



Predictability and stability of sagebrush-steppe restoration in a changing climate

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Abstract The sagebrush steppe is now one of the most imperiled ecosystems in North America, prompting the need for successful restoration. However, restoration efforts often fall short of expectations due to poorly-understood ecological factors and variable outcomes. When, where, and how restoration is initiated could play a large role in community composition in the long-term, but the potential impacts of these contingencies is poorly understood. Plant traits are expected to respond more predictably to restoration treatments than species, but few studies have compared the responses of species and traits in the context of contingencies. In this study, we conducted a preliminary analysis of long-term monitoring data from 13 restored sites in Grand Teton National Park paired with measurements of five traits to understand spatial and temporal community dynamics at two levels of biodiversity. Results show species composition became more similar (converged) across restored sites over time and trajected towards but did not meet reference conditions. Trait composition converged quickly with the reference in early years but diverged among sites. Communities transitioned from volunteer annuals with more resource acquisitive traits to sown species with conservative traits. Future work will use ecological modeling to test whether trends are contingent upon establishment conditions.

Introduction

The sagebrush steppe is one of the most common vegetation types in the Greater Yellowstone Ecosystem (GYE) but it is also one of the most imperiled in North America, having already been reduced to nearly 50% of its original range and facing increasing threats from invasion, land use, and climate change (Miller et al., 2011; Pyke et al., 2018). Though the need for recovery of sagebrush steppe biodiversity is clear, restoration remains notoriously difficult and unpredictable in this system- often falling short of targets due to poorly understood ecological factors and variable outcomes (Pyke et al., 2018). For ex-

ample, in one experimental post-fire restoration, over 90% of sown steppe grasses perished before emergence (James et al., 2012) and other studies have shown that sagebrush cover can remain low or absent even one to two decades after restoration treatment (Pyke et al., 2020). Furthermore, in our study region alone, temperatures have risen 0.6°C and snowfall has decreased by 11% since 1950 (Hostetler et al., 2021). Sagebrush steppe communities are reliant on ground water recharge from snow and are expected to be negatively affected by rising temperatures and decreasing snowpack (Durfee and Ochoa, 2021; Schlaepfer et al., 2012). Therefore, it is likely that climate change will affect restoration success but

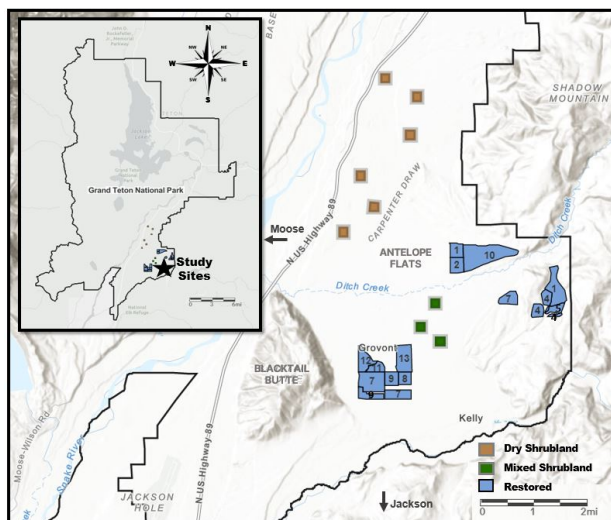


Figure 1. A map of the study sites along Antelope Flats in Grand Teton National Park. Restored sites are bounded by planting year and seed mix used. Reference sites (dry shrubland and mixed shrubland) are bounded by pre-established 10 ha frames per Inventory and Monitoring Network protocols.

the potential impacts are still largely unknown.

If restoration efforts are to meet their full potential, we must identify drivers which explain variation in restoration outcomes with special attention to those that can be controlled through management action and planning (Brudvig, 2017; Brudvig and Catano, 2021). In application, many restoration projects assume that communities will follow deterministic pathways of recovery towards pre-disturbance conditions, following traditional successional theory (Chang and HilleRisLambers, 2016; Matthews and Spyreas, 2010). However, modern community assembly theory proposes that establishment conditions and restoration designs can “filter” out particular species and constrain the final community composition in the long-term based on when, where, and how restoration is initiated (Brudvig, 2017; Hulvey and Aigner, 2014). Such contingencies may limit the success of generalized restoration designs if communities initiated under varied conditions become less similar with time (diverge) and follow pathways to different, less desirable states.

