validation data sets were moderate to high for bluebunch wheatgrass (Mean = 0.748, SE = 0.0008, Fig. 5 ii) and Idaho fescue (Mean = 0.823, SE = 0.0010, Fig. 5 v) and overall comparable to terrain models, while western wheatgrass models showed comparatively low scores (Mean = 0.299, SE = 0.0037, Fig. 5 viii).

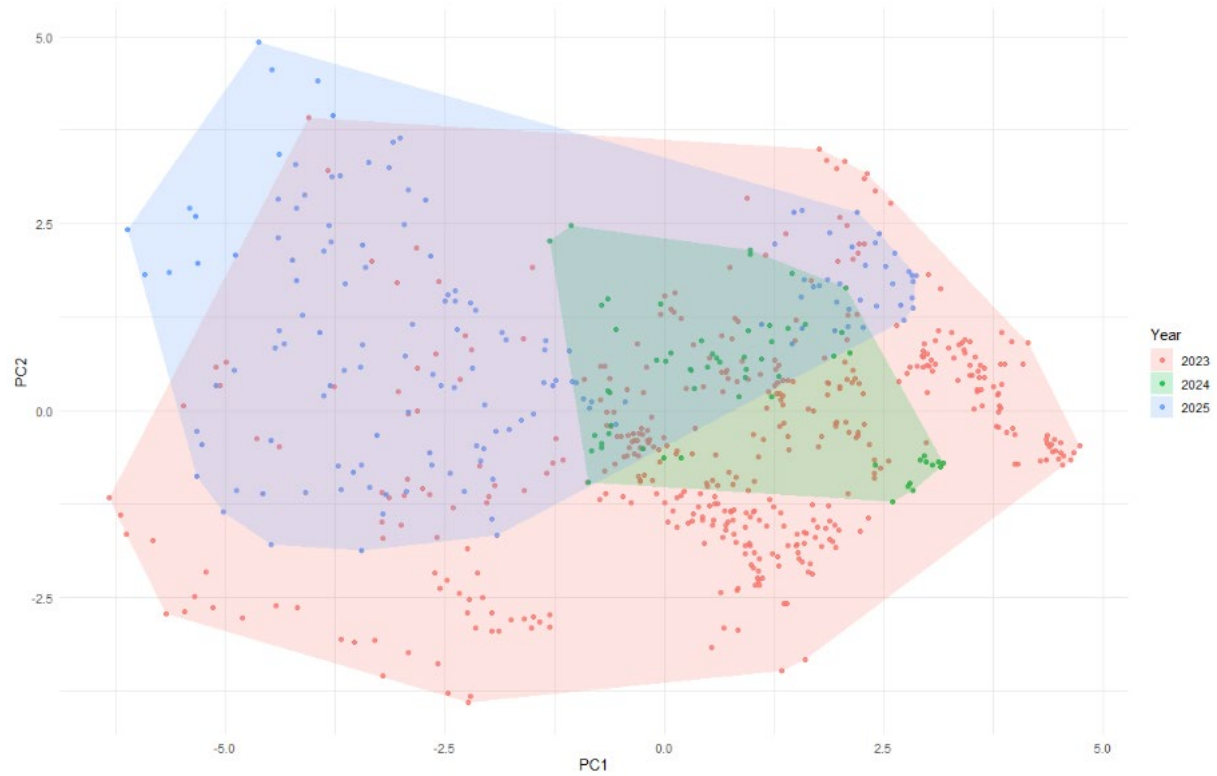


Fig. 3: Principal component analysis for the plant inventories collected across all three years and all continuous variables used in our models. Each point represents a plot from one of our three sets of occupancy data sets when comparing our first (PC1, 52.63% variation explained) and second (PC2, 17.97% variation explained) principal components. Convex hulls were formed around each year's set of plots to visualize an approximate degree of overlap in environmental space across our three years of data.

