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TECHNICAL ARTICLE

Near-infrared spectroscopy aids ecological restoration by classifying variation of taxonomy and phenology of a native shrub

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Plant communities are composed of complex phenotypes that not only differ among taxonomic groups and habitats but also change over time within a species. Restoration projects (e.g. translocations and reseeding) can introduce new functional variation in plants, which further diversifies phenotypes and complicates our ability to identify locally adaptive phenotypes for future restoration. Near-infrared spectroscopy (NIRS) offers one approach to detect the chemical phenotypes that differentiate plant species, populations, and phenological states of individual plants over time. We use sagebrush (*Artemisia* spp.) as a case study to test the accuracy by which NIRS can classify variation within taxonomy and phenology of a plant that is extensively managed and restored. Our results demonstrated that NIRS can accurately classify species of sagebrush within a study site (75–96%), populations of sagebrush within a subspecies (99%), annual phenology within a population (>99%), and seasonal phenology within individual plants (>97%). Low classification accuracy by NIRS in some sites may reflect heterogeneity associated with natural hybridization, translocation of nonlocal seed sources from past restoration, or complex gene-by-environment interactions. Advances in our ability to detect and interpret spectral signals from plants may improve both the selection of seed sources for targeted conservation and the capacity to monitor long-term changes in vegetation.

Key words: **ecological restoration, functional restoration, near-infrared spectroscopy, phenotypes, sagebrush**

Implications for Practice

- Near-infrared spectroscopy (NIRS) uses spectral traits of plants to differentiate vegetation based on taxonomy and phenology.
- NIRS offers an emerging restoration tool that can detect changes in plant composition, distribution, and functional traits that are not obvious from morphology.
- NIRS has the potential to detect taxonomic diversity associated with natural hybridization and reseeding or translocation of local and nonlocal plant sources.
- NIRS can help increase the spatial and temporal scale at which plant traits can be used to monitor restoration outcomes.

Introduction

Pervasive landscape alterations from climate change and human disturbance substantially affect vegetation and associated wildlife communities (Coop et al. 2020). These changes are often met with ecological restoration practices meant to prevent further loss of native species and restore vegetative communities. Past and current restoration efforts include reseeding with locally sourced native seed (Brabec et al. 2015), admixing individuals from different sources to maximize adaptive potential (Bucharova et al. 2019), and introducing species that may shift community types but avoid extirpation (Guerrant Jr &

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Kaye 2007). These restoration practices can alter taxonomic composition of plants (Carlucci et al. 2020), associated communities (e.g. herbivores, Pyke et al. 2020; fungi, Hovland et al. 2019), land use and cover (Cox & Anderson 2004), and ecosystem health and services (Reynolds et al. 2012). The high economic costs of restoration (Boyd & Davies 2012) demand better tools to properly classify and monitor plants and their functional traits for restoration.

Monitoring restoration outcomes requires an understanding of past restoration practices and optimizing present ones; this generally starts with classifying taxa (e.g. species) and functional traits (e.g. morphology, physiology, and phenology). Classifying plants within a community after translocation or reseeding can identify which plants were resilient to restoration (Davidson et al. 2019). Differentiating species can also reveal the extent of local versus foreign recruits from translocation efforts (Keller et al. 2000) and invasive species (Somers & Asner 2013). Landscapes characterized by morphologically distinct plant species may be relatively simple to measure and monitor (Pasquarella et al. 2016) compared to landscapes dominated by plant species that are difficult to classify due to complex or inconsistent morphological traits.

Sagebrush steppe ecosystems are characterized by complex landscapes that contain individual plants from the genus *Artemisia* that can vary morphologically within a species and others that are morphologically indistinguishable among species and subspecies (Jaeger et al. 2016). Sagebrush exhibits high intraspecific genetic diversity and has the ability to hybridize between species and subspecies (Bajgain et al. 2011; Richardson et al. 2012; Davidson et al. 2019), which further complicates classification. The diverse intraspecific phenotypes in sagebrush, including flowering phenology and phytochemistry (e.g. secondary metabolites), are underpinned by a combination of genetics, environmental conditions (i.e. phenotypic plasticity), and complex gene-by-environment (G×E) interactions (i.e. heritable plasticity; Nicotra et al. 2010; Karban et al. 2014; Richardson et al. 2017). Given the genetic basis of these morphological traits, it is possible that sagebrush is adapted to local conditions, which should influence where seeds are collected for restoration efforts (Davidson & Germino 2020). Alongside the natural complexities, sagebrush-dominated ecosystems have a convoluted history of management. In the 1940s, herbicide, controlled burning, and manual techniques (e.g. plowing) cleared the land and increased grass production for livestock (Pechanec et al. 1954). After the Federal Land Policy and Management Act was passed in 1976, wildlife-oriented management, restoration, and conservation became a priority for federal land managers (Knick & Connelly 2011). Despite substantial efforts to restore sagebrush ecosystems, sagebrush habitat continues to decline (Arkle et al. 2014; Requena-Mullor et al. 2019) and threaten the survival of species that rely on it (e.g. sage-grouse [*Centrocercus* spp., Conover & Roberts 2016]; pygmy rabbits [*Brachylagus idahoensis*, Thines et al. 2004]). To protect and restore sagebrush steppe habitats, we need to identify which species and subspecies of sagebrush exist across the landscape.

