








ARTICLE

Testing the hierarchy of predictability in grassland restoration across a gradient of environmental severity

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Abstract

Ecological restoration is critical for recovering degraded ecosystems but is challenged by variable success and low predictability. Understanding which outcomes are more predictable and less variable following restoration can improve restoration effectiveness. Recent theory asserts that the predictability of outcomes would follow an order from most to least predictable from coarse to fine community properties (physical structure > taxonomic diversity > functional composition > taxonomic composition) and that predictability would increase with more severe environmental conditions constraining species establishment. We tested this “hierarchy of predictability” hypothesis by synthesizing outcomes along an aridity gradient with 11 grassland restoration projects across the United States. We used 1829 vegetation monitoring plots from 227 restoration treatments, spread across 52 sites. We fit generalized linear mixed-effects models to predict six indicators of restoration outcomes as a function of restoration characteristics (i.e., seed mixes, disturbance, management actions, time since restoration) and used variance explained by models and model residuals as proxies for restoration predictability. We did not find consistent support for our hypotheses. Physical structure was among the most predictable outcomes when the response variable was relative abundance of grasses, but unpredictable for total canopy cover. Similarly, one dimension of taxonomic composition related to species identities was unpredictable, but another dimension of taxonomic composition indicating whether exotic or native species dominated the community was highly predictable. Taxonomic diversity (i.e., species richness) and functional composition (i.e., mean trait values) were intermittently predictable. Predictability also did not increase consistently with aridity. The dimension of taxonomic composition related to the identity of species in restored communities was more predictable (i.e., smaller residuals) in more arid sites, but functional composition was less predictable (i.e., larger residuals), and other outcomes showed no

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significant trend. Restoration outcomes were most predictable when they related to variation in dominant species, while those responding to rare species were harder to predict, indicating a potential role of scale in restoration predictability. Overall, our results highlight additional factors that might influence restoration predictability and add support to the importance of continuous monitoring and active management beyond one-time seed addition for successful grassland restoration in the United States.

KEYWORDS

aridity, community composition, ecological restoration, functional composition, grasslands, physical structure, restoration outcomes, restoration success, richness

INTRODUCTION

Ecological restoration is a critical strategy for repairing degraded ecosystems worldwide and is key to meeting global environmental and climate commitments (Suding et al., 2015; UNEP, 2019). However, achieving restoration targets is challenging because similar restoration actions often lead to varied results (Brudvig & Catano, 2021; Brudvig et al., 2017; Suding, 2011). A broad range of outcomes are used to evaluate success in restoration projects, such as vegetation structure, community diversity, and ecosystem functioning (Ruiz-Jaen & Mitchell Aide, 2005; Wortley et al., 2013), but some of these outcomes might be inherently more variable than others (Brudvig et al., 2017). Understanding which outcomes are more predictable and less variable following restoration efforts could help practitioners set realistic goals and improve restoration effectiveness by more successfully anticipating outcomes (Brudvig & Catano, 2021; Cooke et al., 2019; Laughlin et al., 2017).

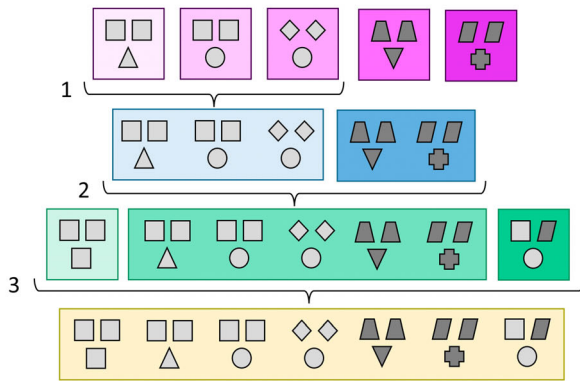
The so-called hierarchy-of-predictability hypothesis (Brudvig et al., 2017; Laughlin et al., 2017) proposes that the predictability of restoration outcomes would follow an order from most to least predictable based on how many different ways an outcome can be achieved. At one end, the most predictable restoration outcomes would be coarse metrics such as vegetation structure or total biomass, for which similar results can be achieved with different combinations of species or levels of diversity (Lockwood & Pimm, 1999; Yachi & Loreau, 1999). At the other end, the least predictable outcome would be taxonomic composition, which requires specific combinations of species. If stochastic processes such as dispersal and first-year weather effects impact the species that become established, we would expect these finer metrics to be more variable and, thus, less predictable than coarse metrics (Brudvig et al., 2017). Hence, there would be a hierarchy of predictability between metrics according to their nested nature (Figure 1).

The hierarchy of metrics that fall in the middle is less certain (Laughlin et al., 2017), but we expect taxonomic diversity indices (e.g., richness, evenness) to be less constrained than functional indices (e.g., community weighted mean of traits, functional diversity) (Brudvig et al., 2017; Laughlin et al., 2017). The same values of these metrics can be achieved with different species combinations (i.e., different taxonomic compositions), but different values can result in the same physical structure, so they would be intermittently predictable. Taxonomic diversity indices such as species richness consider all species equally, where many different combinations of a specific number of species can be assembled from a finite species pool. However, functional metrics add additional constraints based on species traits and thus can be considered a more detailed outcome that would be more constrained and less predictable than taxonomic diversity (Brudvig et al., 2017; Laughlin et al., 2017).

The hypothesis also states that the predictability of restoration would depend on the number of factors constraining the outcomes (Figure 1). That is, any given outcome would become more predictable with a higher number of constraints limiting the combinations of species inhabiting a site (Brudvig et al., 2017). Environmental filters restricting which species are able to establish and survive would decrease variation and thereby increase the predictability of restoration under more severe environmental conditions (Brudvig et al., 2017). For example, as site mean annual precipitation or precipitation in the year following restoration decreases, the restored community may be limited to species with drought-resistant strategies (Butterfield et al., 2023). Evidence for the two aspects of the hypothesis is, however, still in its initial stages. Previous tests of the hierarchy focused on single sites or ecosystems and demonstrated contrasting results (Abella et al., 2018; Laughlin et al., 2017). Moreover, to our knowledge, no one has tested the secondary hypothesis that more constraints on vegetation development would increase the predictability of restoration.

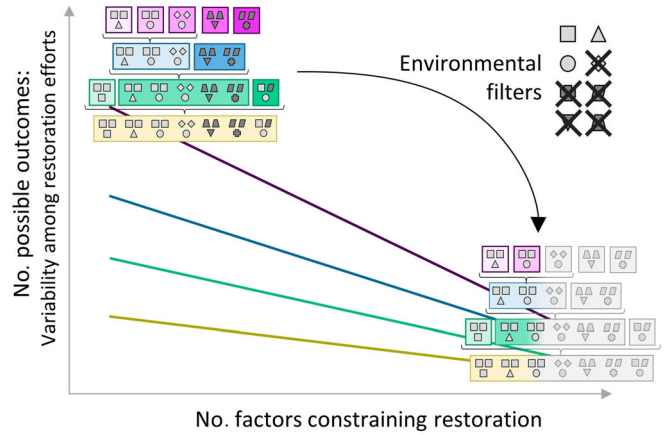
(a) QUESTION 1

Does the predictability of grassland restoration outcomes follow the hierarchy of predictability?



(b) QUESTION 2

To what extent do changes in environmental severity influence the predictability of each outcome?



LEGEND

- x △ x ○ ≠ shapes: ≠ species
- △ x ▼▲ ≠ colors: ≠ traits
- x ◇◇ ≠ groupings: ≠ communities
- ◇◇ similar-colored boxes: similar outcomes
- Taxonomic composition
- Functional composition
- Taxonomic diversity
- Physical structure

FIGURE 1 The hierarchy-of-predictability hypothesis proposed that the variability among restoration efforts was expected to change according both to the different outcomes (a) and to the number of factors constraining the outcomes (b). Panel (a) depicts how the nested nature from fine to coarse metrics can determine a hierarchy of predictability among restoration outcomes. For example, communities with different taxonomic compositions (different-colored boxes in the top row) can have similar functional composition (communities dominated by species with similar traits grouped in the same box in second row) (1), while communities with different functional composition (different-colored boxes in the second row) can have the same taxonomic diversity (communities with same number of species grouped in the same box in the third row) (2). Finally, communities with different taxonomic diversity (different colored boxes in the third row) can have the same physical structure (communities dominated by species represented by four-sided geometrical shapes grouped in the same box in the fourth row) (3). Hence, more possibilities for different taxonomic composition exist than for physical structure, making the latter potentially less variable and, thus, more predictable than the former. Panel (b) depicts how an increase in the number of factors constraining restoration (e.g., environmental filters caused by increased aridity) can limit the species capable of occupying restoration sites, reducing variability and potentially increasing predictability of restoration outcomes. In this paper, we posed two research questions, depicted above in the figure, related to the two aspects of the hierarchy of predictability hypothesis.