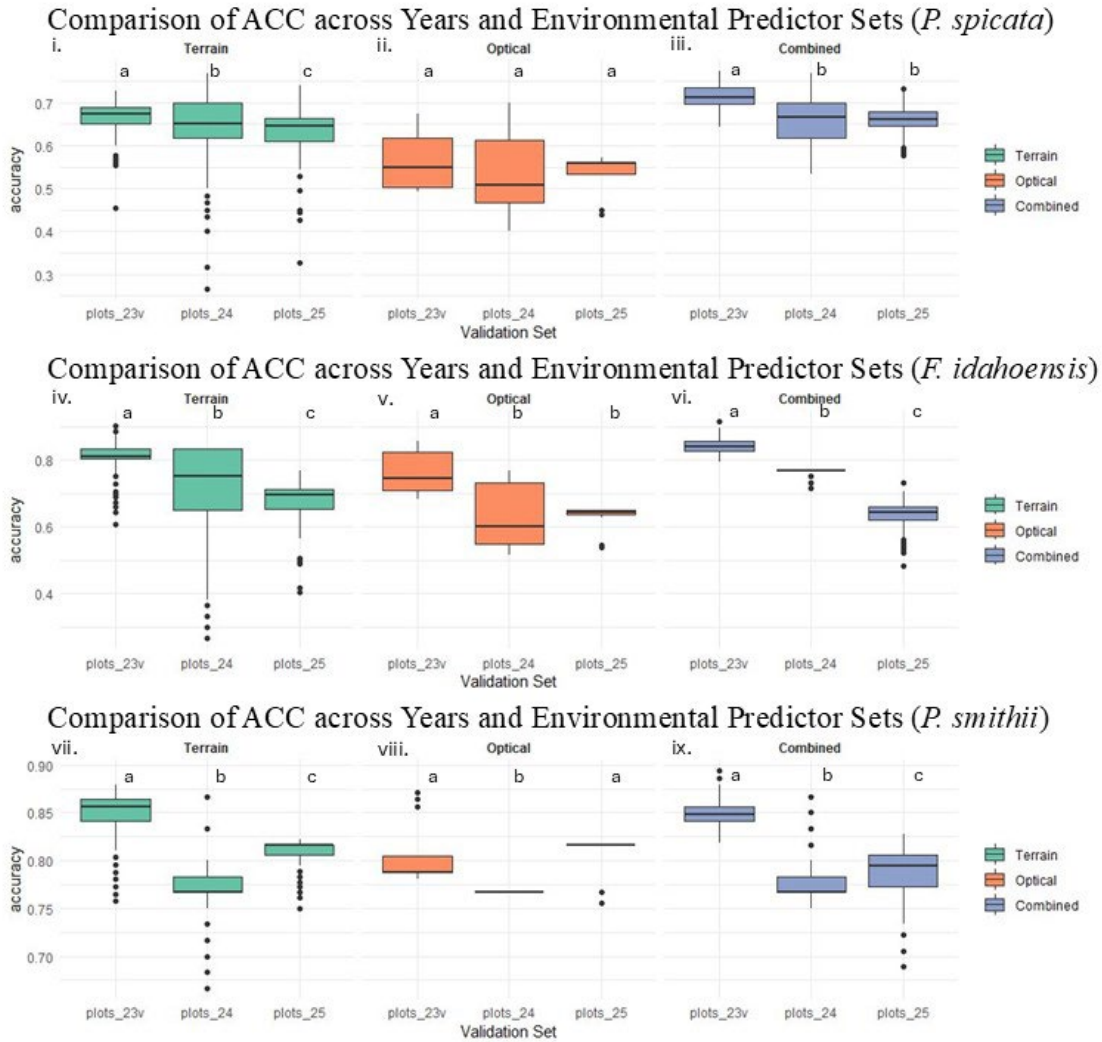


Fig. 4: Boxplot comparing the accuracy (ACC) of SDMs across three focal grass species (*P. spicata* (Bluebunch wheatgrass), *F. idahoensis* (Idaho fescue), *P. smithii* (Western wheatgrass)), as well as the three predictor class sets (terrain, optical, combined), and 3 sets of validation data (plots_23v, plots_24, plots_25). Letters (a, b, c) denote significant differences ($p < .05$) in accuracy across validation sets within each set of models by predictor class. Each set of boxplots per species and model predictor set is differentiated by Roman numerals (i-ix).