Functional traits, or measurable attributes of plants

that influence growth, survival, and reproduction in a given environment (Violle et al., 2007), provide promise for anticipating how communities will respond to restoration efforts. Environmental conditions are expected to filter for functional traits that are a match for available niches, leading to a deterministic response, while several functionally-similar species may establish and follow random trajectories based on order of arrival or other stochastic factors (Fukami et al., 2005). Therefore, it is expected that traits will respond more predictably to restoration treatments (Laughlin et al., 2017). However, studies which compare the responses of species and trait diversity to restoration efforts are still rare and have seldom been tested in the context of contingencies (Brudvig and Catano, 2021; Catano et al., 2021).

Over a decade ago, Grand Teton National Park (GTNP) initiated a large-scale sagebrush steppe restoration project in the area of Antelope Flats where Mormon homesteading converted the landscape to monocultures of smooth brome (*Bromus inermis*) in the 1800s (Figure 1). Since then, 534 ha have been treated with herbicide to remove brome and then seeded in the fall of eight different years at multiple sites, allowing us to test how different establishment conditions have shaped outcomes in the long term. In this study, we combined plant community monitoring data from thirteen of these sites with functional trait measurements, soil analyses, climate data, and restoration design records to test if species and trait compositions were contingent upon establishment conditions and to identify key drivers that constrain restoration success in the long-term. The UW-NPS grant funded the 2020 field season of plant community monitoring and allowed for the collection of samples for trait measurements on 70 species.

Specifically, our objectives were to:

1. Quantify trajectories of species and trait diversity in sagebrush steppe communities after initiation of restoration by seeding.
2. Test whether communities follow deterministic pathways of succession or if restoration outcomes are contingent upon establishment conditions (planting-year weather, soil properties,

	Mean	SD	Range
Predictors			
<i>Planting Year Weather</i>			
Growing season temperature average (°C)	15.501	0.507	14.628 - 16.151
Dormant season temperature average (°C)	-0.088	0.754	-1.185 - 0.878
Growing season precipitation average (°C)	10.664	3.926	4.15 - 15.88
Average snowfall (cm)	380.463	76.730	274.2 - 468.2
Average snow depth (cm)	28.412	7.641	14.741 - 36.606
<i>Soil Properties</i>			
Sand (%)	32.485	13.334	16.4 - 58.5
Silt (%)	55.066	11.035	38 - 69
Clay (%)	12.740	7.880	4.5 - 25
Nitrate Nitrogen (ppm)	2.740	4.660	0.1 - 15.1
AB-DTPA Phosphorous (ppm)	13.704	4.580	4.85 - 19.022
AB-DTPA Potassium (ppm)	160.079	61.142	97.017 - 266.65
Organic matter (%)	4.770	0.784	3.8 - 6.3
pH	6.326	0.335	5.85 - 7
<i>Seed Mix</i>			
Species richness	12.308	4.871	8 - 24
Graminoid ratio	15.923	16.359	1.02 - 65.667
Seeding density (seeds/m2)	42.548	17.153	25-90
Responses			
<i>Compositional Metrics</i>			
Indicator species richness	0.569	0.584	0 - 1.76
Seeded species richness	3.460	1.097	1.875 - 5.76
Volunteer richness	1.726	0.761	0.5 - 3.25
Herbaceous invadedness index (0-1)	0.412	0.145	0.187 - 0.64
Shannon diversity (H')	1.657	0.172	1.342 - 1.872
Pielou's evenness (J')	0.772	0.034	0.708 - 0.811
<i>Community Weighed Trait Means (CWM)</i>			
Specific Leaf Area (cm2 g-1)	160.129	12.288	140.863 - 178.356
Leaf dry matter content (g g-1)	0.331	0.037	0.25 - 0.375
Turgor loss point (MPa)	-3.277	0.382	-3.865 - -2.692
Height at maturity (cm)	40.125	8.368	28.274 - 53.169
Dry seed mass (g)	0.003	0.001	0.001 - 0.004
	1.496	0.252	1.011 - 1.816
<i>Dissimilarities</i>			
Species composition to reference (Bray)	0.920	0.030	0.845 - 0.964
Species composition among restored (Bray)	0.686	0.050	0.592 - 0.762
CWM traits to reference (Euclidean)	3.522	0.817	2.36 - 5.053
CWM traits among restored (Euclidean)	3.494	0.228	3.141 - 3.857