Unfortunately, classifying sagebrush taxa based on morphology alone is challenging (Rosentreter et al. 2021) and misclassification may lead to errors in land cover maps (Fremgen-Tarantino et al. 2021). Although genetic tools for classification of sagebrush are emerging (Richardson et al. 2012), there is a need for inexpensive and rapid approaches to identify and monitor specific sagebrush taxa in the field. Near-infrared spectroscopy (NIRS) can meet this need by detecting distinctive phytochemical traits (Vance et al. 2016). NIRS has been shown to be as accurate, if not more, in classifying vegetative phenotypes than manual approaches (Espinoza et al. 2012). Furthermore, spectral information collected by NIRS that differentiates taxa and phenotypes of interest can be scaled up to landscape and global extents with air- and satellite-borne hyperspectral sensors (Ustin & Middleton 2021). We used NIRS to differentiate sagebrush across four biological scales to demonstrate how spectral signals can detect taxonomic and temporal variation that can benefit ecological restoration, including: (1) sagebrush species within a community, (2) geographically distinct populations within a single subspecies, (3) annual variation within a single population, and (4) seasonal variation within individual plants.

Methods

Study Sites

Sagebrush leaves were collected from four field sites in Idaho, U.S.A: the Magic site (43°14′N, 114°19′W, elevation 1,465–1,480 m), Cedar Gulch site (44°41′N, 113°17′W, elevation 1,890–1,940 m), Craters site (42°57′N, 113°23′W, elevation 1,300–1,650 m), and Raft River site (42°9′N, 113°24′W, elevation 1,380–2,140 m). Previous research on Greater Sage-grouse (*Centrocercus urophasianus*; Ulappa 2011; Fremgen 2015) and pygmy rabbits (Ulappa 2011; Nobler 2016) at these sites demonstrated high phenotypic diversity among sagebrush species. All study sites were predominantly sagebrush (*Artemisia* spp.) but varied in taxonomic (e.g. species) and functional (e.g. morphology, phytochemistry) traits within the sagebrush community and environmental conditions (i.e. terrain, elevation, climate, year, and season collected) (Fig. 1).

Taxonomic and Temporal Phenotypes

Taxonomic phenotypes included sagebrush species and subspecies and geographically distinct populations within the Wyoming big sagebrush subspecies (*Artemisia tridentata* ssp. *wyomingensis*). Sagebrush species and subspecies were identified prior to NIRS analysis using plant morphology, environment type (e.g. elevation, soil type, and depth; Rosentreter 2005), and phytochemical profiles identified in previous research (Fremgen-Tarantino et al. 2020; Olsoy et al. 2020). Sagebrush taxonomic groups included Wyoming big, three-tip (*Artemisia tripartita*), black (*Artemisia nova*), low (*Artemisia arbuscula*), and “dwarf” sagebrush (Fig. 1). Although there are morphological and phenotypic differences between black and low sagebrush (e.g. stem color, stem stature, and soil type; Rosentreter 2005), samples were identified as

