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Leveraging projection models to evaluate long-term dynamics of scrub mint translocations

Federico López-Borghesi[1] | **Stephanie M. Koontz**[2] | **Stacy A. Smith**[3] | **Sarah J. Haller Crate**[4] | **Pedro F. Quintana-Ascencio**[1] | **Eric S. Menges**[2]

[1]Department of Biology, University of Central Florida, Orlando, Florida, USA
[2]Plant Ecology Program, Archbold Biological Station, Florida, USA
[3]Department of Agronomy, University of Florida, Gainesville, Florida, USA
[4]North Carolina Department of Agriculture and Consumer Services, North Carolina Forest Service, Raleigh, North Carolina, USA

Correspondence
Federico López-Borghesi, Department of Biology, University of Central Florida, 4110 Libra Dr., Orlando, FL 32816, USA.
Email: flopezborghesi@knights.ucf.edu

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Abstract

Translocated populations often show vigorous initial dynamics but eventually collapse. Modeling tools that incorporate basic ecological knowledge and allow for propagation of uncertainty can help identify potential risks. Here, we use Bayesian Integral Projection Models to estimate population growth rates (λs), associated elasticities, and extinction risks for the endangered *Dicerandra christmanii*. Our study compared natural populations in gaps (open areas) within the shrub matrix and roadsides, unoccupied gaps augmented with transplants, and introduced populations. These populations experienced different management, including prescribed fires, and had different initial conditions. Augmented gaps showed lower means but similar variation in λs as natural gaps. Yet, simulations indicate that augmentations can delay quasi-extinction (40% of simulations) by 4 years at the population level. Introduced populations showed higher means and variation in λs as wild gaps. While vital rate estimates suggested initial translocation success, time to quasi-extinction was projected to be 7 years shorter for introductions in gaps than for natural gap populations. These contradictory results are partially explained by the lack of established seed banks in introduced populations, which affected the response of early life stage transitions to a prescribed fire. This study highlights the need to account for site-specific information in models of population dynamics, including initial conditions and management history, and especially cryptic life stages such as dormant seeds.

KEYWORDS
augmentation, Bayesian, fire, habitat management, integral projection models, introduction, rare plants, seed bank, translocations

1 | INTRODUCTION

Populations of endangered and rare species are particularly vulnerable to anthropogenic pressures, requiring effective management for their persistence. In the last 25 years, the use of translocations as a tool for species rescue has surged (Abeli & Dixon, 2016; Falk et al., 1996). The term translocation refers to the movement of species, or other ecological material, performed by people (Dalrymple et al., 2021). Our study included two types of translocations: augmentations—the addition of individuals to an existing population—and introductions—the addition of individuals to a historically unoccupied site within the historic range of the species (IUCN, 2013).

Translocations can help to alleviate reductions in suitable habitat and environmental change (Sgrò et al., 2011). Properly evaluating differences in the dynamics of translocated and wild populations, however, can be challenging (Bell et al., 2003; Menges, 2008), as they are subject to different sources of process error, including time-lagged responses to management decisions (Royama, 2012). Transplants rarely replicate the size distribution of wild populations, lacking particularly in cryptic life stages like seed banks. Because seeds are often the most abundant life stage, a reduced seed bank can have profound impacts on demographic dynamics. Accounting for cryptic life stages in demography is critical, particularly when dealing with dynamic and unpredictable conditions like those that usually characterize translocations. In addition, transplants are often provided with initial support, such as watering, which can reduce mortality (Dillon et al., 2018) and help individuals outperform natural recruits during early stages (Halsey et al., 2017). The inability to accurately evaluate long-term performance might prevent corrective measures and ultimately lead to translocation failure (Drayton & Primack, 2012). In fact, the success of translocations tends to decrease with time and failures are under-reported compared to successes (Godefroid et al., 2011).

Structured population models allow us to investigate questions pertinent to conservation and management because they help connect the effect of biotic and abiotic factors on individuals of different age, stage, or size to population dynamics (Doak et al., 1994; Methot Jr & Wetzel, 2013). Of the wide range of available options, Integral Projection Models (IPMs) have been increasingly adopted for studying issues of population growth rate and derived metrics (Merow et al., 2014). IPMs have the same analytic advantages of traditional matrix models but are constructed from continuous distributions instead of discrete classes (Easterling et al., 2000). This has the added advantage of avoiding arbitrary class divisions while significantly reducing parameter estimation (Easterling et al., 2000; Ellner & Rees, 2006). Modeled population growth rates and associated metrics are succinct indicators of relative demographic status. They can help identify possible population threats and compare management alternatives (Regan et al., 2017).

Typically, an IPM kernel is constructed with statistical models of individual-scale vital rates, such as survival, growth, and fecundity (Ellner & Rees, 2006). These models have commonly been fitted within frequentist and maximum-likelihood frameworks. While simpler, these approaches lack the flexibility necessary to explicitly account for different sources of process and observation error (Conn et al., 2008) inherent in translocation experiments. The use of Bayesian methods in ecology has been rising for the past three decades, facilitated by advances in technology (Gimenez et al., 2009). Their use in IPM studies, however, has been fairly limited (e.g., Diez et al., 2014; Elderd & Miller, 2016; Rees & Ellner, 2009), partly due to their heavy computational requirements.

Bayesian approaches, however, provide several advantages in the construction of IPMs (Elderd & Miller, 2016), making them better suited to our current study. The main advantage of using Bayesian approaches to parameterize IPMs lies in the ability to translate the posterior distribution of the vital rate parameters into posterior distributions of other metrics such as population growth rate (Elderd & Miller, 2016). This allows tracking different sources of variation.

In a companion paper, we used Bayesian methods to compare vital rate variation of *Dicerandra christmanii* across five types of populations, including natural and translocated populations in different habitats (Koontz et al., 2023). Our goal here was to combine these vital rates into IPMs and evaluate differences in the population dynamics of *D. christmanii* across the different population types. We used an IPM framework to estimate population growth rates and associated stochastic elasticities to determine the influence of stage transitions on the mean and variance of these growth rates. We also performed simulations to explore long-term trends when site history (disturbances and initial conditions) is considered.

