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Estimating vital rate variation to assess early success of scrub mint translocations

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Abstract

Species translocations are increasingly common in rare plant conservation. Wild populations can provide basic ecological knowledge to improve their chance of success. In the heavily fragmented Florida scrub, USA, many listed species require translocations to persist, including *Dicerandra christmanii*. In 1994, we began monitoring the only protected population of *D. christmanii* growing both in gaps (open areas) within the shrub matrix and on roadsides. In 2010, we augmented this population by adding plants and seeds to unoccupied gaps. In 2012, we introduced plants to a separate protected site to create a new population. We evaluated early translocation success using generalized linear mixed-effect models of vital rate variation among habitat types. Survival probability increased with size, peaking at 0.6–0.8, and was lowest in augmentations and highest in introductions. Growth increased with plant size across all habitat types, except for the largest adults which experienced senescence. Naturally recruited plants in gaps showed the highest reproduction probability and fecundity at smaller sizes, but larger plants in translocations had the highest fecundity. Yearling recruitment was higher in translocated plants relative to naturally recruited plants in gaps during the initial years following outplanting. Experimental components of translocations also affected outplanting performance with positive effects of fire. These analyses suggest a high potential for translocations to become established and contribute to species recovery.

KEYWORDS

augmentation, fire, Florida scrub, habitat management, introduction, mixed effects models, rare plants, translocations

1 | INTRODUCTION

Protected natural areas are often effective in conserving biodiversity (Bruner et al., 2001), but some taxa, such as plants, are dispersal-limited and poorly equipped to move to protected habitats (Clark et al., 2007). Species translocations, either within or outside historic ranges, are an increasingly common practice in efforts to preserve biodiversity. We define translocation as the human-mediated movement of a species (Griffith et al., 1989).

Translocations include augmentations, adding plants to an existing population, and introductions, adding plants to a historically unoccupied site but within the historic range of the species (IUCN, 2013).

Detailed data on translocation success or failure is critical to improve future management strategies and can be a valuable source of general ecological information (Abeli & Dixon, 2016; Menges, 2008). Unfortunately, the majority of translocations go unreported (Silcock et al., 2019). Moreover, surveys of unpublished data reveal that failures are poorly documented and subsequent monitoring is often insufficient (Godefroid et al., 2011). While there is robust documentation for measures of early translocation success (Menges, 2008; Pavlik, 1996), indicators may shift in importance as populations become established. Year-to-year variation in environmental drivers and transient effects of experimental treatments can cause restored populations to behave unpredictably over time (Stuble et al., 2017; Trowbridge et al., 2016). According to reports, many initially successful translocations failed after as few as 15 years (Drayton & Primack, 2012).

Estimation of vital rates (growth, survival, reproduction, fecundity, recruitment) is a popular tool for assessing the initial success of translocations (Menges, 2008). Comparing the dynamics of wild and translocated populations may offer insights on experimental considerations such as site suitability, source material, and planting density. Many studies use a priori data from wild populations to inform translocation designs (Abeli et al., 2015; Maschinski & Quintana Ascencio, 2016), but few include concurrent wild population dynamics to evaluate translocation success (Maschinski & Albrecht, 2017). Such comparisons can provide much-needed context (Menges, 2008). A translocated population of *Limonium perplexum* fluctuated drastically in size; however, examination of the wild population revealed similar trends, all in response to rainfall (Laguna et al., 2016). Data from multiple translocations of the endangered *Pseudoziziphus celata* showed high annual survival of transplants, yet other vital rates were less vigorous compared with wild populations (Menges et al., 2016), suggesting key components of recovery were still lacking. Vital rates of introduced populations of the endemic *Centaurea corymbosa* differed from wild populations, but overall population growth rates (λ) were not clearly different (Colas et al., 2008). These and other studies highlight the value in comparing population dynamics of translocations to their wild counterparts.