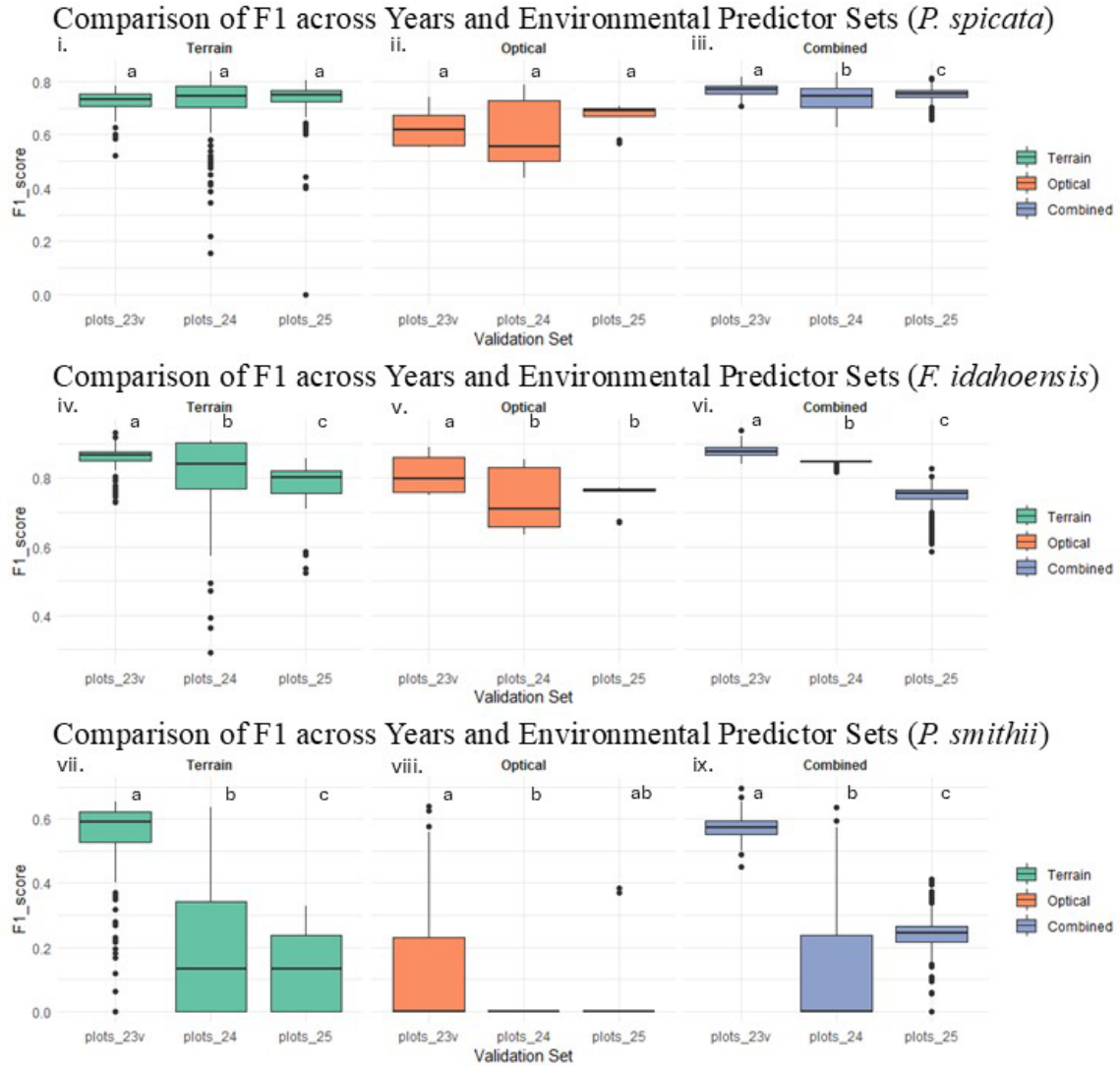


Fig. 5: Boxplot comparing the F1 score of SDMs across three focal grass species (*P. spicata* (Bluebunch wheatgrass), *F. idahoensis* (Idaho fescue), *P. smithii* (Western wheatgrass), as well as the three predictor class sets (terrain, optical, combined), and 3 sets of validation data (plots_23v, plots_24, plots_25). Letters (a, b, c) denote significant differences ($p < .05$) in accuracy across validation sets within each set of models by predictor class. Each set of boxplots per species and model predictor set is differentiated by Roman numerals (i-ix).

Individual effects

Accuracy was not improved by addition of any specific environmental variables (see column “Var”), but many environmental variables had significant impact on the slope (column “Corr”) of the relationship between model fit ($\Delta AICc$) and accuracy (Table 1). The degree and

direction of the effect of predictor presence varied among validation data sets, sometimes dramatically. Some terrain variables like slope, elevation, and elevation squared, consistently decrease the slope of the relationship between accuracy and $\Delta AICc$ when present across all validation sets for bluebunch wheatgrass and Idaho fescue, representing an increase in the strength of the relationship between model fit and accuracy. However, those same variables when included in western wheatgrass model, consistently weakened the relationship between model fit and accuracy.