Evaluating the predictability of restoration over larger spatial extents, across multiple sites, and in different environmental conditions can provide a powerful test of the ideas and yield more generalizable evidence of patterns of predictability between restoration outcomes. Nonetheless, while the hierarchy-of-predictability hypothesis does not explicitly incorporate scale, restoration outcomes can be different at local and regional scales (Ladouceur et al., 2023). For example, in a series of surveys across grassland restoration sites, differences in species richness as a function of time since restoration were not as detectable at small local scales but were notable at

regional scales (Sluis, 2002). Moreover, the relative importance of community assembly processes determining restoration outcomes can vary depending on the spatial extent considered (Catano et al., 2021; de Bello et al., 2013; Viana & Chase, 2019). This could in turn impact the predictability of restoration outcomes when assessed at a larger scale.

Here, we conducted a broad-scale analysis of the predictability of grassland restoration using multiple projects along a gradient of environmental severity. Grasslands cover over one-third of the Earth’s land surface (Strömberg & Carla Staver, 2022) and are one of the most

degraded ecosystems worldwide (Bardgett et al., 2021; Blair et al., 2014), making their restoration a pressing global issue (Buisson et al., 2022; Tölgyesi et al., 2022). In the United States, thousands of restoration projects are conducted in grasslands on public and private lands that move billions of dollars annually (BenDor et al., 2015). Most of these projects share comparable restoration practices through the addition of seed mixes (seeding treatments) containing a high abundance of grasses (Barr et al., 2017; Török et al., 2021) and aim to achieve similar outcomes. This includes reducing exotic species cover and restoring native species diversity and a vegetation structure similar to undisturbed sites (Buisson et al., 2022; Prach et al., 2017). Hence, projects like these present a great opportunity to investigate drivers of variation among restoration efforts. In addition, grasslands are strongly responsive to precipitation variability and are found in the United States along an annual precipitation gradient of <200 mm in the west to 1000 mm in the east (Lauenroth et al., 1999). This represents an axis of environmental severity that can constrain community assembly during restoration, allowing a test of the hypothesis related to environmental constraints.

In this study, we tested whether some outcomes of restoration actions were more predictable than others in grassland restoration projects across the United States. Specifically, we posed two questions (Figure 1): (1) Does the predictability of grassland restoration outcomes follow the hierarchy of predictability? (2) To what extent do changes in environmental severity—as measured by aridity—influence the predictability of each outcome? If the nested nature of outcomes from coarse to fine metrics influences restoration predictability as proposed in the hierarchy-of-predictability hypothesis, then we expect restoration outcomes to decrease in predictability in the following order: physical structure, taxonomic diversity, functional composition, and taxonomic composition (Brudvig et al., 2017; Laughlin et al., 2017). Furthermore, if stronger environmental filters constraining species establishment and survival determines restoration predictability, then we expect that all outcomes would be less variable and, thus, more predictable with increasing aridity (Brudvig et al., 2017).

METHODS

To understand the variation in restoration outcomes and, in turn, the predictability of various response variables of interest, we conducted a synthesis of primary data obtained from the Global Restore Project (GRP), the largest database of restoration outcomes in the world (Ladouceur et al., 2022; Ladouceur & Shackelford, 2021).

When synthesizing these data, our focus was not on the effect of restoration treatments on restored communities or on grand mean and variances of those effects, but rather on variation in restoration outcomes as a way to interpret predictability and sources of unpredictability. Projects included in the database were also diverse. Therefore, we directly used the raw data rather than mean and variances of individual projects (Ladouceur & Shackelford, 2021; Mengersen et al., 2013) to embrace this variability and employ it to empower our understanding of variation in restoration outcomes (Brudvig et al., 2017).

Our general methodological strategy (detailed in the topics below) was to first quantify restoration outcomes for physical structure, taxonomic diversity, functional composition, and taxonomic composition of restored communities based on raw data from restoration projects (Figure 2). Then, to quantify the variation in these responses to restoration treatments and, in turn, their predictability, we fit a generalized linear mixed model for each outcome with data from all projects at once (Figure 2). Generalized linear mixed models are powerful tools for such analyses because they allow for non-normality of response variables and nonindependence of observations and are flexible enough to deal with high variability across studies (Bolker et al., 2009). We used a common set of predictor variables (i.e., fixed effects) for all models and had a common set of random effects. After fitting the models, we analyzed the predictability of restoration outcomes in two different ways. As the first question focused on comparing predictability between different outcomes, we used the total variance explained by the model fitted for each outcome as an indicator of predictability. We expected that outcomes hypothesized to be more predictable based on the hierarchy of predictability would have a higher proportion of variance explained by the models (Figure 2). The second question compared the predictability of the same outcome between restored communities across different aridity conditions. Hence, we extracted the model residuals for each community as an indicator of unexplained variability (or unpredictability) of restoration outcomes in those communities. For this question, we expected that unexplained variability (i.e., model residuals) would be smaller in more arid conditions (i.e., smaller values of the aridity index) (Figure 2).

GRP dataset

Restoration projects in the GRP database are organized in a structure containing monitoring plots within restoration treatments within restoration sites (Figure 2).

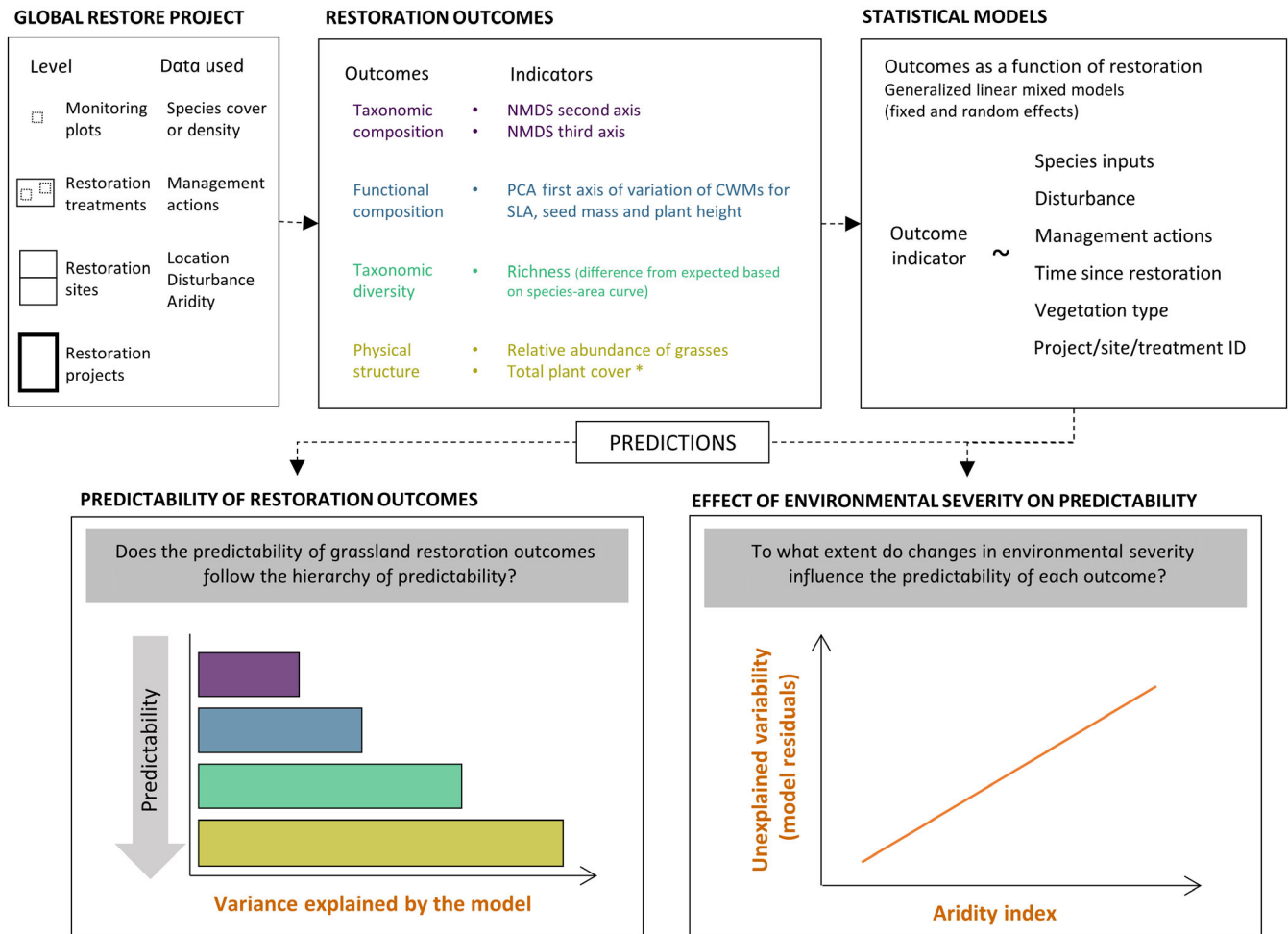


FIGURE 2 Flow diagram of methods used to answer the two research questions, with their specific predictions based on the hierarchy-of-predictability hypothesis. CWM, community-weighted mean; NMDS, nonmetric multidimensional scaling; PCA, principal component analysis; SLA, specific leaf area.