Our study included natural populations in gaps (open areas in the shrub matrix) and roadside habitats, augmented populations in gaps, and introduced populations in both gaps and roadsides. These populations underwent different management practices, including prescribed burning and initial assistance of transplants. We hypothesize that (1) local extinction probabilities are higher in roadside populations, due to higher population variances, than in gap populations immersed within the habitat matrix, (2) local extinction will be lower in periodically augmented populations with supplemented individuals than in populations without management, and (3) local extinction will be higher in recently introduced population than in native populations.

2 | METHODS

2.1 | Study species and sites

Dicerandra christmanii is a narrow endemic Lamiaceae native to Florida, United States. It is listed at the state and federal levels, and considered critically imperiled (NatureServe, 2019; USFWS, 1999). Both the South Florida multi-species recovery plan (USFWS, 1999) and local conservation groups (Turner et al., 2006) recommend translocations for its persistence.

Dicerandra christmanii is found on yellow sands of oak-hickory scrub (Weekley et al., 2008), a shrubland of oaks and palms maintained by periodic fires (with a return interval of 5–12 years; Menges, 2007). It grows in gaps within the shrub matrix and on the side of sandy roads (Menges, 1999). Aboveground individuals are killed by fire, but populations recover from persistent soil seed banks. *Dicerandra christmanii* has been recorded in fewer than 10 sites (FNAI, 2010) with only one population in a protected site: the Flamingo Villas (FV) unit of the Lake Wales Ridge National Wildlife Refuge (LWRNWR), which is managed by the US Fish and Wildlife Service (USFWS). More detailed descriptions on the species can be found in the companion manuscript (Koontz et al., 2023).

2.2 | Data collection

We began collecting data in 1994 at a gap area in FV using a 45 × 2 m belt transect and six nearby 1 m^2 quadrants. We added two additional gap areas: one in 2000 and another in 2010. Since 1999, we started monitoring two roadside areas with transects along firebreaks. In 2010, we augmented 40 gaps previously unoccupied by *D. christmanii* using both seedlings (200 total) and sown seeds (4000). Half of these gaps burned in a prescribed fire the year prior to the augmentation, and the other half remained unburned. Seedling and stem cutting transplants received supplemental irrigation the first year. In 2012, we introduced *D. christmanii* in 50 areas at Carter Creek (CC) using only transplants (216 total) but no seeds. This unit of the LWRNWR occurs 8 km north of FV and just 4 km from the northernmost known occurrence of *D. christmanii* (FNAI, 2010). Sixteen of these areas occurred along human-modified firebreaks (roadsides) while the remaining 34 were gaps within the scrub. All plants received initial irrigation, but only half received supplemental hand-watering through the end of 2012. Three years post-outplanting, this site was affected by a prescribed fire on May 2, 2015, burning 35 of the 50 study areas, most of them gaps.

We conducted annual censuses during peak flowering in October. We marked plants with numbered aluminum tags and pin flags or plastic toothpicks located near tags. We recorded the survival, life history stage (yearlings, vegetative adults, and reproductive adults), number of branch tips (>2 cm in length), and number of flowering branch tips (>2 cm in length) of marked plants. We collected fruits in late 2018 from natural populations in gaps and roadsides at FV and counted their seeds in the lab. We used 10 randomly selected light-to-medium brown, unopened schizocarps from each of 13 plants. Seeds light in coloration, small in size, or damaged by light pressure were considered unviable. We obtained fruits-per-branch counts in late 2019 from both FV and CC. Additional information on data collection can be found in Koontz et al. (2023).

2.3 | Evaluating vital rates

The overall IPM combined sub-models that estimated vital rates as a function of population type, habitat, and pulses due to translocation and fire effects. We recognized three life history stages—seed, yearling (new plant that survives to its first census), and adult—and used the natural logarithm of individual number of branches as the continuous state variable, with a quadratic response for survival. In a companion manuscript, we modeled vital rate variation using generalized linear mixed models (Koontz et al., 2023). We used binomial error distributions and logit link for survival (σ), probability of reproduction (φ0), and proportion of reproductive branches (φ1). Normal distributions were assessed for changes in number of branches for yearlings and adults (γ). Mean count of fruits per branch (φ2) was assessed with a normal distribution that was consistent with the distribution of log-transformed data. Mean number of seeds per fruit was estimated using a Poisson distribution of the overall fruit data. We ignored the occasional reproductive contribution from yearlings since the data were unreliable due to low sample size. The models describing survival (σ) and growth (γ) of yearlings and adults and probability of flowering (φ0) and proportion of flowering branches (φ1) of adults were defined in general as:

$$\begin{aligned} G(\mu|(i,j,k,m,r,s,y)) = {} & \alpha_0 + \alpha_1 \times B_i + \alpha_2\left[S_j\right] \\ & + \sum \beta_{index}\left[other\_variables\right] + \alpha_{s(y)} \\ & + \alpha_y \end{aligned} \tag{1}$$

where μ is the estimated mean for each of the dependent variables as a function of study drivers including size state (*i*; number of branches, *B*), stage (*j*; yearling/adult, *S*), burn condition (*k*; yes/no), habitat (m; gap/roadside), and initial translocation treatment (*r*; yes/no). The state variable (number of branches) was centered to facilitate the interpretation of the coefficient and to improve model convergence. Site within year $\alpha_{s_j(y_i)}$ and year α_{y_i} were included, when data permitted, as random effects centered in the estimate at the intercept. The coefficient α_0 was the posterior estimate for the focal vital rate variable for adults as a function of the mean value of branches in natural gaps without fire or translocation; α_1 was a coefficient for the number of branches per individual (B_i); α_2 the coefficient for the effect of stage (S_j); and β are coefficients for each additional driver and interactions (implicit in the formula). Excepting the size variable, levels for independent variables were incorporated as dummy variables against a reference level. Estimates of the variance of the error from models with normal distribution were evaluated but omitted in the equation above (for more information on decisions about variances, see Figure S1a,b).

Not all these variables were included in a particular vital rate model. We fitted several competing models (15–20 per vital rate) using frequentist inference—to take advantage of their computational speed—and performed model selection based on Akaike Information Criterion (Burnham & Anderson, 2002). We then fitted the top 3–4 models for each vital rate using Bayesian approaches and compared them via Widely Applicable Information Criteria (Wantabe, 2013) to gauge the consistency with the frequentist approach. In the Supporting Information, we present the selected model for each vital rate (Table S1) as well as their fit to data (Figure S4a–f) and model validation plots (Figure S5a–f).

