Forecasting natural regeneration of sagebrush after wildfires using population models and spatial matching

Andrii Zaiats · Megan E. Cattau · David S. Pilliod · Rongsong Liu · Juan M. Requena-Mullor · T. Trevor Caughlin

Abstract

Context Addressing ecosystem degradation in the Anthropocene will require ecological restoration across large spatial extents. Identifying areas where natural regeneration will occur without direct resource investment will improve scalability of restoration actions.

Objectives An ecoregion in need of large scale restoration is the Great Basin of the Western US, where increasingly large and frequent wildfires threaten ecosystem integrity and its foundational shrub species. We develop a framework to forecast where post-wildfire regeneration of sagebrush cover (*Artemisia* spp.) is likely to occur within the burnt areas across the region ($> 900{,}000$ km^2).

Methods First, we parameterized population models using Landsat satellite-derived time series of sagebrush cover. Second, we evaluated the out-of-sample performance by predicting natural regeneration in wildfires not used for model training. This model assessment reproduces a management-oriented scenario: making restoration decisions shortly after wildfires with minimal local information. Third, we asked how accounting for increasingly fine-scale spatial heterogeneity could improve model forecasting accuracy.

Results Regional-level models revealed that sagebrush post-fire recovery is slow, estimating > 80-year time horizon to reach an average cover at equilibrium of 16.6% (CI95% 9–25). Accounting for wildfire and within-wildfire spatial heterogeneity improved out-of-sample forecasts, resulting in a mean absolute error of $3.5 \pm 4.3\%$ cover, compared to the regional model with an error of $7.2 \pm 5.1\%$ cover.

Conclusions We demonstrate that combining population models and non-parametric spatial matching provides a flexible framework for forecasting plant population recovery. Models for population recovery applied to Landsat-derived time series will assist restoration decision-making, including identifying priority targets for restoration.

A. Zaiats (✉) · M. E. Cattau · T. T. Caughlin
Boise State University, Boise, ID, USA
e-mail: andriizaiats@u.boisestate.edu

D. S. Pilliod
U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, ID, USA

R. Liu
University of Wyoming, Laramie, WY, USA

J. M. Requena-Mullor
Department of Biology and Geology. Andalusian Center for the Assessment and Monitoring of Global Change (CAESCG), University of Almeria, C/ Sacramento s/n 04120, Almeria, Spain

Introduction

Natural regeneration of native plant communities in disturbed landscapes can be an economical and ecologically attractive option for restoration (Shono et al. 2007; Jones et al. 2018; Strassburg et al. 2019). As climate change induces increasingly large disturbances the need for economically feasible strategies, such as natural regeneration, will become even more acute (Holl and Aide 2011). Yet, adopting natural regeneration as a management tool is challenged by variable rates of ecological succession, particularly at large spatial extents (Zahawi et al. 2014; Brancalion et al. 2016; Caughlin et al. 2019). Developing quantitative models that can forecast spatial variability in natural regeneration is a long-standing and largely unrealized goal in restoration ecology (Brudvig and Catano 2021). Ecological forecasts of ecosystem recovery derived from quantitative models would support land management by identifying sites where natural regeneration is a feasible restoration strategy (Marescot et al. 2013; Chazdon and Guariguata 2016; Dietze et al. 2018; Strassburg et al. 2019; Crouzeilles et al. 2020). However, multiple barriers have impeded the development of forecasting models in restoration ecology. These barriers include multivariate patterns of environmental heterogeneity, the complexity of ecological process models, and the lack of species-level time series data across large spatial extents.

One difficulty in developing forecasts for ecological succession stems from the multivariate, non-linear, and interactive effects of biotic and abiotic factors across scales (Rollinson et al. 2021). Such interactions lead to changing relationships among environmental and biological variables across space and time, thereby making ecological forecasts difficult (Zipkin et al. 2021). Non-parametric methods can overcome difficulties associated with multivariate effects and often show superior performance in ecological predictions compared to regression-based models that quantify effect sizes for each environmental covariate directly (*e.g.*, Barnard et al. 2019). Spatial matching is a non-parametric approach that provides a flexible way to predict an unknown ecological process based on the environmental similarity between geographically distant locations (Kirkman et al. 2013; Adler et al. 2020). This method relies on a similarity score to find a physical, or construct a synthetic, reference site to a focal location where an ecological forecast

is needed (Butsic et al. 2017; Ribas et al. 2021). Spatial matching also allows for hierarchical combinations that can account for environmental variation across multiple scales (Rollinson et al. 2021). For example, Renne et al. (2021) used spatial matching to overcome computational challenges in a cross-scale analysis of individual plant performance as a function of ecosystem water balance. Spatial matching has also enabled causal inference on the effectiveness of policy interventions from observational data (Brandt et al. 2019; Fick et al. 2021; Simler-Williamson and Germino 2022). Interpretable spatial matches based on ecological similarity are likely to benefit model adoption by managers, including potential recognition of model strengths and shortcomings when confronted with local knowledge and observations (Radchuk et al. 2019a). Multi-scale, hierarchical matching is particularly relevant for heterogeneous landscapes where environmental variation crosses scales from regional gradients to locally varying site characteristics (Diaz et al. 1998; Mertes et al. 2020).

In addition to multivariate environmental heterogeneity, the complexity of ecological processes complicates the development of forecasting models. For example, relationships between population dynamics and abiotic drivers at the plot level can be challenging to transfer to other locations (Davies et al. 2011; Applestein et al. 2021). Process-based models are expected to improve forecasting accuracy, relative to phenomenological regression-based models, by representing mechanistic relationships (Purves and Pacala 2008; Dietze 2017; Hefley et al. 2017). Such process-based models often include endogenous feedbacks of population change, such as density dependence, that lead to non-linear system dynamics (Hastings et al. 1993, 2018). Therefore, a fundamental challenge to confronting process models with real data is balancing the trade-off between complex, but more realistic, and parsimonious, but potentially oversimplified models (Clark et al. 2020; Fer et al. 2021). Population models present a potential solution to this trade-off by simplifying ecological complexity while focusing on the population dynamics of a single species (Tredennick et al. 2016). For example, the Gompertz model for unstructured populations (i.e., the per capita growth rate is the same for all individuals in the population, regardless of individual characteristics such as size, genotype, or health status) is a simple, regression-based framework that quantifies growth

rate and density dependence and is widely used to model time series of population data in fisheries and wildlife applications (Rossetto et al. 2015; Barbraud et al. 2018, p. 20; Johnson-Bice et al. 2021). However, despite its potential utility for forecasting plant population recovery after disturbance, the Gompertz model has not been widely used in plant ecology (but see Damgaard et al. 2002; Tredennick et al. 2016).

Data limitation provides one explanation for the relative lack of models to forecast plant population recovery after large-scale disturbances. Whereas field-based monitoring of individual plants is the foundation of plant population ecology, these data are logistically difficult to collect over large spatial and temporal extents (Gurevitch et al. 2016). Trajectories of population-level changes provide an alternative to marking and monitoring individual plants. In some cases, unstructured population models informed by temporal changes in percent cover offer equivalent predictive power to structured population models that rely on individual-level data (Tredennick et al. 2017; Goodsell et al. 2021). The utility of modeling time series of plant cover with unstructured population models, such as the Gompertz model, hints at using remote sensing as a data source for plant demography. Remotely sensed data, such as the multi-decadal, globally extensive Landsat satellite imagery archive, can accurately map species and functional group cover over large areas (Homer et al. 2020; Larson and Tuor 2021). We propose that satellite imagery provides an unprecedented data source to model plant population recovery at broad spatial extents relevant for land management.

In this paper, we use Landsat satellite-derived cover trajectories to forecast population recovery of foundational shrub species (sagebrush, *Artemisia* spp.) in the Western United States. Over the last century, altered wildfire regimes and other disturbance factors have reduced or altered intact sagebrush steppe habitat to nearly half of its former extent (Pyke et al. 2015; Mahood and Balch 2019). Despite active restoration efforts aimed to counteract ecosystem degradation (Pilliod et al. 2017; Copeland et al. 2018), including over US $100 million spent annually, restoration of the sagebrush steppe remains a challenge (James et al. 2013; Knutson et al. 2014). A large proportion of the restoration and conservation efforts aim to assist post-fire recovery of sagebrush stands, which provide wildlife habitat and dominate

large areas of the western US (Miller et al. 2011; Davies et al. 2011; Chambers et al. 2017; Pilliod et al. 2020). The geographical scope of historic degradation and the increasing impacts of altered wildfire regimes call for cost-efficient restoration strategies. Allocating restoration interventions in sagebrush steppe will benefit from spatial forecasts of natural regeneration to limit the geographical scope of potential interventions (James et al. 2013; Copeland et al. 2021; Duchardt et al. 2021).