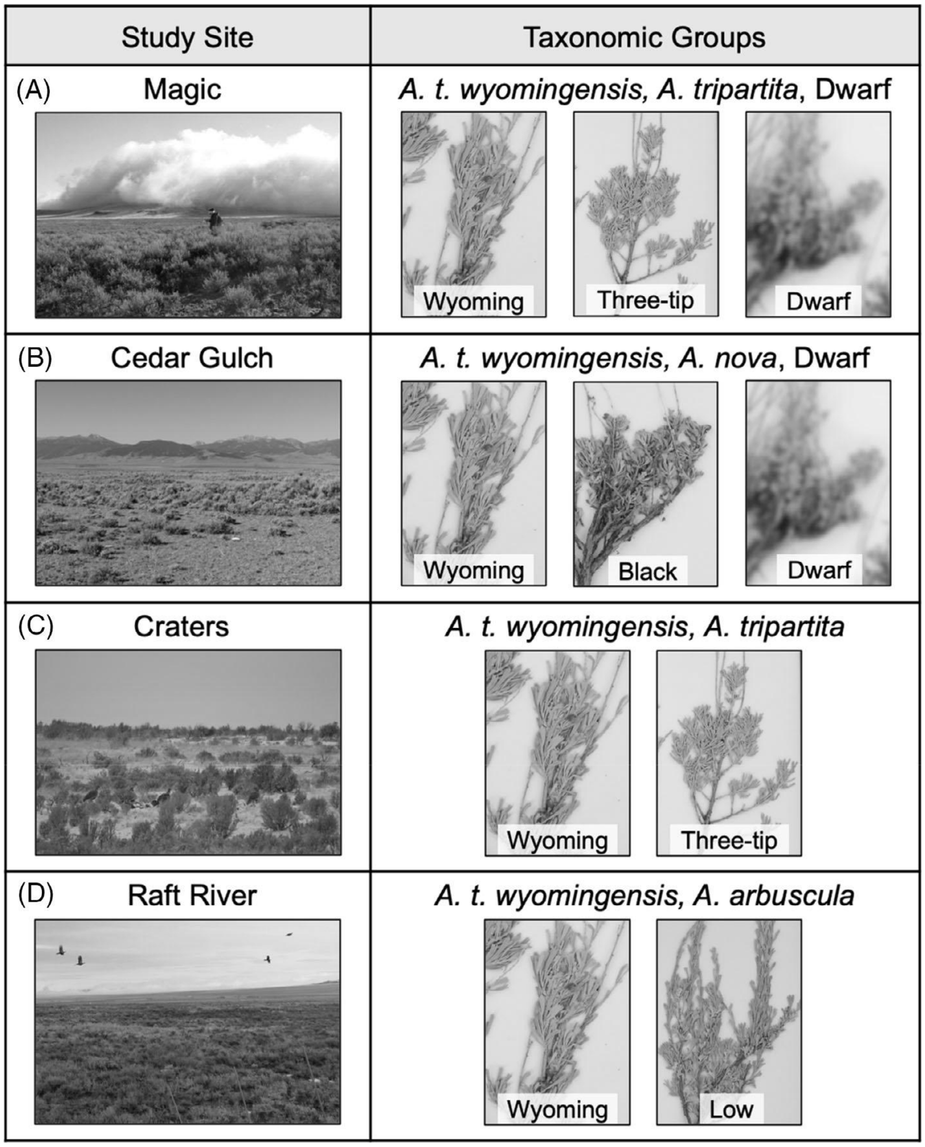

Figure 1. Taxonomic groups of sagebrush (*Artemisia* spp.) classified using near infrared spectroscopy within four geographically distinct study sites in Idaho, U. S.A.: (A) Magic, (B) Cedar Gulch, (C) Craters, (D) Raft River. Species photos came from the Consortium of Pacific Northwest Herbaria (https://www.pnwherbaria.org/data/search.php). The dwarf photo is intentionally blurred to represent a general dwarf sagebrush species.

dwarf when they had smaller morphological size relative to big sagebrush species at the site or occurred within micro-topographically unique patches but did not have clear morphological features to distinguish them as black or low.

Temporal phenotypes represent phenological states and included year (2013 vs. 2015) within a single Wyoming big sagebrush population at one study site (Magic) and season (summer vs. winter) within individual plants of Wyoming big sagebrush at two different study sites (Magic and Cedar Gulch). Within-species analysis (classifying populations, year, and season) focused on Wyoming big sagebrush because it was the only subspecies present at all of our study sites.

Sample Collection

Sampling collection methods were standardized across sites and seasons. To reduce potential noise from user differences, individuals collecting sagebrush tissues within a site collected all morphotypes across all seasons and a subset of collectors were consistent across sites. Approximately 2.0 g (wet weight) of biomass was clipped per plant and stored in individual bags on ice until transfer to −20°C freezers. Sagebrush samples from Magic ($n = 1{,}089$) and Cedar Gulch ($n = 625$) were representative of plant parts consumed by pygmy rabbits (for the broader purpose of that study, see Olsoy et al. 2020) and included both stems and leaves. Sagebrush samples from Craters ($n = 94$) and Raft River ($n = 263$) were representative of plant parts consumed by

