Landscape heterogeneity is key to forecasting outcomes of plant reintroduction

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Abstract. Conservation and restoration projects often involve starting new populations by introducing individuals into portions of their native or projected range. Such efforts can help meet many related goals, including habitat creation, ecosystem service provisioning, assisted migration, and the reintroduction of imperiled species following local extirpation. The outcomes of reintroduction efforts, however, are highly variable, with results ranging from local extinction to dramatic population growth; reasons for this variation remain unclear. Here, we ask whether population growth following plant reintroductions is governed by variation at two scales: the scale of individual habitat patches to which individuals are reintroduced, and larger among-landscape scales in which similar patches may be situated in landscapes that differ in matrix type, soil conditions, and other factors. Quantifying demographic variation at these two scales will help prioritize locations for introduction and, once introductions take place, forecast population growth. This work took place within a large-scale habitat fragmentation experiment, where individuals of two perennial forb species were reintroduced into eight replicate ~50-ha landscapes, each containing a set of five ~1-ha patches that varied in their degree of isolation (connected by habitat corridors or unconnected) and edge-to-area ratio. Using data on individual growth, survival, reproductive output, and recruitment collected one to two years after reintroduction, we developed models to forecast population growth, then compared forecasts to observed population sizes, three and six years later. Both the type of patch (connected and unconnected) and identity of the landscape to which individuals were reintroduced had effects on forecasted population growth rates, but only variation associated with landscape identity was an accurate predictor of subsequently observed population growth rates. Models that did not include landscape identity had minimal forecasting ability, revealing the key importance of variation at this scale for accurate prediction. Of the five demographic rates used to model population dynamics, seed production was the most important source of forecast error in population growth rates. Our results point to the importance of accounting for landscape-scale variation in demographic models and demonstrate how such models might assist with prioritizing particular landscapes for species reintroduction projects.

Key words: Carphephorus; conservation biology; demography; ecological forecasting; habitat fragmentation; integral projection model; landscape corridor; Liatris; longleaf pine savanna; prediction; restoration ecology.

INTRODUCTION

Conservation and restoration projects often involve starting new populations by introducing individuals into portions of their native or projected future range. Species introductions and reintroductions serve many conservation goals, such as creating habitat, reestablishing populations of locally extirpated species, promoting biodiversity of dispersal-limited species, assisting species migration in the face of climate change, and increasing carbon storage (e.g., Hoegh-Guldberg et al. 2008, Foster et al. 2009, Grman et al. 2015, Shoo et al. 2016, Holl 2017). Introductions are therefore central to major

conservation and restoration initiatives (Chazdon 2008, Cao et al. 2017) and a significant component of an emerging multibillion-dollar ecological restoration industry (Kimball et al. 2015).

In practice, however, the effectiveness of reintroductions is unpredictable (Armstrong and Seddon 2008) and the success of plant species reintroductions is generally low. A review of 249 reintroduction experiments concluded that only 52% of populations survive for three years (Godefroid et al. 2011), a success rate that is likely biased upward due to under-reporting of failures and the short time scale of monitoring efforts (Drayton and Primack 2012). Forecasting whether transplants will successfully establish new populations is a critical research need that would aid decision-making during reintroduction efforts (Converse et al. 2013, Butterfield et al. 2016) and contribute to broader efforts of developing predictive capacity in ecology and restoration (Brudvig et al. 2017, Dietze et al. 2018). In particular, such information could help with landscape-level planning by prioritizing reintroductions to locations where they are most likely to succeed (Neeson et al. 2015, Barbosa and Asner 2017). However, this information is generally unavailable due to the difficulty of tracking demographic trajectories of populations at landscape scales.

Understanding and forecasting the outcomes of plant reintroductions across landscapes will require quantifying how variation at different scales relates to specific demographic processes of reintroduced species. In particular, reintroduction outcomes may differ among individual patches of habitat within a landscape or among landscapes, and influences at different scales may operate on different demographic rates (Holl et al. 2003). For example, due to habitat loss and fragmentation, patches within a landscape may differ in area, edge-to-area ratio, or connectedness; these patch-scale differences may affect key demographic processes, including rates of pollination, seed germination, recruitment, and growth (Bruna 1999, 2003). At broader among-landscape scales, reintroduction outcomes may differ due to large-scale variation in soil conditions, elevation, or other factors that influence survival and/or other demographic processes (e.g., Pywell et al. 2002, Holl et al. 2003). Considering variation at different spatial scales has important pragmatic consequences for practitioners seeking to prioritize limited resources (Meinke et al. 2009, Wilson et al. 2011).

How variation at among-landscape scales affects reintroduction is still poorly understood because few studies have conducted demographic studies that explicitly compare among patches or landscapes during reintroduction (but see Münzbergová et al. 2005). Moreover, despite the myriad effects of landscape-scale environmental variation on metrics of plant demography, their combined effect on population growth rate is unclear. The same environmental variable can have a range of effects across life stages, from positive to negative (Schupp 1995), suggesting that population-level consequences of environmental variation depend on whether combined effects across the life cycle are opposing or synergistic (Dalgleish et al. 2011). Thus, it is important to not only quantify how population growth varies among patches within a landscape, but also to quantify how particular demographic rates underlie this variation. Because different demographic rates are affected by different management strategies, knowing which demographic rates contribute most to population growth rate can yield further insights and enable targeted management actions (Neubert and Caswell 2000, Buckley et al. 2005).

We suggest that quantitative models can be used to scale up demographic data to forecast reintroduction success across heterogeneous landscapes. Size-structured models, including matrix models and integral projection models (IPM), have generated widespread interest due to their ability to predict population outcomes based on demographic rates (Crone et al. 2011, Merow et al. 2014, Rees et al. 2014). In theory, these process-based models could be parameterized using commonly collected data on individual plant growth, survival, and reproduction and then applied to forecast reintroduction success over longer time periods and larger spatial scales. In practice, the track record of size-structured models to accurately forecast population outcomes is mixed. For example, across a range of plant populations spanning three continents, forecast accuracy of matrix models was very low, with correlations between predicted and observed population growth rates near zero (Crone et al. 2013). While IPMs tend to decrease bias and variance of population growth rate predictions relative to matrix models (Ramula et al. 2009), Tredennick et al. (2017) found that forecast horizons of IPMs for four grass species were limited to <5 yr. In general, however, we know little about the accuracy of forecast horizons for ecological process models, including models for population dynamics (Dietze et al. 2018). Incorporating spatial variation into size-structured models has the potential to improve forecasting ability (Van Mantgem and Stephenson 2005, Ehrlén and Morris 2015, Crone 2016). Accounting for landscape-scale variation, such as attributes of patches or landscape identity, can improve model accuracy (Quintana-Ascencio et al. 2018); however, these benefits remain unclear because the majority of demographic models are based on data from less than three sites (Gurevitch et al. 2016).