We used hierarchical spatial matching and regression-based unstructured population growth models to develop spatio-temporal forecasts of sagebrush cover in post-wildfire landscapes that had no documented restoration treatments. We applied our framework to a subset of wildfires that occurred between 1987 and 2007 and evaluate the forecasting accuracy of our approach using out-of-sample validation. By leaving out entire wildfire sites for model validation, we directly quantify how well our models can forecast the recovery (i.e., the trajectory of sagebrush cover post-wildfire) at wildfires where no data are available. Our validation approach corresponds to the management need to make decisions with minimal site-level information on plant demography. We asked the following questions:

(i) How accurately can a simple population growth model, i.e., the Gompertz model, forecast natural regeneration of post-wildfire sagebrush cover?

(ii) How does spatial matching of wildfires combined with the population model improve the forecasting accuracy of natural regeneration?

(iii) Does accounting for within-wildfire heterogeneity improve the forecasting accuracy of natural regeneration?

Methods

The central data source in our study is the National Land Cover Database (NLCD, now rebranded as RCMAP; Rangeland Condition Monitoring Assessment and Projection), which maps the annual cover of plant functional groups at 30-m spatial resolution across the Western US, including the Great Basin ecoregion (Rigge et al. 2019; Homer et al. 2020). The
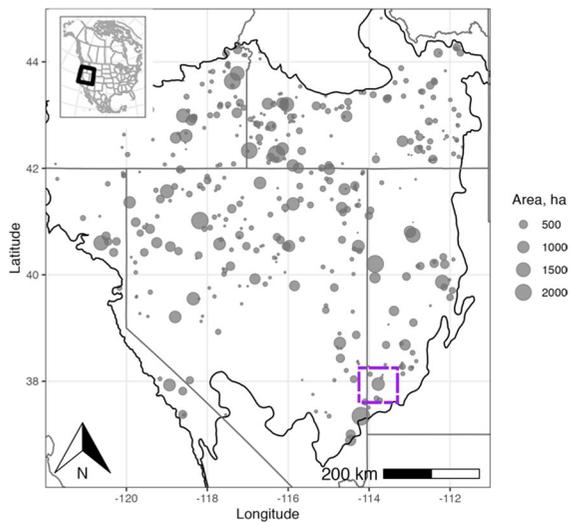
Fig. 1 The extent of the study area showing the Great Basin ecoregion over the US state boundaries (gray lines). Naturally regenerating wildfire polygons are indicated by grey points, with the size of the points indicating the polygon area. Map lines delineate study areas and do not necessarily depict accepted national border lines

NLCD database is derived from the Landsat satellite archive, with back-propagated estimates of sagebrush cover resulting in a time series from 1985 to 2018 with cross-validated accuracy of RMSE at 3.4%

cover and R^2 of 0.63. We focus on modeling the sagebrush fractional component at the genus level (*Artemisia* spp.) as a trade-off between NLCD accuracy and demographic similarity within *Artemisia* spp. (Shultz 2009). The sagebrush fractional component is mostly representative of big sagebrush (*Artemisia tridentata*); but also includes several less common congeneric species with similar demographic traits (Shultz 2009; Rigge et al. 2019). We selected locations that burnt only once since 1950 until present time, had at least 10 years of post-fire recovery, and had no documented restoration treatments after wildfire events (Fig. 1). We used a historic wildfire dataset (Welty and Jeffries 2021) and the Land Treatment Digital Library (Pilliod et al. 2019) to select the sites that met these criteria. As none of our sites received restoration treatments (sensu Holl and Aide 2011), we consider all sites to be naturally regenerating, albeit at different rates. See the Zenodo repository referenced in the Data Availability statement for documented geospatial processing steps. Our selection process resulted in N = 430 wildfire areas (polygons) burnt once between 1987 and 2007 without subsequent wildfires until the end of the NLCD time series (2018). Although some wildfire polygons in our dataset represent a non-treated portion of a larger wildfire, we refer to our sample units as wildfires for the rest
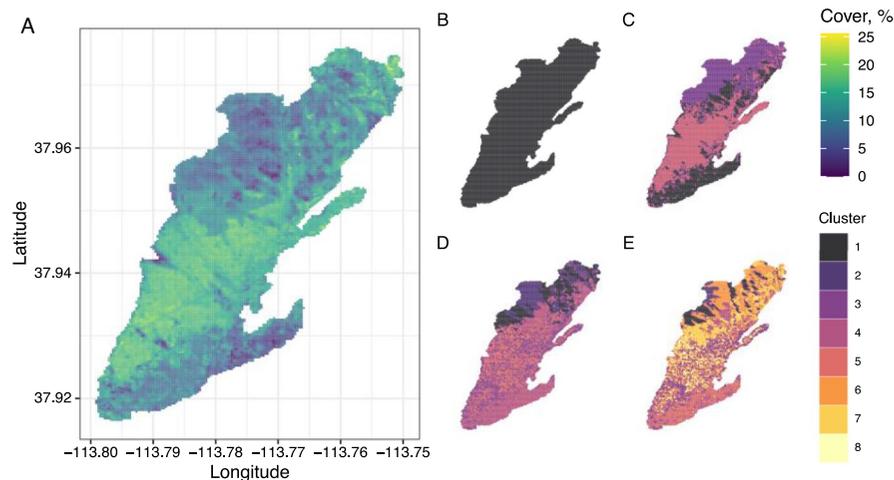

Fig. 2 An example of a wildfire polygon highlighted by the purple dashed line in Fig. 1 with color intensity indicating sagebrush cover before the wildfire event based on the National Land Cover Database (**A**). Clusters of pixels within the same wildfire (**B**–**E**) grouped by similarity in topography, soil organic carbon, and pre-disturbance sagebrush cover. Starting from a single cluster (**B**) where pixels are assumed identical, (**C**–**E**) show a progressively higher degree of pixel clustering, with the color indicating cluster identity

of the manuscript. The area of wildfires ranged from 41 to 2465 ha, resulting in a total of 1,269,744 wildfire pixels from the NLCD time series (Figs. 1 & 2). The length of the time series ranged between 11 and 31 years since a wildfire event.

Hierarchical spatial matching

The Great Basin ecoregion is characterized by a high degree of environmental variation at both local and regional extents (from less than 0.1 to $> 900,000$ km², including elevation, soil, and climate patterns. We used spatial matching to forecast sagebrush cover trajectories for each wildfire by identifying environmentally similar reference locations. We limited the number of possible covariates in spatial matching to variables with demonstrated relationships to sagebrush population dynamics. Specifically, higher elevation and higher annual precipitation positively correlate with sagebrush regeneration, while temperature extremes and heat load are associated with slower recovery and lower sagebrush density (Knutson et al. 2014; Tredennick et al. 2016; Requena-Mullor et al. 2019). Similarly, soil characteristics and its water holding capacity, particularly in early spring, can determine sagebrush seedling recruitment and juvenile survival (Shriver et al. 2019; O'Connor et al. 2020). Based on these results, we extracted remotely sensed data products, including topographic (Farr et al. 2007; Theobald et al. 2015), climate (Daly et al. 2015), soil (Chaney et al. 2019; NASA: http://nsidc.org/data/smap), and pre-wildfire sagebrush (Homer et al. 2020) to develop covariates for matching (see Appendix S1: Table S1 for the full list of covariates used in the spatial analysis).

The spatial matching procedure included two successive and nested steps. First, at the wildfire level, the spatial matching included finding a reference wildfire, i.e., a biophysically similar site, from the entire dataset based on a suite of abiotic and biotic covariates (i.e., wildfire-to-wildfire matching, Appendix S1: Table S1). We used the shortest Mahalanobis distance metric to form each pair of ecologically similar wildfires. The Mahalanobis distance accounts for the covariance between the environmental factors and represents a distance measure in an orthogonal multivariate space where covariates are centered on their means and pairwise correlations between them are zero (McCune et al. 2002). Second, to account

for within-wildfire variation, i.e., within each wildfire polygon, we grouped ecologically similar pixels into clusters based on a set of abiotic and biotic covariates at the pixel level (Table S1). Based on the identified clusters within each wildfire, we matched two environmentally similar clusters from the reference and focal wildfires using the shortest pairwise Mahalanobis distance between the means of cluster-level covariates. To group environmentally and ecologically similar pixels into clusters, we scaled and centered pixel-level values and applied *k-means* algorithm with the number of clusters, M, ranging between 2 and 14. Our goal with *k-means* clustering was to quantify within-wildfire heterogeneity at progressively finer resolution. The maximum number of clusters, $M = 14$, was dictated by the ability of *k-means* algorithm to converge for each wildfire when grouping pixel-level covariates under increasingly higher number of clusters. As a result, the average area of clusters decreased with the increasing M, i.e., the number of distinct spatial units within a wildfire. Given the average wildfire area at 265.7 ha, the average area of the spatial units under $M = 3$, 6, 14 clusters was at 88.5, 44.3, and 17.7 ha., respectively.