	BLUEBUNCH WHEATGRASS				IDAHO FESCUE				WESTERN WHEATGRASS			
	Accuracy		F1		Accuracy		F1		Accuracy		F1	
	Var	Corr.	Var	Corr.	Var	Corr.	Var	Corr.	Var	Corr.	Var	Corr.
SLOPE		+	+	+		+		+		-		
ELEV		+		+		+		+				
ELEV^2		+	-	+		+		+		-	-	
ASPECT			-			+		+		-		
TRI		+	+	+								
TPI		+	-	+								
SOIL UNIT										-		
ROUGHNESS				+								
MAY ST		+		+								
JULY ST		+		+								
SNOW		+										
MEAN_MSAVI2			-									
MAX_MSAVI2			-									
SD_MSAVI2							-					
MEAN_SAVI			-									
MAX_SAVI			-									
SD_SAVI			+				-					
MEAN_NDVI			-									
MAX_NDVI			-									
SD_NDVI							-					

Table 1. Effect environmental predictor presence on the relationship between model fit ($\Delta AICc$) and mean accuracy and F1 score of our models. “Var” columns represent the effect of each predictor on accuracy and F1 scores of the top fitting models. “+” indicate predictors that consistently improved accuracy or F1 scores of the top fitting models across all validation sets, while “-“ indicates a decrease in accuracy or F1 scores of at least one of the top models. “Corr” columns represent the effect of each predictor on the slope of the relationship between accuracy and F1 scores and model fit ($\Delta AICc$), where “+” represents predictors that consistently increased the relationship between model fit on accuracy or F1, where decreasing model fit (increasing $\Delta AICc$) leading to decreasing accuracy or F1.

For bluebunch wheatgrass, model fit (lower ΔAIC_c) and F1 or mean accuracy scores were more strongly and positively correlated, when slope, elevation, elevation square, TRI, TPI, roughness, May average surface temperature, or July average surface temperature were present in the model. In other words, the presence of these variables meant that model fit was a better indicator of transferability. However, these variables did not necessarily improve transferability when present; only slope and TRI contributed to higher F1 scores for bluebunch wheatgrass. Other predictors either had no effect or consistently decreased the F1 score of the top performing models, even while improving the correlation between fit and transferability. The only remotely sensed productivity index that had a consistently positive effect on transferability was the standard deviation of SAVI, which improved the F1 scores of all bluebunch wheatgrass models. The maximum and mean of all of remotely sensed productivity indicators consistently decreased F1 scores of the top fitting bluebunch wheatgrass model and we found no variables that improved model accuracy when included.

We also found that no environmental variables increased the F1 scores of the top performing Idaho fescue models, although slope, elevation, elevation squared, aspect, TRI and TPI all improved the slope of the relationship between model fit and both, F1 scores and accuracy. While the standard deviation of SAVI increased F1 scores for bluebunch wheatgrass, the standard deviations of all productivity variables decreased F1 scores of the top fitting Idaho fescue models. No variables had a consistent effect on western wheatgrass model transferability. Indeed most variables that appear to improve the transferability of models for our other two bunch grasses, seem to have the opposite or neutral effects on western wheatgrass models. For western wheatgrass models, only the inclusion of the soil map consistently impacted the slope of

the relationship between model fit and sensitivity, suggesting that western wheatgrass occupancy may be influenced by differences in soil.

DISCUSSION

Assessing Transferability

If goodness of fit metrics are useful for identifying environmental factors driving species presence, and if models trained using only direct drivers have better transferability, models with better fit should also be more transferable (He et al., 2015; Deblauwe et al., 2016; Werkowska et al., 2017). Furthermore, many fit metrics, including AICc, account for parsimony, which is also hypothesized to improve transferability (Wenger and Olden, 2012; Merow et al., 2014). For these reasons, we hypothesized that AICc, our measure of model fit, would correlate with transferability.

More often than not, we found a significant correlation between model fit and accuracy or F1 scores (Figs. 1, 2). Furthermore, for most of these instances, model fit increased as accuracy increased, with some exceptions for models validated using 2025 data. These examples support the idea that internal fit metrics can convey information regarding transferability. However, none of these effects were strong enough to be practically useful for model selection, as large differences in AICc translated to minimal changes in accuracy. Additionally, model accuracy cannot fully capture model transferability, because accuracy can be inflated when a high number of correctly predicted absences results in highly accurate but questionably useful SDMs that might fail to predict species presence correctly (Sequeira et al., 2017; Rousseau and Betts, 2022). Sensitivity and precision have been used to study transferability, particularly when researchers care about maximizing true positive observations and minimizing either missed or