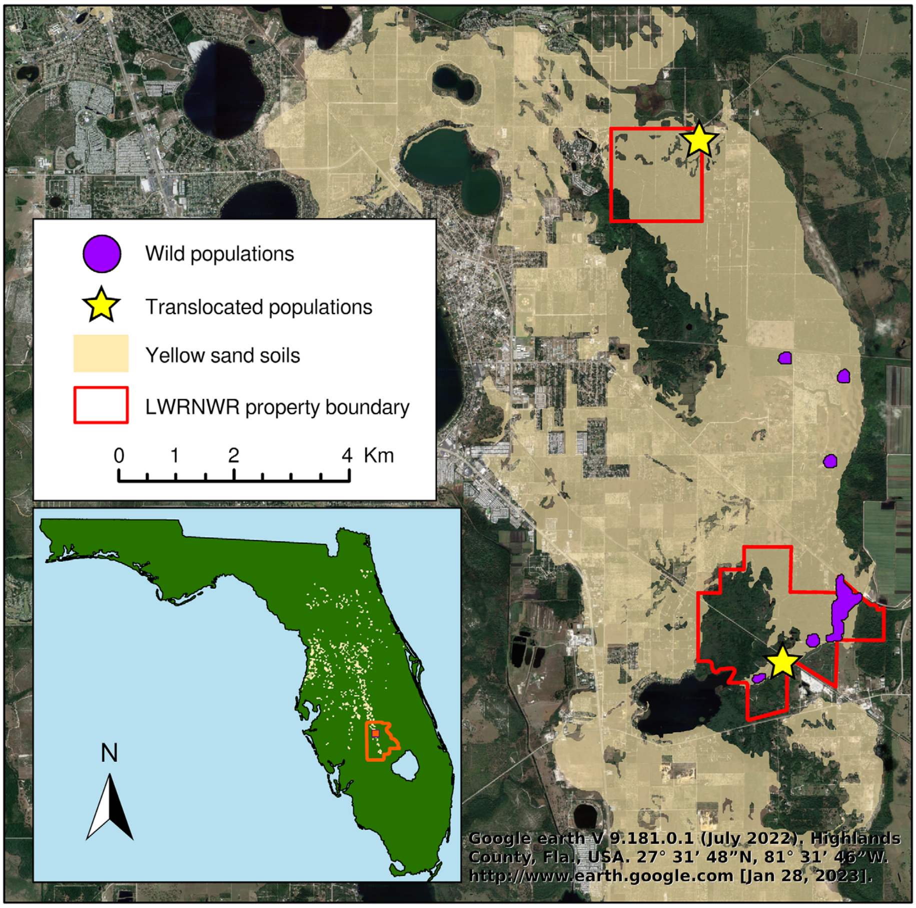
Our goal was to compare the dynamics of natural and translocated populations of *Dicerandra christmanii* growing in two types of habitat—gaps (open areas) within the shrub matrix and sandy roadsides. In total, we consider five population types: natural populations in gaps, natural populations in roadsides, augmented populations in gaps, introduced populations in gaps, and introduced populations in roadsides. Here, we assess the variation of vital rates (survival, growth, reproduction, fecundity, and recruitment) associated with translocations, other management activities, and habitat. In a companion manuscript, we combine these vital rates into Integral Projection Models (IPMs) to evaluate differences in population viability while accounting for other ecological factors (López-Borghesi et al., 2023). Work on *Hypericum cumulicola*, another gap specialist of Florida scrub, has shown that populations in human-modified habitats, such as roadsides, often have more variable vital rates than populations in gaps (Quintana-Ascencio et al., 2007). In addition, transplanted populations typically receive initial support, such as habitat improvement and supplemental water. This can lead to increased survival (Dillon et al., 2018) and robust individuals which at first outperform natural recruits (Halsey et al., 2017). Therefore, we hypothesized that translocated populations would outperform wild populations, at least for the first few years. Once we account for the outplanting boost, however, our expectation is that transplanted populations will perform at least as well as natural populations. This is our main conservation goal.

2 | METHODS

2.1 | Study species

Dicerandra christmanii is a herbaceous perennial species in the Lamiaceae family. It is a Florida endemic listed as endangered at the federal and state levels and ranked as critically imperiled (NatureServe, 2019; USFWS, 1999). The genus *Dicerandra* includes many rare species and is, by one measure, the rarest genus in the southeastern United States (Estill & Cruzan, 2001). Many of these species require aggressive conservation actions, including land acquisition, propagation, fire management, and translocations (Evans et al., 2008; Menges, 1999; Menges et al., 2019; Peterson et al., 2013). Both the USFWS Recovery Plan (1999) and Turner et al. (2006) recommend translocations as necessary for *D. christmanii* conservation.

Dicerandra christmanii occurs exclusively on yellow sands of oak-hickory scrub (Menges et al., 2007), a shrubland dominated by oaks and palms and maintained by fire (fire-return-interval of 5–12 years; Menges, 2007). It occupies gaps within the shrub matrix and open areas along sandy roadsides (Menges, 1999). In other types of Florida scrub, gaps support high diversity, especially of



Google earth V 9.181.0.1 (July 2022). Highlands County, Fla., USA. 27° 31′ 48″N, 81° 31′ 46″W. http://www.earth.google.com [Jan 28, 2023].

FIGURE 1 Known population range of *Dicerandra christmanii* on yellow sand soils in Highlands County, Florida, USA. Wild populations are shown in pink and translocated populations are shown with yellow stars. The only protected site for *D. christmanii* is at Flamingo Villas Lake Wales Ridge National Wildlife Refuge (LWRNWR) which was also augmented in 2010. A new population was introduced to the Carter Creek LWRNWR in 2012.

herbaceous plants and subshrubs (Menges et al., 2008). Gaps expand and merge with fire, then contract and fragment between fire. Since gap size determines the occupancy of many species, fire strongly affects community and population patterns (Menges et al., 2017).

Like with most species in the genus (Evans et al., 2008; Menges et al., 2006; Menges et al., 2019; Peterson et al., 2013), *D. christmanii* individuals are killed by fire. Populations recover through a persistent soil seed bank (Menges unpub. data). Seedling cohorts are often large after fires, given favorable weather conditions (e.g., wet winters). While the response of *D. christmanii* to fire remains understudied, its close relatives *D. frutescens* and *D. thinicola* show strong demographic responses, with increased recruitment and relative growth, and reduced time to flowering (Menges et al., 2006, 2019).

2.2 | Study sites

Dicerandra christmanii subsists in fewer than 10 sites (FNAI, 2010; Figure 1), with only one site protected: the Flamingo Villas (FV) unit of the Lake Wales Ridge National Wildlife Refuge (LWRNWR). This 575-ha property is managed by the US Fish and Wildlife Service (USFWS) and contains a mix of upland Florida scrub and lower-lying flatwoods, bayheads, and depression marshes. While USFWS land managers have recently succeeded in introducing prescribed fires, most of the area of FV remains long-unburned.

Patches of *D. christmanii* occur across several management units of FV, both in natural gaps and along sandy firebreaks (roadsides). Data collection started in 1994 at FV1, sampling within a 45 m × 2 m belt transect across a gap area as well as 6 nearby 1 m × 1 m quadrats. In 1999, we started sampling 2 roadside areas: FV2 in a 51 m × 1 m transect on the west edge of a firebreak and FV3 in a 31 m × 1 m transect on the east edge. We later added 2 additional gap areas with natural populations: FV4 consisting of 16 gaps in 2000 and FV5 consisting of 11 gaps in 2010.