Model fitting

The population process in our models hinges on the Gompertz growth model for single-species population dynamics. The discrete-time Gompertz equation can be written as $\frac{y_{t+1}}{y_t} = \exp(\alpha)y_t^\delta$, where α and δ are parameters for growth and density dependence, respectively, and y_t is the population size at time t. The model has been widely applied to model population time series in wildlife study systems with demonstrated inferential and forecasting value (Zhang 1997; Lebreton and Gimenez 2013; Koons et al. 2015). Population dynamics under the Gompertz model include exponential growth rates at low population densities that slow down as population size increases (Gamito 1998). While the model accounts for nonlinear growth, it can be parametrized in a regression-based framework on the log–log scale (Eq. 1).

Our modeling work borrows from previous studies that used generalized linear models (GLMs) and the Gompertz model to predict population cover using NLCD (Tredennick et al. 2016). The NLCD data for

sagebrush cover is an integer-valued number format, which motivated several of our modeling decisions. First, we used a Poisson generalized linear model for count data to be consistent with the data generation process (Tredennick et al. 2016). Second, because the Gompertz model in a Poisson regression requires a natural log-transformation of current cover in year t, we excluded pixels with zero values from the predictor of Eq. 1, resulting in $y_t > 0$, and left the response variable intact ($y_{t+1} \geq 0$). The exclusion of zero-valued observations is demographically justifiable for Eq. 1: a transition of the population cover in pixel p from zero in the current year t ($y_{t,p} = 0$) to a positive value in the next year ($y_{t+1,p} > 0$) could be due to seeds or seedlings present in the pixel that are not detectable via satellite imagery. We fitted a Poisson GLM with a log-link function (Eq. 1) to obtain the population growth and density dependence parameters, α and δ, respectively. To account for spatial heterogeneity within wildfires we added cluster identity of a pixel as a random effect and fit Poisson generalized linear mixed model (GLMM) to the same response (random effect indices in Eqs. 1 & 2 not shown).

To estimate sagebrush cover immediately after a wildfire event (the initial population cover, θ_0), we subset the sagebrush trajectories to include only the first five years after a wildfire and fit a Poisson GLM (at the regional and wildfire levels) and GLMM (at the level of clustered pixels) models with a log-link function using time since wildfire as a predictor and cluster as a random effect (Eq. 2). In the absence of subsequent wildfires this model assumed an exponential, density-independent growth of sagebrush with rate θ during the initial years post-wildfire event and was parametrized using the first five years of the sagebrush cover trajectory, where the initial post-wildfire population size, θ_0, is estimated by the intercept.

$$y_{t+1} \sim Poisson\left(\exp(\alpha + \delta \log\left(y_t \right) + \log\left(y_t \right)) \right) \quad (1)$$

$$y_t \sim Poisson\left(\exp(\theta_0 + \theta t) \right), \text{ for } t = 1, 2, \ldots, 5 \quad (2)$$

Forecasting and accuracy assessment

In order to account for environmental variation, we fit the statistical models following Eqs. 1 & 2 at various levels of spatial heterogeneity represented by the *k-means*-based clusters. In total, we fit the regional model and set of models for each wildfire ($N = 430$) at each level of spatial heterogeneity ($M = 14$), resulting in 6021 models (i.e., 430×14 and the regional model). We incorporated within-wildfire spatial heterogeneity as random effects corresponding to variation at the level of clustered pixels. Consequently, the terms of the equations and the estimated parameters corresponding to growth and density dependence were indexed by i-th wildfire and j-th cluster of pixels within that wildfire, i.e., $\alpha_{i,j}$ and $\delta_{i,j}$. The formulation of the Gompertz growth model in Eq. 1 and initial values parametrized statistically following Eq. 2 allowed us to project sagebrush cover in time using an analytical solution of the Gompertz model (see Appendix S1 for more details):

$$u(t)_{[i,j]} = K_{[m,n]} \exp \left(C_{[m,n]} e^{\delta_{[m,n]} t} \right) \quad (3)$$

where, $u(t)$ is the predicted sagebrush cover in time t, K is a population estimated carrying capacity calculated as $\exp(-\alpha/\delta)$, and C is a constant equal to $\log(\theta_0/K)$. Indices i and j correspond to the wildfire and the cluster of pixels within that wildfire, respectively. For the out-of-sample forecasts, indices m and n in Eq. 3 indicate spatially matched wildfire m to i and cluster n to cluster j based on environmental similarity.

We evaluated the forecasting accuracy by estimating out-of-sample prediction errors according to our three research questions. To address the first question, how well the Gompertz model can predict sagebrush cover after a wildfire event, we randomly subsampled 5% of the pixels from each dataset (without replacement) and obtained estimates of sagebrush natural regeneration at the regional level. We validated the regional model by calculating the errors between regional predictions and sagebrush cover trajectories in each wildfire. This approach represented ecological forecasting using pooled, region-wide population parameters only. To address the second question, how does spatial matching of wildfires improve the regional model, we generated predictions for each wildfire using population parameters transferred from the reference wildfire using the matching steps at the wildfire polygon level. Lastly, we matched two environmentally similar clusters of pixels between the reference and focal wildfires identified at the wildfire

polygon level to test how within-wildfire variation impacts forecasting accuracy.

We calculated several metrics of forecasting accuracy to summarize in- and out-of-sample errors. To account for wildfires that occurred in different years and had varying lengths time series, we calculated mean absolute error (MAE) and root-mean-squared error (RMSE) ten years after a wildfire event (Eqs. 4 & 5). The mean absolute error weighs all the errors in the dataset equally, while the root mean squared error puts more weight on larger errors than smaller deviations between observed and predicted data. We also calculated proportional MAE and RMSE metrics to put the errors in each site relative to its pre-wildfire average sagebrush cover (Eqs. 6 & 7). Second, we computed the Bias of the predictions for each year to estimate the directionality of the error and how it changed over the forecast time (Eq. 8). We averaged the pixel-level sagebrush cover values within each wildfire for the validation, and present accuracy metrics based on the difference between our forecasts and the spatial average of sagebrush cover in each wildfire.

$$MAE = \frac{1}{N} \sum_{i=1}^{N} |e_i| \qquad (4)$$

$$RMSE = \sqrt{\frac{1}{N} \sum_{i=1}^{N} (e_i)^2} \qquad (5)$$

$$MAE\% = \frac{1}{N} \sum_{i=1}^{N} \frac{|e_i|}{K_i^*} \qquad (6)$$

$$RMSE\% = \sqrt{\frac{1}{N} \sum_{i=1}^{N} \frac{(e_i)^2}{K_i^*}} \qquad (7)$$

$$BIAS_t = \frac{1}{N} \sum_{i=1}^{N} |e_{i,t}|, \text{ for } t = 0, 1, \ldots, T \qquad (8)$$

where $e_i = (\hat{y}_i - \bar{y}_i)$ is the difference between the predicted, $\hat{y}$, and an average observed sagebrush cover, $\bar{y}$, in wildfire i. For models where we accounted for within-wildfire heterogeneity, we calculated an average error per wildfire as $e_i = \sum (\hat{y}_{i,j} - \bar{y}_{i,j})/M$, where

j indicates the cluster identity and $M \in \{2, 3, \ldots, 14\}$ is the number of clusters. The MAE% and RMSE% metrics show proportional error relative to the wildfire average cover before the wildfire event, K^*.

We used '*brms*' package to fit the regional model and the '*lme4*' package for wildfire and cluster level models to obtain the estimates of the population parameters (Bates et al. 2007; Bürkner 2017). For all data processing and figures we used R software (R Core Team 2021), including the following packages: '*raster*', '*sf*', '*tidyverse*', and '*ggplot2*' (Wickham 2011; Hijmans et al. 2015, p. 20; Pebesma 2018; Wickham et al. 2019).