false detections (Liu et al., 2009; Ruete and Leynaud, 2015). When balancing these two factors is important, F1 can be used to assess the harmonic balance of sensitivity and precision (Wunderlich et al, 2022; Anselmetto et al., 2025). Besides accuracy, F1, sensitivity and precision, many different confusion matrix derived indices and statistical methods have been used to assess transferability (Sequeira et al., 2017). When we measured transferability using precision and sensitivity, we saw distinct differences in model performance across species (Appendix A, Figs. A1, A2), which is also represented in F1 scores (Fig. 2). Model transferability differed among species, depending on the predictors and validation data sets used as well as weaker relationships between model fit and transferability. In real world, SDM applications where sensitivity and precision are important, model fit metrics may provide even less information about transferability than cases where only accuracy is considered. While accuracy may be an appropriate metric for land managers hoping to apply SDMs, most use-cases value correct species detection, rather than just producing accurate models (Meineri et al., 2012; Addison et al., 2013; Sequeira et al., 2017).

Variation in Predictions Among Species

Top models were generally able to accurately predict the occupancy of all three species, especially in the combined predictor set (Fig. 1). When we evaluate F1 score, however, it becomes apparent that the western wheatgrass models were primarily successful at predicting lack of occupancy instead of species presence (Fig. 2 g-i). In fact, Western wheatgrass SDMs regularly failed to predict any true Western wheatgrass occurrences. This drastic difference in model performance across species is not unexpected, as the ecology of species, including their lifespan, is known to affect model quality (Rousseau and Betts, 2022). Species with shorter

lifespans tend to be more difficult to model using SDMs than species with longer lifespans, potentially due them responding more to short-term trends and less to long term ecological gradients used to train SDMs (Petitpierre et al., 2017). A possible driver of the inconsistency in western wheatgrass SDMs might be the species relationship with disturbance. Western wheatgrass positively responds to disturbances such as overgrazing and automotive impacts (USDA, 2002, Lessica et al., 2022). Disturbance may not correlate consistently with the environmental variables included in our models, such as topography. Overall, SDMs may have lower quality when predicting more generalist or disturbance loving species (Morán-Ordóñez et al., 2012; Werkowska et al 2016). While variables such as elevation, slope and elevation by slope interactions may indirectly affect land use, for example by cattle and sheep as on the Red Bluff Research Ranch, and therefore disturbance, our models lacked a variable directly measuring disturbance, which may have contributed to the overall poor western wheatgrass model performance (Cook, 1966; Bailey, 2004).

Training versus Target Environmental Similarity

The degree to which different validation data sets produced differing transferability depended largely on the species, likely driven by species-specific habitat preferences (Figs. 4, 5) (Petitpierre et al., 2016; Werkowska et al 2016). The 2023 dataset, comprised of randomly located sites, contained the most observations and covered the greatest amount of environmental variation as can be seen in the first two principal components of terrain variation (Fig. 3). We hypothesized that, if transferability degrades with distance from training space, transferability should be better for 2024 than 2025 (Rouseau and Betts, 2022). This hypothesis was not

supported by our analysis, as we found significant differences in accuracy and F1 scores across survey years, but the strength and direction of effect depended on the species.

We note that in this study, both the training and testing locations were at the same study site, Red Bluff Research Ranch, albeit separated by two years and different in sampling methodology. Nonetheless, the environmental differences between training and testing data were as small as any a distribution modeler might encounter when extrapolating models. These results may represent a best-case-scenario for model transferability, and yet the environmental differences between surveys were enough to limit transferability, especially for western wheatgrass. These results call into question the applicability of SDMs for extrapolating occupancy predictions even across very small spatial scales, in the absence of validation data.

Terrain vs Optical Environmental Predictors

The type of environmental variables used as predictors are known to affect the transferability of species distribution models (Elith and Leathwick, 2009; He et al., 2015; Petitpierre et al., 2016). Choosing environmental predictors that most closely relate to a species ecology, and physiological requirements should maximize transferability, however it's unclear how predictors should be selected or what type of variables are best. Our results suggest that the use of terrain vs. optical variable classes may affect transferability, however comparisons are difficult due to the difference in the total number of models in each class (Figs. 1, 2). It is worth noting that, while the optical models were able to produce models with adequate F1 and accuracy scores and using few predictors, these models produced slightly lower average transferability than models fit on landscape variables or the combined variable set (Figs. 4, 5). Since parsimonious models generally transfer better than more complex models, remotely sensed

reflectance data may be an increasingly valuable source of training data for SDMs (Elith and Leathwick, 2009; Merow et al., 2014; He et al., 2015; Wang et al., 2024). However, the highest transferability was possible when all candidate variables were included, indicating that more data sources may be better when selecting variables for SDMs (Figs. 1, 2).