We estimated the variation in annual recruitment of yearlings (N) per site as a function of initial translocation treatment (r; yes/no, T) and average number of viable seeds (Ss) from the current year (c) and the previous years (p; $Ss_{\mathrm{p}} = [1 - G_c] \times V \times Ss_{\mathrm{c}}$).

$$ln\left(N_{ys}\right) = \alpha_w + \beta_r[T_r] + G_c \times V \times Ss_c + G_{sb} \times D \times Ss_p + G_{sb} \times D \times D \times Ss_p + \alpha_{(y)} \tag{2}$$

where α_w was the mean yearlings and β_r was the coefficient for the effect of initial translocation treatment. Variation among years was included as random effects ($\alpha_{(y_i)}$). Seed viability (V) was a constant. Germination from new seeds (G_c) and from seeds in the seed bank (G_{sb}), and dormancy (D) were latent variables in the model. We used diffuse prior probabilities in all our models (McElreath, 2016) except for this model, where we used informative priors for germination and dormancy. These prior probabilities were based on data from *Dicerandra frutescens*, a congeneric species from similar habitats (Menges et al., 2006).

2.4 | Implementing the integral projection model

We modeled these data using fixed and random effects of the most plausible GLMM models in the set assessed to simulate the demographic variation of *D. christmanii* in response to management effects: pulses (first and second year after outplanting) and fire. We conducted statistical analyses using R version 3.4.4 (R Core Team, 2019) and version 2.18.0 of Stan (Carpenter et al., 2017; Stan Development Team, 2018).

We built the kernels of IPMs (Easterling et al., 2000; Ellner et al., 2016; Ellner & Rees, 2006) to summarize the life cycle of *D. christmanii* for each population type. We modeled nine populations combining different habitats and treatment: three natural populations in gaps; two natural populations in roadsides; two augmented populations in gaps (half burned and half not burned); and two introduced populations in different habitats (gaps and roadsides), which experienced fire 3 years after outplanting.

The continuous form of these IPMs (using the midpoint rule approximation; Ellner et al., 2016) was a Goodman matrix (Goodman, 1969) model (with 96 × 96 cells; Figure 1) describing the population dynamics of three stages, one discrete (dormant seeds) and two continuous (yearlings and adults). Every IPM consisted of the merger of four sub-matrices, two vectors, and one scalar: one sub-matrix of 80 × 80 cells for the annual change of adults; one sub-matrix of 15 × 80 cells for the production of yearlings from reproductive plants; one sub-matrix of 80 × 15 describing the transition of yearlings to adults; one sub-matrix of 15 × 15 with structural zeroes because the absence of yearling reproduction; one vector for germination of dormant seeds and their survival to the annual census (95 cells; 15 cells for information on size distribution of yearlings plus 80 with structural zeros); another vector for recently produced seeds (95 cells; 15 cells with zeros and 80 for the production of dormant seeds per size class); and one scalar describing long-term seed dormancy (Figure 1).

For the adults, the responses of coupled equations are integrated over $L = 0$ and $U = 6.8$ (natural logarithm values of 1–900 branches, respectively) using the midpoint approximation into $m = 80$ size classes of width $h = (U - L)/m$. We used the first 15 of these cells for yearlings ($L = 0$ and $U = 1.21$; natural logarithm values of 1–3.35 branches). Projections of models with 100 and 300 bins for adults or a larger portion of cells for yearlings were commensurate, so we kept 80 and 15 size classes for adults and yearling, respectively.

The discrete form of the IPM is described as:

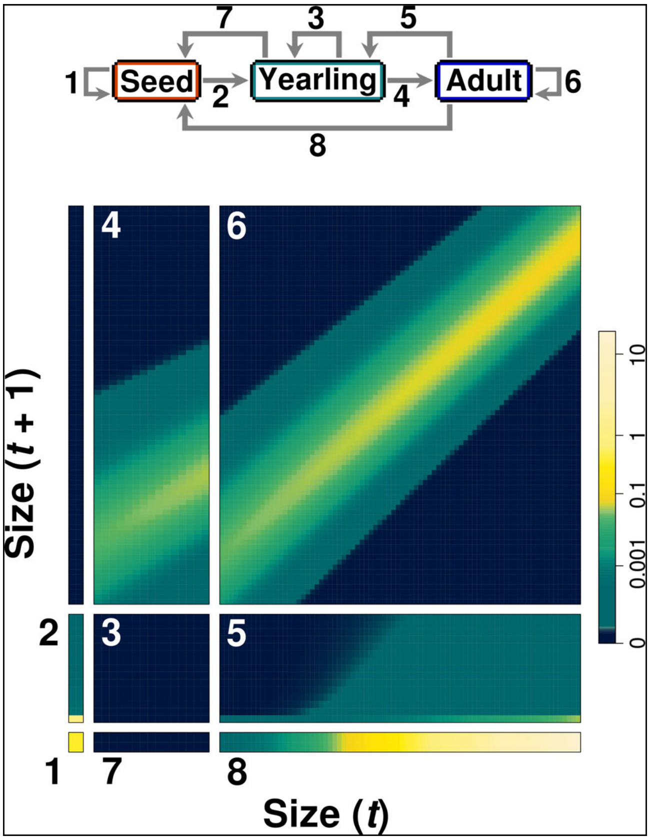

FIGURE 1 (Top) Life cycle of *Dicerandra christmanii* consisting of three stages (seeds, yearlings, and adults) and eight life history transitions (numbered). (Bottom) Demographic processes represented in a Goodman's matrix for a sample Integral Projection Model of a natural gap population. Size of aboveground individuals was measured as total number of branch tips. Numbers match life stage transitions to the section of the Goldman's matrix representing them: (1) long-term seed dormancy; (2) recruitment from dormant seeds; (3) recruitment from yearlings; (4) transitions from yearlings to adults; (5) recruitment from adults; (6) annual growth and survival for adults; (7) production of dormant seeds by yearlings; and (8) production of dormant seeds by adults. Color gradient shows the relative size of transitions and is customized to accommodate different scales.