For every project, the database contains plant species canopy cover or density for each monitoring plot over time, as well as metadata related to the restoration project, such as location and associated characteristics of restoration sites (e.g., type of disturbance that prompted restoration, aridity, mean annual precipitation) and management actions applied to each treatment (e.g., species seeded, seeding rate, type of weed control, seedbed preparation) (Figure 2). All species names and measurement units were standardized before being added to the database, and the specific details for these processes as well as other information included in the database are described in Shackelford et al. (2021).

In November 2021, we downloaded from the GRP database plot vegetation data that were located in the United States and that were classified when entered into the database as grassland (i.e., less than 10% tree cover) according to the description of World Formation Types (Faber-Langendoen et al., 2016). From each site, we only

analyzed seeding restoration treatments to focus on the variability in response across restoration treatments, rather than average differences between restored and unrestored sites (Brudvig et al., 2017). To calculate outcomes for whole communities, we only used projects that collected data for every species present and not just seeded target species. Plots had to be monitored for at least 2 years after seeding to allow for initial establishment of restored communities, and we only used the first monitoring point after 2 years of seeding. We also excluded plots subjected to manipulation of irrigation or to repeated restoration treatments more than 4 weeks after seeding (Appendix S1: Section S1). Finally, we excluded one project that had almost all plots completely dominated by an invasive forb, resulting in most observations having the same value for outcomes and thus inflating the variance explained by predictor variables (see Appendix S2: Section S4 for results including this project). The resulting data set encompassed 1829 plots

from 227 different restoration treatments, spread across 52 restoration sites and 11 projects (Figure 3, Appendix S1: Section S1). This encompassed sites from arid to humid conditions, with aridity index values varying between 0.12 and 0.87 (Figure 3).

Quantifying restoration outcomes

We used physical structure, taxonomic diversity, functional composition, and taxonomic composition as the restoration outcomes of interest. Of the 1829 plots included in this study, 286 measured species density while 1543 measured canopy cover (Appendix S1: Section S1). To be able to compare outcomes across all plots, we first transformed species density or canopy cover into relative abundances, with the exception of the calculation for total canopy cover (see below). For physical structure, we focused on grasses, as they are the most abundant plant family in restoration seedings and contribute most to vegetation structure of grasslands (Wilsey, 2018). Thus, we used the relative abundance of grasses in each plot as an indicator of structure (Table 1, Appendix S3:

Section S1). Different combinations of species composition, functional composition, and species diversity can result in the same relative abundance of grasses, thus being an indicator of physical structure (Brudvig et al., 2017; Lockwood & Pimm, 1999). Moreover, the relative proportion of grasses as opposed to forbs influences many ecosystem processes in grasslands, such as seedling recruitment and invasion susceptibility, and is thus an important indicator for grassland restoration (Dickson & Busby, 2009; Wilsey, 2021). We also used total canopy cover as an additional indicator of physical structure (Table 1, Appendix S3: Section S1), calculating it in a filtered data set for which we excluded plots that measured density. Because of differences in sample sizes between the full and filtered data sets, caution must be taken when comparing results for total canopy cover and other restoration outcomes. Results for all other outcomes in the subset of projects that measured canopy cover are presented in the supplementary material (Appendix S2: Section S1).

We used species richness for the taxonomic diversity outcome. Due to the effect of scale of measurement (i.e., plot area) on species richness (Spake et al., 2021),

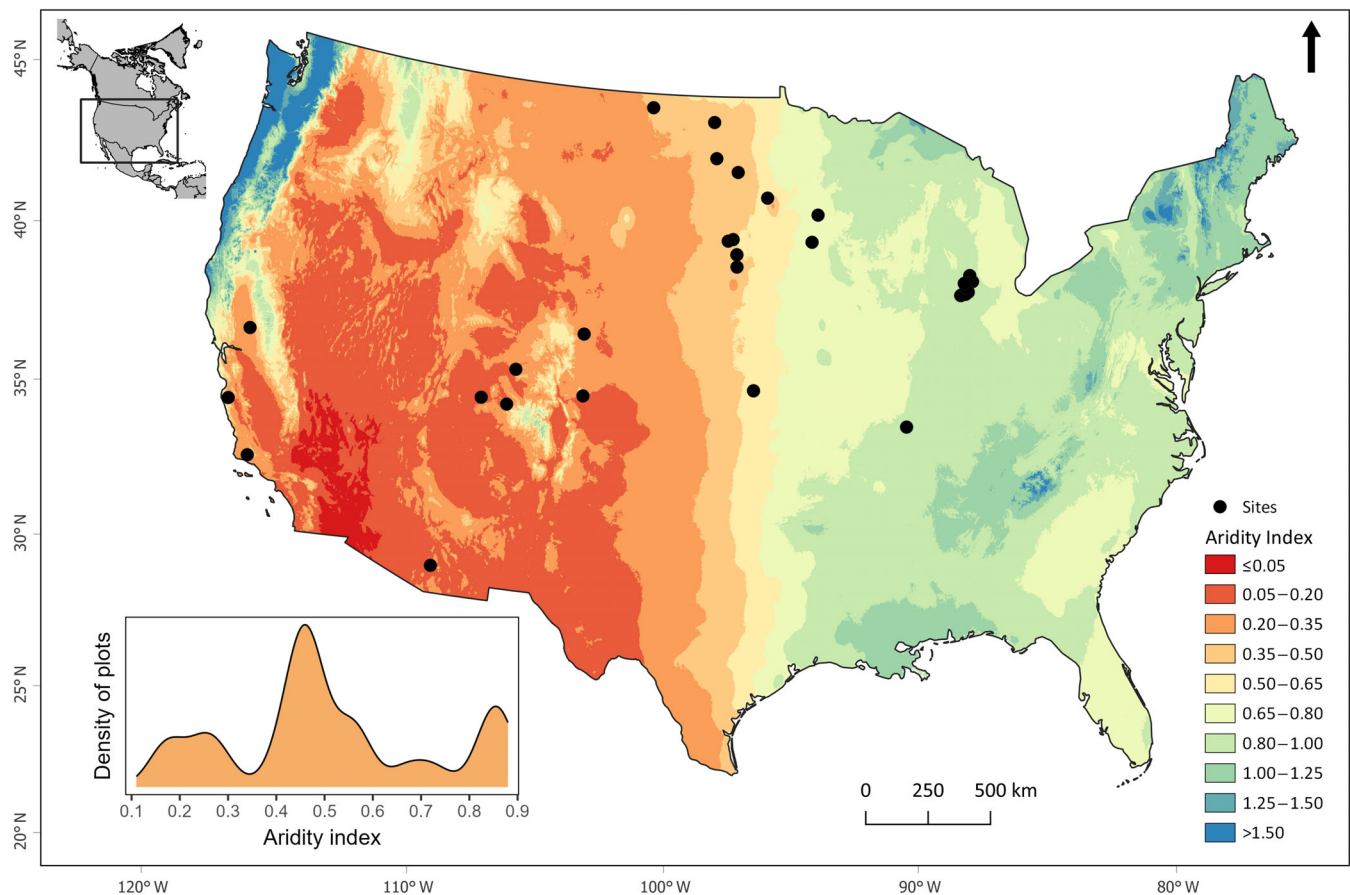


FIGURE 3 Location of restoration sites used to test hierarchy of predictability in North American grassland restoration along aridity gradient. Drier values are represented in red (lower values) and wetter in blue (higher values).

TABLE 1 Description of indicators of restoration outcomes of grassland restoration projects across the United States.

Restoration outcome	Indicator	Description
Physical structure	Relative abundance of grasses	Sum of canopy cover or density of grass species in plot divided by total canopy cover or density
Physical structure	Total cover	Sum of canopy cover values for all species in plot; calculated only for projects that measured cover as an abundance metric
Taxonomic diversity	Residuals of richness-area model	Residuals of linear model of $\log(\text{richness})$ as a function of $\log(\text{area})$; expresses how many more or fewer species each plot had when compared to expectations based solely on plot area
Functional composition	First axis of variation	Scores of each plot on first component identified by conducting PCA on community-weighted means of specific leaf area (SLA), seed mass, and plant height calculated using species relative abundances; represents a gradient from communities dominated by taller plants with smaller SLA and seed mass to communities dominated by shorter plants with higher SLA and seed mass (Figure 4)
Taxonomic composition	Second NMDS axis	Plot values on second axis identified by extracting three dimensions with NMDS on species relative abundances; divides restored communities along broad-scale vegetation types and whether dominant group of species was composed of exotics or natives (Figure 4)
Taxonomic composition	Third NMDS axis	Plot values on third axis identified by extracting three dimensions with NMDS on species relative abundances; represents identity of particular exotics or native species, among the most dominant species, that were present in each plot (Figure 4)

Note: Each indicator was used as a response variable in models using the same set of predictor variables related to characteristics of restoration projects to investigate the predictability of different restoration outcomes. Detailed methods for calculations of each outcome indicator are presented in Appendix S3: Section S1.