Results

How accurately can a simple population growth model, i.e., the Gompertz model, forecast natural regeneration of post-wildfire sagebrush cover?

The regional model trained on 5% of the pixels sampled randomly from each post-wildfire polygon predicted an asymptotic sagebrush cover of 16.6% (CI95%: 9 – 25; SD = 4.0). In the absence of
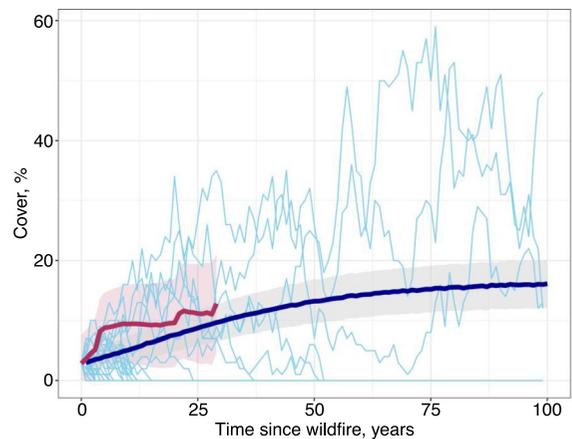

Fig. 3 The results of the regional model representing the Gompertz population growth model fit to a subsample of pixels from each wildfire. The time series plot shows the NLCD and predicted sagebrush cover at the regional level. The red and blue thick lines show the average NLCD and predicted sagebrush trajectories, respectively, with shaded regions corresponding to one standard deviation (SD) around the mean. The thin blue lines illustrate 30 stochastic realizations of sagebrush cover over time using a subset of population parameters sampled from the posterior distribution

repeated wildfires, sagebrush recovery trajectories at the regional level followed a monotonic logistic population growth curve (Fig. 3, blue thick line). In contrast to pixel-level stochastic realizations that are highly variable, the average recovery is predicted to be positive but slow, with an estimated recovery time, indicated by the sagebrush trajectory reaching a plateau, of more than 80 years. The predicted asymptotic sagebrush cover (16.6%) was greater compared to the average pre-wildfire sagebrush cover across sites at 11.6% (5% and 95% quantiles at 3.0% and 20.5%, respectively). We attribute this difference of 4% in cover to the dramatic increase in sagebrush cover following initial years after the wildfire in the NLCD (Fig. 3): increasing the intrinsic growth rate under constant density-dependence in the Gompertz model would lead to higher asymptotic cover value at equilibrium. Nevertheless, the NLCD cover estimates were within 2 SD of the predictions in asymptotic cover. The MAE for the regional model was higher than the wildfire- and cluster-level models regardless of whether the validation data set was in- or out-of-sample. For the regional model, the average out-of-sample MAE ten years after a wildfire event was 7.5% cover (±5.1% SD), and the proportional error was 0.65. The regional predictions considerably underestimated sagebrush cover during the initial years

after a wildfire event, although the negative bias in the predictions diminished over time (Fig. 4, trajectory labeled as "Region"). The median bias was greatest seven years after a wildfire event. Specifically, the regional model underestimated the averaged sagebrush cover by -7.3% (CI95%: -14.92 – -0.43; SD=4.76), and this value decreased over time to -2.84% cover (CI95%: -12.02 – 6.03; SD=3.8) in the last year of the validation data set.

How does spatial matching of wildfires combined with the population model improve the forecasting accuracy of natural regeneration?

Matching pairs of environmentally similar wildfires led to a nearly two-fold reduction in out-of-sample MAE, relative to the regional model. The MAE for sagebrush cover predicted using data from spatially matched wildfires was 4.8% (±5.2% SD) with a proportional error of 0.49 (Fig. 5, Appendix S1: Table S2). The bias observed at the level of matched wildfires was considerably lower than the regional predictions. However, the forecasts still underpredicted sagebrush cover trajectories for almost the entire duration of the validation dataset (Fig. 4, trajectory labeled as "Site"). The greatest bias was between the 6th and 11th years at -2.7%, and the temporal patterns in the bias were comparable to the regional model.

Fig. 4 Bias in the out-of-sample forecasts of sagebrush cover by each of the tested environmental clustering scheme complexity. The cluster number refers to the number of environmental clusters used in the k-means algorithm for spatial matching. The bias is calculated as the mean of the out-of-sample errors for each year. The colored lines indicate average bias across all wildfires, whereas the shaded regions show one standard deviation (SD) around the mean
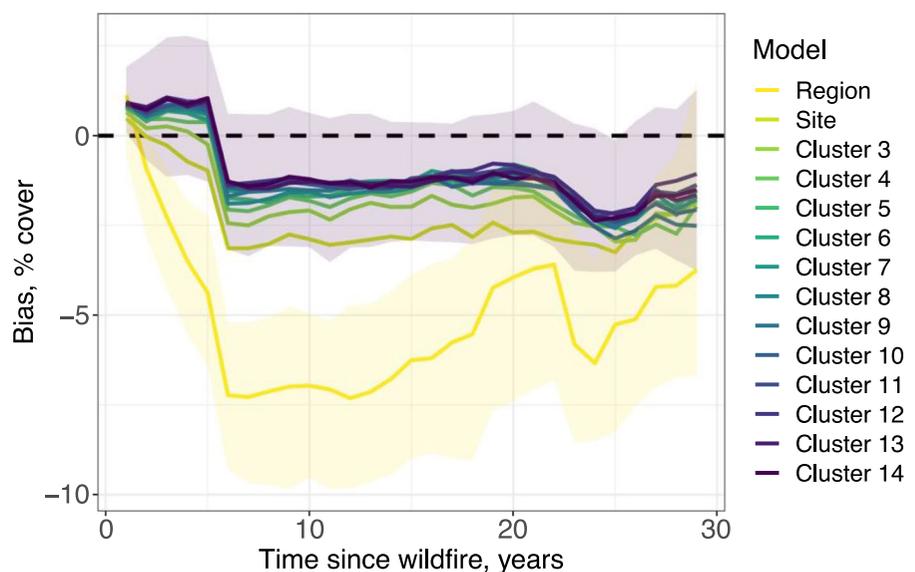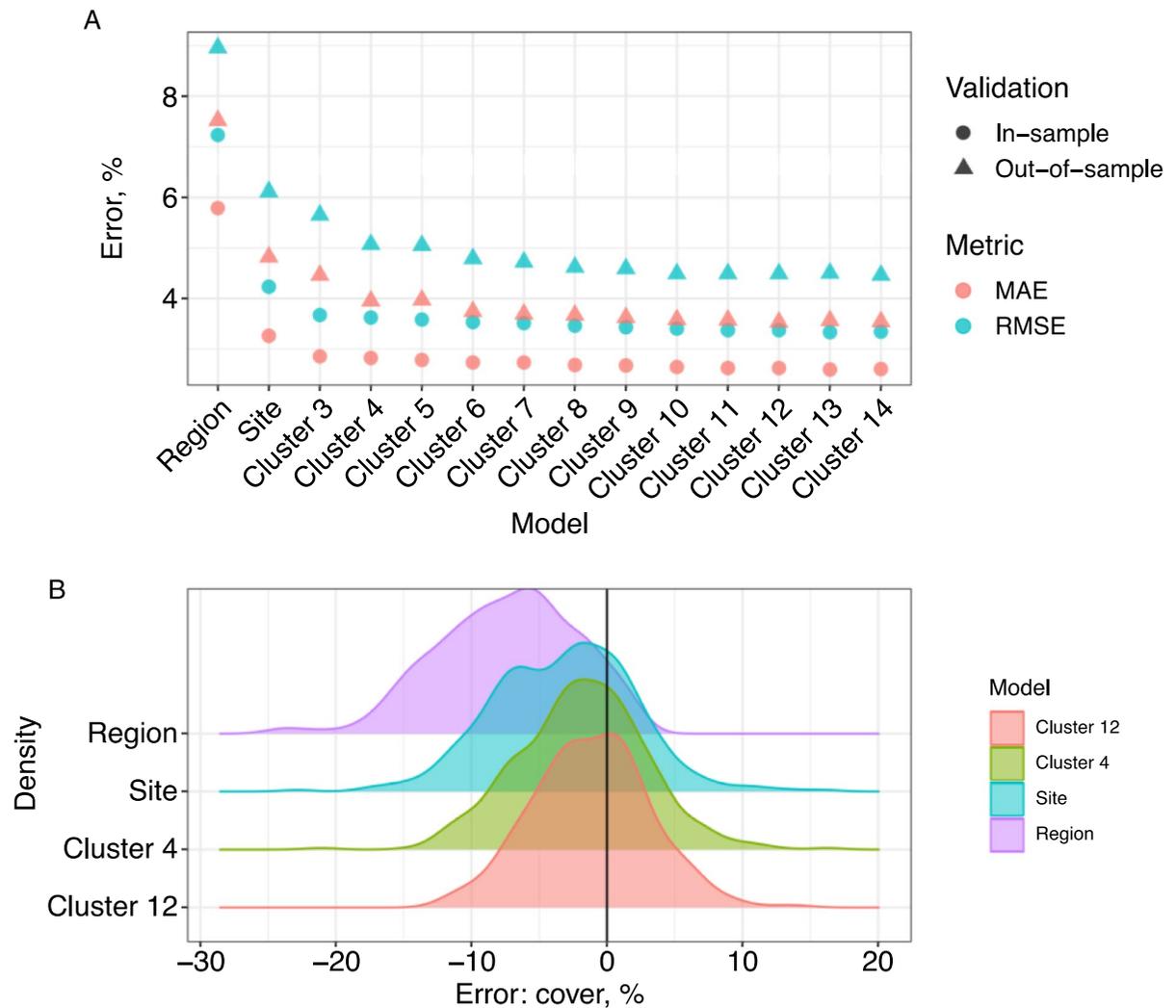
Fig. 5 The relationship between forecasting accuracy and environmental clustering scheme complexity. (A) shows the error between predicted and observed sagebrush cover 10 years after a wildfire event. (B) shows the distribution of errors across wildfires calculated as the difference between the predicted and observed average trajectories