In August 2010, we augmented 40 gaps at FV in appropriate habitat unoccupied by *D. christmanii*. We used 3 source materials harvested within FV, including 4000 sown seeds, 160 greenhouse-grown seedling transplants, and 40 greenhouse-grown stem-cutting transplants. The Conservation Program at Bok Tower Gardens (BTG) in Lake Wales, Florida, propagated the stem-cutting transplants, while Archbold Biological Station propagated the seedling transplants. All gaps were initially 1–10 m^2 in

TABLE 1 Cumulative number of observations of aboveground *Dicerandra christmanii* individuals (n) by population type, subset by number of yearlings and by total number of identified unique adults.

Population type	First year[a]	Observations (n)	Yearlings	Adults (unique ID)
Natural in gaps	1994, 2000, 2010	8687	1807	1693
Natural in roadsides	1999	4618	1317	980
Augmentation	2010	7937	2300	1685
Introduction in gaps	2012	3601	891	896
Introduction in roadsides	2012	2840	1331	686
Total	—	27,683	7646	22,314

[a] Beginning of sampling for sites within management treatment.

area, with half ($n = 20$) burned by a prescribed fire in June 2009—prior to outplanting—and half not burned. All transplants received supplemental irrigation from individual feeder hoses off a main line gravity-fed from a tank. Irrigation ceased in June 2011.

The Carter Creek (CC) unit of the LWRNWR is located 8 km north of FV, just 4 km from the northernmost natural occurrence of *D. christmanii* (FNAI, 2010; Figure 1). The northern half of this 254-ha property consists mostly of upland sandhill and Florida scrub habitat. In September 2012, we outplanted 102 greenhouse-grown seedling transplants and 114 greenhouse-grown stem-cutting transplants into 50 open areas. Sixteen of these areas occurred along sandy firebreaks (roadsides) while the remaining 34 were gaps within the scrub matrix. BTG collected and propagated seeds and stem-cuttings from an unprotected population with landowner permission and state collection permits. All plants received water initially, but only half got supplemental hand-watering through the end of 2012. All translocations followed guidelines outlined by the IUCN Species Survival Commission (2013). In May 2015, 3 years post-outplanting, a prescribed fire affected the introduction site, burning 35 of the 50 study areas, most of them gaps.

2.3 | Data collection

We conducted annual censuses every October, during peak flowering. We marked all plants within study boundaries with numbered aluminum tags and pin flags, or with plastic toothpicks located near tags. We visited each plant and recorded its survival, life history stage (yearlings, vegetative adults, or reproductive adults), number of branch tips (>2 cm in length), and number of flowering branch tips (>2 cm in length). All standing plants entered the dataset as yearlings (new recruits at census) or new adults (new plants at census with ≥4 branch tips). We recorded 27,683 observations of stage and survival and 13,216 observations of growth across 5 population types (Table 1). This included data on 7646 yearlings and 5940 unique adult plants. Subsampling started in 2014 and 2017 for the augmentation and introduction, respectively, due to rapid increases in number of plants.

In late 2018, we estimated number of seeds per fruit using material collected at FV from gaps and roadsides. From each of 13 plants, we randomly selected 10 light to medium brown, unopened schizocarps and counted their seeds in the lab. We avoided seeds light in coloration, small in size, or damaged by light pressure, considering them unviable.

We obtained fruit-per-branch counts in late 2019 at both sites (FV and CC), in all study areas except FV1 and FV5 which had been burned that year. We collected data for the 5 population types (natural in gaps, natural in roadsides, augmented in gaps, introduced in gaps, and introduced in roadsides), and for the 2 fire treatments (burned and unburned) in the augmentation. For each of the 6 combinations (population + fire treatment), we counted the number of fruits on a single, intact branch from 30 plants ($n = 180$). We selected these plants by first binning all plants based on the number of flowering branch tips (1–6, 7–17, >17) using 2019 demographic data.

2.4 | Models for vital rates

Our main goal was to contrast vital rate variation among the five population types to determine early translocation success using natural populations in gaps as reference. We used generalized linear mixed-effect models (GLMMs) to assess variation in survival, growth (changes in number of branch tips), probability of reproduction, fecundity (proportion of flowering branch tips), and recruitment. For each vital rate, we proposed a set of potential models, selected to help assess the relative importance of specific factors such as outplanting pulses and prescribed fires. We fitted these models using frequentist inference to take advantage of the speed of these algorithms. We then identified the most likely models from each set using Akaike Information Criteria (Burnham & Anderson, 2002). We then fitted the top models from each group using Bayesian inference to better convey the uncertainty of vital rate estimates and enable the propagation of errors in integrated models. We compared these models using Widely Applicable Information Criteria (Watanabe, 2013) to verify consistency with the frequentist approach (see Tables S1A-3B in appendix for comparisons). 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).

All proposed models, except for recruitment models, used population type and number of branch tips as predictor variables. Population type included only 4 levels: natural gaps, natural roadsides, augmentations, and introductions. To model the differences between introduced populations in gaps and roadsides, we used a separate habitat variable. In addition, these models included site nested within year as random effects.

Growth models used normal errors with the identity link. Models of survival, probability of reproduction, and fecundity (proportion of flowering branches) used binomial errors and logit links. Due to the scarcity of reproductive yearlings (<10 individuals), we excluded this stage for all models describing reproduction.