Abbreviation: NMDS, nonmetric multidimensional scaling.

much of the variation in species richness across plots was explained by plot area and not by restoration actions (Appendix S4: Section S1). Hence, we used an indicator for species richness that discounted this effect. To do this, we first fitted a linear model of the log-transformed richness as a function of the log-transformed plot area, as this is the function that best fits the species-area curve of grasslands (Dengler et al., 2020). Then we used the residuals of this model as the indicator of taxonomic diversity (Table 1, Appendix S3: Section S1). This indicator expresses how many more or fewer species were observed in each plot when compared to what would be expected based on plot area alone and, thus, represents the variation in richness that might be explained by restoration action.

Plant functional traits are important drivers of ecological processes and, hence, have received increasing attention as key indicators of restoration success (Laughlin, 2014). Here, we used a multivariate approach to identify the main axis of variation in community functional composition for specific leaf area, seed mass, and plant height. We focused on these traits because together they represent the main dimensions of plant form and function (Díaz et al., 2016; Westoby, 1998) and capture important physiological and life history characteristics of plants (Díaz et al., 2016; Reich, 2014; Wright et al., 2004).

We retrieved species-average values for these traits from the TRY global trait database (Kattge et al., 2020; Appendix S1: Section S2). By restricting our analysis to more than 2 years after seeding, we ensured alignment between plants in restored communities and values of mature plants retrieved from TRY (Havrilla et al., 2021). We calculated the mean of all values available for each species if at least three different values were available. Trait data were available for species comprising more than 80% of total abundance across all plots for all traits (Májeková et al., 2016; Pakeman, 2014; Appendix S1: Section S2). We then combined relative abundances from the GRP database and the trait data from the TRY database to calculate the community-weighted means (CWM) for each trait in each plot, using only species for which trait data were available. We performed principal component analysis (PCA) on the CWMs and used the first principal component representing the main axis of CWM trait variation across the restored communities as the indicator variable for functional composition (Table 1, Appendix S3: Section S1). This axis represents a gradient from communities dominated by native perennial grasses and forbs that are taller and have a smaller specific leaf area (SLA) and seed mass to communities dominated by exotic annual grasses and forbs that are shorter and have higher SLA and seed mass (Figure 4, Appendix S4: Section S1).

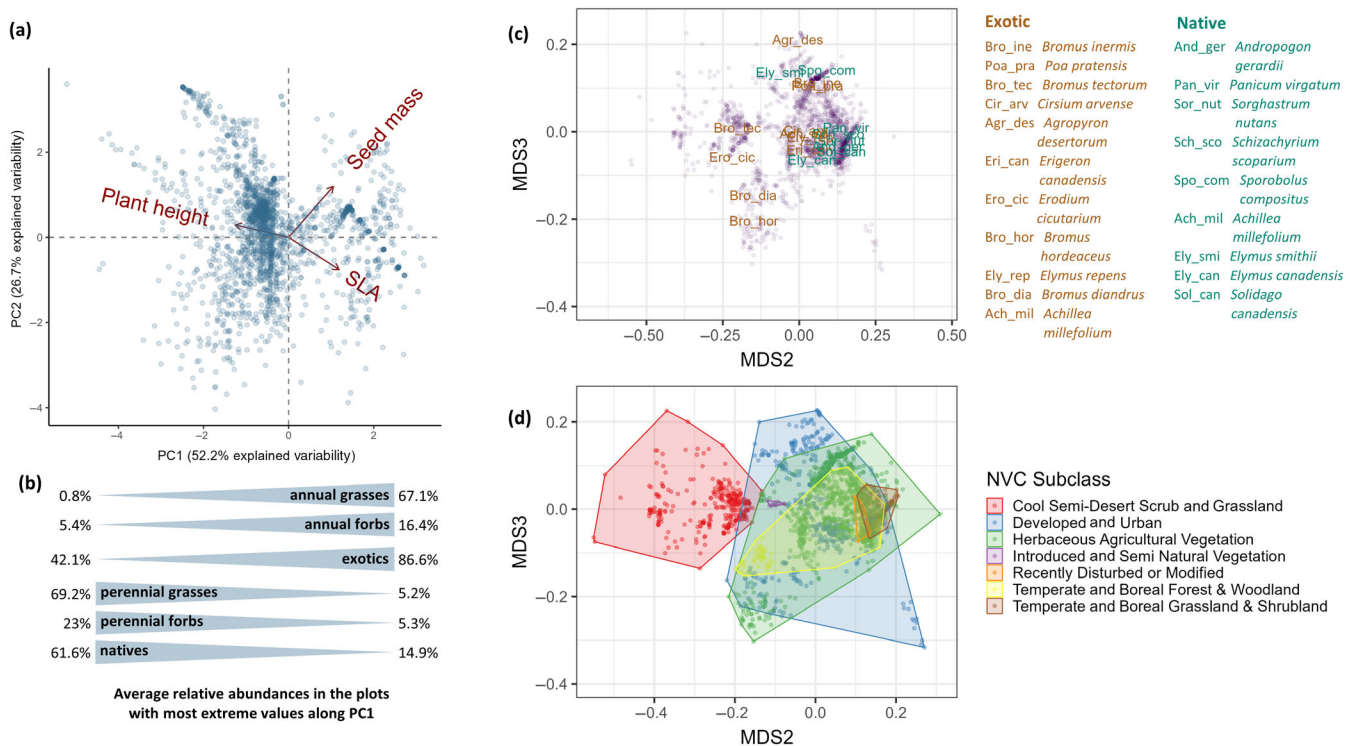


FIGURE 4 Multivariate analyses used to calculate outcome indicators for functional composition (a, b) and taxonomic composition of restored grassland communities in the United States (c, d). (a) Principal component analysis of community-weighted means for specific leaf area, seed mass, and plant height, showing plot scores (points) and trait relationships (arrows) with the two first components, as well as (b) trends for functional groups along the first axis. (c) Nonmetric multidimensional scaling of species relative abundances, showing the location of plots in the second and third dimensions with the location of the 20 most common exotic and native species on the multidimensional space or (d) plots grouped by their vegetation type. Two plots with extreme values on MDS3 were excluded from the figures to facilitate the visualization of patterns (see Appendix S4: Section S1 for figure with all plots). NVC, national vegetation classification.

Finally, for taxonomic composition, we reduced the variation in our data set into two indicator variables that expressed differences in relative abundances of species across plots. As recommended for species composition data, we calculated the Bray–Curtis pairwise species dissimilarity index between plots and used nonmetric multidimensional scaling (NMDS) to produce a visual representation that preserved as best as possible the dissimilarity between plots (Borcard et al., 2018). Many multivariate analyses identify axes for interpretation based on amount of variability explained (e.g., PCA), but NMDS axes are arbitrary and do not necessarily align with axes of high variation (Borcard et al., 2018). Hence, to choose the most relevant axes for our analysis, we first explored extracting two and three dimensions. The first NMDS axis of the solutions with two and three dimensions separated plots of a single project that shared few species with other plots (Appendix S4: Section S1.3). Because we were not interested in predicting the species composition of a single project, this axis did not provide a meaningful description of variation in

community composition for our question. Hence, we chose the second and third NMDS axes of the solution with three dimensions (stress = 0.045) as indicators of taxonomic composition because they provided information about the variation in community composition across all plots (Figure 4). The second axis (MDS2) divided restored communities along broad-scale vegetation types and whether the dominant group of species was composed of exotics or natives (i.e., lower values on the axis represent communities dominated by exotics while larger values represent communities dominated by natives) (Table 1, Figure 4, Appendix S3: Section S1). The third axis (MDS3) represented the identity of the particular exotic or native species, among the most dominant species, that were present in each plot (i.e., different values on the axis indicate presence of different species) (Table 1, Figure 4). All calculations were conducted in the R environment (R Core Team, 2021) using the tidyverse (Wickham et al., 2019), traitor (Götzenberger, 2015), FD (Laliberté & Legendre, 2010), ggbiplot (Vu, 2011), and vegan (Oksanen et al., 2022) packages.

Statistical models

To explain the restoration outcomes, we fit each outcome indicator as a function of restoration predictors, using plots from all restoration sites together in a single univariate model for each indicator (six univariate models in total). Each outcome indicator was the response variable in a generalized linear mixed model using the same structure for fixed and random effects in all models. A detailed description of the modeling approach is presented in Appendix S3: Section S3.