$$n\left(z_{jk}, t+1\right) = h\sum_{i=1}^{m} K\left(z_{jk}, z_{ik}\right) n\left(z_{ik} t\right) \tag{3}$$

where $n\left(z_{jk}, t+1\right)$ is the number of individuals in size class j and stage k at time $t+1$ from individuals in size class i and stage k at time t given the matrix kernel (K) and number of individuals $\left[n\left(z_{ik} t\right)\right]$ at time t. We defined two continuous kernel functions for yearlings and adults, one including survival and growth ($P_{j.i}$) and another for recruitment ($F_{j.i}$; as surviving dormant seeds [$Seed_{(j,i)}$] and yearling recruitment [$Yearling_{(j)}$]).

$$K_{z(j,i)} = P_{(j,i)} + F_{(j,i)} \tag{4}$$

$$P_{(j,i)} = \sigma_{(i)} \times \gamma_{(j,i)} \tag{5}$$

$$F_{(j,i)} = Seed_{(j,i)} + Yearling_{(j)} \tag{6}$$

where j is the index for the vector of size classes n at $t + 1$, and i the one of time t.

Recruitment as (dormant) seeds included, for each size class (x) at time t, estimates of probability of reproduction (φ0), number of reproductive branches (φ1 × *exp* (γ); proportion of total reproductive branches × total number of branches); number of fruits per branch (φ2), number of viable seeds per fruit (φ3), and dormancy ($D \times [1 - G]$); where D is the proportion of seeds going dormant, and G is the proportion of seeds germinating

$$\begin{aligned} Seed_{(y,t+1)} = {} & Seeds_{(x,t)} \times D \\ & \times (1-G)\sum_{L}^{U}\left(\varphi_0(x) \times \varphi_1(x) \times exp(\gamma(x))\right) \\ & \times \varphi_2 \times \varphi_3 \times (1-G) \end{aligned} \tag{7}$$

Recruitment as yearlings (*yling*) included estimates of germination from the seed bank $\left(Seed_{(x,t)} \times D \times G\right)$, probability of reproduction (φ0), reproductive branches (φ1 $\times exp(\gamma)$; proportion of total branches × total number of branches); number of fruits per branch (φ2) and number of viable seeds per fruit (φ3), germination probability (G), and seedling survival to census (φ4).

$$\begin{aligned} yling_{(y,t+1)} = {} & Seed_{(x,t)} \times D \times G \\ & + \sum_{L}^{U}\left(\varphi_0(x) \times \varphi_1(x) \times exp(\gamma(x))\right) \times \varphi_2 \times \varphi_3 \\ & \times G \times \varphi 4 \end{aligned} \tag{8}$$

We assigned an initial number of branches to yearlings at census time using a gamma distribution with coefficients specific to yearling data per population type. We used the eigen-structure of our models to quantify the population growth rate (λ) for each population. We used 200 posterior estimates from our models to bracket variation in stochastic lambda (after 220 iterations with the first 20 discarded) as a function of the combinations of studied drivers (site, translocation, and fire).

2.5 | Elasticities

We estimated the elasticity of the stochastic growth rate λs with respect to the mean μ_{ij} and variance σ_{ij} of each element X_{ij} of the projection matrices (Tuljapurkar et al., 2003) for natural and roadside populations. We used 200 posterior estimates to characterize the uncertainty around these estimates (Elderd & Miller, 2016). We then summarized these results to represent the effect on each life stage transition.

2.6 | Projected simulations

We projected the population dynamics for combinations of treatments and habitats and estimated their extinction probabilities after 100 simulated years:

1. Natural gap populations: For the initial vector, we used the average number of individuals at natural gaps, distributed as in the stable stage distribution of the average gap model.
2. Natural roadside populations: We used as the initial vector the average number of individuals at roadsides, distributed as in the stable stage distribution of the average roadside model.
3. Augmented gap populations: We modeled sites as following natural gap dynamics but added a simulated augmentation every 20 years. Augmented plants were simulated in parallel to the wild gap plants for 7 years, then both groups of plants were merged in a common vector and simulated for another 13 years using natural gap dynamics. The overall simulation lasted 100 years and involved four augmentations (at 20, 40, 60, and 80 years). We combined previously burned and unburned gaps. For the augmentations, we used the actual initial number of plants and seeds augmented as the initial vector.
4. Introduced gap populations: We projected an introduction into gaps for 7 years, including a fire in the third year and post-fire conditions in Years 3, 4, and 5. Then the population was simulated with natural gap dynamics for 93 years. We used the actual initial number of plants introduced in the gap as the initial vector (which did not include seeds).
5. Introduced roadside populations: We projected an introduction to roadsides for 7 years, with two-thirds burned. Then the population was simulated with the natural roadside dynamics for 93 more years. We used the actual number of plants introduced in the roads as the initial vector (which did not include seeds).

We used the time to reach the quasi-extinction (Ginzburg et al., 1982) threshold of 40% of the simulated populations having <1 plant, as an indicator to compare the relative performance of different simulated population types. We are convinced that this threshold is informative for managers since it still provides time to respond with adaptive management strategies to any potential threats identified.

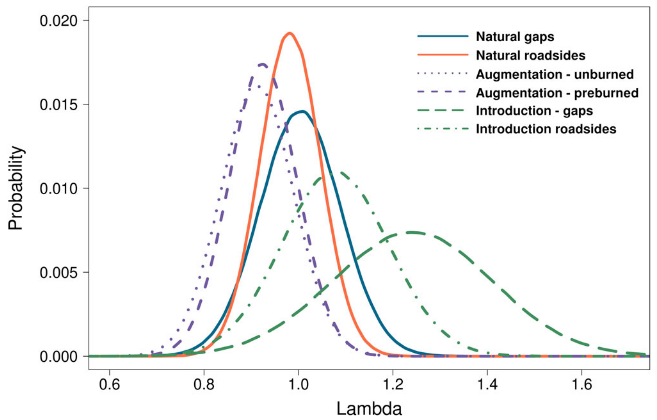

FIGURE 2 Probability distribution of stochastic lambda values for each population evaluated: natural gaps (solid blue), natural roadsides (solid orange), unburned augmented gaps (dotted purple), burned augmented gaps (short-dashed purple), introduced gaps (long-dashed green) and introduced roadsides (dot-dashed green).