We also evaluated the response of vital rates to other relevant but confounding variables. While important for management and conservation, these variables can hinder comparisons of long-term performance between treatments. Augmentation and introduction actions created short-term disturbances and pulse effects where vital rates may have been stronger due to outplanting vigor (Dillon et al., 2018; Halsey et al., 2017). We included variables that identified plants outplanted or recruited during the first and second years of translocation (analyzed together or separate) independently for the augmentation and introduction. Because responses of plant growth and survival to translocations were expected to differ for yearlings and adults, we assessed growth of these stages in independent models.

Fire is an important disturbance in Florida scrub with profound effects on the vital rates of *D. christmanii* (Menges, 1999; Slapcinsky et al., 2010). Prescribed fires affected both translocations during the course of this study—the augmented population in 2009, prior to outplanting, and the introduced population in 2015, 3 years after outplanting. We assumed fire effects persisted until the end of this study. We evaluated these effects as binary responses (burned vs. not burned) instead of time-since-fire (time elapsed since burn) because the data were insufficient. For survival in the introduced population, we considered 3 fire stages: pre-burn (<2014), burn year (2014) and post-burn (>2014).

Finally, we modeled recruitment variation per population (number of yearlings) as a function of population type and available number of seeds and assuming a negative binomial distribution. We considered the contribution of recently produced seeds, 1- and 2-year-old seeds, and estimated 2 latent variables: germination and dormancy. These were consistent across habitats, population types, and seeds with different ages. This model included only random effects of year (and not site) due to data limitations. To estimate the seeds available for recruitment, we modeled number of fruits per branch for each population type and overall number of seeds per fruit.

For Bayesian models, we included diffuse priors (McElreath, 2016) for all parameters, except for germination and dormancy in the recruitment model, where we used data from *D. frutescens*. We generated 3 chains with 3000 (120,000 only for recruitment data) iterations with half used for the warm-up phase. We inspected all our model posteriors for proper mixing of chains and r-hats close to 1.00. Coefficients were commensurate between frequentist and Bayesian models in all cases.

Here, we focus on vital rate variation of *D. christmanii* as a function of plant size (natural logarithm of number of branches), stage (yearling and adult), population type, pulse effects of translocations, fire, and habitat. In a companion paper (López-Borghesi et al., 2023), we assessed the combined effects of these variables on the population dynamics of this species using IPMs built with the most likely models identified here.

3 | RESULTS

Table 2 presents the top model for each vital rate. Subsequent models appear in Supplementary tables—survival (Tables S1A,B), growth (Tables S2A,B), reproduction probability and fecundity (Tables S3A,B). Figure 2 presents the fit of the top model for each vital rate, comparing across all population types. More detailed representations of each model fitted to the data appear in the supplementary figures (Figure S4A–F).

3.1 | Survival

The most likely model for survival was complex (Table 2) with mean probabilities ranging from just under 0.2 to over 0.8 across all population types. Survival probability increased with plant size but at a greater rate in yearlings

TABLE 2 Most likely model for each vital rates of *Dicerandra christmanii* as determined with AIC; except for "adult growth" where second top model was selected.

Vital rate	Life stage	Model	dAIC	Df	Weight
Survival	All	branches $(x + x^2)$*MT + stg + branches $(x + x^2)$*stg + Aug + pre-burn + habitat + post-burn + habitat*burn	0.0	18	0.87
Growth	Yearlings	branches*MT + aug1 + aug2 + pre-burn + habitat	0.0	15	0.62
	Adults	branches*MT + Int-A + habitat	0.6	13	0.35
Reproduction	Adults	branches*MT + aug1 + aug2 + pre-burn + habitat + burn	0.0	15	0.50
Fecundity	Adults	branches*MT + aug1 + aug2 + pre-burn + habitat + burn	0.0	15	0.51

Note: Variables include: *branches*, the (ln) number of branch tips; *MT*, management treatment; *stg*, life stage; *pre-burn*, if the site was burned prior to augmentation; *aug1* and *aug2*, first and second pulse years of augmentation (or *Aug* if combined); *burn*, if introduced site had a prescribed fire; *post-burn*, years after prescribed fired; *Int-Y* and *Int-A*, pulse effect of introduction on yearlings and adults respectively; and *habitat*, if introduction was on interior or edge gaps.