Fixed effects included variables that represented three main predictors of restoration outcomes: previous land-use history, restoration management actions, and species inputs. For land-use history, we used a categorical variable assigned by data contributors expressing the disturbance that prompted restoration efforts: agriculture, invasion, and/or grazing (Table 2, Appendix S3: Section S2). For management actions, we included the most common management actions (Appendix S1: Figure S2) as four binary variables indicating whether or not each action was applied at each plot (Table 2, Appendix S3: Section S2). To represent species input, we used the characteristics of the seed mixes. This variable was different in each model, and it corresponded to the outcome indicator used as the response variable in the model (Table 2, Appendix S3: Section S2). For example, to predict species richness in the restored communities, we used the number of species in the seed mix as the fixed effect related to species input, but to predict the relative abundance of grasses in the restored communities, we used the relative abundance of grasses in the seed mix (Table 2, Appendix S3: Section S2). Finally, we also included time since restoration as an additional fixed effect because the first monitoring point after 2 years of seeding was different for each project (Table 2, Appendix S3: Section S2).

For random effects, we included treatments, sites, and projects as nested random intercepts to consider the nonindependence of plots within the data set (Table 2). In addition, plots that share climatic conditions due to similar macro-ecological drivers such as latitude and altitude are expected to be occupied by similar vegetation and, thus, have more similar restoration outcomes. Hence, we also used the vegetation type of each site as a random intercept (Table 2). Vegetation type was defined as the formation subclass of the site where plots were located according to the GAP/LANDFIRE National Terrestrial Ecosystems Dataset, classified following the United States National Vegetation Classification (FDGC, 2008; USGS GAP, 2016). This level describes communities in terms of general appearance of vegetation and growth forms of dominant taxa, which is adequate to describe variation at continental scales (Faber-

Langendoen et al., 2014), such as in the case of the projects included in our data set (Figure 3). As this spatial data layer was developed based on satellite imagery, the specific subclass classification for each coordinate might be different than the ecosystem description provided by data contributors, but it is expected to group restoration sites based on similar vegetation. Taken together, the random structure of models captures the broad sources of variability that influence outcomes such as the biogeographic location of each restoration plot and due to the different experimental designs and methodologies among studies.

To decide on the appropriate family of distribution for the response variables, we compared models fitted with different distributions and selected the best fit using the lowest Akaike's information criterion (AIC_c) (Appendix S4: Section S3). All models were fitted using the *glmmTMB* package (Brooks et al., 2017) in R (R Core Team, 2021), using the following formula: `outcome indicator ~ disturbance + bed preparation + weed control + shelter + grazer removal + species input + time since restoration + (1|vegetation type) + (1|project/site/treatment)`. The assumptions of each model were verified using the *DHARMA* package (Hartig, 2021) to check for uniformity in simulated residual distributions, zero inflation and overdispersion, and the *sjPlot* package (Lüdtke, 2021) to inspect Q-Q plots of random effects (Appendix S4: Section S4).

Predictability of restoration outcomes (Question 1)

We were interested in the variability that can be explained—and thus predicted—in the course of a restoration project. Thus, we compared the proportion of variance between restoration plots that was explained by the models to investigate if the predictability of outcomes followed the hierarchy hypothesis (Figure 2). To do this, we calculated the marginal (explained by fixed effects) and conditional (explained by fixed and random effects) variance of the models (Nakagawa et al., 2017; Schielzeth & Nakagawa, 2013). Then we ordered outcomes from most to least predictable based on decreasing variance explained by fixed effects. The higher the variance explained by the fixed effects in the model, the more predictable we considered the restoration outcome.

Effect of aridity on predictability of outcomes (Question 2)

To investigate whether the predictability of restoration outcomes increased with the severity of environmental

TABLE 2 Details of fixed (a–d) and random effects (e–h) used in six different models predicting restoration outcome indicators of grassland restoration projects across the United States.

Predictor variable	Description	Transformation	Model used
(a) Previous disturbance	Categorical variable indicating combinations of disturbances that led to restoration efforts (agriculture, invasion, grazing, invasion and agriculture, invasion and grazing, or all three)	None	All six models
(b) Management actions			
Bed preparation	Binary variable (yes/no) indicating whether or not seedbed was prepared (e.g., tilling, raking)	None	All six models
Weed control	Binary variable (yes/no) indicating whether or not some sort of weed control (chemical or physical removal) was applied	None	All six models
Shelter	Binary variable (yes/no) indicating whether or not some sort of shelter (built shelters using natural materials such as brush) for seeded species was applied	None	All six models
Grazer removal	Binary variable (yes/no) indicating whether or not grazers (livestock or undomesticated animals such as deer) were excluded from restoration treatments	None	All six models
(c) Species inputs			
Relative abundance of grasses in the seed mix	Continuous variable representing proportion of seeds from grass species in seed mix	Scaling	Model predicting relative abundance of grasses
Total seeding rate	Continuous variable representing sum of seeds from all species seeded per square meter	Log, scaling	Model predicting total cover
Seed mix richness	Discrete variable representing no. different species seeded	Log, scaling	Model predicting richness
Seed mix functional composition	Continuous variable representing position of each seed mix in gradient defined by functional composition first axis variation; species seeding rates were used to calculate seed mix community-weighted means for specific leaf area, seed mass, and plant height and used principal component analysis (PCA) model to predict values for each seed mix in first axis of functional composition	Scaling	Model predicting functional composition
Seed mix first axis of variation	Continuous variable representing variation in richness, proportion of grasses, and functional composition between seed mixes, calculated by performing PCA with other seed mix indicators	Scaling	Models predicting taxonomic composition indicators

TABLE 2 (Continued)

Predictor variable	Description	Transformation	Model used
	and extracting first principal component (Appendix S4: Section S2); with this variable, taxonomic composition of community is understood as being result of multiple components of seed mix		
(d) Time since restoration	Continuous variable indicating no. weeks since species were seeded	Scaling	All six models
(e) Vegetation type	Categorical variable indicating formation subclass of site where plots were located, according to United States National Vegetation Classification (FDGC, 2008; USGS GAP, 2016)	None	All six models
(f) Project ID	Categorical variable identifying each unique restoration project	None	All six models
(g) Site ID	Categorical variable identifying each unique restoration site	None	All six models
(h) Treatment ID	Categorical variable identifying each unique restoration treatment	None	All six models

Note: Values in bold represent different categories of predictor variables used in all models. Management actions (b, bold) were represented by four binary variables (below b, normal text) indicating whether each action was applied or not at each plot. The specific predictor variable for species inputs (c, bold) was different for each model (below c, normal text), and it corresponded to the outcome indicator used as the response variable in the model (rightmost column). Detailed methods for calculations of each variable are presented in Appendix S3: Section S2.

conditions, we extracted the difference between the observed value and the values predicted by the models (i.e., the model residuals) and looked at how the residuals varied along the aridity gradient. The larger these residuals in absolute terms, the more variability is left unexplained by the model and, hence, the less predictable the outcome.

For this question, we used treatments instead of plots as observations, because monitoring plots are typically different replicates used to estimate average-treatment outcomes. An outcome can differ greatly between plots but still present an average for the treatment that is similar to the model prediction, which thus makes it highly predictable at the treatment level. The hierarchy of predictability focuses on the variability in outcomes across entire restoration treatments rather than the variability that occurs at a meter scale from one plot to another. This is a real-world approach to how restoration treatments affect systems. Hence, we first averaged the residuals of plots within each treatment and then used the absolute value of this average as the response variable.

We fit generalized linear models with the treatment-level residuals as response variables and aridity as a predictor variable (see Appendix S3: Section S3 for a

detailed description of modeling approach). Because the number of plots in each treatment and plot area can influence the variability of all community-level outcomes (Spake et al., 2021), we included the plot area and number of plots as additional predictor variables in the models, using the following notation in R: treatment-level residuals ~ aridity + plot area + number of plots. We then focus on describing the effect of aridity on model residuals after taking into account the effect of plot area and number of plots. We also conducted a supplementary analysis to investigate whether the severity of environmental conditions due to the temporal variability of precipitation, which is usually higher in more arid sites (Paruelo & Lauenroth, 1998), influenced our results. For this, we retrieved annual precipitation values for each site from the PRISM database (Prism Climate Group, 2014) and ran the same models with additional variables related to absolute rainfall (in seeding or monitoring years) or seeding-year rainfall relative to mean annual precipitation (Appendix S2: Section S2). Number of plots and plot area were log-transformed, and all predictor variables were standardized before being used in the analysis. Exploratory analysis and model validation were conducted as described above.

RESULTS

Predictability of restoration outcomes

We found that the most predictable outcome was the dimension of taxonomic composition related to the dominance of exotics or native species (second NMDS axis), with 66.2% of the variance explained by fixed effects (Figure 5). Second, physical structure indicated by relative abundance of grasses and functional composition had over 25% of the variance explained by fixed effects (Figure 5). Taxonomic diversity, total plant cover, and the dimension of taxonomic composition related to fine-scale species identity (third NMDS axis) were the least predictable outcomes, with less than 16% of the variance explained by fixed effects (Figure 5).