Does further accounting for within-wildfire heterogeneity improve the forecasting accuracy of natural regeneration?

The addition of random effects to the GLMs at the level of within-wildfire variation, i.e., the results of *k-means* clustering corresponding to within-wildfire heterogeneity, resulted in a reduction in the errors compared to the wildfire-level models (Fig. 5). Overall, a higher number of clusters led to improvements in MAE, MAE%, and bias (Appendix S1: Table S2), but the pattern was non-linear and led to diminishing improvements as the number within-wildfire clusters increased. After we included the random effects and spatial matching at the wildfire and within-wildfire levels, the MAE was reduced to 3.5%, with a marginally improved proportional error of 0.48. Similarly, the standard deviation of the errors was the smallest for the model with 14 clusters. The bias in these errors was marginally positive initially, indicating that models overpredicted sagebrush cover. Negative bias began the 6th year after a wildfire, and was smallest in the model with 14 clusters. After the 6th year, the trend stabilized at -1.17% (CI95%: -8.43 – 6.25;

SD = 4.58) for the subsequent years of the time series (Fig. 4, trajectories labeled as "Cluster 3–14"). As the number of clusters increased, the forecasting accuracy also increased, indicating the benefits of accounting for environmental heterogeneity when matching environmentally similar wildfires and clusters of pixels. However, the improvements in forecasting accuracy largely plateaued in models with ten clusters or greater.

Discussion

In this study, we combined remotely sensed data with population models to forecast natural regeneration of sagebrush after wildfire, foundational shrub species in the Great Basin. Our study represents a step towards developing models for natural regeneration that could be used to help prioritize restoration efforts in the sagebrush steppe (Duchardt et al. 2021). Ecological forecasts of post-wildfire natural regeneration could point land managers to where the recovery potential is high and sagebrush can recover with minimal intervention. The relatively low level of absolute error (i.e., MAE 3.54% cover for the Cluster 14 model) achieved by the best-performing model illustrates how the combination of simple and robust analytical tools can result in satisfactory forecasting accuracy with relevance for land management decisions. In contrast to field plot-level studies that suggest the rate of natural regeneration of sagebrush steppe is low and vegetation treatment effects are highly variable (Knutson et al. 2014; Copeland et al. 2018; Germino et al. 2018), our analysis at the regional level demonstrates that on average, sagebrush population recovery after a single wildfire tends to follow similar trajectories.

The regional-level model provides insights into natural regeneration processes in sagebrush at a broad geographical scale, despite relatively low forecasting accuracy. In the absence of repeated wildfires, our results suggest that sagebrush recovery is likely to be slow, with an estimated recovery time of more than 80 years (Fig. 3). Illustrative of this pattern, ten years after a wildfire, the average recovery across all sites was 62% relative to the pre-wildfire sagebrush cover, while only 14% of the sites were predicted to recover at or above the pre-wildfire levels at this stage. The estimated rate is lower than the rate of natural regeneration characteristic of higher-elevation

sagebrush populations, where the recovery could take 20–45 years (Ziegenhagen 2003; Baker 2006; Ziegenhagen and Miller 2009). Although the NLCD represents sagebrush at the genus level, the mean and median average elevation across our sites was under 1700 m and is likely to be more representative of the Wyoming big sagebrush (*A.t. wyomingensis*). Wyoming big sagebrush in lower elevation landscapes historically has longer fire-return intervals and slower rates of natural regeneration (Miller et al. 2011; Bates et al. 2020), making them vulnerable to altered fire regimes and ecosystem transformation (Mahood and Balch 2019).

The negative bias in the regional model supports the evidence from previous field studies that satellite-derived estimates of shrub cover, such as the NLCD, may overestimate cover in the initial stages, i.e., 1–3 years, after a wildfire event (Applestein and Germino 2021). Starting from the second year post-wildfire, our model's underestimation of sagebrush cover, relative to NLCD time series, likely emerges from the model's representation of demography. The combination of growth rate and density dependence feedbacks in the Gompertz model predicts considerably slower recovery in the early stages of regeneration than that observed in the NLCD. We consider this underestimation a feature of the Gompertz model, not an analytical shortcoming, as our biologically meaningful models atone for the tendency in the NLCD data to overestimate early recovery, likely due to satellite measurement error (Applestein and Germino 2021). The mortality of young sagebrush recruits during the transient stages of regeneration post-wildfire is another demographic mechanism that may slow down the rate of natural regeneration and is undetectable from the analysis of satellite data alone (Shriver et al. 2019). In addition to demographic mechanisms, errors in the NLCD data, including potential missed detections of small-statured sagebrush and errors propagated from the Landsat spectral reflectance, may lead to inflated estimates of density dependence and contribute to the negative trend in forecasting bias (Lebreton and Gimenez 2013). Explicitly accounting for noise in the statistical Gompertz models will likely improve the future forecasts of post-wildfire regeneration of sagebrush populations.

Our framework corresponds to a scenario where land managers must decide on restoration action immediately after a wildfire, with minimal

site-specific data on sagebrush population dynamics. The capacity to achieve transferable forecasts across the Great Basin ecoregion relied upon spatial matching to account for environmental heterogeneity. The spatial matching of wildfires and within-wildfire pixel clusters revealed that accounting for spatial heterogeneity by dividing wildfires into 5–10 environmentally distinct units may be a suitable scale for out-of-sample sagebrush cover forecasts (Fig. 5). When evaluating the performance of the models ten years after a wildfire, spatial matching enabled absolute error in sagebrush forecasts within 1% cover of those using the in-sample predictions (Appendix S1: Table S2). We observed an increasing improvement in forecasting accuracy from the regional level to higher clustering levels within wildfires. This trend illustrates how spatial heterogeneity within and among wildfires driven by climate, soil properties, topography, and pre-disturbance conditions can represent a significant source of variation in plant demography and forecasting errors. Our results suggest that an optimal spatial grain for forecasting natural regeneration and restoration planning may include coarsely divided spatial units within wildfires, while increasingly fine-scale spatial units bear diminishing returns and may present logistical and analytical costs.

We observed the most significant reduction in the forecast errors between the regional and wildfire-level models with subsequent diminishing improvements after accounting for heterogeneity at progressively finer spatial grain (Fig. 5). While within-wildfire variation proved important, the relationship between the errors and the degree of spatial clustering largely plateaued beyond ten clusters, contrasting with experimental and observational evidence that highlights local conditions as a strong driver of post-wildfire sagebrush recovery (*e.g.*, Arkle et al. 2022; Germino et al. 2018). Specifically, our results suggest that land management units, *e.g.*, relatively small wildfires or grazing allotments, could be a representative spatial grain to account for spatial heterogeneity when forecasting an average trajectory for the recovery of sagebrush cover. One potential explanation for this discrepancy is that cover trajectories reflect temporal changes that integrate over the entire plant life cycle. In contrast, focusing on a single demographic stage, *e.g.*, individual recruits or seedlings, leaves more room for demographic stochasticity and stage-specific environmental responses (Yang et al. 2022).