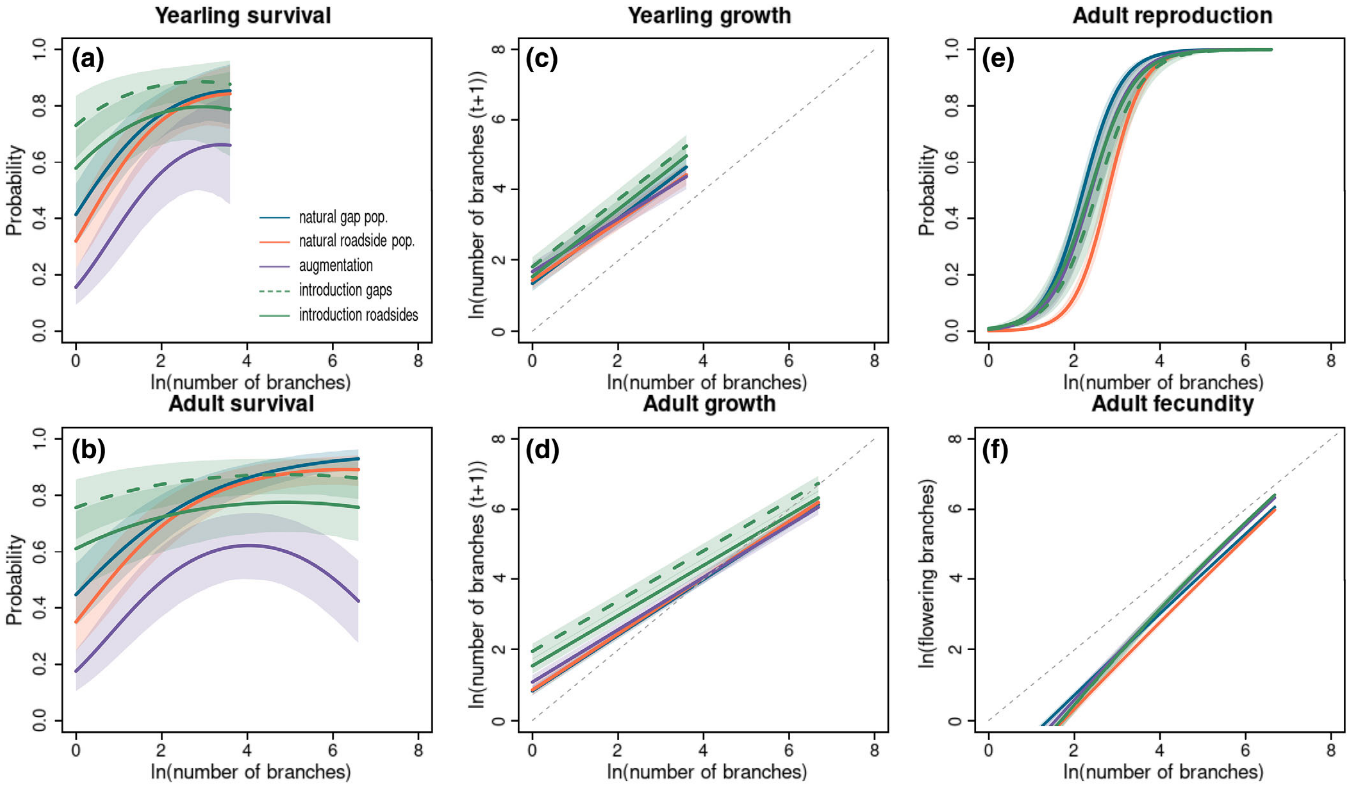


FIGURE 2 Vital rates of *Dicerandra christmanii* in response to plant size (ln of number of branches) across five population types. Natural gap populations are shown in blue and natural roadside populations are in orange. The only protected site was augmented into unoccupied gaps in 2010 (purple). Plants were introduced to a new, previously unoccupied site in 2012 (green). Introductions occurred in gaps (dashed) and roadsides (solid). Generalized linear mixed models for yearling survival (a), adult survival (b), reproduction (e), and fecundity (f) were used to estimate vital rate variation. Linear mixed effects model estimated yearling growth (c) and adult growth (d). Shaded areas represent 75% credibility intervals. The diagonal dashed line (c and d) indicates zero growth. In fecundity (f), the diagonal dashed line indicates all branch tips were flowering (100%).

than adults (Figure 2a,b). Survival probability peaked at around 50–60 branch tips for adults. Overall, roadside populations had a lower survival probability than gap populations. In the augmentation, survival was the lowest among all population types, peaking just under 0.6 at 50–60 branch tips but then declining sharply, a trend not observed in other populations. Survival was highest in the introduction (>0.7), especially for smaller plants.

The probability of survival in the augmentation, both for yearlings and adults, was highest in the first 2 years (peaking at ∼0.8)—comparable to natural populations in gaps—but declined in later censuses (peaking at ∼0.5; Figure S1a,b). Pre-burned gaps had marginally higher survival than unburned gaps. For the introduction, survival pre-fire was higher in gaps than in roadsides, with similar values than natural populations in gaps for both yearlings and adults (Figure S1c,d). In the burn year, survival declined, mostly in gaps (<0.1), but recovered in post-fire years to similar probabilities as before, but only for smaller individuals (<30 branch tips). Survival probability in roadsides continued to decline from pre-burn to post-burn years.

3.2 | Plant size and growth

Most yearlings (72%) across population types had a single branch tip their first year, but yearlings in translocations were larger (3–7 branches) in their second year compared with natural populations (2–3 branches; Figure 2c). Plants in natural populations in gaps and roadsides did not differ in size. In the augmentation, growth of yearlings was low (1–3 branches) relative to plants in natural gaps (2–3 branches) but increased markedly in the second pulse year (6–7 branches; Figure S2a). Unburned gaps of the augmentation produced larger yearlings (5–6 branches) than pre-burned gaps (4–5 branches)—both were larger than yearlings in natural gaps (3–4 branches). Yearling growth in roadside areas of the introduction was similar to yearlings in natural gaps (2–3 branches) but lower than in gaps of the introduction (4–5 branches; Figure S2b).

Adult growth was similar for augmented populations and natural populations in both roadsides and gaps, with positive growth up to 50–60 branch tips. We did not find evidence that growth of adults in the augmentation was affected by any experimental factors (Table 2). In the introduction, plants were significantly larger and showed less senescence in larger plants than elsewhere (Figure 2d). Adults were on average larger for introductions in gaps (8–9 branches) than introductions in roadsides (6–7 branches), but both were larger than plants in natural gaps (4–6 branches). Growth in the first 2 years after outplanting was lower than all other years, but still greater than in natural gaps (Figure S2c).

3.3 | Reproduction and fecundity

The probability of becoming reproductive was low for small plants but increased quickly among individuals with 10–30 branch tips, surpassing 0.8 probability for plants with 40 branch tips or more across all population types (Figure 2e). Reproduction probability in relation to number of branch tips increased fastest in natural gaps, reaching a probability of 0.5 at just 6–7 branch tips. In comparison, plants in translocations reached this probability at 8–9 branch tips. Plants in natural roadside populations were the slowest to pass this threshold, doing so at 16–18 branch tips.