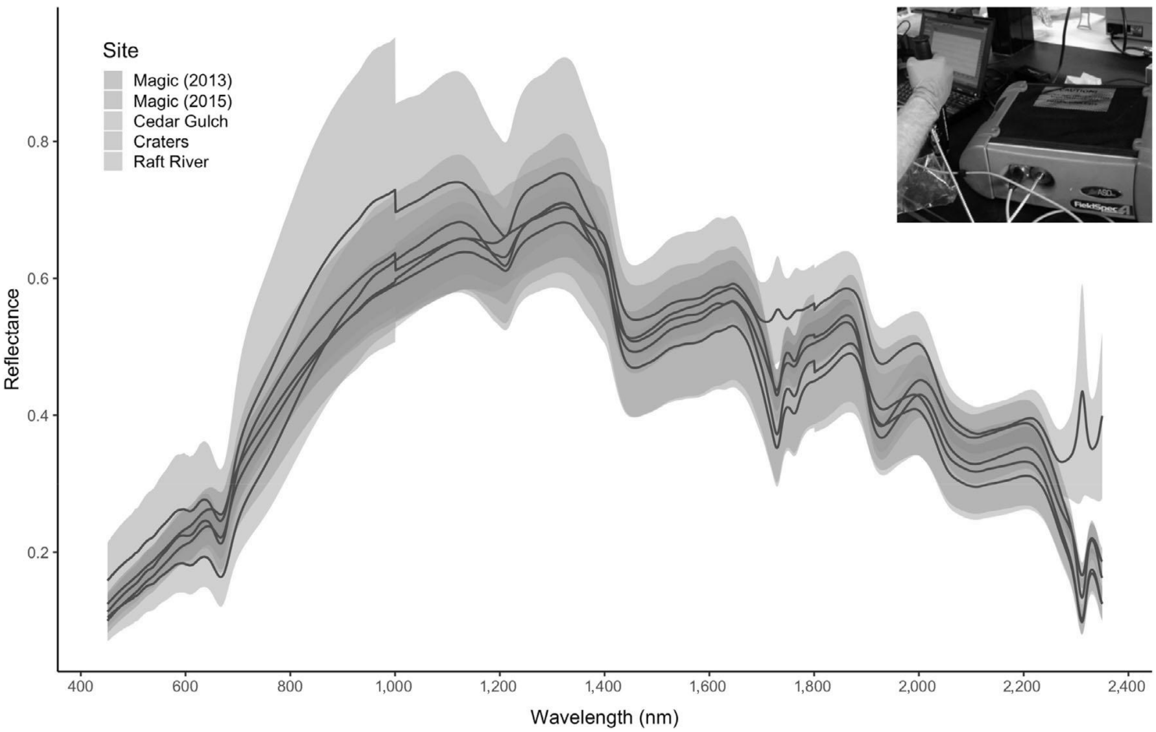

Figure 2. Example of near infrared reflectance spectra from geographically distinct populations of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) samples collected from four study sites (Magic, Cedar Gulch, Craters, and Raft River; Fig. 1) and over 2 years at one study site (Magic in 2013 and 2015) in Idaho, U.S.A. Spectra from plant material were collected using a benchtop ASD FieldSpec 4 spectroradiometer (inset). The *x*-axis is the electromagnetic spectrum from 450 to 2,350 nm and the *y*-axis is the proportion of reflectance out of 1.0, where 1.0 is 100% reflectance.

Table 1. Classification accuracies from support vector machines (SVMs) using NIRS to predict distinct taxonomic groups of sagebrush (*Artemisia* spp.) at four study sites (Fig. 1) in Idaho, U.S.A. Sagebrush taxonomic groups include Wyoming big (*A. tridentata* ssp. *wyomingensis*), three-tip (*A. tripartita*), black (*A. nova*), low (*A. arbuscula*), and "dwarf" sagebrush. Dwarf sagebrush were identified by their smaller size and disparate morphology but did not have clear morphological features associated with a specific dwarf species of sagebrush.

Study Site	*Taxonomic Group*	*Overall Accuracy (%)*	*Kappa*	*Producer's Accuracy (%)*	*User's Accuracy (%)*
Magic	Species (overall)	95.74	0.79		
	Three-tip			100.00	33.33
	Dwarf			75.00	95.45
	Wyoming			98.54	96.67
Cedar Gulch	Species (overall)	76.42	0.25		
	Black			80.00	80.00
	Dwarf			4.17	50.00
	Wyoming			98.70	76.77
Craters	Species (overall)	96.15	0.91		
	Three-tip			100.00	88.89
	Wyoming			94.44	100.00
Raft River	Species (overall)	74.60	0.00		
	Low			100.00	74.60
	Wyoming			0.00	N/A

Greater Sage-grouse (for the broader purposes of that study, see Fremgen-Tarantino et al. 2020) and included only leaves.

NIRS Analysis

The ASD FieldSpec 4 spectroradiometer (Malvern Panalytical, Westborough, MA, U.S.A.) was used to measure continuous near-infrared wavelength reflectance (350–2,500 nm) on samples. Each sagebrush sample was ground (~2 mm) with liquid nitrogen and dried at 60°C for 48 hours and then spread homogeneously on a black surface within a sealed clear plastic bag. After calibrating and optimizing the spectroradiometer, NIRS reflectance was collected with a contact probe (Fig. 2). Thirty replicate scans were collected per sample. The instrument was recalibrated and optimized every 15 samples using a white reference material. The replicate scans were checked for visual outliers using Camo Analytics (now AspenTech) Unscrambler spectral plotting interface. Any spectral signatures that were the result of mis-scans (e.g. scan signatures at or close to 0 or 100% reflectance) were removed. Replicate spectral scans were then averaged to one spectral profile. Each spectrum was converted to absorbance values using a log($1/R$) transformation, where R is reflectance. After visual inspection of reflectance spectra, spectral absorbance values were truncated to 450–2,350 nm to eliminate systematic noise near spectrometer detection limits. To minimize error, all NIRS steps were collected in one lab by the same researcher using this standardized approach.

Statistical Analysis

All response variables (i.e. species, population, year, and season) were joined with their associated near-infrared (NIR) spectra and imported into R 3.6.2 (R Core Team 2020). The e1071 package (Meyer et al. 2020) in R was used to perform support vector machine (SVM) analyses to classify taxonomic and temporal phenotypes of sagebrush using NIR spectra. The SVM type used was C-classification, with a linear kernel and C value of 1.0 (i.e. large margin). Each model was independently calibrated and validated using 75:25 train-to-test datasets. Samples were assigned to training and testing datasets in a stratified manner to ensure representative selection among source populations and phenotypes. The resulting confusion matrices from the SVM analyses were used to evaluate the overall accuracy of NIRS to classify phenotypes. Kappa statistics, which reflect the difference between actual agreement and agreement expected by chance, were obtained for each model. Further accuracies were calculated to differentiate the proportion of phenotypes on the ground that were accurately classified by NIRS (i.e. producer's accuracy) versus the proportion of phenotypes classified by NIRS that were actually present on the ground (i.e. user's accuracy).

Table 2. Classification accuracy from a support vector machine (SVM) using near infrared spectroscopy to predict geographically distinct populations of sagebrush within a subspecies (Wyoming big sagebrush; *Artemisia tridentata* ssp. *wyomingensis*) across four study sites (Fig. 1) in Idaho, U.S.A.