We evaluated the roles of within-landscape (patch) and among-landscape (landscape identity) attributes for forecasting population growth rates of two plant species that we reintroduced into experimental landscapes. The within-landscape patch attributes we examined were patch connectivity and edge-to-area ratio, which we hereafter refer to as patch types. These patch types were created through a large-scale habitat fragmentation experiment, and the spatial scale of their influence on plant populations is roughly the size of a patch (~1 ha). We evaluated the influence of patch type by considering

how reintroduced populations grew in connected vs. unconnected and low vs. high edge-to-area ratio patches. To assess the influence of among-landscape attributes, groups of patches were arranged into replicate blocks (landscapes) with a spatial scale of influence of ~50 ha. We evaluated the influence of landscape identity by comparing population growth among these replicate landscapes.

This study fills two critical gaps in our understanding of plant species reintroduction in heterogeneous landscapes. First, our experimental design enables us to explore effects of patch connectivity and edge-to-area ratio on demography, while the use of replicate landscapes (blocks) allows us to examine effects of landscape identity while controlling for patch type. Effectively, this enables us to compare within-patch effects on demography to among-landscape effects. Second, we apply a modeling approach that combines spatial data on multiple plant demographic rates to forecast population growth rates of reintroduced native plant species at three and six years post-introduction. Because our forecasting models integrate survival, individual growth, and recruitment data, we are further able to determine which demographic rates most affect the accuracy of forecasted population growth rates. Like many conservation and restoration monitoring efforts, our detailed demographic data are limited to the first two years after planting and monitored plants are transplanted founders, not natural recruits. Thus, our study addresses whether these commonly collected, yet short-term, data can forecast longer-term conservation and restoration outcomes. Specifically, we ask three questions: (1) How well do demographic models parameterized from the initial two years of data forecast population sizes, three and six years after reintroduction? (2) Does accounting for within-landscape patch type (connectivity, edge-to-area ratio) and among-landscape identity improve forecasting ability? (3) Which plant demographic rates are most important for accurately forecasting population growth rate?

<center>METHODS</center>

We conducted our research at the Savannah River Site, a National Environmental Research Park in Aiken, Allendale, and Barnwell Counties, South Carolina. Like most of the coastal plain of the southeastern United States, the 800-km^2 site was historically dominated by longleaf pine (*Pinus palustris*) savanna. Following a history of predominantly agricultural land use, much of the Savannah River Site was converted to dense pine plantations (both *Pinus taeda* and *P. palustris*) incapable of supporting the diverse, fire-maintained, herbaceous understory of open-canopy longleaf pine savanna.

<center>*Experimental design*</center>

Our study took place within a habitat fragmentation experiment that manipulates patch connectivity and

patch edge-to-area ratio while controlling for patch area. Eight experimental landscapes were created in 2000 (*n* = 6) and 2007 (*n* = 2) by clearing pine plantation forest and restoring the resulting open patches to upland longleaf pine savanna (retaining the plantation matrix between patches; Tewksbury et al. 2002). Experimental landscape blocks ranged from 2 to 21 km apart (Fig. 1) and while all share the same plant community type (upland longleaf pine savanna), they vary in their history of agricultural land use, plant community diversity, and composition, microtopography, soil types, and other factors that might underpin effects of landscape identity on population growth. Each experimental landscape consisted of four peripheral patches arrayed around one 100 × 100 m center patch. All peripheral patches had an area of 1.375 ha, but patches varied in connectivity and edge-to-area ratio. There were three types of peripheral patch (Fig. 1). Each landscape had a single peripheral patch (termed a "connected patch") that was 100 × 100 m and connected to the center patch in each landscape by a 150 × 25 m corridor of identical habitat to the patches. The other three peripheral patches in each landscape were also 150 m away from, but were not connected to, the center patch and were randomly assigned to be a "rectangle" (100 × 137.5 m) or "winged" (with two 75 × 25 m wings extending into the matrix from a 100 × 100 m core patch); this resulted in one duplicate rectangle or winged patch per landscape. This experimental design disentangles impacts of the edge-to-area ratio (comparison of winged and rectangle patches) and connectivity (comparison of connected and winged patches) on ecological dynamics in fragmented landscapes. In this study system, previous work has shown that patch types differ in a variety of processes that might impact reintroduction outcomes including fire intensity (Brudvig et al. 2012), seed dispersal (Levey et al. 2005), herbivory (Evans et al. 2012, Brudvig et al. 2015), pollination (Townsend and Levey 2005), and plant community diversity and composition (Damschen et al. 2008). For our analyses of population growth rate, we used data from the connected, rectangle, and winged patches, but not the center patch. We consider each patch to be a replicate plant population because seed dispersal is predominantly local for our two focal species (>94% of seeds fall within 2 m of parent plants; C. Warneke, E. I. Damschen, N. M. Haddad, D. J. Levey, and L. A. Brudvig, *unpublished data*) and because the pine plantation matrix between patches is typically unsuitable habitat for our focal species. In total, this design results in 32 replicate populations (four peripheral patches in each of eight blocks) for each of our study species.

We reintroduced two native forb species into each patch in 2007/2008. These species, both perennial plants in the Asteraceae, are *Carphephorus bellidifolius* (hereafter, *Carphephorus*) and *Liatris earlei* (synonym of *Liatris squarrulosa*; hereafter, *Liatris*). They are native to, and of restoration interest in, longleaf pine savannas. Both species
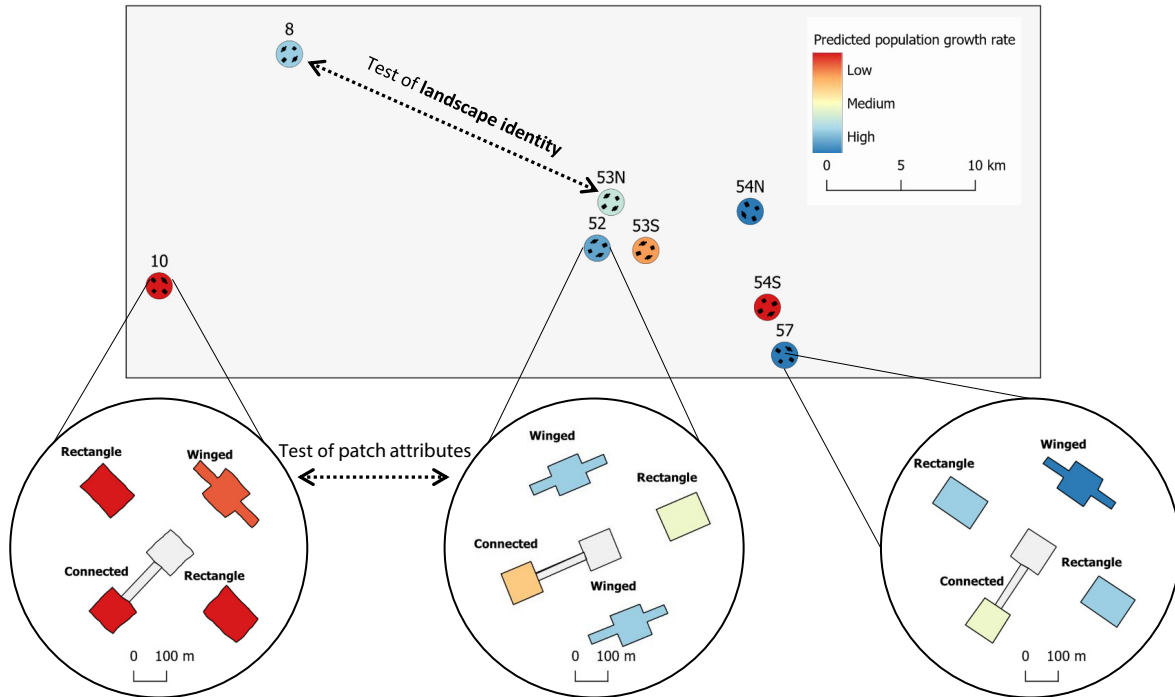
FIG. 1. Predicted effects of landscape identity and patch attributes on population growth rate. This figure illustrates landscape structure at our study site. The top panel represents the eight landscapes used in the study, while the three insets represent patch types within three landscapes. Different colors represent forecasts of population growth rate (λ_p) for *Carphephorus bellidifolius*. Labels above each landscape are code for landscape identity and match *x*-axis labels in Fig. 2.