During the first year of the augmentation, a 0.5 reproduction probability was restricted to larger plants (21–23 branch tips) compared to the second year (7–8) and to natural populations in gaps (6–7; Figure S3a). Reproduction probability in pre-burned gaps was greater compared to plants of the same size in unburned gaps. Both habitats of the introduction had a slower increase in reproduction probability, reaching .5 probability with 8–9 branch tips in roadsides and 10–11 in gaps (Figure S3c).

Fecundity was relatively consistent across all population types. For smaller individuals, it was lower in both translocations relative to natural gap populations, but increased faster with size, approaching 100% of branches flowering for plants with over 400 total branch tips (Figure 2f). Fecundity in the augmentation was marginally higher in the second year after outplanting, although the effect size was small (Pulse second year in Table 3), compared to natural populations in gaps, but similar in all other years (Figure S3b). Fecundity in the introduction showed an effect of burn year relative to all other years (Figure S3d), but the effect size of this trend was also low (Table 3).

3.4 | Recruitment

Recruitment varied strongly by census year and among sites (Figure 3). Because of mismatched sampling areas, direct comparisons of recruits among sites were not informative. However, patterns of variation in number of seedlings helps describe some key differences between population types. Recruitment in the initial years of most translocations showed values above site averages, 25%–60% larger than any values observed in natural gap populations. The exception was in unburned augmentations, where the initial value was similar in magnitude to those occurring in natural gap populations. Introduced populations in gaps experienced initial recruitment values up to 55% greater than those in introduced roadside populations, except in the year of the fire (2015), when recruitment in gaps fell to under 0.01 of the site average. In the last 2 years (2017 and 2018), yearling recruitment had similar patterns in all sites.

TABLE 3 Results of selected generalized linear mixed effects models for each vital rate of Dicerandra christmanii across all 5 population types (introductions modeled as habitats), with the site and year included in all models as random effects. Parameters with CI overlapping 0 appear in gray.

		Growth				
	Survival	Yearlings	Adults	Reproduction	Fecundity	Recruitment
Factor	β (CI)	β (CI)	β (CI)	β (CI)	β (CI)	β (CI)
Natural gaps (reference)	−0.25 (−1.08 to 0.60)	1.06 (0.53 to 1.67)	1.09 (0.97 to 1.21)	−4.97 (−5.32 to −4.61)	−1.42 (−1.57 to −1.27)	−2.98 (−5.21 to −0.95)
ln (number of branches)	0.66 (0.84 to 1.05)	0.94 (0.84 to 1.15)	0.79 (0.77 to 0.80)	2.25 (2.14 to 2.35)	0.23 (0.22 to 0.24)	NE
ln (number of branches)^2	−0.03 (−0.06 to −0.01)	NE	NE	NE	NE	NE
Roadsides	−0.43 (−0.69 to −0.16)	0.11 (−0.12 to 0.25)	0.01 (−1.25 to 1.36)	−2.04 (−2.63 to -1.47)	−0.67 (−0.82 to −0.53)	0.81 (0.38 to 1.29)
Augmentation	−1.40 (−1.84 to −0.98)	0.43 (0.03 to 0.84)	0.24 (0.09 to 0.41)	−0.12 (−0.80 to 0.55)	−0.57 (−0.80 to −0.51)	1.21 (0.65 to 1.78)
Introduction	1.40 (0.77 to 1.99)	0.51 (0.16 to 0.97)	0.94 (0.76 to 1.10)	−0.05 (−0.68 to 0.58)	−0.98 (−1.22 to −0.73)	−0.83 (0.20 to 1.46)
Branches × roadside	0.22 (0.03 to 0.40)	−0.13 (−0.28 to 0.10)	0.01 (−0.01 to 0.04)	0.26 (0.07 to 0.46)	0.08 (0.06 to 0.09)	NE
Branches × augmentation	0.40 (0.22 to 0.59)	−0.16 (−0.32 to −0.01)	−0.05 (−0.08 to −0.02)	−0.13 (−0.33 to 0.08)	0.19 (0.17 to 0.21)	NE
Branches × introduction	−0.32 (−0.50 to −0.14)	0.03 (−0.10 to 0.17)	−0.07 (−0.10 to −0.04)	−0.27 (−0.45 to −0.10)	0.29 (0.28 to 0.31)	NE
Branches^2 × roadside	−0.03 (−0.07 to 0.01)	NE	NE	NE	NE	NE
Branches^2 × augmentation	−0.10 (−0.14 to −0.06)	NE	NE	NE	NE	NE
Branches^2 × introduction	−0.001 (−0.04 to 0.03)	NE	NE	NE	NE	NE
Stage	−0.14 (−0.29 to 0.01)	NE	NE	NE	NE	NE
Stage × branches	0.34 (0.02 to 0.66)	NE	NE	NE	NE	NE
Stage × branches^2	−0.06 (−0.24 to 0.12)	NE	NE	NE	NE	NE
Augmentation pulse						
Both	1.01 (0.19 to 1.82)	—	—	—	—	NE
First year	—	−1.52 (−2.07 to −0.98)	—	−1.50 (−2.58 to −0.42)	0.30 (−1.11 to 1.70)	NE
Second year	—	0.12 (−0.12 to 0.40)	—	0.71 (−0.49 to 1.91)	0.28 (−1.11 to 1.65)	NE
Augmentation pre-burn	0.15 (0.00 to 0.31)	−0.17 (−0.01 to 0.33)	—	0.33 (0.08 to 0.58)	0.01 (−0.02 to 0.04)	NE
Introduction pulse						
Adults	—	—	0.35 (0.26 to 0.44)	—	—	NE
Yearlings	—	—	NE	NE	—	NE
Introduction fire						
Burn year	−5.68 (−6.23 to −5.14)	—	—	0.25 (0.02 to 0.51)	0.06 (0.04 to 0.09)	NE
Post-burn	−1.06 (−1.81 to −0.30)	—	—	—	—	NE
Habitat	−0.72 (−0.90 to −0.30)	−0.32 (−0.47 to −0.16)	−0.26 (−0.34 to −0.19)	0.45 (0.17 to 0.73)	0.03 (0.00 to 0.06)	NE
Habitat × burn year	5.27 (4.72 to 5.87)	NE	NE	NE	NE	NE