Study Site	*Overall Accuracy (%)*	*Kappa*	*Producer's Accuracy (%)*	*User's Accuracy (%)*
Population (overall)	98.74	0.98		
Magic			100.00	100.00
Cedar Gulch			100.00	100.00
Craters			83.33	93.75
Raft River			93.75	83.33

Results

Our results demonstrated that NIRS can accurately classify taxonomy in sagebrush. The accuracy of NIRS to classify sagebrush species was high, but varied among study sites (Table 1). At the Magic site, the overall accuracy of the training dataset to predict the sagebrush species of the test dataset was 95.7%, with a Kappa statistic of 0.79. At Cedar Gulch, the overall accuracy was 76.4%, with a Kappa statistic of 0.25. At Craters, the overall accuracy was 96.2%, with a Kappa statistic of 0.91. At Raft River, the overall accuracy was 74.6%, with a Kappa statistic of 0.00. The accuracy of NIRS in classifying geographically distinct populations within Wyoming big sagebrush was 98.7%, with a Kappa statistic of 0.98 (Table 2).

NIRS can also accurately classify temporal phenotypes within a population and within individual plants (Table 3). NIRS classified years of collection (2013 vs. 2015) for Wyoming big sagebrush at one study site with an overall accuracy of 99.5% and Kappa statistic of 0.99. NIRS classified seasons (summer vs. winter) within the same individual Wyoming big sagebrush plants at two study sites with an overall accuracy of 99.2% and Kappa statistic of 0.97.

Discussion

Overall, we demonstrated that NIRS can classify species within a genus within and across communities, differentiate geographically distinct populations within a subspecies, and detect annual changes within a population and seasonal changes within

Table 3. Classification accuracies from support vector machines (SVMs) using near infrared spectroscopy to predict phenological state of sagebrush phenotypes, including year (2013 vs. 2015) within a Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) population at one study site (Magic) and between seasons (summer vs. winter) within individual plants of Wyoming big sagebrush at two study sites (Magic and Cedar Gulch; Fig. 1) in Idaho, U.S.A.

Study Site	*Phenological State*	*Overall Accuracy (%)*	*Kappa*	*Producer's Accuracy (%)*	*User's Accuracy (%)*
Magic	Year (overall)	99.51	0.99		
	2013			100.00	99.23
	2015			98.70	100.00
Magic	Season (overall)	97.40	0.95		
	Summer			97.37	97.37
	Winter			97.44	97.44
Cedar Gulch	Season (overall)	100.00	1.00		
	Summer			100.00	100.00
	Winter			100.00	100.00

individual plants. Specifically, NIRS provides a tool for detecting taxonomic phenotypes and phenological states of plants that may not be obvious from morphology alone. Given the standardized collection methods used between sites, the consistency of individuals collecting data at each site, and the ability of NIRS to differentiate between species and locations over time, we are confident NIRS is detecting biologically relevant signals. Although we focused on a widespread plant genus in western North America, this case study showcases how spectral traits could aid in monitoring changes in vegetation within and across landscapes that could benefit restoration ecology.

Proper classification of sagebrush is critical for locating desired species or populations for reseeding of locally adapted (e.g. drought tolerant; Barron et al. 2020) or functional (e.g. palatable; Olsoy et al. 2020) phenotypes and identifying which seed sources of sagebrush survive and reproduce after restoration projects. When distinct morphological characteristics of sagebrush allow for proper identification in the field, the accuracy of NIRS to classify species increases. For example, three-tip, which is easy to identify based on deeply lobed leaf morphology (Rosentreter 2005), was still classified accurately with a very small sample size ($n = 8$), compared to the large sample size of Wyoming big sagebrush plants ($n = 807$) at the Magic field site. We propose that when morphotypes are distinct among species (e.g. Wyoming vs. three-tip [Fremgen-Tarantino et al. 2020]; Wyoming vs. black [Frye et al. 2013]), large sample sizes may not be required for NIRS to correctly classify species.

However, distinct morphology may not always indicate different species. Despite distinct morphology between dwarf and Wyoming big sagebrush at Cedar Gulch, the majority of the dwarf ($n = 100$) samples were classified as Wyoming (i.e. 92% of the time). NIRS data indicate that the dwarf taxa at Cedar Gulch are Wyoming big sagebrush with a small growth form that may reflect young age, shallow soil, or disturbance (e.g. browsing or mowing). In support of our NIRS classification, the dwarf and Wyoming big sagebrush morphotypes had similar levels of crude protein, coumarins, and monoterpenes (Olsoy et al. 2020), further indicating they are the same subspecies. On the other hand, 75% of the dwarf plants at Magic were classified discretely from Wyoming big sagebrush, suggesting that at least some of the dwarf morphotypes at this site represent a distinct taxonomic group, which was supported by distinct phytochemistry (Olsoy et al. 2020). Misclassification of dwarf species as Wyoming big sagebrush occurs both on-ground (this study) and in commonly used land cover datasets (Fremgen-Tarantino et al. 2021). Our results demonstrate that NIRS is capable of differentiating sagebrush species that are morphologically complex or ambiguous and could be used to rapidly validate species classifications that are remotely collected at higher spatial scales (i.e. unoccupied aerial systems and satellites) for conservation and restoration purposes.