were absent from our experimental landscapes prior to our reintroduction (Brudvig et al. 2015). In May 2007 and May 2008, 2–4 month old seedlings grown from locally sourced seeds were transplanted into 16 plots (1 × 4 m) per patch. Plots were located along four diagonally projecting transects and positioned at distances of 1, 14.5, 27, and 51 m from the patch corners (1, 10, 19, and 36 m from the nearest patch edge). Each plot contained one seedling of each of our focal species ($n = 1,024$ total plants). Plots were prepared for planting by removal of pre-existing vegetation via hand weeding 4–6 weeks prior to transplanting and herbicidal treatments two weeks prior. Any transplants that died in the establishment period were replanted up until April 2009, after which dead individuals were not replaced. Plots were weeded once annually for the first two years of the study.

Demographic rate data

To parameterize demographic models (detailed in *Demographic modeling* subsection), we collected data within two years of reintroduction, on six demographic rates that span the life cycle of our study species: inflorescence production, seed production, seedling establishment, first-year growth, and survival and growth of established plants (Table 1). These data were collected at each of the transplant plots, ensuring replication of patch type and landscape identity for all demographic rates. Inflorescence production was recorded as counts

TABLE 1. Demographic rate data and models.

Demographic rate	Sample size, n		Distribution
	LE	CB	
Inflorescence production	181	220	negative binomial (log link)
Seed production per inflorescence	306	336	negative binomial (log link)
Seedling establishment	302	296	binomial (logit link)
First-year growth (initial size of newly recruited seedlings)	171	569	truncated normal (identity link)
Annual growth	348	370	truncated normal (identity link)
Annual survival	451	398	Bernoulli (logit link)

Notes: The six demographic rates used to construct the integral projection model (IPM). In sample size column, LE stands for *Liatris earlei* and CB stands for *Carphephorus bellidifolius*.

of the total number of flowering heads during the 2009 flowering season (September–October). We collected developed seeds from a subset of these heads ($n = 1$–3 heads per plant) and counted numbers of developed seeds per head (more details in Brudvig et al. [2015]). For these insect-pollinated species, inflorescence production represents plant reproductive potential, while seed production largely reflects pollination success (Brudvig et al. 2015). We quantified seedling establishment rates

using a seed addition experiment, in which 40 seeds of each of our focal species were added near transplant plots in February 2010, and the number of emerged seedlings was counted in September 2010. First-year growth was recorded as the volume (in cm^3, length × width × height) of offspring of founder plants in September 2009, reflecting one season of individual growth post-germination. Finally, survival and growth were measured in September 2009 for founder plants. All demographic data are archived at the Dryad Digital Repository (see *Data Availability*).

Demographic modeling

The goal of our demographic modeling was to evaluate the forecasting ability of population projection models for our study species. We used integral projection models (IPM), developed with generalized linear mixed-effects models (GLMM), fit to our demographic rate data. IPMs are increasingly used to model population dynamics of organisms described by a continuous state variable (usually size) in discrete time steps (Merow et al. 2014, Rees et al. 2014). Because the demographic rates used to construct IPMs can be parameterized in a regression model context, incorporating multiple predictors of organism state is straightforward. In our case, we developed GLMMs that included plant size as a predictor of survival, growth, inflorescence production, and seed production, and used landscape identity and patch type as predictors of all demographic rates (Table 1; Eq. 1). Seed production was the only demographic rate with multiple measures from the same individual (as three inflorescences were sampled per plant) and thus we included an individual-level random effect for this life stage. For all demographic rate models, we represented patch type (connected, winged, or rectangle) as a fixed effect and landscape identity as a normally distributed random effect. The following equation represents the predicted mean (μ) for one of these demographic rate models, where the index i represents individual plants, the index j represents patch type, and the index k represents landscape units:

$$\mu_{i,j,k} = \alpha + \beta_k \text{Patch}_{i,k} + \gamma \text{Size}_i + \rho_k \text{Landscape}_{i,k} \tag{1}$$

$$\rho_k \sim \text{Normal}(0, \sigma^2)$$

Modeling demographic rates in a GLMM context enabled us to pool demographic data from all patches and all landscapes while accounting for variation in individual size (Size$_i$). The GLMMs were the foundation of our IPM kernels, resulting in patch and landscape-specific population models that leveraged sample sizes of >200 individual plants for each demographic rate (sample sizes presented in Table 1).

For each demographic rate, we assumed data were drawn from an appropriate distribution. To fit models

for established plant growth and first-year growth, we used a truncated normal distribution, constrained to ±1.1 times the observed size range. This distribution enabled us to avoid "evicting" individuals near the size limits of our IPM kernel (see Williams et al. 2012). The seedling establishment model was fit to a binomial distribution using the logit-link function, with the number of trials equal to the number of seeds ($n = 40$) added in each plot of the seed addition experiment. We assumed that all seeds either germinated or died by the end of the first growing season after seed addition. For both inflorescence and seed production, we found the negative binomial distribution provided a better fit to the data than the Poisson distribution, so we used the former distribution in our models, fit with a log-link function. We assumed survival was drawn from a Bernoulli distribution, fit with a logit-link function.

We parameterized our demographic models in a hierarchical Bayesian framework. This approach is advantageous in providing posterior samples that propagate uncertainty through to IPM output (Elderd and Miller 2016). To fit our demographic rate models, we applied a Markov chain Monte Carlo (MCMC) algorithm in JAGS 3.4.0 (Plummer 2003). We ran each model with three chains, with the number of draws and the thinning parameter sufficient to produce 1,000 posterior samples. We checked convergence using the $\hat{R}$ statistic (Gelman and Rubin 1992) and through visual examination.