TABLE 3 (Continued)

Factor	Survival	Growth		Reproduction	Fecundity	Recruitment
		Yearlings	Adults			
	β (CI)	β (CI)	β (CI)	β (CI)	β (CI)	β (CI)
Germination	NE	NE	NE	NE	NE	0.04 (0.00 to 0.18)
Dormancy	NE	NE	NE	NE	NE	0.44 (0.16 to 0.82)
Sigma site	0.45 (0.37 to 0.55)	0.36 (0.10 to 1.41)	0.05 (0.01 to 0.20)	0.51 (0.39 to 0.63)	0.26 (0.23 to 0.31)	NE
Sigma year	1.99 (1.43 to 2.82)	0.24 (0.15 to 0.37)	0.38 (0.27 to 0.5)	0.46 (0.28 to 0.68)	0.30 (0.27 to 0.36)	1.18 (0.78 to 1.73)
Sigma	—	0.78 (0.76 to 0.80)	0.67 (0.66 to 0.68)	—	—	—

Note: (β) effect size; (SD) standard deviation; (−) factors excluded by AIC; (NE) factors not evaluated.

3.5 | Seeds per fruit and fruits per branch

Seeds per fruit were bounded between 0 and 4 seeds with a mean of 1.7 and median of 2. Of 130 examined fruits, 25 had no viable seeds. Mean fruits per branch (ln transformed) varied somewhat among population types (Figure S5). It was highest in the introduced gap populations (mean = 1.9; CI: 1.64–2.16), and the introduced roadside population (mean = 1.8; CI: 1.58–2.02), and it was lowest in pre-burned augmented gap (mean = 1.2; CI: 0.92–1.48) and natural gap (mean = 1.3; CI: 1.08–1.52) populations.

4 | DISCUSSION

Comparing demographic dynamics between translocated and wild populations has been a challenge when restoring rare plant populations (Abeli et al., 2015; Bell et al., 2003; Godefroid et al., 2011). Here, we compared vital rate variation of two translocated populations to those of natural populations to evaluate as metrics of success. Our results indicate that translocations can be a useful tool for the conservation of *D. christmanii*. Overall, during the first years post-outplanting, vital rates of augmented populations were comparable to or exceeded those of natural gap populations, while introduced populations had consistently more robust vital rates (Figure 2). Our ability to measure the early dynamics of translocated populations and compare them with wild populations is critical to evaluate efforts and adjusting management strategies.

Augmented populations showed patterns similar to natural gap populations for most vital rates except for survival, which was lowest among all population types (Figure 2), albeit still ∼.6 probability. The reduced survival probability of augmentations may be due to density-dependent effects. While initial recruitment in augmented gap populations was 4 times greater than in natural gap populations, those gaps had the smallest area (mean 2.0 m^2 ± 0.8 *SD*) compared with gaps of natural populations (3.1 m^2 ± 1.2) and introduced populations (2.8 m^2 ± 1.2). Density was excluded from models since gap areas change over time and were not measured in all censuses. In the introduction, large gap areas may have been able to accommodate larger seedling recruitment cohorts and support more vigorous vital rates (Menges et al., 2017).

Maschinski and Albrecht (2017) recommend designing translocations as experiments so that they can contribute information for future management efforts. Disturbances are critical drivers of population viability

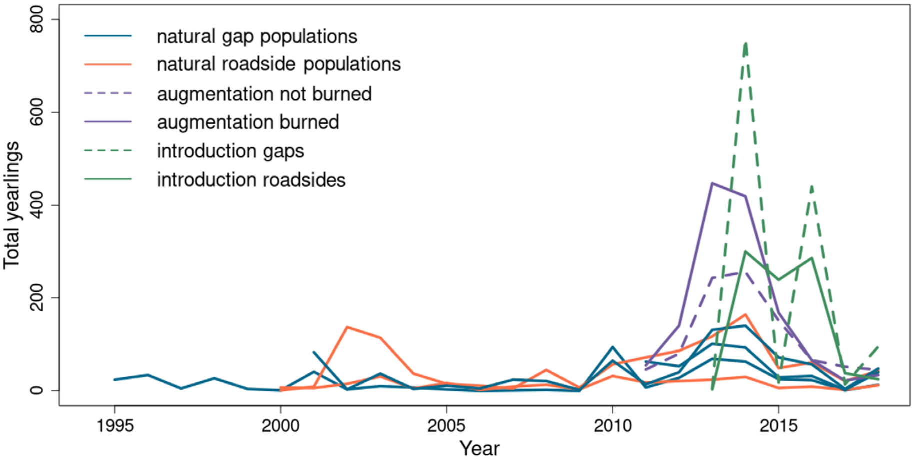


FIGURE 3 Total number of *Dicerandra christmanii* yearlings recruited annually in permanent plots or marked gaps from 1994 through 2018 at 7 areas, including the 3 natural gap areas (blue), both natural roadside areas (orange), the augmentation (purple) separated between unburned gaps (dashed line) or burned (solid line), and introduction (green) in either gaps (dashed line) or roadside habitats (solid line).

and important management tools (Bazzaz, 1983), so we incorporated both fire and outplanting effects into our models. Florida scrub is a fire-maintained habitat with many species reliant on this disturbance (Menges, 1999; Slapcinsky et al., 2010). Both translocations in our study experienced fire events, which had clear positive effects on most vital rates of *D. christmanii*. Responses to the disturbance of outplanting, described as pulse effects (Dillon et al., 2018) and site selection (Halsey et al., 2017; Wendelberger & Maschinski, 2016), were also vital components in determining outplanting success.