Table 1. A summary of environmental/restoration design predictor variables and univariate metrics planned for later use in models to test for contingency effects. Indicator species were determined by SIMPER analysis as the top 7 species associated with reference communities. Volunteer species are any species not included in seed mixes. The herbaceous invadedness index is the total cover of non-native herbaceous species divided by total herbaceous cover, a useful calculation for a system dominated by only native shrubs. Functional dispersion measures the effective number of functionally distinct species and is a measure of trait diversity.

seed mix design).

3. Identify the drivers which explain variation in restoration outcomes and lead to divergence from target reference conditions.

The results of this work will aid GTNP in adaptive management and the development of scientifically-backed restoration designs while acting as an acid-test of community assembly and functional trait theory in a broader, real-world context.

Methods

Plant community surveys

GTNP staff have monitored each of the 13 focal restored sites (11–75 ha in area) using permanently established 60 m line-point intercept transects over a total of five years. This method involves recording the plant species which intersect transects at every meter mark in each of four canopy layers for a total of 50 m. Transect data was converted to percent cover by summing the number of intervals in which a species was recorded in at least one canopy layer and dividing by the total number of intervals (50). Communities were surveyed on a rotational basis starting one to four years after establishment with an average of one year between surveys and an average of five transects established at each site. With the help of a field assistant and GTNP staff, we completed an additional survey of all transects in 2020 (year six). Total years of data for each site range from three to six depending on establishment year. Data for target reference communities (uncultivated sagebrush steppe) was sourced from the Greater Yellowstone Inventory and Monitoring Network (Jean et al., 2014). We selected nine reference sites located within Antelope Flats to represent major sagebrush steppe community subtypes: dry shrubland ($n=6$) and mixed shrubland ($n=3$). It should be noted that sampling protocols for reference communities use a nested 1m² quadrat/10 ha frame method that differs from the protocols used for restored sites (details in Jean et al., 2014). Though this necessitates caution in comparisons between restored and reference sites, especially for metrics like richness, we opted to use them together due to availability and the valuable duration

and intensity of data collected. Examination of the datasets suggests that comparisons will likely lead to a more conservative estimate of restoration success.

Functional traits

For the 70 most common species representing >99% of total species abundances across all restored and reference sites, we measured five quantitative traits in the field from 2020–2021: specific leaf area (SLA, mm² one-sided area mg⁻¹ dry mass), leaf dry matter content (LDMC, mg dry mass mg⁻¹ fresh mass), leaf turgor loss point (TLP, mPa), mature vegetative height ($H_{\max}$, cm), and oven dry seed mass (seed mass, mg). The selected traits represent major plant strategies for survival (Blackman, 2018; Laughlin et al., 2010; Westoby, 1998): a leaf economic spectrum (SLA, LDMC), competitive ability/fecundity ($H_{\max}$), dispersal/seedling survival (seed mass), and drought tolerance (TLP). Traits were measured on healthy, unshaded individuals just before or at the onset of flowering following standardized protocols (Perez-Harguindeguy et al., 2013). Leaf traits (SLA, LDMC, TLP) were measured on 4–5 samples per species, heights were measured on 10–30 individuals, and seed mass was calculated as the average of a minimum of 50 seeds. TLP was estimated from minimum osmolarity as measured by vapor pressure osmometer (Wescor VAPRO 5600) using separate linear models developed for forbs, shrubs, and graminoids (Bartlett et al., 2012; Griffin-Nolan et al., 2019).