Combining the Gompertz growth model with the NLCD trajectories and hierarchical spatial matching enabled a scalable approach to quantify the population process underpinning natural regeneration in sagebrush across the Great Basin. Our approach estimates biologically interpretable parameters at large spatial extents, a historically challenging task in plant ecology (but see Schultz et al. 2022; Shriver et al. 2019). These parameters include population growth rate and density dependence, both relevant to address applied and theoretical questions. For example, the intrinsic growth rate of a foundational shrub species directly links to ecosystem resilience, a characteristic that is central to conservation management and ecosystem integrity (Chambers et al. 2017). A cross-scale analysis of sagebrush resilience could aid resource managers in determining restoration plans based on the already established management guidelines of habitat resilience and resistance (Chambers et al. 2019; Arkle et al. 2022). Our study qualitatively expands previous efforts in predicting sagebrush steppe resilience (mainly based on biophysical site characteristics) by incorporating endogenous population processes that are quantified from observed cover trajectories following a wildfire event. Studies that relate satellite-derived population dynamics to biophysical conditions will improve our understanding of natural regeneration in the sagebrush steppe. For example, in conjunction with site-specific biophysical data, predicted positive recovery in low-resilience sites could provide valuable insights to improve the forecasting models or reveal biological relationships that warrant further empirical investigations. Lastly, the strength of density dependence in a population quantified by the Gompertz model can be a determinant of multiple dimensions of population and community stability, including resistance and persistence responses to environmental variation (Harrison 1979; Radchuk et al. 2019b).

Remote sensing opens new ways to detect and analyze density dependence and coexistence in natural ecosystems on a large scale. Nevertheless, remotely sensed data also presents new problems related to imperfect detection of vegetation cover from space-borne satellites (Caughlin et al. 2021). In the context of the NLCD vegetation cover trajectories, some error in cover measurements is likely inescapable (Rigge et al. 2019; Applestein and Germino 2021). Methods that can account for imperfect

detection when modeling population trends, such as state-space models widely used in wildlife population ecology are likely to prove invaluable for quantifying plant population trends from remotely sensed data (*e.g.*, Dennis et al. 2006). As an example, models that rely on the state-space approach are promising to improve ecological inference and predictions (Auger-Méthé et al. 2021). The state-space approach would help disentangle measurement errors from the endogenous and exogenous sources of variation (Dietze 2017), and allow for a more nuanced analysis of spatio-temporal demographic shifts (Schultz et al. 2022). Taxa-specific time series data, such as the Landsat-derived percent cover data used in our study, are increasingly available (Gudex-Cross et al. 2017; Singh et al. 2020). However, when species-specific time series data are not available, our approach can be applied to taxonomically coarse data, such as time series of per cent tree cover. For example, Caughlin et al. (2021) modeled forest recovery using the logistic growth model. A combination of remote sensing, spatial matching, and state-space models that account for temporal autocorrelation will likely expand the forecasting horizon for population changes (Adler et al. 2020).

In the context of the Great Basin ecological restoration, forecasts of natural regeneration can be instrumental during the time-sensitive planning and implementation of management interventions after a wildfire (Bradford et al. 2020). A prompt management response to a wildfire event can be critical given the time-sensitive decisions in light of the reduced resistance to cheatgrass (*Bromus tectorum*) invasions or favorable weather windows for a restoration treatment (Applestein et al. 2021; Copeland et al. 2021; Pilliod et al. 2021). Our forecasting framework enables early predictions of natural regeneration without local field data, making the information available for the initial management response. To date, managers and practitioners already use landscape and wildfire information that can help predict the likelihood of natural regeneration, including topographic information, burn severity, and site resilience indices (USDI 2007; Arkle et al. 2014). Additional ecological data is available from the NLCD and Land Treatment Exploration Tool that provide pre-wildfire estimates of sagebrush cover and management-oriented site characteristics (Pilliod et al. 2018). To further assist management decisions, our study contributes quantitative

forecasts of sagebrush population recovery that could be used to develop rapid response plans for restoration, with minimal data collection.

The predictions can also readily integrate site-specific information that will have become available during the first years of monitoring, paving the way to improvements in the forecasts over time and adaptive management practices (Applestein et al. 2022; Brudvig and Catano 2021; Dietze 2017). The early-stage forecast based on spatial matching of the reference and the focal wildfires assumes that the latter follows the same recovery trajectory as the former based on ecological similarities between them. However, we suggest that empirically estimated sagebrush cover based on local ecological monitoring can substitute the statistically estimated parameter (i.e., θ_0 in Eqs. 2 & 3) to reflect the initial population cover at the onset of recovery. Similarly, post-wildfire monitoring could provide an updated, site-specific parameter for the density-independent population growth, α, indicating the direction of a growth trajectory and how fast the population may approach its predicted equilibrium. Post-wildfire monitoring data will be essential to reflect the effect of local climate fluctuations and site-specific biotic conditions that can dramatically change long-term population dynamics (Shriver et al. 2019; O'Connor et al. 2020). Importantly, forecasts may point to post-wildfire areas with high resilience and recovery potential that may obviate the need to apply active restoration measures and reallocate resources to other areas. Taken together, the initial and iteratively improved forecasts of resilience in the foundational shrub species provide a platform for an adaptive management framework and productive feedback between ecological monitoring, modeling, and decision making (McCord and Pilliod 2021).

Our approach provides modeling tools for forecasting, following calls to advance simple and transparent ecological forecasts (Dietze et al. 2018; Shriver et al. 2018). Several improvements are within reach to adapt our framework to local applications and enhance forecasting accuracy. These may include: (i) improved remotely sensed data products and statistical methods to account for measurement error (Allred et al. 2021); (ii) informing predictive models with local knowledge and monitoring data (McCord and Pilliod 2021); and improving spatial matching without the necessity to refit the statistical models. For example, combining

spatial and temporal matching may address differences among wildfires separated by decades as climate change continues (Kleinhesselink and Adler 2018). Non-parametric matching can also utilize other remotely sensed data, including the occurrence or abundance of invasive annual grasses (*e.g.*, *Bromus tectorum*) that can affect the recovery. Finally, analytical additions to the framework could include scenarios of repeated wildfires, reduced fire-return intervals, and non-stationary ecological interactions that evolve with changing disturbance regimes (Mahood and Balch 2019).

Conclusions

The presented forecasting framework combines satellite information, spatial matching and simple population process models that can be readily integrated into management scenarios and support local decision-making. In contrast to land cover change methods that rely on detecting linear trends (*e.g.*, Shi et al. 2022), the Gompertz model represents biologically meaningful processes, including leveling off for populations near carrying capacity. The Gompertz model is also straightforward to fit using widely available software packages for generalized linear models (GLMs). In conjunction with the Gompertz model, spatial matching can account for regional heterogeneity by incorporating diverse sources of information. Our spatial matching approach could be adapted to integrate experiential and traditional ecological knowledge, providing opportunities for cross-disciplinary collaborations and co-development of management strategies (Berkes et al. 2000; Kimmerer 2011; Fleischman et al. 2022). Altogether, our approach provides scalable forecasts of natural regeneration to support cost-efficient restoration strategies in post-wildfire landscapes.

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Data availability The data used in the manuscript are already publicly available and can be accessed from Homer et al. 2020, Pilliod et al. 2019, Welty et al. 2021 (full citations in the Reference section). The data processing and analysis R scripts are available from the Zenodo code repository (10.5281/zenodo.7737647).