To further pursue the idea that spectra can differentiate plants within a subspecies with indistinguishable morphology, we assessed if NIRS could classify populations within Wyoming big sagebrush. NIRS was able to predict source populations of samples with 99% overall accuracy (100% at Magic, 100% at Cedar Gulch, 94% at Raft River, and 83% at Craters), with the worst classification accuracy associated with the smallest sample size (i.e. Craters, $n = 94$). Classifying sagebrush species and differentiating unique phenotypes in the field is challenging, yet imperative to the restoration, monitoring, and future protection of sagebrush landscapes. Errors in classification in the field and by NIRS, such as those at Raft River where all of the plants (low, $n = 197$; Wyoming, $n = 65$) were classified as low sagebrush, may be due to unique environmental factors that elicit plastic responses in plants (Gratani 2014), high phenotypic and genetic variation (Richardson et al. 2012; Davidson et al. 2019), or hybridization (McArthur et al. 1988). Although NIRS can detect known genetic variation in model plant species, including wheat (*Tricitum aestivum*; Rincent et al. 2018; Krause et al. 2019), poplar (*Populus nigra*; Rincent et al. 2018), and Eucalyptus (*Eucalyptus globulus*; Raymond & Schimleck 2002), it is unknown to what degree trait variation seen below the species level in sagebrush is determined by genetic variation, phenotypic plasticity, or heritable phenotypic plasticity. To elucidate these mechanisms in sagebrush, we recommend that NIRS be included in G×E studies (Richardson et al. 2017) as a high-throughput measure of phenotyping that could account for trait variation among and within plants (i.e. "modular" concept of plasticity; de Kroon et al. 2005; Forsman 2015), especially studies with shared environmental conditions like common gardens. Such G×E studies, coupled with measures of stress (e.g. herbivory) and phytochemicals (e.g. auxins, crude proteins), can further tease apart the phenotypic underpinnings of NIRS signatures.

We suggest that NIRS can aid in restoration by correctly classifying sagebrush species in the field, reveal sites with high phenotypic variation of sagebrush, and improve our ability to select or avoid taxonomic groups for seed collection and planting (Erickson & Halford 2020). For example, further experimentation with NIRS could identify whether sagebrush that appears morphologically homogeneous are spectrally heterogeneous (i.e. divided among more classification classes) or homogeneous (i.e. shared within a classification class). Sites containing diverse taxonomic variation, as indicated by NIRS, may contain plants most appropriate for reseeding at sites with diverse microclimates (Broadhurst et al. 2008) and may benefit from restoration practices that use seed mixtures of sagebrush species. The potential for NIRS to detect hybrids (Wan-hong et al. 2019) is important for selecting seeds for restoration, as hybrids may have higher fitness within ecotones but lower fitness than parents within parental habitats (Wang et al. 1997). To better characterize hybrids in the sagebrush steppe, NIRS analyses will need to be coupled with high resolution genetic data (Richardson et al. 2012) to classify and detect hybrid individuals and their parents across ecotones. To confirm that NIRS can detect hybridization and assess fitness consequences of hybrids, NIRS should be coupled to common garden studies that include both parents and hybrids. We anticipate that the application of NIRS to classify species and detect hybrids is most useful in taxonomically homogeneous landscapes, where preservation of the locally adapted genotype for future seed collection may improve successful reseeding within that site.

The ability to detect temporal variation in phenotypic responses of plants to environmental conditions may also benefit restoration efforts. We offer evidence that the annual and seasonal phenology of plants can be spectrally distinguished. NIRS accurately classified the year in which samples of Wyoming big sagebrush were collected (99.5%), as well as the season (>97%). The ability of NIRS to distinguish sagebrush between years may reflect plastic responses to biotic and abiotic stressors that changed leaf growth, senescence, or survival of plants (Wilt & Miller 1992). The ability of NIRS to distinguish sagebrush between seasons within individual plants may be associated with emergence and senescence of photosynthetic (ephemeral leaves; Rosentreter 2005) and reproductive phenology (Rosentreter 2005; Richardson et al. 2017). We propose NIRS is detecting changes in phytochemistry associated with these annual and seasonal changes (Wilt & Miller 1992). The next step is to link NIRS to these phytochemical changes as a spectral biomarker that could predict developmental stage and productivity traits of plants (see Rincent et al. 2018). Relatively dynamic NIR spectra within a plant without an obvious change in environmental conditions or growth form could offer an early signal of biotic (e.g. pathogen) or abiotic (e.g. drought) stress. Temporal variation observed in NIRS within a season and species at previously restored landscapes may suggest variation in the sources of seed used for restoration, which could create a mismatch in reproductive phenology.

We used sagebrush as a case study to demonstrate that NIRS offers a valuable tool to discriminate among plant phenotypes, taxonomy, and phenology, which is important to the restoration of sagebrush-dominated landscapes. Broader use of NIRS could help monitor changes in plant composition, identify previously translocated plants that are distinct from local populations and are resilient to restoration, and identify phenotypically homogeneous or heterogeneous sites and potential hybrid zones. Using NIRS to quantify dynamics in leaf phenology could be used to detect biotic or abiotic stressors or identify mismatches in timing of reproductive stage among plants. However, realizing the benefits of NIRS for the conservation and restoration of plant communities across landscapes requires scaling up from benchtop measurements to remote sensing platforms. Scaling up is increasingly possible with greater availability of spectral sensors with increased electromagnetic ranges and resolutions and unoccupied aerial systems and satellite platforms (Ustin & Middleton 2021). NIRS data can be integrated with similar spectral traits across sensors to minimize the loss of resolution associated with scaling up spatially and temporally (Xiao et al. 2019). Finally, NIRS can help isolate and identify functional links between plant traits of interest (e.g. crude protein) and key spectral bands to develop more targeted remote sensors that align with restoration needs. Until scaling up is realized, NIRS of collected plants provides a restoration tool to classify phenotypes, identify locations where hybridization or past restoration influenced taxonomic diversity, select specific taxonomic phenotypes to optimize ongoing restoration practices, and monitor vegetative outcomes of restoration into the future.