Environmental variables

We collected data on several variables that we hypothesized to be drivers of restoration outcomes and which represented differences in when, where, and how restored communities were initiated in GTNP: inter-annual climatic variation (i.e. planting year weather), soil composition, and seed mix design (Table 1). Soil cores were collected along each transect at approximately 20, 35, and 50 m at a depth of 6 cm using a soil probe, homogenized, and sent to the Colorado State University Soil, Water & Plant Testing Laboratory (Fort Collins, CO, USA) for analysis of 8 variables related to productivity and plant wa-

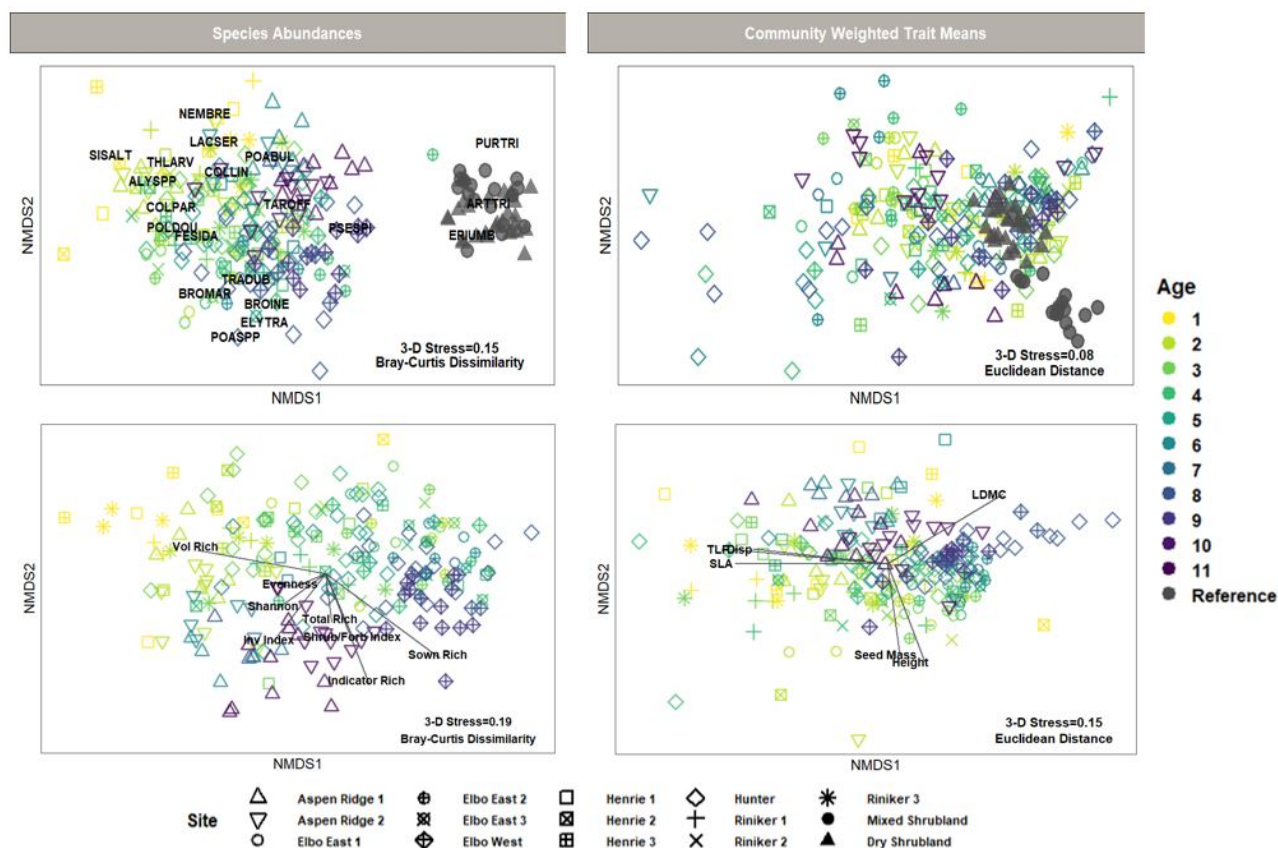


Figure 2. NMDS ordinations of species abundances (left column) and community weighted means (right column) of five traits across all sites and ages since restoration. Only the top 20 species contributing to overall dissimilarity between restored and reference sites are displayed for clarity. The top row compares restored and reference sites and the bottom row shows significant gradients ($p < 0.05$) of univariate species and trait metrics as determined by envfit. Vector length relates to size of R^2 values. Vector Codes: Vol Rich, Volunteer Species Richness; Evenness, Pielou's J' ; Shannon, Shannon Diversity H' ; Inv Index, Herbaceous Invadedness Index; Total Rich, Total Richness; Shrub/Forb Index, Ratio of Shrubs/Forbs to Graminoids; Indicator Rich, Indicator Species Richness; Sown Rich, Sown Species Richness; FDisp, Functional Dispersion; TLP, Turgor Loss Point; SLA, Specific Leaf Area; Seed Mass, Seed Mass; Height, Plant Height; LDMC, Leaf Dry Matter Content. Species Codes: ALYSPP*, *Alyssum spp*; ARTTRI, *Artemisia tridentata*; BROINE*, *Bromus inermis*; BROMAR, *Bromus marginatus*; COLLIN, *Collomia linearis*; COLPAR, *Collinsia parviflora*; ELYTRA, *Elymus trachycaulus*; ERIUMB, *Eriogonum umbellatum*; FESIDA, *Festuca idahoensis*; LACSER*, *Lactuca serriola*; NEMBRE, *Nemophila breviflora*; POABUL*, *Poa bulbosa*; POASPP*, *Poa spp*; POLDOU, *Polygonum douglasii*; PSESP, *Pseudoroegneria spicata*; PURTRI, *Purshia tridentata*; SISALT*, *Sisymbrium altissimum*; TAROFF*, *Taraxacum officinale*; THLARV*, *Thlaspi arvense*; TRADUB*, *Tragopogon dubius*. * Indicates non-native species

ter availability: texture by hydrometer (percent sand, silt, and clay), organic matter content, pH, nitrate nitrogen, AD-DTPA phosphorous, and AD-DTPA potassium (Epstein et al., 2019; Scharwies and Dinneny, 2019). Data on inter-annual climatic variation were sourced from the NOAA National Climatic Data Center station in Moose, WY located approximately 4 km west of Antelope Flats. Because sites were seeded in the fall, we considered temperature and precipitation variables for both the dormant season (September–May) and the growing season (June–August) of the seeding year. Seed mix design records were provided by GTNP. Though this report does not outline the models used to assess these data, the planned analyses are discussed in the future work section.

Data analyses