Fire had an overall positive effect on vital rates of both translocations, except survival during the fire year in the introduced population, when many plants were killed (Figure S1c). Most *Dicerandra* species have plants uniformly killed by fires (Evans et al., 2008, 2010; Menges et al., 2006; Menges et al., 2019; Peterson et al., 2013). In gaps burned prior to augmentation, most vital rates, including recruitment, were stronger than those in unburned gaps, except for yearling growth (Figure S2). For the introduction, there was a confounding effect of habitat and fire, with higher mortality in gaps due to a more complete burn (91% of plants consumed and 9% partially burned, leading to >99% dead) than in roadsides (19% partially burned and 81% unburned plants, leading to ~23% dead). Survival in introduced gap populations recovered quickly, surpassing post-burn survival in roadside introductions but still falling below natural gap populations. Appropriate fire management of introduced populations of other rare plant species has contributed to overall stronger vital rates (Bladow et al., 2017; Bowles et al., 2015), a typical response for many species adapted to fire-maintained habitats (Slapcinsky et al., 2010).

Initial pulse effects during translocation had clear impacts on vital rates with mostly negative effects in the first year after outplanting. These transient negative effects of translocation are well known by horticulturists, and there are many proposed methods to ameliorate them (Adams et al., 2008). Negative effects associated with the initial pulse of translocation are most likely due to transplant shock (Close et al., 2005), altered population size distribution, and low seedling recruitment. Populations often recover by the second year.

For *D. christmanii* pulse effects were less important in the introduction than the augmentation, likely due to above-average rainfall in the year of the introduction. Mean annual rainfall in the initial years after the introduction (0.42 cm ±1.106 *SD*) was greater than for all study years prior to outplanting (0.37 ± 1.101 *SD*) and the for initial years after augmentation (0.36 ± 1.110; Archbold Biological Station weather data). Increased precipitation has been shown to have positive effects on vital rates in another *Dicerandra* species (Menges et al., 2019) and Florida scrub species (Petrů & Menges, 2004; Quintana-Ascencio et al., 2007; Weekley & Menges, 2012).

Introduction habitat clearly affected every vital rate except recruitment (Table 3) with populations in gaps showing stronger vital rates than in roadsides. We observed the same trend of reduced vital rate vigor in roadsides relative to gaps for natural populations (Figure 2). While habitat characteristics of roads favor other Florida scrub species (Petrů & Menges, 2004; Quintana-Ascencio et al., 2007; Schafer et al., 2010; Tye et al., 2016), they had negative impacts on vital rates of *D. christmanii* and may serve better as corridors or source populations following disturbances (Andrews, 1990; Meddens et al., 2018). Habitat has been a key factor in other translocations (Dillon et al., 2018; Halsey et al., 2015; Maschinski et al., 2004) and should be carefully considered when designing future translocation of this species.

Based on observations of wild *D. christmanii* and other Florida scrub congeners (Evans et al., 2008, 2010; Menges et al., 2006; Menges et al., 2019; Peterson et al., 2013), we know their preferred habitat is open gaps, and larger gaps sustain greater abundances

(Menges et al., 2008; Menges et al., 2017). By selecting what we considered to be "preferred habitats," we were able to select favorable micro-sites that may have contributed to our early success (Halsey et al., 2017; Ward et al., 2021; Wendelberger & Maschinski, 2016). In addition, the use of healthy plants and initial supplemental water may have increased vital rates in translocations relative to wild populations. Other studies have found translocation techniques can temporarily inflate translocation success, but long-term monitoring is essential in determining population persistence (Albrecht et al., 2019; Maschinski et al., 2004).

The current study highlights the value in comparing vital rates of translocated and wild populations of *D. christmanii* to evaluate translocation success even after only a few years post-outplanting. Our analysis demonstrates translocations of *D. christmanii* can be a viable strategy for increasing existing populations and creating new populations of this rare species. While both translocations are still relatively new (10 and 8 years post-outplanting), populations have successfully reproduced, dispersed viable seeds, and multiple generations of seedlings have grown to the reproductive stage. The introduction has even survived a major fire disturbance, rebounding quickly with post-fire cohorts recruiting and flowering. In fact, population growth rates (lambdas) for introduced populations in gaps had the highest mean value among all population types (1.241 vs. 1.003 for natural populations in gaps), suggesting positive population growth (López-Borghesi et al., 2023). However, it is important to note that they also had the greatest variability in population growth ($SD = 0.169$ compared to 0.085 for natural gaps). This leads to an increased risk of extinction in transplanted populations compared to natural ones. The impact of such uncertainty on future trends, particularly when accounting for ecological factors such as disturbances and cryptic life stages, is investigated in the companion manuscript. Overall, our demographic and comparative approach to evaluating translocations provides opportunities to explicitly address confounding effects, enabling a fair assessment of early success.

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DATA AVAILABILITY STATEMENT

Demographic measurements from annual censuses (from 1994 to 2018), seeds per fruit, fruits per reproductive 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.

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SUPPORTING INFORMATION

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

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