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LITERATURE CITED

Arkle RS, Pilliod DS, Hanser SE, Brooks ML, Chambers JC, Grace JB, Knutson KC, Pyke DA, Welty JL, Wirth TA (2014) Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin. Ecosphere, 5, art31.

Bajgain P, Richardson BA, Price JC, Cronn RC, Udall JA (2011) Transcriptome characterization and polymorphism detection between subspecies of big sagebrush (*Artemisia tridentata*). BMC Genomics 12:370

Barron R, Martinez P, Serpe M, Buerki S (2020) Development of an in vitro method of propagation for *Artemisia tridentata* subsp. *tridentata* to support genome sequencing and genotype-by-environment research. Plants 9:1717

Boyd CS, Davies KW (2012) Spatial variability in cost and success of revegetation in a Wyoming big sagebrush community. Environmental Management 50:441–450

Brabec MM, Germino MJ, Shinneman DJ, Pilliod DS, McIlroy SK, Arkle RS (2015) Challenges of establishing big sagebrush (*Artemisia tridentata*) in rangeland restoration: effects of herbicide, mowing, whole-community seeding, and sagebrush seed sources. Rangeland Ecology & Management 68:432–435

Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, Vesk PA, Yates C (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. Evolutionary Applications 1:587–597

Bucharova A, Bossdorf O, Hölzel N, Kollmann J, Prasse R, Durka W (2019) Mix and match: regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. Conservation Genetics 20:7–17

Carlucci MB, Brancalion PHS, Rodrigues RR, Loyola R, Cianciaruso MV (2020) Functional traits and ecosystem services in ecological restoration. Restoration Ecology 28:1372–1383

Conover MR, Roberts AJ (2016) Declining populations of greater sage-grouse: where and why. Human–Wildlife Interactions 10:217–229

Coop JD, Parks SA, Stevens-Rumann CS, Crausbay SD, Higuera PE, Hurteau MD, et al. (2020) Wildfire-driven forest conversion in western North American landscapes. Bioscience 70:659–673

Cox RD, Anderson VJ (2004) Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. Rangeland Ecology & Management 57:203–210

Davidson BE, Germino MJ (2020) Spatial grain of adaptation is much finer than ecoregional-scale common gardens reveal. Ecology and Evolution 10: 9920–9931

Davidson BE, Germino MJ, Richardson B, Barnard DM (2019) Landscape and organismal factors affecting sagebrush-seedling transplant survival after megafire restoration. Restoration Ecology 27:1008–1020

Erickson VJ, Halford A (2020) Seed planning, sourcing, and procurement. Restoration Ecology 28:S219–S227

Espinoza JA, Hodge GR, Dvorak WS (2012) The potential use of near infrared spectroscopy to discriminate between different pine species and their hybrids. Journal of Near Infrared Spectroscopy 20:437–447

Forsman A (2015) Rethinking phenotypic plasticity and its consequences for individuals, populations and species. Heredity 115:276–284

Fremgen M (2015) Plant toxins influence diet selection and intestinal parasites in a specialist herbivore. MS thesis. Boise State University, Boise, Idaho

Fremgen-Tarantino MR, Olsoy PJ, Frye GG, Connelly JW, Krakauer AH, Patricelli GL, Forbey JS (2021) Assessing accuracy of GAP and LANDFIRE land cover datasets in winter habitats used by greater sage-grouse in Idaho and Wyoming, USA. Journal of Environmental Management 280:111720

Fremgen-Tarantino MR, Peña JJ, Connelly JW, Forbey JS (2020) Winter foraging ecology of greater sage-grouse in a post-fire landscape. Journal of Arid Environments 178:104154

Frye GG, Connelly JW, Musil DD, Forbey JS (2013) Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. Ecology 94:308–314

Gratani L (2014) Plant phenotypic plasticity in response to environmental factors. Advances in Botany 2014:1–17

Guerrant EO Jr, Kaye TN (2007) Reintroduction of rare and endangered plants: common factors, questions and approaches. Australian Journal of Botany 55:362

Hovland M, Mata-González R, Schreiner RP, Rodhouse TJ (2019) Fungal facilitation in rangelands: do arbuscular mycorrhizal fungi mediate resilience and resistance in sagebrush steppe? Rangeland Ecology & Management 72:678–691

Jaeger DM, Runyon JB, Richardson BA (2016) Signals of speciation: volatile organic compounds resolve closely related sagebrush taxa, suggesting their importance in evolution. The New Phytologist 211:1393–1401

Karban R, Wetzel WC, Shiojiri K, Ishizaki S, Ramirez SR, Blande JD (2014) Deciphering the language of plant communication: volatile chemotypes of sagebrush. New Phytologist 204:380–385

Keller M, Kollmann J, Edwards PJ (2000) Genetic introgression from distant provenances reduces fitness in local weed populations. Journal of Applied Ecology 37:647–659

Knick ST, Connelly JW (2011) Greater sage-grouse: ecology and conservation of a landscape species and its habitats. 1st ed. Berkeley, CA: University of California Press