Constructing the Integral Projection Model

For our population projection model, we assumed an annual time step, corresponding to the September censuses of most demographic rates. This model represents a pre-reproductive census scheme, as seed and stalk production occurs in September, and the count and size of new recruits (determined by germination and first-year growth models, respectively) is tallied the following September. We used our demographic rate models to construct an IPM kernel that predicts the number of individuals of a given size as a probability density function of size at the previous time step, patch attributes, and landscape identity. We discretized the kernel using the midpoint rule (Rees et al. 2014). After testing various grid sizes, we found that eigenvalues were not sensitive to grid dimensions >60, and used a grid of 100 bins for discretization. For all population-level results, we propagated uncertainty from parameter estimation by using posterior samples from demographic rate models to construct sets of 1,000 IPM kernels.

To evaluate whether landscape covariates improve forecasting ability of IPMs, we developed four separate IPM kernels for each species: a nonspatial kernel that included size as the only predictor of demographic rates, a kernel including size and landscape identity, a kernel including size and patch type, and a kernel that included size and both landscape identity and patch type,

representing the full spatial model. We constructed each of these IPM kernels by predicting demographic rates from GLMMs that either lacked or included the patch and landscape covariates in Eq. 1. As a result, while our study included 32 replicate patches of each species, the full model resulted in 24 unique predictions (8 landscapes × 3 patch types), the landscape identity model resulted in eight unique predictions (eight landscapes), the patch type model resulted in three unique predictions, and the nonspatial model resulted in a single prediction of population growth rate for all patches. We used the IPM kernels to calculate both the asymptotic population growth rate (λ_p) and transient population growth rates, by initializing models with size and abundance data of all plants in 2009 and projecting forward three and six years (to 2012 and 2015, respectively). Asymptotic λ provided a better fit to observed population growth rates than transient population growth rates, so all results we present are comparisons of the dominant eigenvalue of the IPM kernel (henceforth λ_p) and observed population growth rates from 2009–2012 (λ_{3yr}) and 2009–2015 (λ_{6yr}). To facilitate comparison between population growth rates, we rescaled λ_{3yr} and λ_{6yr} to annual rates by raising these rates to the power of 1/3 and 1/6, respectively.

Confronting demographic models with population growth rate data

To measure population size, we counted all recruited individuals of each species in a circle with a 1.5 m radius centered on the location of each founder plant. We did this in September–October of both 2012 and 2015, representing the third and sixth years after transplanting.

We selected the best model from our set of four IPM kernels (nonspatial, patch type only, landscape identity only, and the full model) by calculating mean absolute error (MAE) between observed and predicted population growth rates. For the best-fit model for each species, we quantified forecasting ability in multiple ways. First, we fit zero-intercept linear regressions to predicted vs. observed λs. Comparing the resultant slope to a slope of 1 (i.e., a perfect fit between predicted and observed data) measures the magnitude and direction of bias (Crone et al. 2013). Second, we quantified Pearson correlations (r) between predicted and observed λ Finally, we estimated our ability to forecast whether a population is growing ($\lambda > 1$) or shrinking ($\lambda < 1$) by calculating the probability that the IPM correctly predicts whether observed populations had either increased or decreased. Our Bayesian methodology enabled us to propagate uncertainty from parameter estimation to metrics of model fit, including Pearson's r.

Sensitivity analysis

We quantified the relative importance of demographic rates for population growth rate and forecast error of population growth rate using global sensitivity analysis (GSA). GSA is a model-independent technique for quantifying how variability in model input affects model output (Ellner and Fieberg 2003, Saltelli et al. 2008). Our approach differs from perturbation analyses based on the partial derivative of population growth rate (as in Easterling et al. 2000) in two important ways. First, all parameters are perturbed simultaneously, rather than one at a time. Second, the scale of parameter perturbation is determined by the scale of variation in the data, rather than by an arbitrary amount. As input to our GSA, we used the posterior draws ($n = 1,000$) from the MCMC algorithm used to fit demographic rate models for data. The MCMC draws represent total uncertainty across each of our five demographic rate models (because seed production and stalk production were jointly estimated, we combined these rates in the GSA). The proportion in output variance explained by each input variable (demographic rate) in the GSA represents both uncertainty in parameter estimation as well as the influence of demographic rate on population dynamics (Caughlin et al. 2015). We quantified the sensitivity of regional population growth rate and forecasting error to uncertainty in demographic rates. For these analyses, we used the full IPM model, including both patch type and landscape identity. We elected to run the GSA on the full IPM model, as this model generally provided the best fit to the data (see *Results*). Because our models assume geometric growth rates, we defined regional population growth rate as the largest population growth rate out of all patches. Forecast error was defined as the MAE between the observed and predicted population growth rate after six years.

RESULTS

Overview of demographic models

Within-landscape patch type and among-landscape identity had varying impacts on demographic rates (Appendix S1: Fig. S1). In general, the effect of landscape identity was greater than that of patch type (Appendix S1: Figs. S2, S3). The patch type effect tended to be inconsistent across demographic rates (Appendix S1: Fig. S2). For example, winged patches were the worst patch type for survival, but the best type for seedling establishment and seed production. In contrast, particular landscapes tended to have consistently positive or negative effects on most demographic rates for both species (Appendix S1: Fig. S4). An exception was individual growth rate, which was relatively unaffected by landscape identity. Survival, growth, and inflorescence production were strongly size-dependent for both species (Appendix S1: Fig. S5), while seed production per inflorescence did not depend on plant size (Appendix S1: Fig. S6).

Population growth rates

IPMs predicted growing populations, with a median λ_p (predicted population growth rate) of 1.47 (95% CI:

1.07–2.00) for *Carphephorus* and 1.20 (0.92–1.96) for *Liatris*. Observed population growth rates were lower than predicted growth rates for both species, with a median λ_{3yr} of 1.23 (0.77–1.62) for *Carphephorus* and 1.00 (0.69–1.91) for *Liatris*. Observed λ decreased for *Carphephorus* after six years, with a median λ_{6yr} of 1.16 (0.87–1.46), and increased for *Liatris* with a median λ_{6yr} of 1.13 (0.81–1.49). Overall, from populations beginning with 16 plants per patch, after six years, abundance of plants per patch (mean $\pm$ SD) was 109.28 $\pm$ 76.91 for *Carphephorus* and 41.78 $\pm$ 43.96 for *Liatris*. None of the reintroduced populations went extinct at the patch scale during the study.