3 | RESULTS

3.1 | Population trajectories

Observed populations in natural gaps and roadsides fluctuated from <50 aboveground individuals to >300, with higher numbers between 2010 and 2015 (Figure S1). Recruitment of yearlings was more variable in roadsides than in gaps. In the augmented populations, observed aboveground individuals increased from 200 at the time of translocation to >800 5 years later, subsequently declining to ~500 plants 7 years post-outplanting. The introduction consisted of a total of 216 plants. The number of aboveground individuals in the introduced gap populations fluctuated strongly; first increasing to >800 in the second year, decreasing to <30 after fire, and rebounding to ~400 the following year. The site continued to fluctuate strongly the last 2 years of sampling. In roadsides of the introduction, aboveground individuals were less affected by fire and increased gradually over the study period, reaching >600 individuals by the end of sampling.

Overall population lambdas for natural gap and roadside populations had mean values close to 1 with relatively narrow distributions (Figure 2). Populations introduced to gaps had the highest mean lambda values (1.24) but with the widest distribution (highest uncertainty). Augmented populations in previously burned gaps had slightly higher mean lambdas than

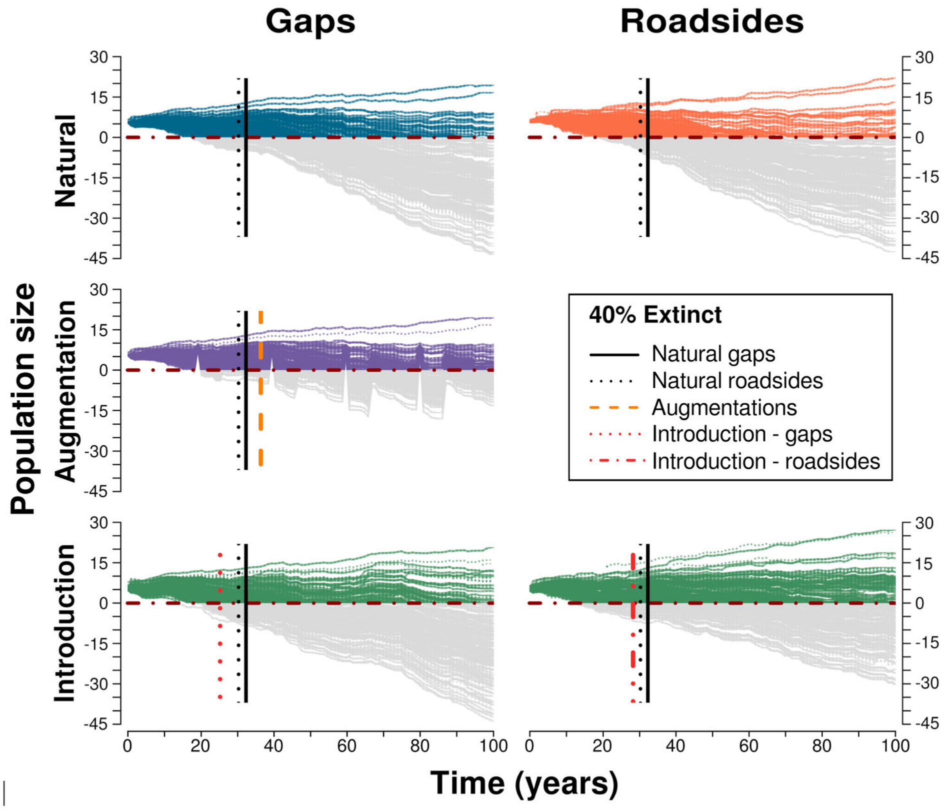

FIGURE 3 Projected trajectories for different population types simulated: natural gaps (blue), roadsides (orange), gaps augmented every 20 years (purple), introduced populations in gaps (green; left), and introduced populations in roadsides (green; right). The horizontal red dashed line indicates the threshold of one individual. The vertical lines indicate the quasi-extinction year when 40% of simulations go under the one-individual threshold. The year of natural gap (vertical solid black) and natural roadside (vertical dotted black) pseudo-extinctions is included in every panel as reference.

those in unburned gaps (0.92 vs. 0.91) but both had distributions similar in width to the wild populations.

Projected lambdas per year reasonably mimicked observed sequences in annual population changes (N_{t+1}/N_t) for the longest sequences observed in natural gaps and roadsides (Figure S2). Some peaks in recruitment, such as those observed in 2009 (Sites 1–4), were not properly recovered by the projected lambdas. This is likely due to a dampening effect by individuals in the seed bank (which are included in λ). In fact, the projected change in aboveground individuals (N0) better recovered recruitment peaks.

3.2 | Extinction probabilities

All population types had clear risk of extinction (59.0%–91.5%) in the long-term (100 years) under current conditions (Figure 3). Augmented gaps had the longest times to quasi-extinction (37 years). Roadside populations had shorter times to quasi-extinction (31 years) than wild gap populations (33 years). Introductions had the shortest times to quasi-extinction, with populations introduced to gaps showing shorter times (26 years) than those introduced to roadsides (29 years).

3.3 | Elasticities

Elasticities of λs with respect to the mean were highest for adult growth followed by early-stage transitions in both gap and roadside habitats (Figure 4). Seeds remaining in the seed bank had the second highest impact, followed by yearling-to-adult transitions and germination from the seed bank. The large role of adult growth was contributed mainly by mid-sized plants (20–150 branches; Figure S3). The elasticity of λs with respect to the variance showed a similar pattern, being by far stronger for adult growth, followed by yearling-to-adult transitions.