Krause MR, González-Pérez L, Crossa J, Pérez-Rodríguez P, Montesinos-López O, Singh RP, et al. (2019) Hyperspectral reflectance-derived relationship matrices for genomic prediction of grain yield in wheat. G3: Genes, Genomes, Genetics 9:1231–1247

de Kroon H, Huber H, Stuefer JF, van Groenendael JM (2005) A modular concept of phenotypic plasticity in plants. New Phytologist 166:73–82

McArthur ED, Welch BL, Sanderson SC (1988) Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. Journal of Heredity 79:268–276

Meyer D, Dimitriadou E, Hornik K, Weingessel A, Leisch F (2020) e1071: Misc Functions of the Department of Statistics, Probability Theory Group (Formerly: E1071), TU Wien

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, et al. (2010) Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15:684–692

Nobler JD (2016) Risky business: tradeoffs between nutrition, toxicity, and predation by a specialist mammalian herbivore. MS thesis. Boise State University, Boise, Idaho

Olsoy PJ, Forbey JS, Shipley LA, Rachlow JL, Robb BC, Nobler JD, Thornton DH (2020) Mapping foodscapes and sagebrush morphotypes with unmanned aerial systems for multiple herbivores. Landscape Ecology 35:921–936

Pasquarella VJ, Holden CE, Kaufman L, Woodcock CE (2016) From imagery to ecology: leveraging time series of all available Landsat observations to map and monitor ecosystem state and dynamics. Remote Sensing in Ecology and Conservation 2:152–170

Pechanec JF, Stewart G, Blaisdell JP (1954) Sagebrush burning: good and bad. Washington, DC: US Department of Agriculture

Pyke DA, Shriver RK, Arkle RS, Pilliod DS, Aldridge CL, Coates PS, Germino MJ, Heinrichs JA, Ricca MA, Shaff SE (2020) Postfire growth of seeded and planted big sagebrush—strategic designs for restoring greater sage-grouse nesting habitat. Restoration Ecology 28:1495–1504

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Raymond CA, Schimleck LR (2002) Development of near infrared reflectance analysis calibrations for estimating genetic parameters for cellulose content in *Eucalyptus globulus*. Canadian Journal of Forest Research 32:170–176

Requena-Mullor JM, Maguire KC, Shinneman DJ, Caughlin TT (2019) Integrating anthropogenic factors into regional-scale species distribution models—a novel application in the imperiled sagebrush biome. Global Change Biology 25:1–15

Reynolds LK, McGlathery KJ, Waycott M (2012) Genetic diversity enhances restoration success by augmenting ecosystem services. PLoS One 7:e38397

Richardson BA, Chaney L, Shaw NL, Still SM (2017) Will phenotypic plasticity affecting flowering phenology keep pace with climate change? Global Change Biology 23:2499–2508

Richardson BA, Page JT, Bajgain P, Sanderson SC, Udall JA (2012) Deep sequencing of amplicons reveals widespread intraspecific hybridization and multiple origins of polyploidy in big sagebrush (*Artemisia tridentata*; Asteraceae). American Journal of Botany 99:1962–1975

Rincent R, Charpentier J-P, Faivre-Rampant P, Paux E, Le Gouis J, Bastien C, Segura V (2018) Phenomic selection is a low-cost and high-throughput method based on indirect predictions: proof of concept on wheat and poplar. G3: Genes, Genomes, Genetics 8:3961–3972

Rosentreter R (2005) Sagebrush identification, ecology, and palatability relative to sage-grouse. Sage-Grouse Habitat Restoration Symposium Proceedings. US Department of Agriculture, Forest Service Proceedings, RMRS-P-38, Boise, Idaho, USA. Pages 3–16

Rosentreter R, Robb BC, Forbey JS (2021) Using the UV light test to improve sagebrush identification and predict forage quality for wildlife. Western North American Naturalist 81:191–200

Somers B, Asner GP (2013) Multi-temporal hyperspectral mixture analysis and feature selection for invasive species mapping in rainforests. Remote Sensing of Environment 136:14–27

Thines NJS, Shipley LA, Sayler RD (2004) Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*). Biological Conservation 119:525–534

Ulappa AC (2011) Nutritional and chemical factors shaping diet selection for two sagebrush specialists: pygmy rabbits and sage-grouse. MS thesis. Boise State University, Boise, Idaho

Ustin SL, Middleton EM (2021) Current and near-term advances in Earth observation for ecological applications. Ecological Processes 10:1

Vance CK, Tolleson DR, Kinoshita K, Rodriguez J, Foley WJ (2016) Near infrared spectroscopy in wildlife and biodiversity. Journal of Near Infrared Spectroscopy 24:1–25

Wang H, McArthur ED, Sanderson SC, Graham JH, Freeman DC (1997) Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): IV. Reciprocal transplant experiments. Evolution 51: 95–102

Wan-hong L, Jie Q, Jian-zhong L (2019) Application of NIRS for discrimination of eucalyptus hybrids. Spectroscopy and Spectral Analysis 39: 1451–1457

Wilt FM, Miller GC (1992) Seasonal variation of coumarin and flavonoid concentrations in persistent leaves of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*: Asteraceae). Biochemical Systematics and Ecology 20:53–67

Xiao J, Chevallier F, Gomez C, Guanter L, Hicke JA, Huete AR, et al. (2019) Remote sensing of the terrestrial carbon cycle: a review of advances over 50 years. Remote Sensing of Environment 233:111383

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