All analyses were conducted in R, primarily with the packages ‘vegan’ and ‘FD.’ To explore multivariate temporal trends across restored communities, we visualized species abundances and community weighted means (CWM) of all five traits via NMDS ordination for all sites in all survey years. Community weighted means are community level trait values weighted by species abundances. We calculated the dissimilarities among sites using the Bray-Curtis method for species abundances and used Euclidean distances for CWMs of traits. Ordination was followed by SIMPER analysis to determine which species contributed most to dissimilarities between ages and PERMANOVA to assess whether site, establishment year, or age explained the most variation in community composition. Univariate community metrics (e.g. richness) were fit to the ordination as vectors using ‘envfit’ to determine whether they significantly related to variation in composition and could be used as indicators of change (Table 1). Decomposing community responses to metrics which represent species and trait diversity will provide clarity and management-relevant contexts to how restoration outcomes are impacted by establishment conditions. Finally, we averaged dissimilarities/distances for each site at each age to quantify convergence among sites and with the reference.

Preliminary results

Our initial analyses quantified functional and compositional temporal change at all thirteen sites from both multivariate and univariate perspectives. Community surveys recorded a total of 101 species across restored sites (site mean=27) and reference sites (site mean=41). The three-dimensional NMDS ordinations of species abundances (stress=0.19) and community weighted means (stress=0.15) reveal differences in temporal trends at each level of biodiversity (Figure 2). Species composition generally trended towards but did not meet reference conditions while trait composition converged with the reference in early years but then diverged slightly in mid-late years. All selected univariate metrics were significantly correlated with community variation ($p < 0.05$). The metrics with the highest correlations were indicator species richness ($R^2=0.45$), sown species richness ($R^2=0.43$), LDMC ($R^2=0.47$), and TLP ($R^2=0.50$). Axis 1 of each ordination represented a gradient of high volunteer richness to high sown richness and high SLA, TLP, and functional dispersion to high LDMC. Axis 2 represented a gradient of high to low values for all other species metrics, seed mass, and height. A major split in the community trajectories of different sites appears to occur around years 6–8 based on these axes. SIMPER analysis identified key species contributing to dissimilarity between ages. The youngest sites were dominated by *Sisymbrium altissimum*, *Lactuca serriola*, and *Nemophila brevifolia* while the oldest sites were dominated by *Poa bulbosa* and *Taraxacum officinale* or *Elymus trachycaulus* and *Poa spp.* depending on which axis they followed. In contrast, reference communities were dominated by *Artemisia tridentata*, *Purshia tridentata*, and *Eriogonum umbellatum*. These species alone cumulatively contributed 45% to dissimilarity between restored and reference sites. Time-series plots of dissimilarities/distances confirmed that the species composition of restored sites converged (became more similar) with time (~35% decrease in dissimilarity) but only marginally converged (~10% decrease in dissimilarity) with reference sites over time (Figure 3). In contrast, CWMs of traits in restored sites converged quickly with reference sites from years one to five (~50% de-