Predicted and observed λ at 3 and 6 yr show differences between patch types and experimental landscapes (Figs. 2, 3). The difference in λ_p (predicted λ) between the best- and worst- landscapes had a mean of 0.17 for *Carphephorus* and 0.58 for *Liatris*, compared to a mean difference in λ_p between best and worst patch type of 0.24 for *Carphephorus* and 0.17 for *Liatris*. This result demonstrates strong predicted differences in λ_p across

both scales (landscape identity and patch type). Nevertheless, landscape identity was a consistently better predictor of observed λ than patch type. Observed λ_{6yr} and λ_{3yr} revealed large differences between experimental landscapes, and the ranking of experimental landscapes was broadly similar to that predicted by the IPM for both species (Table 2). Observed effects of patch type on λ_{6yr} and λ_{3yr} did not match predicted effects for either species (Table 3). The ability of IPMs to correctly forecast the landscapes and patch types with the best and worst population growth rates declined over time for *Carphephorus* but increased for *Liatris* (Tables 2–3).

Model selection

Our primary measure of forecast accuracy was MAE (mean absolute error), which represents the absolute value of the difference between predicted and observed λ. We found substantial differences in forecasting error between species and models (Fig. 4). MAE was lower for *Liatris* than *Carphephorus*, meaning we had greater
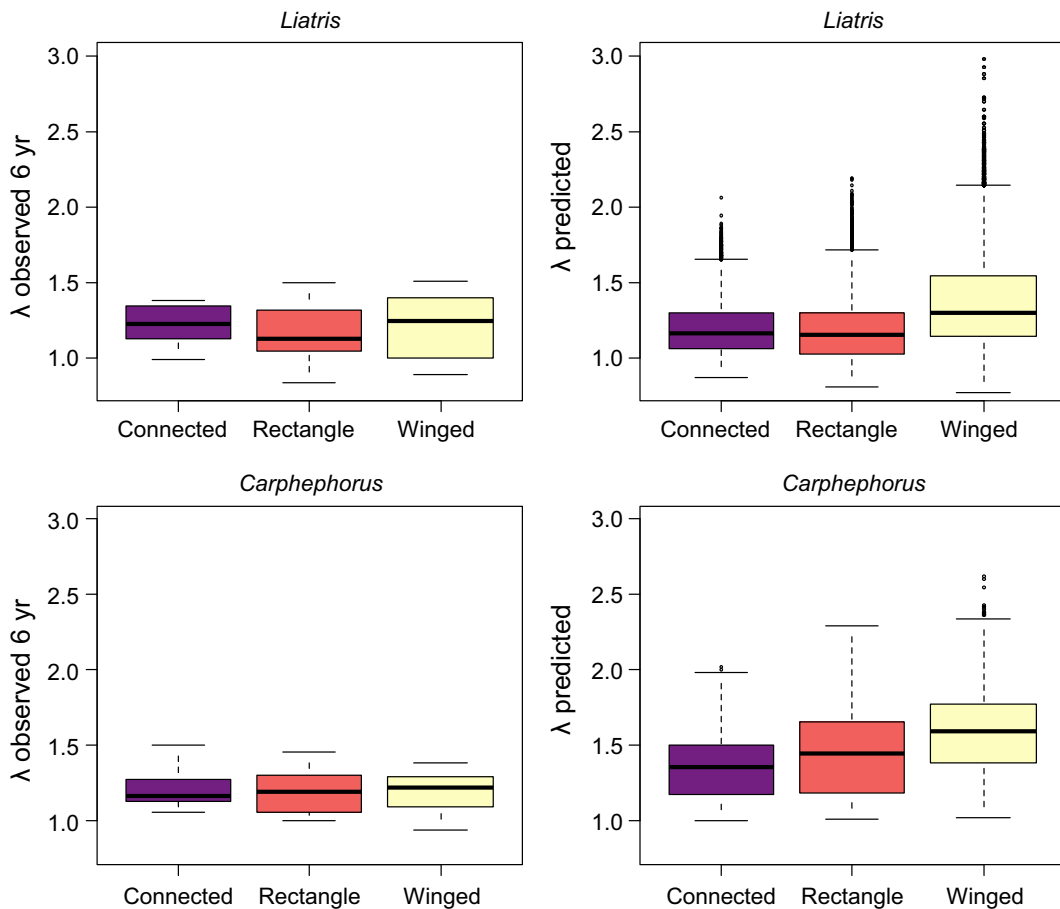

FIG. 2. Effect of patch type on population growth rate differs between observed (left) and predicted (right) values. Boxes represent first to third quartiles. The thick black line in the center of the box shows the median value, "whiskers" represent observations within 1.5 times of the upper and lower quartiles, and dots represent outliers. Predicted values represent model output, including model uncertainty. Observed values represent variation between 32 replicate populations. For simplicity, only 6-yr lambdas are shown. However, 3-yr lambdas were qualitatively similar.
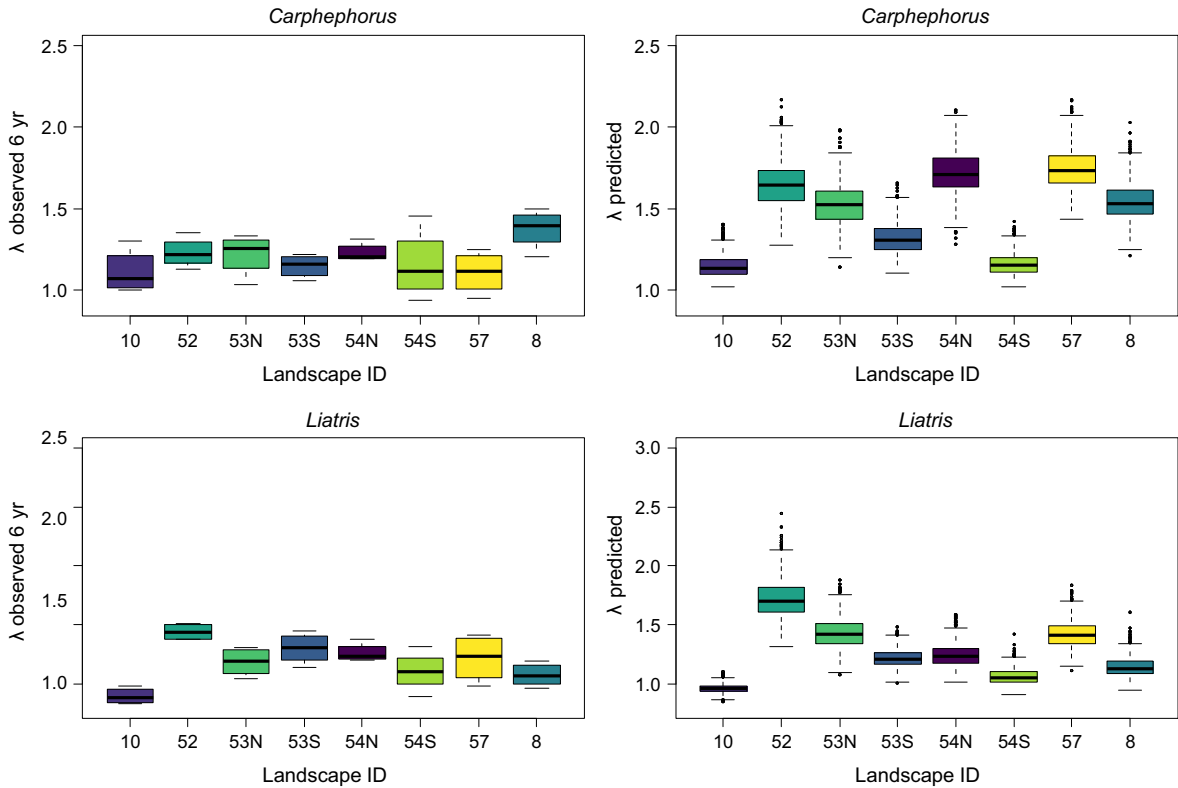
FIG. 3. Effect of landscape unit on predicted and observed population growth rate (λ). Box and whiskers plots as in Fig. 2. For simplicity, only 6-yr lambdas are shown. However, 3-yr lambdas were qualitatively similar.