4 | DISCUSSION

Species translocations are labor-intensive endeavors. Besides the addition of propagules, they may require strategies aimed at restoring ecological conditions such as hydrology and disturbance patterns (Menges, 2008). Because the biological and ecological knowledge needed for these efforts is often lacking, it is essential to evaluate translocations as experiments (Kaye, 2008; Schemske et al., 1994). Long-term monitoring is seen as an essential part of any translocation experiment; however, practical

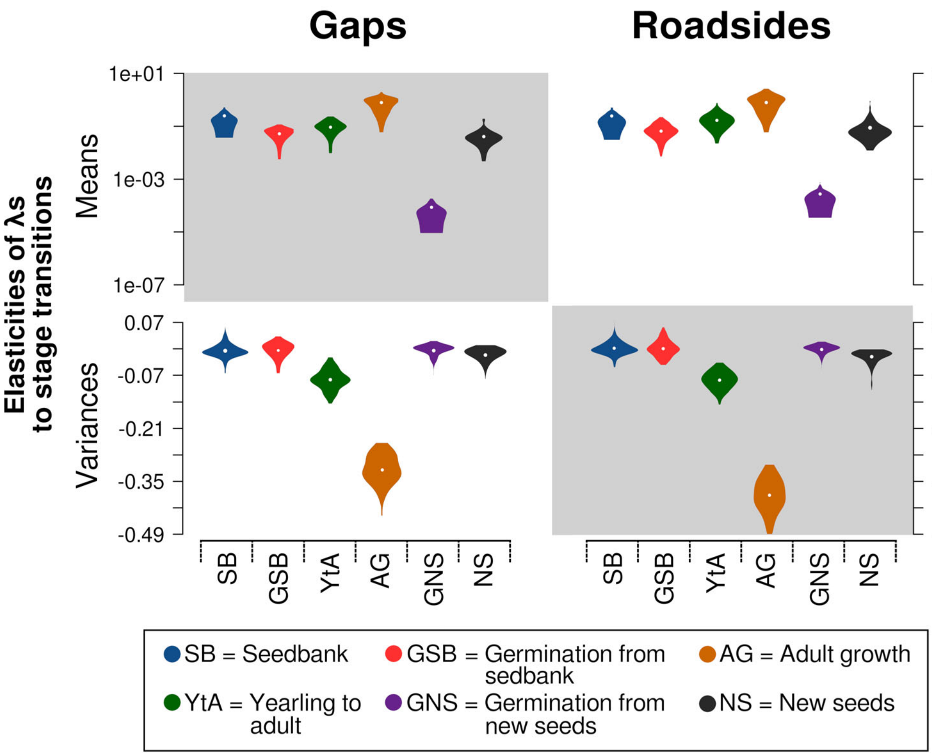

FIGURE 4 (Top) Elasticities of λs with respect to the mean values of life-stage transitions in natural gaps and roadside habitats. (Bottom) Elasticities of λs with respect to the variances of life-stage transitions in natural gaps and roadside habitats. Elasticities of variances are negative because higher variance reduces stochastic lambda. The violin graphs show the result of 100 iterations.

constrains usually limit monitoring to just a few years (Godefroid et al., 2011). More importantly, monitoring alone cannot provide the mechanistic perspectives necessary to understand and predict risk of failure (Menges, 2008). Here, we demonstrate the benefits of using Bayesian IPMs to estimate population growth rates, associated elasticities, and extinction risks. By allowing us to track how uncertainty around vital-rate estimates translates into uncertainty around population-level parameters, these methods can help formulate hypotheses on future trends and identify potential reasons for failure. Furthermore, by explicitly considering pulse effects (translocation and fire) and seed bank dynamics, these IPMs allow us to perform stochastic simulations that account for site and population characteristics.

In tandem with the companion manuscript (Koontz et al., 2023), our results paint a complex picture of translocation dynamics and suggest likely reasons for the often-observed long-term failure of initially successful translocation efforts (Godefroid et al., 2011). For *D. christmanii*, vital rate estimates indicate initial translocation success, with values for introductions as strong or stronger than those for natural populations (Koontz et al., 2023). This might be partially explained by the vigor of the plants used in outplanting, which were grown in more favorable greenhouse conditions, and short-term actions including small scale disturbances and initial irrigation. Regardless, these results provide support for the choice of site and outplanting strategies. Conversely, projected simulations indicate a higher risk of extinction for introductions than natural populations. Time to quasi-extinction for introduced populations in gaps is estimated to be 7 years shorter than for natural gap populations (33 vs. 26 years). These seemingly contradictory results highlight the need to properly account for uncertainty and to include site-specific information in our models, including previous management, habitat heterogeneity, and population history (legacies).

Results of the elasticity analyses emphasize the importance of early life-stage transitions for *D. christmanii*, particularly that of seed bank dynamics (dormancy and germination). These phenomena match results seen with other translocations (e.g., Gross & Mackay, 2014) and highlights the need to account for cryptic life stages. While often hard to assess, these life stages can be critical under conditions of extreme variability (Nguyen et al., 2019). Describing the role of different seed bank parameters on population dynamics is key to predict population trends under different scenarios (Adams et al., 2008). The formation of persistent seed banks provides a means of long-term security when aboveground conditions are unfavorable, for instance in long-unburned habitats (Menges & Quintana-Ascencio, 2004). Simultaneously, large germination events after fires, coupled with occasional recruitment into open areas of unburned habitats, result in growth and reproduction of aboveground individuals that help replenish the seed bank (Quintana-Ascencio et al., 2003). Our results indicate that a change in the mean value of either seed bank dormancy or germination would have a positively correlated effect on the stochastic lambda (Figure 4). However, it is important to note that these two parameters (germination and dormancy) are not independent from each other, and an increase in one can only occur in detriment of the other (Benton & Grant, 1996; Paniw et al., 2017). Notwithstanding the importance of the seed bank and other cryptic life stages, they are often neglected in demographic studies and frequently ignored in population counts due to the difficulty of its measurements (López-Borghesi, 2018; Nguyen et al., 2019).

When considering the known history of disturbance, the results of our analysis suggest a potential explanation for the greater risk of extinction predicted for introduced populations. While *D. christmanii* is adapted to a habitat with a typical fire-return-interval of 5–12 years (Menges, 2007), a prescribed fire was performed only 3 years after outplanting. Given that seeds were not added as part of the introduction, it is likely that such an early disturbance occurred before a permanent seed bank was fully formed. A sudden depletion of the incomplete seed bank could account for the increase in risk of extinction. Appropriate fire management is essential to improve vital rates in species adapted to fire-maintained habitats (Slapcinsky et al., 2010), and it has been key in the introduction of other rare plant populations (Bowles et al., 2015).