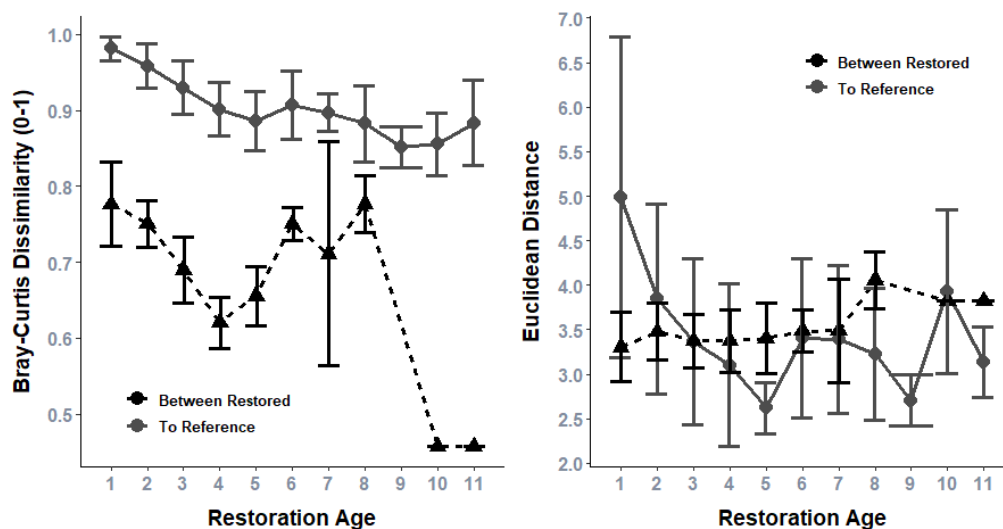


Figure 3. Time-series plots of species and trait-based dissimilarities/distances among restored sites and between restored and intact sites. Decreasing dissimilarity/distance indicates convergence. Error bars indicate one standard deviation from the mean based on variance across sites at a given age. Note: scales are not directly comparable between the left and right panels.

crease in distance) but trait composition diverged slightly among restored sites with time (~20% increase in distance). Variation among sites at each age was generally greater for CWMs of traits than species abundances as indicated by error bars. According to the PERMANOVA results (Table 2), variation in species composition was explained most by seeding year ($R^2=0.32$, $p=0.001$), followed by site ($R^2=0.08$, $p=0.001$) and restoration age ($R^2=0.08$, $p=0.001$). Trait composition was nearly equally explained by seeding year ($R^2=0.13$, $p=0.001$) and site ($R^2=0.15$, $p=0.001$) with little variance explained by age ($R^2=0.06$, $p=0.001$).

The univariate time-series plots (Figure 4) revealed that CWMs of traits generally trajected towards and met reference values with time while species metrics either fell short of targets (e.g. lower indicator richness) or trajected away from targets (e.g. higher invadedness). As communities aged, volunteer native and invasive annuals were replaced by seeded species, reference indicator species, and non-native grasses. Shannon diversity remained lower than reference communities after 11 years and evenness exceeded that of the reference with little change over time. Functionally, communities shifted from species

with acquisitive trait strategies (high SLA, low LDMC) towards species with more conservative, drought tolerant strategies (low SLA, high LDMC, low TLP) with age. Seed mass decreased slightly over time, functional dispersion marginally increased, and height remained relatively unchanged across time steps.