TABLE 2. Predictive accuracy of Integral Projection Model (IPM) in identifying best and worst experimental landscapes for population growth rate after three and six years.

Species and time span	Probability of successful identification of	
	Best landscape (%)	Worst landscape (%)
Carphephorus bellidifolius after 3 yr	13.23	36.80
Carphephorus bellidifolius after 6 yr	1.40	33.87
Liatris earlei after 3 yr	30.23	31.10
Liatris earlei after 6 yr	92.00	64.50

Notes: Because there were eight experimental landscapes, we would expect a success rate of 12.5% through chance alone.

TABLE 3. Predictive accuracy of Integral Projection Model (IPM) in identifying best and worst patch type for population growth rate after three and six years.

Species and time span	Probability of successful identification of	
	Best patch type (%)	Worst patch type (%)
Carphephorus bellidifolius after 3 yr	37.38	16.93
Carphephorus bellidifolius after 6 yr	25.81	16.93
Liatris earlei after 3 yr	44.99	34.14
Liatris earlei after 6 yr	56.48	36.18

Notes: Because there were three treatments, we would expect a success rate of 33.33% through chance alone.

ability to forecast *Liatris* population growth rates than *Carphephorus.* For *Liatris,* median MAE of the different models ranged from 0.16 to 0.29, while for *Carphephorus,* median MAE ranged from 0.28 to 0.65. An interpretation of these MAE values is that, relative to a population that is not changing ($\lambda = 1$), our best model among those we tested for *Carphephorus* had an average error of 28% change in population size per year (including both growth and shrinkage), while the best model for *Liatris* had an average error of 16% change in

population size per year. Including landscape identity was necessary to forecast *Carphephorus* population growth rates, and models without this term performed poorly, while the inclusion of patch type had almost no impact on forecasting error. *Liatris* was similar in that the nonspatial model tended to have higher forecasting error. However, unlike *Carphephorus,* patch type resulted in slight improvements of forecasting ability for λ_{3yr} for *Liatris.* At six years, the pattern of *Liatris* forecasting error became more similar to *Carphephorus,* with

decreases in MAE for both models that included landscape identity. We did not find strong evidence that forecasting error increased over time, with a relatively small increase in forecasting error for *Carphephorus*, and decreased forecasting error after six years for *Liatris*.

Best model evaluation

Best-fit models for both species performed well at forecasting population growth rates and discriminating between growing and shrinking populations. Pearson correlations between λ_p and the best-fit model for λ_{3yr} were 0.40 (95% CI: 0.25–0.52) for *Liatris* and 0.43 (95% CI: 0.31–0.50) for *Carphephorus*. After six years, Pearson correlations increased for *Liatris* to a median Pearson's *r* of 0.65 (95% CI: 0.53–0.74) and decreased for *Carphephorus*, to a median of 0.19 (95% CI: 0.03–0.34). We note that 95% CI for Pearson's *r* that do not overlap zero can be considered statistically significant. Although the relationship between predicted and observed values was approximately linear for both species (Fig. 5), slope terms for the zero-intercept regression were below one.
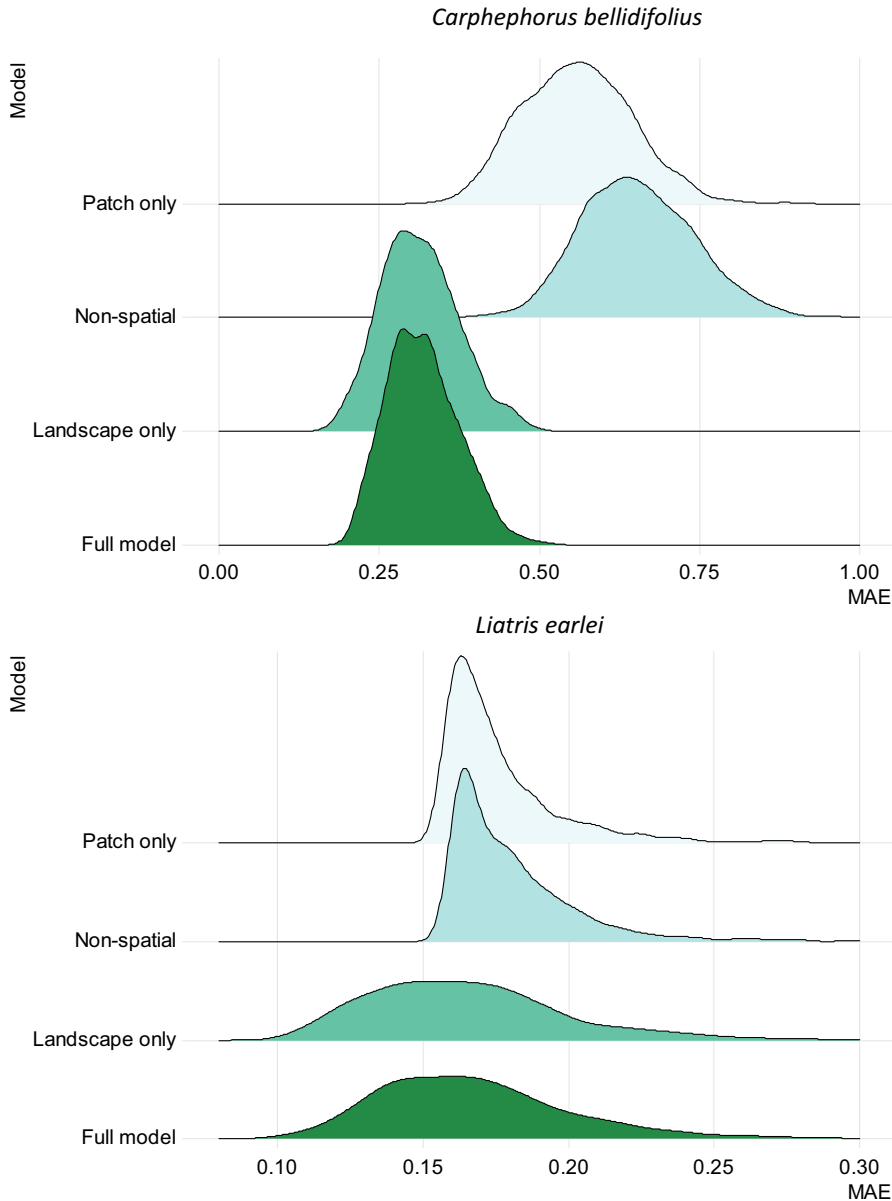