The specific restoration predictors explaining the variability in restoration outcomes across communities varied across indicators. Seed mixes appeared as significant predictors for total cover and species richness, with higher seeding rates and seed mix richness resulting, on average, in higher total cover and species richness (Figure 6). Time since restoration affected relative abundance of grasses, total cover, and species richness, with longer times since restoration resulting in, on average, higher relative abundance of grasses, lower total cover, and fewer species (Figure 6). Previous disturbance and specific management actions were a significant predictor of relative abundance of grasses, functional composition, and the dimension of taxonomic composition related to the dominance of native or exotic species (second NMDS axis). In addition, disturbance also affected richness while specific management actions affected the dimension of taxonomic composition related to fine-scale species identity (third NMDS axis) (Figure 6).

Effect of environmental severity on predictability of restoration outcome

The unexplained variability of restoration—as measured by model residuals—was higher at sites with intermediate levels of aridity for most outcomes (Figure 7), but this was mostly explained by the fact that these residuals were averaged across treatments that had fewer and smaller plots (Appendix S4: Section S4). When keeping plot area and number of plots constant, most relationships between aridity and unexplained variability of restoration outcomes were weak and nonsignificant (Figure 7). Functional composition, however, showed significantly lower predictability (i.e., higher unexplained variability) with increasing aridity, while the dimension of taxonomic composition related to fine-scale species identity (third NMDS axis)

became significantly more predictable (i.e., smaller unexplained variability) with increasing aridity (Figure 7). These effects were the same when including additional variables related to the temporal variability of precipitation in the models (Appendix S2: Section S2).

DISCUSSION

Predictability of restoration outcomes

We did not find consistent support for the hypothesis that the predictability of outcomes would decrease from coarse to fine response metrics according to their nested nature (physical structure > functional composition > taxonomic diversity > taxonomic composition). On the one hand, in accordance with our predictions, one indicator of physical structure (relative abundance of grasses) was among the most predictable outcomes, and one dimension of taxonomic composition (related to fine-scale species identity) was among the least predictable (Figure 5). On the other hand, total plant cover was one of the least predictable outcomes (Figure 5), contradicting the expectation that structural attributes would be highly predictable. Additionally, although taxonomic composition was hypothesized to be unpredictable, our measured dimension of taxonomic composition related to dominance of exotics or natives (second NMDS axis) was the most predictable outcome (Figure 5). While previous research in a ponderosa pine restoration site found species composition to be unpredictable (Laughlin et al., 2017), these results are similar to findings from a study encompassing 24 oak-savanna prairie sites that did not follow the hierarchy of predictability but rather found species composition to be among the most predictable restoration outcomes (Abella et al., 2018). Overall, these results indicate that coarse to fine organization of response metrics might have a role in influencing the predictability of some restoration outcomes, but that additional factors are also at play.

First, how outcome metrics are measured might be an important factor influencing their predictability. We measured physical structure and taxonomic composition using two different indicators each, and those indicators showed different predictability trends. Physical structure represented by the relative abundance of grasses was highly predictable but unpredictable if represented by total canopy cover, and the same pattern occurred for the two dimensions of taxonomic composition. Indeed, community taxonomic composition is a multivariate property of communities composed both of species identities and the relative abundances of each species (Blowes et al., 2022; Magurran & McGill, 2011). As such, it can be

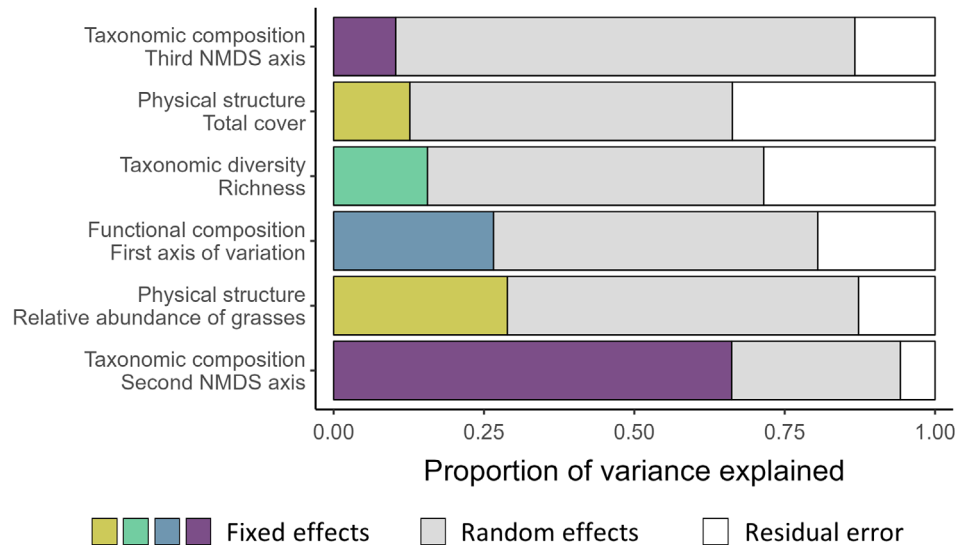


FIGURE 5 Proportion of variance explained by fixed and random effects and residual error in each of the models predicting restoration outcomes, organized from least predictable (top) to most predictable (bottom). Indicators of the same outcome are shown in the same color. Total plant cover was calculated using a subset of projects that used canopy cover as an abundance metric. NMDS, nonmetric multidimensional scaling.

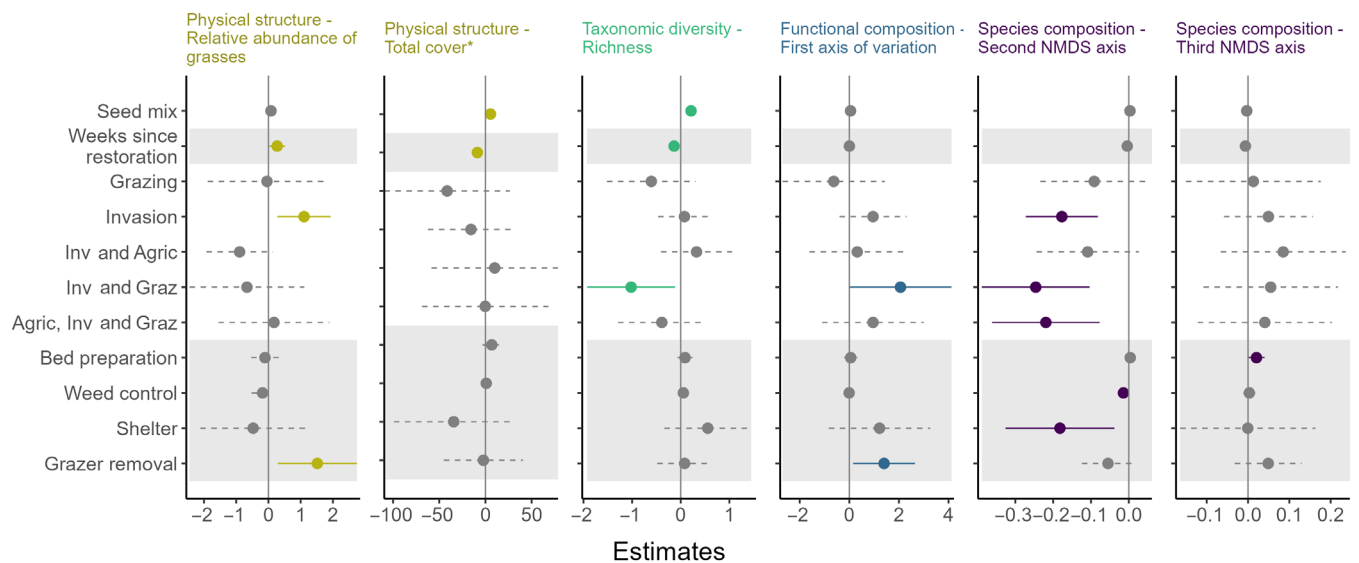


FIGURE 6 Estimated model coefficients (circles) and CIs (lines) for each predictor of each restoration outcome. Significant coefficients are presented in color and with continuous lines, while nonsignificant coefficients are presented in gray and with dashed lines. The reference level for the disturbance variable was the “agriculture” category. *Total plant cover was calculated using the subset of projects that used canopy cover as an abundance metric. Agric, agriculture; Graz, grazing; Inv, invasion; NMDS, nonmetric multidimensional scaling.

described by different dimensions, with potentially different degrees of predictability. The dimension related to the identity of native and exotic species, captured by the third NMDS axis in our study, is a highly specific measure of taxonomic composition. Hence, the low predictability encountered for this dimension is in accordance with the original hypothesis that fine/specific restoration goals achieved by particular combinations of species are less predictable than coarse/broad goals (Brudvig et al.,

2017). Nonetheless, this represents only one potential measure of taxonomic composition. Our results indicate that if taxonomic composition is alternatively measured as coarser patterns in dominant species, such as predominance of exotics or natives captured in our second NMDS axis, it might be more predictable in the course of a restoration project.