Individual Environmental Variable Impact on Transferability

We found no single variable that significantly improved the accuracy of our top models (Table 1). While multiple studies have found that variables relating to plant productivity and thermal ground conditions can increase model accuracy (Elith and Leathwick 2009; Morán-Ordóñez et al., 2012; He et al., 2015), our data did not support this scenario. Inclusion of some variables, such as slope and elevation, did improve the relationship between fit and accuracy for bluebunch wheatgrass and Idaho fescue, but these had the opposite effect on Western wheatgrass models.

While no variables directly improved the accuracy of the top fitting models, slope, TRI and the standard deviation of SAVI, all consistently improved F1 scores of the top fitting bluebunch models (Table 1). It is worth noting that the other remotely sensed indices, NDVI and MSAVI2, consistently decreased the F1 scores of our top models. SAVI and MSAVI2 are designed to account for variation in soil reflectance and exposure, when assessing plant greenness (Rondeaux et al., 1996; Voitik et al., 2023). Our study suggests that SAVI may be more appropriate for SDM applications in our study system compared to other indices, although this trend was only seen in the bluebunch models. No predictors consistently improved F1 scores of the top fitting models for the other two species, which may be due to interspecific differences in environmental responses generally and across out validation data sets. The effect of

environmental predictors on the slope of the F1 by AICc relationship largely mirrored these results. Our findings support current research suggesting that SDM transferability is driven by species-specific responses to environmental gradients, meaning any assessment of transferability must consider both species identity and the target environmental space (Petitpierre et al., 2016; Werkowska et al., 2017).

CONCLUSION

Local-scale occupancy predictions represent realistic challenges faced by restoration and conservation professionals, where a local reference site is used to train an ecological niche model which then informs restoration or management planning. Reference sites are often nearby intact ecosystem, intentionally chosen to represent the ecological potential of the target area. Ideally differences in environmental space between the reference site and the target site are minimal, similar to the distribution of occupancy data across our 13,000-acre study site, thus this study represents a near best-case scenario for applying SDM's for occupancy predictions. Our results are most relevant to local-scale modeling, where extrapolation in environmental niche space is assumed to be small, and geographic distances are modest. However, SDMs are also being used to predict the impact of invasive species and climate change on species distributions, requiring far more extreme extrapolation and a more complex understanding of transferability. Such tasks require further research into SDM transferability and strategies for maximizing model transferability outside of the environmental training space. The ability to estimate an ecological model's predictive performance is imperative for improving the applicability of SDMs for real world applications in conservation, restoration, and land management. $\Delta AICc$ does not appear

to adequately predict model transferability; however, the inclusion of specific variables can affect the relationship between model fit and transferability, and even improve the performance of the top model. These differences in transferability, however, are largely species and environment specific. Additionally, it is apparent that remotely sensed reflectance data hold a lot of valuable information regarding plant community distribution. Regardless, while some models transferred well, we could identify no consistent scheme for selecting variables that produced the best-transferring models or identifying problems of model transferability *a priori*. Further research is needed to develop a viable strategy for predicting the optimal variables for transferability.

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CHAPTER FOUR

THESIS CONCLUSION

This thesis evaluates how remotely sensed data can be used to better understand and predict patterns of rangeland biodiversity in western production grasslands. Rangelands represent large complex ecosystems and are a critical aspect of the culture and economy of the Montana and the American West. However, assessing biodiversity across such large-scale systems is difficult, costly, and often impossible to adequately do by hand. As a result, there is a growing need for scalable strategies for biodiversity monitoring and modeling.

This thesis is comprised of two complementary studies in which remotely sensed data were utilized to study different aspects of plant diversity across a GYE rangeland system. In chapter 1, we used imaging spectroscopy data to detect β -diversity across our study site, outside of the growing season. We were able to explain roughly half of the variation in plant community composition across sites based on spectral variation. Differences in terrain and snow cover among sites also influenced spectral variation but to a lesser degree. This study shows the potential of imaging spectroscopy for mapping and monitoring plant diversity at scales greater than can be sampled just by hand.

In chapter 2, we focused on modeling the occupancy of individual species, exploring the relationship between model fit and transferability, as well as the effect that remotely sensed data products had on this relationship. While we were able to identify consistent significant relationships between model fit and our transferability metrics (mean accuracy and F1 scores), these relationships were too weak to be practically useful for managers. We did, however, find differences in model predictive ability across different validation data sets, predictors, and

species, supporting the current consensus that model transferability is significantly impacted by the environmental distances between training and prediction space, and that model transferability is highly species specific.