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

References

Adler PB, White EP, Cortez MH (2020) Matching the forecast horizon with the relevant spatial and temporal processes and data sources. Ecography 43:1729–1739

Allred BW, Bestelmeyer BT, Boyd CS et al (2021) Improving Landsat predictions of rangeland fractional cover with multitask learning and uncertainty. Methods Ecol Evol 12:841–849

Applestein C, Germino MJ (2021) Detecting shrub recovery in sagebrush steppe: comparing Landsat-derived maps with field data on historical wildfires. Fire Ecol 17:5

Applestein C, Caughlin TT, Germino MJ (2021) Weather affects post-fire recovery of sagebrush-steppe communities and model transferability among sites. Ecosphere 12:e03446

Applestein C, Caughlin TT, Germino MJ (2022) Bayesian modeling can facilitate adaptive management in restoration. Restor Ecol 30:e13596

Arkle RS, Pilliod DS, Hanser SE et al (2014) Quantifying restoration effectiveness using multi-scale habitat models: implications for sage-grouse in the Great Basin. Ecosphere 5:art31

Arkle RS, Pilliod DS, Germino MJ et al (2022) Reestablishing a foundational species: Limitations on post-wildfire sagebrush seedling establishment. Ecosphere 13:e4195

Auger-Méthé M, Newman K, Cole D et al (2021) A guide to state–space modeling of ecological time series. Ecol Monogr 91:1470

Baker WL (2006) Fire and restoration of sagebrush ecosystems. Wildl Soc Bull 34:177–185

Barbraud C, Bertrand A, Bouchón M et al (2018) Density dependence, prey accessibility and prey depletion by fisheries drive Peruvian seabird population dynamics. Ecography 41:1092–1102

Barnard DM, Germino MJ, Pilliod DS et al (2019) Cannot see the random forest for the decision trees: selecting predictive models for restoration ecology. Restor Ecol 27:1053–1063

Bates D, Sarkar D, Bates MD, Matrix L (2007) The lme4 package. R package version 2:74. https://doi.org/10.18637/jss.v067.i01

Bates JD, Boyd CS, Davies KW (2020) Longer-term post-fire succession on Wyoming big sagebrush steppe. Int J Wildland Fire 29:229

Berkes F, Colding J, Folke C (2000) Rediscovery of traditional ecological knowledge as adaptive management. Ecol Appl 10:1251–1262

Bradford JB, Weltzin J, Mccormick M et al (2020) Ecological forecasting—21st century science for 21st century management. US Geol Surv. https://doi.org/10.3133/ofr20201073

Brancalion PH, Schweizer D, Gaudare U et al (2016) Balancing economic costs and ecological outcomes of passive and active restoration in agricultural landscapes: the case of Brazil. Biotropica 48:856–867

Brandt JS, Radeloff V, Allendorf T et al (2019) Effects of ecotourism on forest loss in the Himalayan biodiversity hotspot based on counterfactual analyses. Conserv Biol 33:1318–1328

Brudvig LA, Catano CP (2021) Prediction and uncertainty in restoration science. Restor Ecol. https://doi.org/10.1111/rec.13380

Bürkner P-C (2017) brms: An R package for Bayesian multilevel models using Stan. J Stat Softw 80:1–28

Butsic V, Lewis DJ, Radeloff VC et al (2017) Quasi-experimental methods enable stronger inferences from observational data in ecology. Basic Appl Ecol 19:1–10

Caughlin TT, de la Peña-Domene M, Martínez-Garza C (2019) Demographic costs and benefits of natural regeneration during tropical forest restoration. Ecol Lett 22:34–44

Caughlin TT, Barber C, Asner GP et al (2021) Monitoring tropical forest succession at landscape scales despite uncertainty in Landsat time series. Ecol Appl 31:e02208

Chambers JC, Maestas JD, Pyke DA et al (2017) Using resilience and resistance concepts to manage persistent threats to sagebrush ecosystems and greater sage-grouse. Rangel Ecol Manag 70:149–164

Chambers JC, Brooks ML, Germino MJ et al (2019) Operationalizing resilience and resistance concepts to address invasive grass-fire cycles. Front Ecol Evol 7:185

Chaney NW, Minasny B, Herman JD et al (2019) POLARIS soil properties: 30-m probabilistic maps of soil properties over the contiguous United States. Water Resour Res 55:2916–2938

Chazdon RL, Guariguata MR (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48:716–730

Clark AT, Ann Turnbull L, Tredennick A et al (2020) Predicting species abundances in a grassland biodiversity experiment: trade-offs between model complexity and generality. J Ecol 108:774–787

Copeland SM, Munson SM, Pilliod DS et al (2018) Long-term trends in restoration and associated land treatments in the southwestern United States: vegetation treatment trends related to restoration. Restor Ecol 26:311–322

Copeland SM, Baughman OW, Boyd CS et al (2021) Improving restoration success through a precision restoration framework. Restor Ecol 29:e13348

Crouzeilles R, Beyer HL, Monteiro LM et al (2020) Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. Conserv Lett 13:e12709

Daly C, Smith JI, Olson KV (2015) Mapping atmospheric moisture climatologies across the conterminous United States. PLoS ONE 10:e0141140

Damgaard C, Weiner J, Nagashima H (2002) Modelling individual growth and competition in plant populations: growth curves of Chenopodium album at two densities. J Ecol 90:666–671

Davies KW, Boyd CS, Beck JL et al (2011) Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biol Conserv 144:2573–2584

Dennis B, Ponciano JM, Lele SR et al (2006) Estimating density dependence, process noise, and observation error. Ecol Monogr 76:323–341

Diaz S, Cabido M, Casanoves F (1998) Plant functional traits and environmental filters at a regional scale. J Veg Sci 9:113–122

Dietze MC (2017) Prediction in ecology: a first-principles framework. Ecol Appl 27:2048–2060

Dietze MC, Fox A, Beck-Johnson LM et al (2018) Iterative near-term ecological forecasting: needs, opportunities, and challenges. PNAS 115:1424–1432

Duchardt CJ, Monroe AP, Heinrichs JA et al (2021) Prioritizing restoration areas to conserve multiple sagebrush-associated wildlife species. Biol Conserv 260:109212

Farr TG, Rosen PA, Caro E et al (2007) The shuttle radar topography mission. Rev Geophys 45:RG2004

Fer I, Shiklomanov A, Novick KA, et al (2021) Capturing site-to-site variability through Hierarchical Bayesian calibration of a process-based dynamic vegetation model. bioRxiv 2021.04.28.441243. https://doi.org/10.1101/2021.04.28.441243

Fick SE, Nauman TW, Brungard CC, Duniway MC (2021) Evaluating natural experiments in ecology: using synthetic controls in assessments of remotely sensed land treatments. Ecol Appl 31:e02264

Fleischman F, Coleman E, Fischer H et al (2022) Restoration prioritization must be informed by marginalized people. Nature 607:E5–E6

Gamito S (1998) Growth models and their use in ecological modelling: an application to a fish population. Ecol Model 113:83–94

Germino MJ, Barnard DM, Davidson BE et al (2018) Thresholds and hotspots for shrub restoration following a heterogeneous megafire. Landsc Ecol 33:1177–1194

Goodsell RM, Childs DZ, Spencer M et al (2021) Developing hierarchical density-structured models to study the national-scale dynamics of an arable weed. Ecol Monogr 91:e01449

Gudex-Cross D, Pontius J, Adams A (2017) Enhanced forest cover mapping using spectral unmixing and object-based classification of multi-temporal Landsat imagery. Remote Sens Environ 196:193–204

Gurevitch J, Fox GA, Fowler NL, Graham CH (2016) Landscape demography: population change and its drivers across spatial scales. Q Rev Biol 91:459–485

Harrison GW (1979) Stability under environmental stress: resistance, resilience, persistence, and variability. Am Nat 113:659–669

Hastings A, Hom CL, Ellner S et al (1993) Chaos in ecology: is mother nature a strange attractor? Annu Rev Ecol Syst 24:1–33

Hastings A, Abbott KC, Cuddington K et al (2018) Transient phenomena in ecology. Science 361:eaat6412

Hefley TJ, Hooten MB, Russell RE et al (2017) When mechanism matters: Bayesian forecasting using models of ecological diffusion. Ecol Lett 20:640–650

Hijmans RJ, Van Etten J, Cheng J, et al (2015) Package 'raster.' R package 734:

Holl KD, Aide TM (2011) When and where to actively restore ecosystems? For Ecol Manag 261:1558–1563

Homer C, Rigge M, Shi H, et al (2020) Remote sensing shrub/grass National Land Cover Database (NLCD) back-in-time (BIT) products for the Western US. US Geological Survey data release, https://doi.org/10.5066/P9C9O66W

James JJ, Sheley RL, Erickson T et al (2013) A systems approach to restoring degraded drylands. J Appl Ecol 50:730–739

Johnson-Bice SM, Ferguson JM, Erb JD et al (2021) Ecological forecasts reveal limitations of common model selection methods: predicting changes in beaver colony densities. Ecol Appl 31:e02198

Jones HP, Jones PC, Barbier EB et al (2018) Restoration and repair of Earth's damaged ecosystems. Proc R Soc B 285:20172577

Kimmerer R (2011) Restoration and reciprocity: the contributions of traditional ecological knowledge. In: Human dimensions of ecological restoration. Springer, pp 257–276

Kirkman LK, Barnett A, Williams BW et al (2013) A dynamic reference model: a framework for assessing biodiversity restoration goals in a fire-dependent ecosystem. Ecol Appl 23:1574–1587