Another factor potentially influencing the predictability of restoration outcomes in our study is differences in

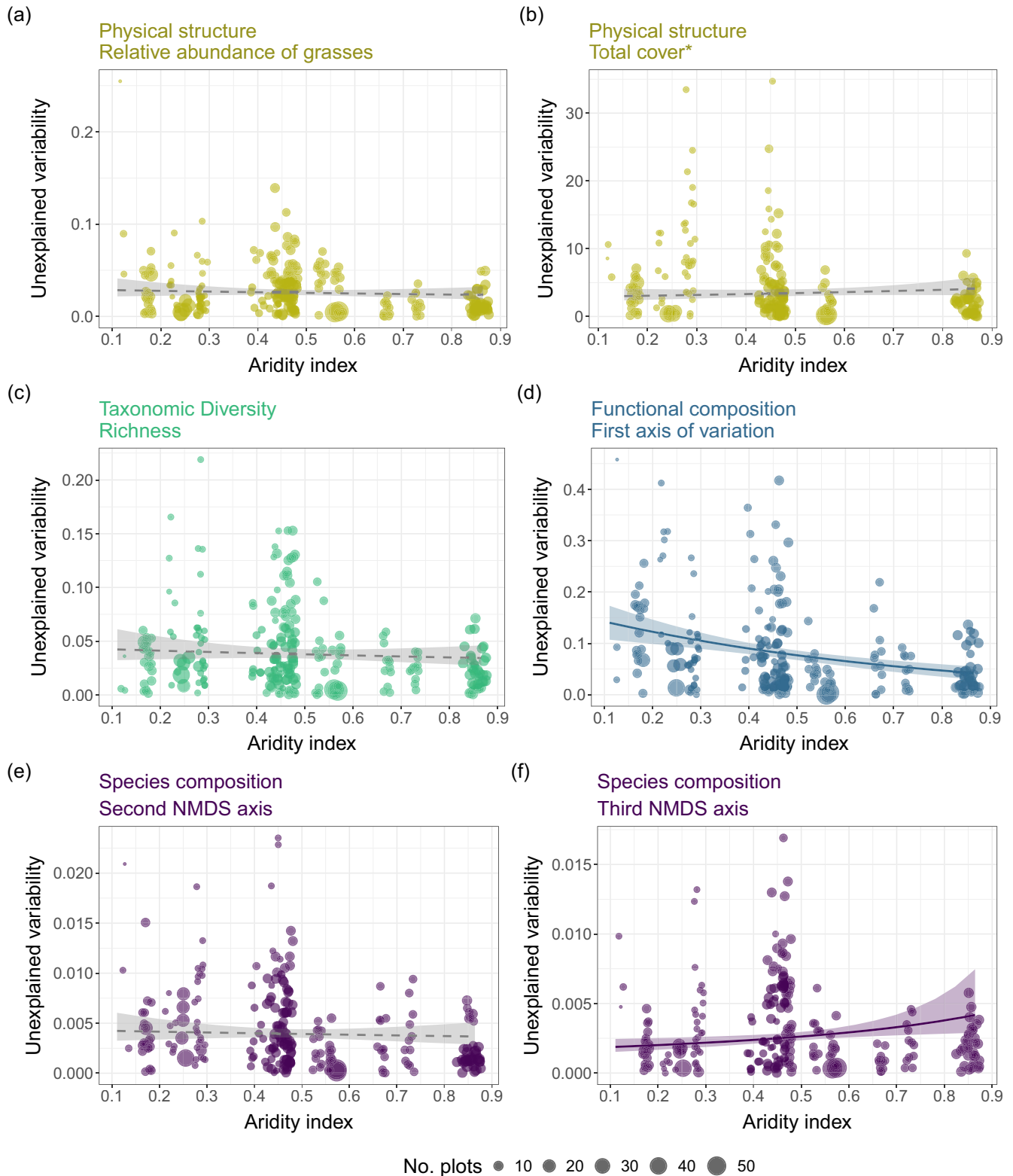


FIGURE 7 Results of generalized linear models of effect of aridity on predictability of restoration outcomes. Plots show predicted lines and 95% CIs for effect of aridity on treatment-average residuals when keeping area and number of plots constant at their mean values. Significant relationships are shown in color and with continuous lines, while nonsignificant relationships are shown in gray and with dashed lines. *Total plant cover was calculated using the subset of projects that used canopy cover as an abundance metric. NMDS, nonmetric multidimensional scaling.

predictability between dominant and rare species of restored grassland communities. The three most predictable indicators were the dimension of taxonomic composition related to the dominance of exotics or natives (second NMDS), the relative abundance of grasses, and the first axis of variation in functional composition. These indicators are driven by variations in the most dominant species within communities rather than changes in rare species. Moreover, the dimension of taxonomic composition related to the identity of dominant species (third NMDS axis), although harder to predict based solely on fixed effects, was mostly explained by random effects representing the biogeographic location of restored sites (Figure 5). This can be a result of species pools being different between regions, suggesting that when comparing sites across a larger spatial extent, it might be possible to determine the identity of dominant species of restored grassland communities based on site location. At the same time, richness, which essentially captures the number of rare species because it disregards species abundances (Magurran & Henderson, 2011), was harder to predict in our study, even when considering random effects (Figure 5). Hence, predicting variation in dominant species might be easier than predicting variation in rare species among restored grassland communities.

Uneven species abundance distributions, with a few abundant species and many rare species, are a common pattern in ecological communities (McGill et al., 2007), and research suggests that dominant and rare species might respond to different assembly processes (Magurran & Henderson, 2003; Matthews & Whittaker, 2015). While dominant species typically respond to deterministic niche-based mechanisms, the presence and identity of rare species might be more influenced by stochastic processes such as random dispersal (Matthews & Whittaker, 2015). Moreover, the richness and composition of rare species typically respond more to interannual weather variation in grasslands than dominant species (Cleland et al., 2013). Hence, more variation would be explained by the niche-based mechanisms of our restoration predictors (e.g., previous disturbances or management actions manipulating biotic filters such as grazer removal) for those indicators responsive to dominant species. The increasing effect of stochastic processes and interannual variability on determining rare species could then in turn explain why richness was less predictable than expected.

The potential importance of dominant and rare species in our predictability results might also be related to the continental extent of our study, which spans different vegetation types and a wide environmental gradient. The relative importance of niche-based versus stochastic assembly processes is scale dependent, with the former usually being stronger when studied across larger spatial

extents (Shinohara et al., 2023; Viana & Chase, 2019). It is thus possible that the higher predictability of indicators responsive to the dominant species is related to a stronger signal of niche-based mechanisms when comparing communities across a regional scale. The original hierarchy of predictability hypothesis relies on stochastic processes such as random dispersal and priority effects driving which particular combination of species becomes established, resulting in outcomes that can be achieved by multiple combinations of species (e.g., structure, species diversity) being more predictable than outcomes that can only be achieved by a single combination of species (e.g., species composition) (Brudvig et al., 2017). We suggest that this might still be the case at smaller spatial extents, where such stochastic processes are expected to be more evident (Viana & Chase, 2019). This effect of spatial extent could explain why Laughlin et al. (2017), looking at a single site, encountered support for the hypothesis, while Abella et al. (2018), looking at multiple sites across a landscape, did not. Moreover, when predicting outcomes separately for each restoration site in a supplementary analysis, we found that richness was one of the most predictable outcomes, as expected by the hierarchy-of-predictability hypothesis, although trends for other outcomes remained similar between the regional and site-level analysis (Appendix S2: Section S3). Still, the patterns of predictability among restoration outcomes and the different predictability of richness encountered between the regional and site-level analyses indicate that further research on the effect of scale on predictability of recovery, regeneration, and restoration is warranted (Ladouceur et al., 2023).

Finally, plant cover was one of the least predictable outcomes. Total cover was only measured on a subset of the data, but it remained one of the least predictable outcomes even after being compared to other outcomes measured on the same subset (Appendix S2: Section S1). On the one hand, this could be a result of the unreliability of plant cover as an estimate of species relative abundance (Klimeš, 2003). On the other hand, similar results were found by Abella et al. (2018), in which restoration outcomes related to physical structure such as herbaceous cover were also unpredictable. This suggests that plant cover might indeed be an unpredictable outcome in grassland restoration. Total biomass is highly variable in grassland ecosystems, and it usually responds to interannual variations in precipitation (Briggs & Knapp, 1995; Gherardi & Sala, 2019). If the variation in biomass results in variable canopy cover, this could partly explain the higher unpredictability of this metric. Moreover, in cases where vegetation structure is dependent on other outcomes, for example, when initial species composition impacts the development of total cover because of

processes such as plant–soil feedbacks (Heinen et al., 2020) or apparent competition (Orrock & Witter, 2010), physical structure would be less predictable than other outcomes (Abella et al., 2018). Hence, how each individual outcome is affected by processes driving community assembly and species abundances, as well as the number of different processes impacting each outcome, might be important additional factors causing differences in predictability among restoration outcomes.