Both chapters utilize existing vegetation community data to study how remote sensing can be used to assess grassland plant diversity. Studies like this help us build towards a future where ecological modeling powered by remote sensing technologies enable accessible large-scale monitoring and active management of rangelands under changing conditions. As research continues, we will be able to more effectively target the relevant spectral ranges and species attributes for accurately capturing spatio-temporal changes in plant community composition. Likewise, remotely sensed data can be incredibly useful for studying and modeling individual species occurrence, but a better assessment and understanding of the drivers of model transferability is required first.

Climate change and shifts in land use are pushing existing plant populations and communities into novel combinations of environmental conditions, and the ways in which they will respond are likely to be similarly novel. Landscape level diversity monitoring and modeling, enabled by the next generations of remote sensing technology and methods, could allow managers to predict or detect rapid changes in plant communities. Such methodology would allow managers to address community changes before potentially costly consequences become apparent in the field. Continued research into the applications of remote sensing in ecology as well as the continued access to high quality remotely sensed data will enable future land managers to make informed decisions and manage land proactively.

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APPENDIX

Additional Species Distribution Model Validation Plots

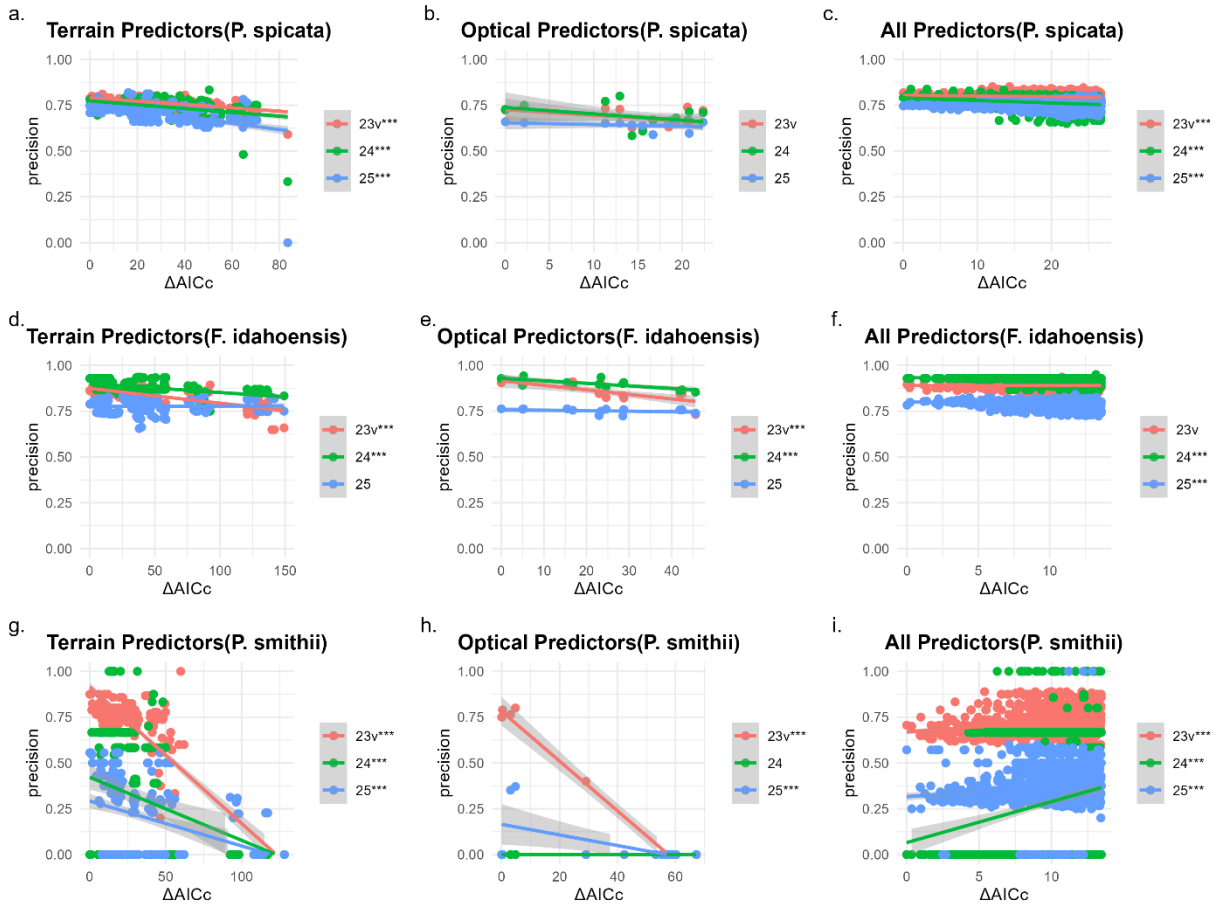
Comparing $\Delta AICc$ and precision (Species, Model Set, Validation Data)

Fig. A1: Scatterplots comparing precision and $\Delta AICc$ across three sets of models (terrain, optical, global) and three years of validation data, for each species. Each plot has a best fit trendline comparing precision and $\Delta AICc$ within each validation set. Sets with a significant relationship between our predictor and response are denoted with "***".