Another important result of the elasticity analyses is the strong effect of the yearling-to-adult variance, especially in roadside *D. christmanii* populations. As the probability of growth from yearling to adult becomes more variable, the stochastic lambda decreases proportionally. This means that any changes in the survival of yearlings will negatively affect population growth rates. When considering the effect of early assistance to adult plants in both types of translocations, this effect provides a potential explanation for the greater uncertainty in translocated populations. As pulse effects disappear, yearling-to-adult transitions become more dependent on natural conditions, changing gradually toward native values. Additionally, yearlings tend to be more susceptible in exposed roadsides than in interior gaps, increasing the variability in their survival probability. When dealing with adult plants, elasticities point at growth of mid-sized plants as having the greatest impact on stochastic lambda. In fact, the shape of elasticities for adult plants of different sizes mimics the frequency distribution of observed plants (Figure S3). This highlights an often-unappreciated aspect of demography—phenomena affecting the more abundant life stages often have the greatest impact.

Effective measures of success for translocations can be hard to determine. Production of seeds and recruitment are often seen as valuable metrics of success (Godefroid et al., 2011), but even the presence of new cohorts of reproductive individuals might not be enough to sustain populations (Menges, 2008). Estimating vital rates of subsequent generations can also be a useful tool, but without placing them in the context of wild populations, they can be misleading (Koontz et al., 2023). Overall, quantifying the uncertainty of vital rates, particularly those with strong effects on population growth rate, can help researchers to account for uncertainty associated with environmental stochasticity (Evans et al., 2010). While monitoring over an extended period is still essential to determine the ultimate success or failure of translocations (Falk et al., 1996; Guerrant Jr & Kaye, 2007), adequate predictive tools can provide hypotheses to understand mechanisms behind observed trends and suggest corrective strategies (Menges, 2008). However, as demonstrated by this study, predictive models need to account for cryptic life stages, such as dormant seeds, and site history, or the interaction between them to provide useful insight on the mechanisms behind observed patterns.

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DATA AVAILABILITY STATEMENT

Demographic measurements from annual censuses (from 1994 to 2018), seeds per fruit, fruits per reproducive branch, and yearling recruitment for all habitat types in comma-separated-value files are provided on Dryad: https://doi.org/10.5061/dryad.bvq83bkf5. The code used for this paper can be accesses on GitHub: https://github.com/FedeLoBo/Dicerandra_chirstmanii.

ORCID

Federico López-Borghesi https://orcid.org/0000-0002-5557-0399
Pedro F. Quintana-Ascencio https://orcid.org/0000-0001-7587-8166
Eric S. Menges https://orcid.org/0000-0002-9486-4189

REFERENCES

Abeli, T., & Dixon, K. (2016). Translocation ecology: The role of ecological sciences in plant translocation. *Plant Ecology*, *217*(2), 123–125.

Adams, C. R., Early, M. P., & Bamford, K. M. (2008). *Principles of horticulture*. Butterworth-Heinemann.

Bell, T. J., Bowles, M. L., & McEachern, A. K. (2003). Projecting the success of plant population restoration with viability analysis. In C. A. Brigham & M. W. Schwartz (Eds.), *Population viability in plants: Conservation, management, and modeling of rare plants* (pp. 313–348). Springer.

Benton, T. G., & Grant, A. (1996). How to keep fit in the real world: Elasticity analyses and selection pressures on life histories in a variable environment. *The American Naturalist*, *147*(1), 115–139.

Bowles, M. L., McBride, J. L., & Bell, T. J. (2015). Long-term processes affecting restoration and viability of the federal threatened Mead's milkweed (*Asclepias meadii*). *Ecosphere*, *6*(1), 1–22.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*(1), 1–32.

Conn, P. B., Diefenbach, D. R., Laake, J. L., Ternent, M. A., & White, G. C. (2008). Bayesian analysis of wildlife age-at-harvest data. *Biometrics*, *64*(4), 1170–1177.

Dalrymple, S. E., Winder, R., & Campbell, E. M. (2021). Exploring the potential for plant translocations to adapt to a warming world. *Journal of Ecology*, *109*(6), 2264–2270.

Diez, J. M., Giladi, I., Warren, R., & Pulliam, H. R. (2014). Probabilistic and spatially variable niches inferred from demography. *Journal of Ecology*, *102*(2), 544–554.

Dillon, R., Monks, L., & Coates, D. (2018). Establishment success and persistence of threatened plant translocations in south West Western Australia: An experimental approach. *Australian Journal of Botany*, *66*(4), 338.

Doak, D., Kareiva, P., & Klepetka, B. (1994). Modeling population viability for the desert tortoise in the western Mojave Desert. *Ecological Applications*, *4*(3), 446–460.

Drayton, B., & Primack, R. B. (2012). Success rates for reintroductions of eight perennial plant species after 15 years. *Restoration Ecology*, *20*(3), 299–303.

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, *81*(3), 694–708.

Elderd, B. D., & Miller, T. E. (2016). Quantifying demographic uncertainty: Bayesian methods for integral projection models. *Ecological Monographs*, *86*(1), 125–144.

Ellner, S. P., Childs, D. Z., & Rees, M. (2016). *Data-driven modelling of structured populations. A practical guide to the integral projection model*. Springer.

Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex demography. *The American Naturalist*, *167*(3), 410–428.

Evans, M. E., Holsinger, K. E., & Menges, E. S. (2010). Fire, vital rates, and population viability: A hierarchical Bayesian analysis of the endangered Florida Scrub mint. *Ecological Monographs*, *80*(4), 627–649.

Falk, D. A., Millar, C. I., & Olwell, M. (1996). *Restoring diversity: Strategies for reintroduction of endangered plants*. Island Press.

FNAI. (2010). *Florida natural areas inventory*. Florida Conservation Lands http://fnai.org

Gimenez, O., Bonner, S. J., King, R., Parker, R. A., Brooks, S. P., Jamieson, L. E., Grosbois, V., Morgan, B. J. T., & Thomas, L. (2009). WinBUGS for population ecologists: Bayesian modeling using Markov chain Monte Carlo methods. In *Modeling demographic processes in marked populations* (pp. 883–915). Springer.

Ginzburg, L. R., Slobodkin, L. B., Johnson, K., & Bidman, A. G. (1982). Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis*, *2*(3), 171–181.

Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A.-D., Aguraiuja, R., Cowell, C., Weekley, C. W., Vogg, G., Iriondo, J. M., Johnson, I., Dixon, B., Gordon, D., Magnanon, S., Valentin, B., Bjureke, K., Koopman, R., Vicens, M., Virevaire, M., & Vanderborght, T. (2011). How successful are plant species reintroductions? *Biological Conservation*, *144*(2), 672–682.