Conclusions

Overall, the restored sagebrush steppe communities trended towards reference conditions but still fell short or trajected away from some targets after 11 years (Figure 4). This was especially true for species metrics. Species composition only ever reached 10% similarity to the reference, which was reflected by the large differences in dominant species found in the oldest sites vs. the dry and mixed shrubland communities (Figure 2, Figure 3). The trait composition of restored communities overlapped with reference communities early on after restoration before reaching a plateau or diverging. Results demonstrate that certain aspects of restored communities may follow somewhat deterministic successional trajectories (i.e. sown species richness and leaf dry matter content) but that others do not respond predictably to age and instead exhibit high variation across sites (i.e.

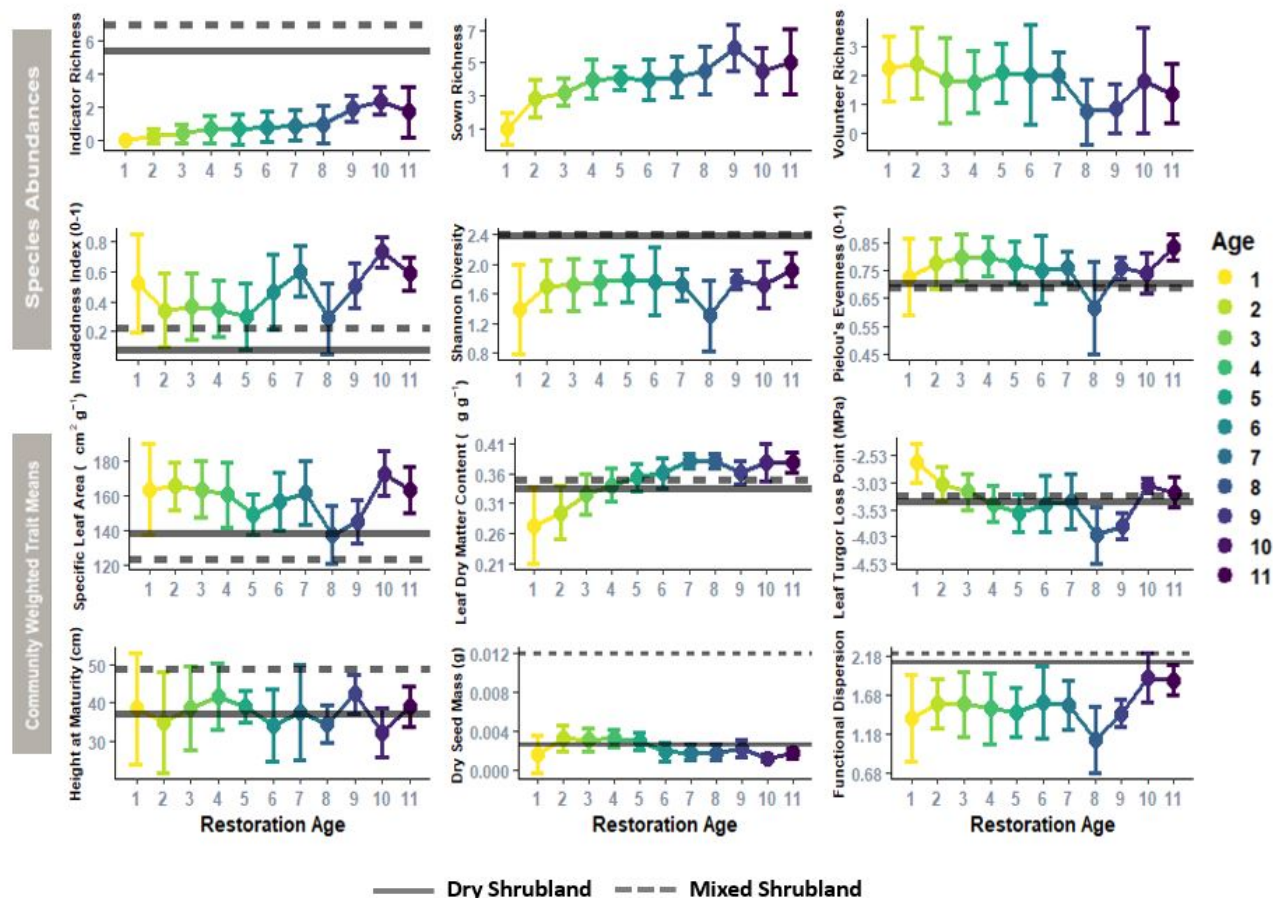


Figure 4. Time-series plots of six species-based and six trait-based community metrics. Error bars indicate one standard deviation from the mean based on variance across transects at a given age. Average values for both reference community types are indicated by horizontal lines (not applicable for sown or volunteer richness).