Kleinhesselink AR, Adler PB (2018) The response of big sagebrush (*Artemisia tridentata*) to interannual climate variation changes across its range. Ecology 99:1139–1149

Knutson KC, Pyke DA, Wirth TA et al (2014) Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. J Appl Ecol 51:1414–1424

Koons DN, Colchero F, Hersey K, Gimenez O (2015) Disentangling the effects of climate, density dependence, and harvest on an iconic large herbivore's population dynamics. Ecol Appl 25:956–967

Larson KB, Tuor AR (2021) Deep learning classification of cheatgrass invasion in the Western United States using biophysical and remote sensing data. Remote Sens 13:1246

Lebreton J-D, Gimenez O (2013) Detecting and estimating density dependence in wildlife populations. J Wildl Manag 77:12–23

Mahood AL, Balch JK (2019) Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984–2014). Ecosphere 10:e02591

Marescot L, Chapron G, Chadès I et al (2013) Complex decisions made simple: a primer on stochastic dynamic programming. Methods Ecol Evol 4:872–884

McCord SE, Pilliod DS (2021) Adaptive monitoring in support of adaptive management in rangelands. Rangelands. https://doi.org/10.1016/j.rala.2021.07.003

McCune B, Grace JB, Urban DL (2002) Analysis of ecological communities. MjM software design Gleneden Beach, OR

Mertes K, Jarzyna MA, Jetz W (2020) Hierarchical multi-grain models improve descriptions of species' environmental associations, distribution, and abundance. Ecol Appl 30:e02117

Miller RF, Knick ST, Pyke DA, et al (2011) Characteristics of sagebrush habitats and limitations to long-term conservation. Greater sage-grouse: ecology and conservation of a landscape species and its habitats Studies in Avian Biology 38:145–184

O'Connor RC, Germino M, Barnard DM et al (2020) Small-scale water deficits after wildfires create long-lasting ecological impacts. Environ Res Lett. https://doi.org/10.1088/1748-9326/ab79e4

Pebesma EJ (2018) Simple features for R: standardized support for spatial vector data. R J 10:439

Pilliod DS, Welty JL, Toevs GR (2017) Seventy-five years of vegetation treatments on public rangelands in the Great Basin of North America. Rangelands 39:1–9

Pilliod DS, Welty JL, Jeffries MI et al (2018) Land treatment exploration tool: (rev. 1.1, October 2018): U.S. Geological Survey Fact Sheet 2018-3042, 2p. https://doi.org/10.3133/fs20183042

Pilliod DS, Welty JL, Jeffries MI (2019) USGS Land Treatment Digital Library Data Release: a centralized archive for land treatment tabular and spatial data (ver. 5.0, July 2022): U.S. Geological Survey data release. https://doi.org/10.5066/P98OBOLS

Pilliod DS, Jeffries MI, Arkle RS, Olson DH (2020) Reptiles under the conservation umbrella of the greater sage-grouse. J Wildl Manag 84:478–491

Pilliod DS, Jeffries MA, Welty JL, Arkle RS (2021) Protecting restoration investments from the cheatgrass-fire cycle in sagebrush steppe. Conserv Sci Pract 3:e508

Purves D, Pacala S (2008) Predictive models of forest dynamics. Science 320:1452–1453

Pyke DA, Knick ST, Chambers JC et al (2015) Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat-Part 2: Landscape level restoration decisions. Circular 1418 Washington, DC: US Department of the Interior; Reston, VA: US Geological Survey 43 p

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Radchuk V, Kramer-Schadt S, Grimm V (2019a) Transferability of mechanistic ecological models is about emergence. Trends Ecol Evol 34:487–488

Radchuk V, Laender FD, Cabral JS et al (2019b) The dimensionality of stability depends on disturbance type. Ecol Lett 22:674–684

Renne R, Schlaepfer D, Palmquist K et al (2021) Estimating complex ecological variables at high resolution in heterogeneous terrain using multivariate matching algorithms. Ecoevorxiv. https://doi.org/10.32942/osf.io/b2ux7

Requena-Mullor JM, Maguire KC, Shinneman DJ, Caughlin TT (2019) Integrating anthropogenic factors into regional-scale species distribution models—a novel application in the imperiled sagebrush biome. Glob Chang Biol 25:3844–3858

Ribas LGS, Pressey RL, Bini LM (2021) Estimating counterfactuals for evaluation of ecological and conservation impact: an introduction to matching methods. Biol Rev 96:1186–1204

Rigge M, Shi H, Homer C et al (2019) Long-term trajectories of fractional component change in the Northern Great Basin, USA. Ecosphere 10:e02762

Rollinson CR, Finley AO, Alexander MR et al (2021) Working across space and time: nonstationarity in ecological research and application. Front Ecol Environ 19:66–72

Rossetto M, Micheli F, Saenz-Arroyo A et al (2015) No-take marine reserves can enhance population persistence and support the fishery of abalone. Can J Fish Aquat Sci 72:1503–1517

Schultz EL, Hülsmann L, Pillet MD et al (2022) Climate-driven, but dynamic and complex? A reconciliation of competing hypotheses for species' distributions. Ecol Lett 25:38–51

Shi H, Rigge M, Postma K, Bunde B (2022) Trends analysis of rangeland condition monitoring assessment and projection (RCMAP) fractional component time series (1985–2020). Gisci Remote Sens 59:1243–1265

Shono K, Cadaweng EA, Durst PB (2007) Application of assisted natural regeneration to restore degraded dropical forestlands. Restor Ecol 15:620–626

Shriver RK, Andrews CM, Pilliod DS et al (2018) Adapting management to a changing world: Warm temperatures, dry soil, and interannual variability limit restoration success of a dominant woody shrub in temperate drylands. Glob Chang Biol 24:4972–4982

Shriver RK, Andrews CM, Arkle RS et al (2019) Transient population dynamics impede restoration and may promote ecosystem transformation after disturbance. Ecol Lett 22:1357–1366

Shultz LM (2009) Monograph of *Artemisia* subgenus *tridentatae* (*Asteraceae-Anthemideae*). Syst Bot Monogr 89:1–131

Simler-Williamson AB, Germino MJ (2022) Statistical considerations of nonrandom treatment applications reveal region-wide benefits of widespread post-fire restoration action. Nat Commun 13:3472

Singh G, Reynolds C, Byrne M, Rosman B (2020) A remote sensing method to monitor water, aquatic vegetation, and invasive water hyacinth at national extents. Remote Sens 12:4021

Strassburg BBN, Beyer HL, Crouzeilles R et al (2019) Strategic approaches to restoring ecosystems can triple conservation gains and halve costs. Nat Ecol Evol 3:62–70

Theobald DM, Harrison-Atlas D, Monahan WB, Albano CM (2015) Ecologically-relevant maps of landforms and physiographic diversity for climate adaptation planning. PLoS ONE 10:e0143619

Tredennick AT, Hooten MB, Aldridge CL et al (2016) Forecasting climate change impacts on plant populations over large spatial extents. Ecosphere 7:e01525

Tredennick AT, Hooten MB, Adler PB (2017) Do we need demographic data to forecast plant population dynamics? Methods Ecol Evol 8:541–551

USDI B (2007) Burned area emergency stabilization and rehabilitation handbook (public). Washington, DC, USA: BLM Handbook H-1742-1, USDI BLM

Welty J, Jeffries M (2021) Combined wildland fire datasets for the United States and certain territories, 1800s-Present: U.S. Geological Survey data release. https://doi.org/10.5066/P9ZXGFY3

Wickham H (2011) ggplot2. Wiley Interdisc Rev 3:180–185

Wickham H, Averick M, Bryan J et al (2019) Welcome to the Tidyverse. J Open Source Softw 4:1686

Yang X, Angert AL, Zuidema PA et al (2022) The role of demographic compensation in stabilising marginal tree populations in North America. Ecol Lett 25:1676–1689

Zahawi RA, Reid JL, Holl KD (2014) Hidden costs of passive restoration: passive restoration. Restor Ecol 22:284–287

Zhang L (1997) Cross-validation of non-linear growth functions for modelling tree height–diameter relationships. Ann Bot 79:251–257

Ziegenhagen LL (2003) Shrub reestablishment following fire in the mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. vaseyana (Rydb.) Beetle) alliance. Oregon State University

Ziegenhagen LL, Miller RF (2009) Postfire recovery of two shrubs in the interiors of large burns in the Intermountain West, USA. WNAN 69:195–205

Zipkin EF, Zylstra ER, Wright AD et al (2021) Addressing data integration challenges to link ecological processes across scales. Front Ecol Environ 19:30–38