Goodman, L. A. (1969). The analysis of population growth when the birth and death rates depend upon several factors. *Biometrics*, *25*, 659–681.

Gross, C. L., & Mackay, D. (2014). Two decades of demography reveals that seed and seedling transitions limit population persistence in a translocated shrub. *Annals of Botany*, *114*(1), 85–96.

Guerrant, E. O., Jr., & Kaye, T. N. (2007). Reintroduction of rare and endangered plants: Common factors, questions and approaches. *Australian Journal of Botany*, *55*(3), 362–370.

Halsey, S. J., Bell, T. J., & Bowles, M. (2017). Initial transplant size and microsite influence transplant survivorship and growth of a threatened dune thistle. *Ecological Restoration*, *35*(1), 52–59.

IUCN Species Survival Commission. (2013). Guidelines for reintroductions and other conservation translocations, Version 1.0. Gland, Switzerland.

Kaye, T. N. (2008). Vital steps toward success of endangered plant reintroductions. *Native Plants Journal*, *9*(3), 313–322.

Koontz, S. M., López-Borghesi, F., Smith, S. A., Haller Crate, S. J., Quintana-Ascencio, P. F., & Menges, E. S. (2023). Estimating vital rate variation to assess early success of scrub mint translocations. *Conservation Science and Practice*. https://doi.org/10.1111/CSP2.12934

López-Borghesi, F. (2018). Buried lies: Incongruities between seed banks in population models and field measures. Ecological Society of America. Annual meeting. New Orleans, Louisiana, USA. Abstract Paper 134. https://eco.confex.com/eco/2018/meetingapp.cgi/Paper/73159

McElreath, R. (2016). *Statistical rethinking a Bayesian course with examples in R and Stan*. CRC Press, Taylor & Francis Group.

Menges, E. S. (1999). Ecology and conservation of Florida scrub. In R. C. Anderson, J. S. Fralish, & J. Baskin (Eds.), *Savannas, barrens, and rock outcrop plant communities of North America* (pp. 7–22). Cambridge University Press.

Menges, E. S. (2007). Integrating demography and fire management: An example from Florida scrub. *Australian Journal of Botany*, *55*(3), 261–272.

Menges, E. S. (2008). Restoration demography and genetics of plants: When is a translocation successful? *Australian Journal of Botany*, *56*(3), 187–196.

Menges, E. S., Quintana Ascencio, P. F., Weekley, C. W., & Gaoue, O. G. (2006). Population viability analysis and fire return intervals for an endemic Florida Scrub mint. *Biological Conservation*, *127*(1), 115–127.

Menges, E. S., & Quintana-Ascencio, P. F. (2004). Population viability with fire in *Eryngium cuneifolium*: Deciphering a decade of demographic data. *Ecological Monographs*, *74*(1), 79–99.

Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., Record, S., Rees, M., Salguero-Gomez, R., & McMahon, S. M. (2014). Advancing population ecology with integral projection models: A practical guide. *Methods in Ecology and Evolution*, *5*(2), 99–110.

Methot, R. D., Jr., & Wetzel, C. R. (2013). Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, *142*, 86–99.

NatureServe. (2019). *NatureServe explorer: An online encyclopedia of life [web application]*. Version 7.1. NatureServe http://explorer.natureserve.org

Nguyen, V., Buckley, Y. M., Salguero-Gómez, R., & Wardle, G. M. (2019). Consequences of neglecting cryptic life stages from demographic models. *Ecological Modelling*, *408*, 108723.

Paniw, M., Quintana-Ascencio, P. F., Ojeda, F., & Salguero-Gómez, R. (2017). Accounting for uncertainty in dormant life stages in stochastic demographic models. *Oikos*, *126*(6), 900–909.

Quintana-Ascencio, P. F., Menges, E. S., & Weekley, C. W. (2003). A fire-explicit population viability analysis of *Hypericum cumulicola* in Florida rosemary scrub. *Conservation Biology*, *17*(2), 433–449.

R Core Team. (2019). R: A language and environmental for statistical computing. R foundation for statistical computing, Vienna,Austria. https://www.R-project.org/

Rees, M., & Ellner, S. P. (2009). Integral projection models for populations in temporally varying environments. *Ecological Monographs*, *79*(4), 575–594.

Regan, H. M., Bohórquez, C. I., Keith, D. A., Regan, T. J., & Anderson, K. E. (2017). Implications of different population model structures for management of threatened plants. *Conservation Biology*, *31*(2), 459–468.

Royama, T. (2012). *Analytical population dynamics* (Vol. 10). Springer Science & Business Media.

Schemske, D. W., Husband, B. C., Ruckelshaus, M. H., Goodwillie, C., Parker, I. M., & Bishop, J. G. (1994). Evaluating approaches to the conservation of rare and endangered plants. *Ecology*, *75*(3), 585–606.

Sgrò, C. M., Lowe, A. J., & Hoffmann, A. A. (2011). Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, *4*, 326–337.

Slapcinsky, J. L., Gordon, D. R., & Menges, E. S. (2010). Responses of rare plants species to fire in Florida's pyrogenic communities. *Natural Areas Journal*, *30*(1), 4–19.

Stan Development Team. (2018). Stan modeling language users guide and reference manual, Version 2.18.0. http://mc-stan.org

Tuljapurkar, S., Horvitz, C. C., & Pascarella, J. B. (2003). The many growth rates and elasticities of populations in random environments. *The American Naturalist*, *162*, 489–502.

Turner, W. R., Wilcove, D. S., & Swain, H. M. (2006). State of the scrub. Conservation progress, management responsibilities, and land acquisition priorities for imperiled species of Florida's Lake Wales ridge. Archbold Biological Station Report, Venus, Florida.

USFWS. (1999). South Florida multi-species recovery plan. Atlanta, GA.

Wantabe, S. (2013). WAIC and WBIC are information criteria for singular statistical model evaluation. Proceedings of the workshop on information theoretic methods in science and engineering (90–94).

Weekley, C. W., Menges, E. S., & Pickert, R. L. (2008). An ecological map of Florida's Lake Wales ridge: A new boundary delineation and an assessment of post-Columbian habitat loss. *Florida Scientist*, *71*(1), 45–64.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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