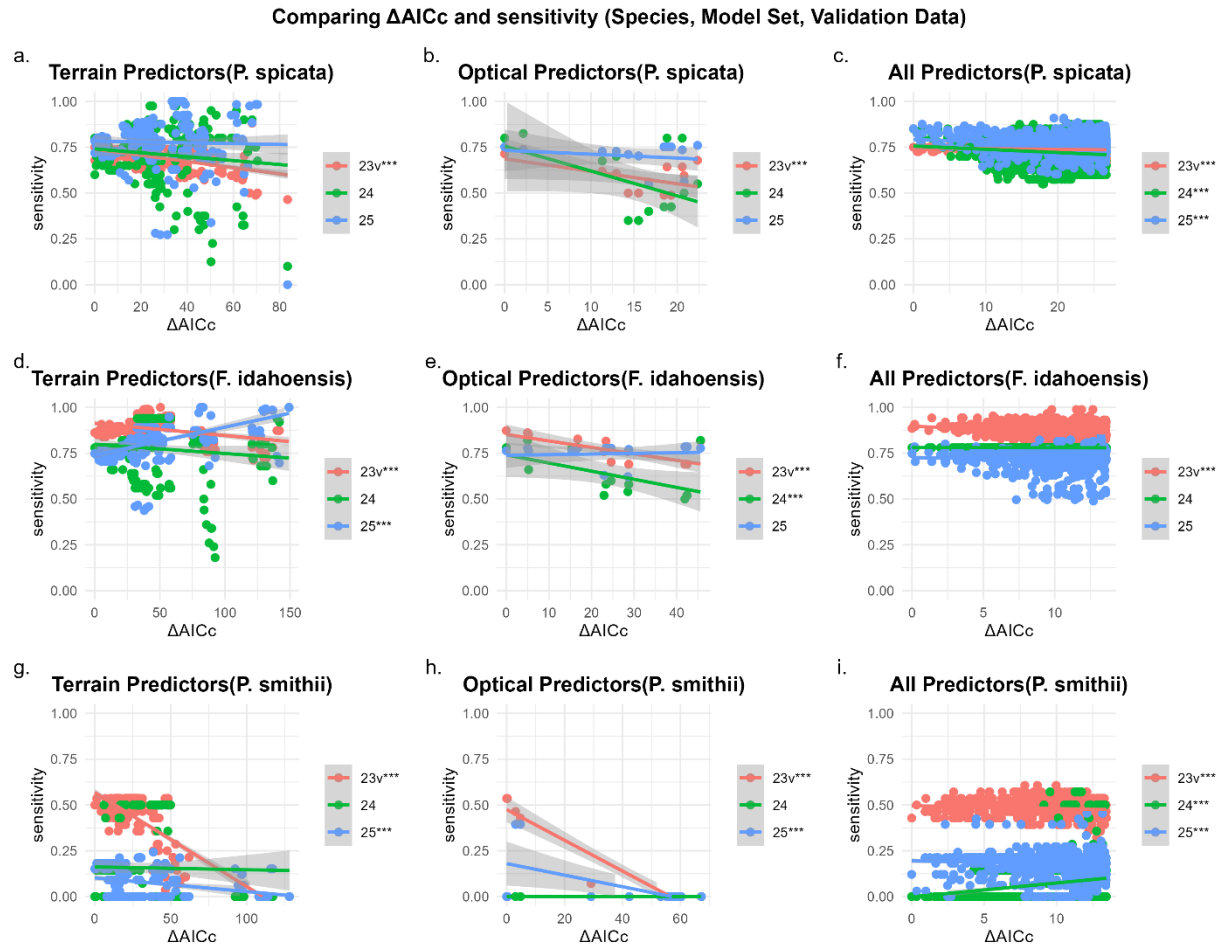


Fig. A2: Scatterplots comparing sensitivity and $\Delta AICc$ across three sets of models (terrain, optical, global) and three years of validation data, for each species. Each plot has a best fit trendline comparing sensitivity and $\Delta AICc$ within each validation set. Sets with a significant relationship between our predictor and response are denoted with “***”.