evenness and height at maturity). This suggests that certain metrics of success are generally less predictable than others or can only be explained in the context of site-specific contingency effects. In contrast to expectations that stochastic processes would drive abundances towards random patterns, species composition appears to be slightly more deterministic with time than traits. The divergence of traits among sites might indicate a greater sensitivity to establishment conditions, which is congruent with trait theory and the environmental filtering concept. PERMANOVA results support that species composition is somewhat more explained by age than trait composition, however, the results indicate that abundances are even more contingent upon the year of seeding (Table 2). Other studies have found that year of plant-

ing can affect the species composition of the resulting community (e.g. sown vs. non-sown richness) via inter-annual variation in climate (Groves and Brudvig, 2019). Trait composition was explained not only by seeding year but also by site, which may hint at the role of site-specific abiotic filters such as soil properties.

Future work

Plant community surveys and functional trait measurements were finished in 2021 and no additional data collection is required for our research. The next steps in our study focus on identifying specific drivers of variation in restoration outcomes with attention to potential contingencies arising from when, where, and how restoration is initiated. We are currently con-

		PERMANOVA				PERMDISP	
		df	<i>F</i>	R ²	<i>P</i>	<i>F</i>	<i>P</i>
Species (% Cover)							
	Seeding Year	7	17.66	0.32	0.001	6.02	<0.001
	Site	5	5.88	0.08	0.001	5.51	<0.001
	Age	1	29.91	0.08	0.001	6.7	<0.001
Traits (CWM)							
	Seeding Year	7	5.69	0.13	0.001	2.88	<0.01
	Site	5	9.2	0.15	0.001	2.11	0.02
	Age	1	16.96	0.06	0.001	3.26	<0.001

Table 2. PERMANOVA results based on Bray-Curtis dissimilarities for species abundances and Euclidean distance for CWMs of traits in relation to seeding year, site, and age since restoration. PERMDISP results indicate differences in dispersion among groups. P-values based on 999 permutations.

ducting model selection for multiple generalized linear mixed effects models to quantitatively test the relative and interactive effects of time since restoration, soil properties, seed mix design, and inter-annual climatic variation on six species-based metrics and six trait-based metrics (Table 1). The inclusion of random effects for site and sample year will allow us to control for repeated measures and determine how much variation remains unexplained by our selected variables. Furthermore, consideration of the under-explored effects of inter-annual climate (i.e. planting year weather) on restoration outcomes (Werner et al., 2020) will provide insight into how climate change in the GYE might affect sagebrush steppe restoration success.

Contingency effects may explain variation in restoration outcomes but it is also possible that certain conditions themselves lead to more variable outcomes (divergence among sites) even when sites are initiated similarly (Catano et al., 2021). Therefore, we will also examine the impacts of establishment conditions on convergence among sites and convergence between restored and reference sites. Based on the stress-dominance hypothesis (Lhotsky et al., 2016), we expect that establishment under “limiting conditions” such as dry planting years or low diversity seed mixes will lead to greater convergence among restored sites (but not necessarily with the reference), especially in the case of traits which represent the fitness-environment relationship. Overall, these

models will uncover what aspects of restored communities follow successional trajectories of recovery towards/away from target reference conditions and which are contingent upon establishment conditions, allowing GTNP and other restoration practitioners to adapt restoration designs for improved predictability and success in a changing climate. This work will be published as a master’s thesis, a peer-reviewed paper, and a research brief/infographic for GTNP. Other planned work includes a second study testing the ability for traits to predict species level responses to inter-annual climatic variation and subsequent impacts on community stability.

Disclaimer

This progress report is intended to disseminate preliminary results of our research and does not represent final results or conclusions. The content of this manuscript does not represent official findings or stances of the National Park Service or its collaborators and has not yet been approved for journal publication.

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