Effect of environmental severity on predictability of restoration outcomes

We also did not consistently find support for our hypothesis relating environmental severity to predictability of restoration. While we expected all outcomes to become more predictable with increasing aridity, only the dimension of taxonomic composition related to fine-scale species identity (third NMDS axis) showed this trend. The predictability of outcomes related to physical structure, taxonomic diversity, and dominance of exotics versus natives was not affected by environmental severity, nor was the predictability of outcomes when predicted separately for each restoration site (Appendix S2: Section S3). The hierarchy-of-predictability hypothesis proposed that harsher environmental conditions would limit the potential combinations of species that are able to establish (Brudvig et al., 2017), but our results suggest this process might not be impacting the predictability of all response metrics. Interestingly, the dimension of taxonomic composition that showed higher predictability in more arid environments is the one related to species identities, which likely responds more than other indicators to variations in the combinations of species inhabiting a particular restoration site. Hence, this indicator expresses more closely the mechanisms behind the original hierarchy-of-predictability hypothesis. Thus, the smaller number of species able to establish and survive in arid grasslands across the United States (Cleland et al., 2013) could underpin the higher predictability of species identity in those sites.

Nonetheless, most outcomes did not follow the original hypothesis. Aridity is an important factor to consider in restoration projects, but the lack of variation in predictability along the aridity gradient for some outcomes suggests that at least some processes impacting restoration outcomes do not vary along the aridity gradient. For example, this might be the case of disturbance as a driver of dominance of exotic species in restored communities. The dimension of taxonomic composition related to the dominance of exotic or native species was strongly impacted by previous disturbance, with sites previously

exposed to invasion being more dominated by exotics (Figure 6). The mechanisms determining the establishment and dominance of non-native species in North American grasslands are complex, but disturbed habitats typically provide an opportunity for non-native species to become established, irrespective of the environmental severity or resource availability of the site (Seastedt & Pyšek, 2011). Because restoration by definition occurs in previously disturbed habitats, it makes sense that predicting the dominance of native and exotic species in restored grassland communities would be equally feasible across the aridity gradient. However, we focused on how broad types of disturbance could predict restoration outcomes, while we did not investigate the effect of different magnitudes of disturbance, which could still potentially vary along the aridity gradient.

The predictability of functional composition, on the other hand, decreased in more severe environments. More arid sites typically have higher intra-annual and interannual variability in precipitation (Puelo & Lauenroth, 1998), and anomalously wet or dry periods in comparison to baseline conditions or long-term averages could potentially make restoration less predictable in those sites. However, the predictability of functional composition was also smaller in more arid sites even after including variables related to interannual variability in precipitation in addition to aridity in supplementary models (Appendix S2: Section S2). Functional composition was also less predictable with lower seeding-year rainfall relative to mean annual precipitation as well as with lower absolute seeding-year rainfall and monitoring-year rainfall (Appendix S2: Section S2). Overall, this suggests that the low predictability of functional composition occurs in more arid sites and in sites that received below average rainfall during and immediately after restoration, indicating that water limitation can increase the variability of functional composition in restored communities. Given the lack of restoration data on temporal resolutions finer than a year, we were not able to assess the impact of intra-annual variability of precipitation on our results. Nonetheless, if relatively larger rainfall events or longer dry spells in arid grasslands led to larger variation in restoration outcomes, we would expect to see a decrease in predictability with increasing aridity for all restoration outcomes. The fact that we only encountered this relationship for our functional composition outcome suggests that other mechanisms might be at play.

A possible mechanism for the smaller predictability of functional composition under higher water limitation is that there may have been stronger priority effects in more arid sites. Priority effects occur when species that arrive early reduce resources available for later arriving

species or modify the abiotic conditions making the environment less harsh (i.e., nutrient enrichment, shading) (Fukami, 2015; Hess et al., 2019). Hence, it is reasonable to expect these effects might be stronger under already harsh environmental conditions (Goodale & Wilsey, 2018; Weidlich et al., 2021). Our results indicate that previous exposure to biological invasion can increase the dominance of exotic annuals (i.e., higher values for our indicator of functional composition) in restored grasslands (Figure 6) but that arid sites also have higher or lower dominance of these species (i.e., higher residuals; Figure 7) when compared to what would be expected based on previous disturbance. We thus propose that stronger effects of early arriving species on subsequent communities in more sites could be causing this higher variability. Indeed, North American arid and semi-arid grasslands are notoriously invaded by annual grasses (Corbin & D'Antonio, 2004; D'Antonio & Vitousek, 1992), which preempt resources from native seedlings, in particular native perennials in more arid sites (Davies et al., 2021; Ray-Mukherjee et al., 2011). Moreover, exotic grassland species have been shown to have strong priority effects, by having a larger impact when arriving first (Schantz et al., 2015; Wilsey et al., 2015) or by benefiting more from facilitation, in particular exotic annuals (Lucero et al., 2019). Thus, if priority effects are stronger in more arid sites, they could cause a higher dominance of exotics annuals when they arrive first or lower dominance of exotics when by chance a native species arrives first in arid grasslands. This could in turn explain the higher variability of outcomes related to exotic versus natives and annuals versus perennials in more arid sites, such as our indicator of functional composition (Figure 4).

Still, our data set includes varied restoration projects implemented and monitored at different spatial and temporal scales. Although we grouped restoration predictors into broad categories, specific restoration actions and disturbance history differ between sites, most certainly contributing to some unexplained variability in restoration outcomes. Other factors known to be important drivers of restoration, such as soil, topography, and landscape context, were not included in our models due to a lack of information or consistent measurement across sites. This heterogeneity in the data prevented us from making strong inferences linking specific restoration characteristics to specific restoration outcomes. Though interesting, these more detailed explorations of restoration drivers were not the focal point of our investigation, which was instead centered on identifying coarse, broad-scale patterns on sources of variation across multiple projects and a large spatial extent. In addition, it is important to note that increasing model complexity does not necessarily

increase model performance, and often simpler models can generate better generalizations (Clark et al., 2020). To take advantage of our data set, we focused on how the early results of grassland restoration were predicted by a simple set of restoration characteristics. Most restored communities will, however, continue to develop long after these initial years, but the potential impacts of these changes to the predictability of restoration over longer timescales lies outside the scope of our study.

Implications for restoration science and practice

Overall, our results indicate that the predictability of certain restoration outcomes in grassland restoration across the United States, such as indicators related to species identities, might follow the hierarchy-of-predictability hypothesis in the initial years of restoration. Predicting whether early-restored grassland communities will contain a specific combination of species is difficult, although this might be more feasible under more severe environments where fewer combinations of species are able to survive. Nonetheless, the trends for other outcomes suggest the mechanisms behind the original hierarchy of predictability hypothesis are not sufficient to explain variation in the predictability of grassland restoration across the United States, both between outcomes and along a gradient of environmental severity. Specifically, our results indicate that looking into differences between processes driving dominant and rare species in restored grassland communities, how those processes might change with scale, and how the strength of priority effects vary along environmental gradients might be important avenues for further research on the predictability of restoration.

Furthermore, we found that restoration outcomes related to the most dominant species of restored communities were easier to predict in grassland restoration projects across the United States. In particular, previous disturbance appeared as an important predictor for the dominance of exotic species in restored communities. This information could serve as a foundation for developing landscape-level tools that help land managers select more favorable restoration sites, develop achievable goals, and estimate effort necessary for restoration plans that account for simultaneously establishing desired species and controlling undesired exotic species. In particular, richness as a metric had low predictability, suggesting that the presence and diversity of rare species were likely less predictable. Dominant and common species are typically important to maintain ecosystem function, but supporting native species diversity, including

rare and dispersal-limited species, is also an important goal of many restoration efforts (Baur, 2014; Maina & Howe, 2000). Thus, our findings also highlight the need for investing in continuous monitoring and active management beyond one-time seed addition for restoration plans that strive to establish rare species (Svejcar et al., 2023; Young & Hamerlynck, 2023). Overall, our results add support to the importance of long-term post-restoration management to achieve multiple goals for grassland restoration in the United States.

AUTHOR CONTRIBUTIONS

Nancy Shackelford and Emma Ladouceur organized the GRP database that provided the data. Diana Bertuol-Garcia and Nancy Shackelford conceptualized the study. All authors provided feedback on the analytical framework. Diana Bertuol-Garcia analyzed the data with assistance from Nancy Shackelford, Daniel C. Laughlin, and Michael F. Curran, and all authors helped with the interpretation of results. The first draft of the article was written by Diana Bertuol-Garcia, and all authors contributed by revising the draft and approving the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Bertuol-Garcia et al., 2023) are available from Borealis at: <https://doi.org/10.5683/SP3/ZMUWWC>.

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