FIG. 4. Distribution of mean absolute error (MAE) between predicted and observed population growth rate for IPMs. Each row represents a different representations of landscape identity and patch attributes in the IPM. A lower value of MAE indicates better model fit. The order of the rows in both figures follows the median values for MAE (from highest MAE at the top to lowest MAE at the bottom). This figure represents uncertainty in parameter estimation propagated through to model predictions.
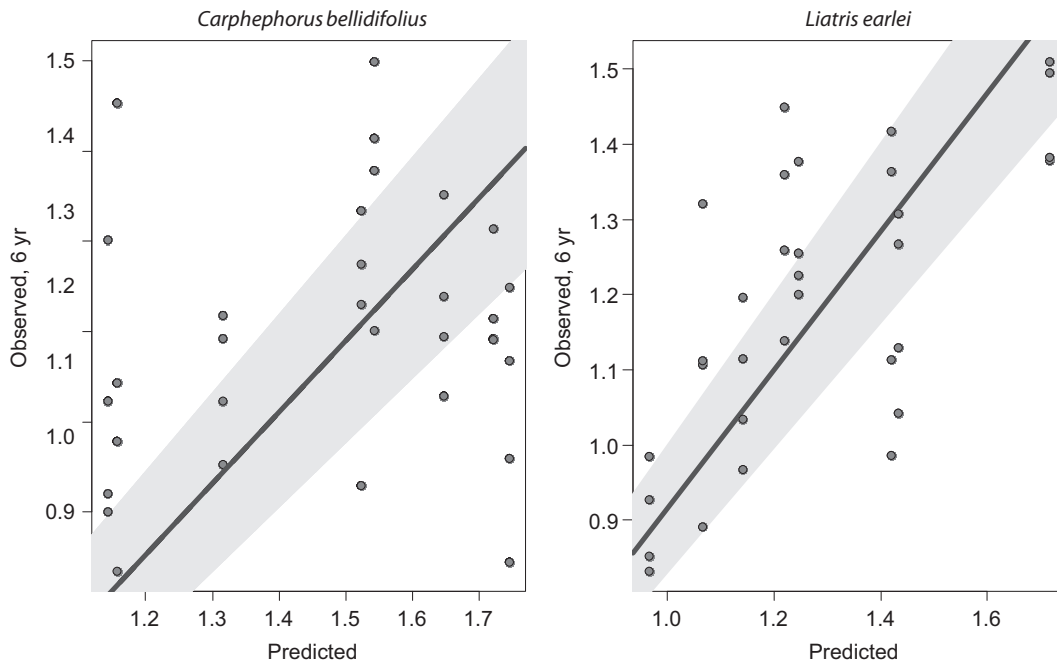
FIG. 5. Predicted vs. observed population growth rate from best-fit IPM for each species by time period. Black dots indicate one of 32 replicate populations. The black line represents the fit of a zero-intercept regression to the data, and the gray polygon represents 95% CI for the slope parameter of this regression.

This result indicates that our IPMs overpredicted population growth rates. Despite overpredicting λ, best-fit models accurately predicted whether populations were shrinking or growing, with median accuracy rates of 90.63% and 93.75% for *Carphephorus* after 3 and 6 yr, respectively, and accuracy rates of 65.62% and 90.63% for *Liatris* after 3 and 6 years.

Global sensitivity analysis

For both species, seed production explained the majority of variance in IPM predictions (Fig. 6). Seed production explained 55.32% (95% CI: 53.90–56.74%) of variation in MAE of forecasted population growth rates for *Carphephorus* and 43.00% (95% CI: 41.36–44.74%) of forecast MAE for *Liatris*. Initial size made negligible contributions to variation in forecast error for both species. For *Liatris*, the growth of established plants was the second-most important demographic rate, while survival was the second-most important demographic rate for *Carphephorus*. The sensitivity of population growth rate to demographic rates was nearly identical to forecast error.

DISCUSSION

Developing near-term forecasts for ecological outcomes is a critical research need for sustainability science (Dietze et al. 2018). We demonstrate that we can forecast the outcomes of plant reintroductions for up to six

years using integral projection models (IPM) parameterized with demographic data on transplanted individuals collected in the first two years after their reintroduction. Consideration of among-landscape identity was critical for improving the accuracy of forecasts for reintroduction outcomes. By replicating our study within patches and across landscapes, we forecasted population-level outcomes across heterogeneous landscapes, including population growth rate, whether populations were growing or shrinking, and which landscapes were better or worse for establishing new populations. These results illustrate the potential for demographic models to provide near-term forecasts for outcomes of native plant reintroduction.

Role of within- vs. among-landscape variability

Accounting for among-landscape differences in demography was key to the success of our approach. Our study included 32 replicate populations from different landscapes with embedded patch types that experimentally manipulated the connectivity and edge-to-area ratio of patches. Consequently, we were able to quantify the consequences of within-landscape patch type and among-landscape identity on our ability to forecast reintroduction success. While both the type of patch and landscape identity influenced predicted population growth rates, only landscape identity was important for forecasting population outcomes six years after initial data collection. From a pragmatic perspective, this
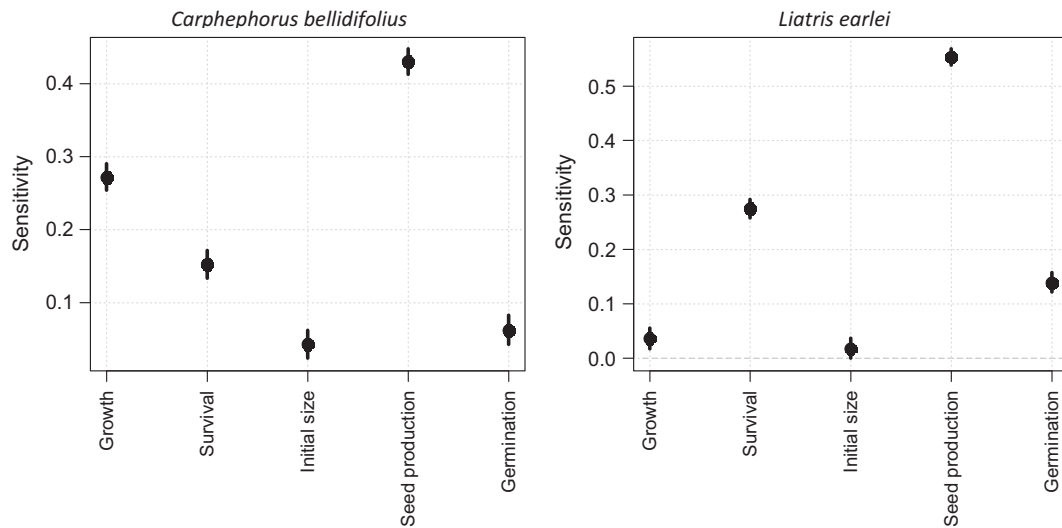
Fig. 6.   Sensitivity of forecast error of population growth rate to demographic rates. This figure indicates the proportion of variance in model output explained by each of the demographic rates. Note that seed production includes both stalk production and number of viable seeds per stalk.

finding suggests that conservation decisions might focus on identifying entire landscapes into which reintroduction will be successful, and that patch configuration (edge-to-area ratio, connectedness) within these "good" landscapes may be of less consequence for reintroduction success.

These results indicate that different scales of environmental variation impact the accuracy of plant reintroduction forecasts. At the local patch scale, the predicted, but not observed, influence of patch attributes on population growth suggests that ecological impacts of patch attributes may be temporally dynamic. Previous work in our system has shown that patch type affects demographically important processes, such as fire temperatures and rates of herbivory (Brudvig et al. 2012, Levey et al. 2016); however, due to the temporally variable nature of these processes, their impacts (which manifest as patch type effects) on population growth may not be predictable from the initial period after transplanting. Indeed, a recent study on long-term (22 yr) population dynamics of a pyrogenic herb found that impacts of patch attributes on population growth rate were mediated by an interaction with time-since-fire (Quintana-Ascencio et al., 2018). Synthesizing these results, we propose a testable hypothesis: patch attributes, whose impacts on plant demography may be mediated by temporally dynamic processes, will be less useful for forecasting restoration outcomes than more permanent landscape features (e.g., the soil variation among landscapes in our study).

Although we do not know the precise reasons why landscape identity best predicted population growth rates in our system, there are several things we do know. First, spatial factors such as habitat area and configuration were held constant across landscapes, so these cannot explain the effects of landscape identity. Second,

given the match between predicted and observed influence of landscape identity for population growth, these among-landscape effects are likely temporally stable, at least for the duration of our study. These may include local-scale factors that covary across patches within a landscape but differ among landscapes (e.g., soil conditions). Alternatively, there could be properties of entire landscapes that covary and were unmeasured, such as subtle differences in matrix composition.

Drivers of model accuracy

While both of our focal species were perennial forbs with similar life histories, including individual growth habit (basal rosettes) and insect-pollinated flowers, we found differences in forecasting ability between them. In general, population models for *Liatris* had higher forecast accuracy than *Carphephorus* after six years, with nearly half the mean absolute error in forecasted population growth rate for the former species. Models for *Liatris* also improved performance from a three- to a six-year forecast window. While forecast accuracy was higher for *Liatris,* differences between the four models with varying landscape-scale predictors were smaller than for *Carphephorus,* implying that variation among landscapes was more important for forecasting population growth for *Carphephorus* than for *Liatris.* Nevertheless, we observed sharp limits to forecasting accuracy for the two *Liatris* models without landscape identity (Fig. 3), suggesting that without including this term in the predictive models, there is an upper bound to how well we can forecast differences between populations. Altogether, the differences in model forecasting between our two relatively similar species point to the need to explore forecasting ability of demographic models over a wide range of species of reintroduction interest.

In our global sensitivity analysis, we found that the majority of variance in forecast error was due to uncertainty in seed production for both of our study species. This result suggests that targeting seed production for further study will yield the biggest gains in forecast accuracy. In our global sensitivity analysis, output uncertainty results from a combination of parameter uncertainty and process error. Parameter uncertainty could be decreased by increasing sampling efforts for seed production. Process error could be decreased with further study of the biological mechanisms that lead to differences in pollination and flowering head production between populations, such as proximity to competitors such as overstory trees (Turley et al. 2017). Uncertainty analysis will play a major role in improving near-term forecasting in ecology by enabling researchers to identify sources of error in complex models (Ellner and Fieberg 2003, Perz et al. 2013). Our approach demonstrates how a fundamental concept from population ecology (sensitivity analysis; Easterling et al. 2000) can be applied to evaluate models that forecast ecological outcomes.

Population forecasting implications

Our success at forecasting population growth is surprising, given the many reasons predictive models might fail when they are fit with data on demographic rates of transplants during the first two years following reintroduction. First, the demographic rates of transplants might differ from the demographic rates of individuals that recruited naturally in the field (Bell et al. 2003). Second, demographic rates are likely to change as population density in establishing population increases, due to negative density dependence (Petermann et al. 2008). Third, environmental stochasticity can alter population dynamics, leading to predictive error in demographic models that ignore year-to-year variability (Crone et al. 2013). Our models were based mostly on demographic data from transplants (albeit, planted as seedlings, individuals that grew primarily in the field), and models did not include negative density dependence, environmental stochasticity, or demographic stochasticity. One or more of these factors are likely responsible for our models' tendency to overpredict population growth rate (Fig. 4). For our fire-maintained system (including plots that experienced several burns during the six-year forecast window), incorporating environmental stochasticity into our demographic models is a top priority.

Despite the simplifications of our models, we were able to forecast demographic performance between landscapes with high accuracy (e.g., >90% accuracy in predicting which *Liatris* populations were growing or shrinking after six years). For the application of our modeling approach to restoration decision-making, the tradeoff of waiting for multiple years of data to parameterize more complicated models is a decreased ability to alter reintroduction plans based on initial data. Overall, we agree with Dietze et al. (2018) that the best path forward for ecological forecasting that supports environmental management is to test predictive models with available data using an iterative approach, rather than waiting for optimal models and datasets.

Conclusions and management implications

Our work focused on population dynamics of two species of reintroduction interest; however, general aspects of our approach and findings provide several take-home messages for a range of conservation and restoration applications. First, our consideration of replicate study populations provided statistical power to quantify reintroduction outcomes and to relate those outcomes to landscape-scale variables. Second, our measurement of multiple demographic rates and use of hierarchical Bayesian methods provide a way to combine data across spatial scales and to propagate uncertainty in parameter estimation into model predictions (Elderd and Miller 2016). Finally, our assessments of those predictions three and six years later illustrate the importance of considering landscape-scale variation (and, in particular, landscape identity) for improving the accuracy of model forecasts. These general lessons could be applied to forecast other restoration metrics, such as biodiversity, carbon sequestration, or canopy closure, using process models fit to landscape-scale data. Across these and other measures, our findings illustrate the importance of considering landscape-scale variation when planning, forecasting, and assessing the outcomes of large-scale restoration projects.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1850/full

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8s7v328.