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Permalink

<https://escholarship.org/uc/item/6p28d0b5>

Journal

Conservation Biology, 38(2)

ISSN

0888-8892

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Publication Date

2024-04-01

DOI

10.1111/cobi.14190

Peer reviewed

Identifying predictors of translocation success in rare plant species

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Article impact statement: Maximizing founder population sizes and committing to adaptive management can improve the success of rare plant translocations.

Abstract

The fundamental goal of a rare plant translocation is to create self-sustaining populations with the evolutionary resilience to persist in the long term. Yet, most plant translocation syntheses focus on a few factors influencing short-term benchmarks of success (e.g., survival and reproduction). Short-term benchmarks can be misleading when trying to infer future growth and viability because the factors that promote establishment may differ from those required for long-term persistence. We assembled a large ($n = 275$) and broadly representative data set of well-documented and monitored (7.9 years on average) at-risk plant translocations to identify the most important site attributes, management techniques, and species' traits for six life-cycle benchmarks and population metrics of translocation success. We used the random forest algorithm to quantify the relative importance of 29 predictor variables for each metric of success. Drivers of translocation outcomes varied across time frames and success metrics. Management techniques had the greatest relative influence on the attainment of life-cycle benchmarks and short-term population trends, whereas site attributes and species' traits were more important for population persistence and long-term trends. Specifically, large founder sizes increased the potential for reproduction and recruitment into the next generation, whereas declining habitat quality and the outplanting of species with low seed production led to increased extinction risks and a reduction in potential reproductive output in the long-term, respectively. We also detected novel interactions between some of the most important drivers, such as an increased probability of next-generation recruitment in species with greater seed production rates, but only when coupled with large founder sizes. Because most significant barriers to plant translocation success can be overcome by improving techniques or resolving site-level issues through

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early intervention and management, we suggest that by combining long-term monitoring with adaptive management, translocation programs can enhance the prospects of achieving long-term success.

KEYWORDS

endangered species, population restoration, reintroduction, seedling recruitment, species recovery, threatened species

Identificación de pronosticadores del éxito de reubicación en especies raras de plantas

Resumen: El objetivo fundamental de la reubicación de plantas raras es la creación de poblaciones autosuficientes con resiliencia evolutiva que persistan a la larga. De todas maneras, la mayoría de las síntesis de estas reubicaciones se enfocan en unos cuantos factores que influyen sobre los parámetros a corto plazo del éxito (supervivencia y reproducción). Los parámetros a corto plazo pueden ser engañosos si se intenta inferir el crecimiento y la viabilidad en el futuro ya que los factores que promueven el establecimiento pueden diferir de aquellos requeridos para la persistencia a largo plazo. Ensamblamos un conjunto grande de datos representativos en general ($n = 275$) de las reubicaciones de plantas en riesgo bien documentadas y monitoreadas (7.9 años en promedio) para identificar los atributos de sitio más importantes, las técnicas de manejo y los rasgos de las especies para seis parámetros de ciclos de vida y medidas poblacionales del éxito de reubicación. Usamos el algoritmo de bosque aleatorio para cuantificar la importancia relativa de las 29 variables de pronosticadores para cada medida del éxito. Los factores en los resultados de las reubicaciones variaron con los marcos temporales y las medidas de éxito. Las técnicas de manejo tuvieron la mayor influencia relativa sobre la obtención de parámetros de ciclos de vida y tendencias poblacionales a corto plazo, mientras que los atributos de sitio y los rasgos de la especie fueron más importantes para la persistencia poblacional y las tendencias a largo plazo. En específico, las grandes cantidades de fundadores incrementaron el potencial de reproducción y reclutamiento de la siguiente generación, mientras que la declinación de la calidad del hábitat incrementó el riesgo de extinción y el trasplante de especies con baja producción de semillas redujo el rendimiento del potencial reproductivo a la larga. También detectamos interacciones novedosas entre algunos de los factores más importantes, como el aumento en la probabilidad del reclutamiento en la siguiente generación en especies con tasas mayores de producción de semillas, pero sólo cuando se emparejó con grandes cantidades de fundadores. Ya que las barreras más significativas para el éxito de la reubicación de plantas pueden superarse al mejorar las técnicas o resolver los temas a nivel de sitio por medio de un manejo y una intervención temprana, sugerimos que con la combinación del monitoreo a largo plazo con el manejo adaptativo los programas de reubicación pueden aumentar el prospecto de lograr el éxito a largo plazo.

PALABRAS CLAVE

especie amenazada, especie en peligro, reclutamiento de plántulas, recuperación de especie, reintroducción, restauración poblacional

确定珍稀植物迁地保护成功的预测因素

【摘要】珍稀植物迁地的基本目标是建立能够自我维持、具有演化恢复力、能够长期续存的种群。然而,大多数对植物迁地计划的综述研究都侧重于影响短期成功基准(如存活和繁殖)的几个因素。这些短期基准可能会对推断未来的生长和生存力产生误导,因为利于种群建立的因素可能与种群长期续存所需要的因素不同。本研究收集了大量($n = 275$)具有广泛代表性的数据集,这些数据集包含了记录详实且受到监测(平均7.9年)的濒危植物迁地计划案例,可用于确定指示迁地保护成功与否的6个生命周期基准及种群统计参数中最重要位点属性、管理技术和物种特征。我们使用随机森林算法量化了29个预测变量对每个迁地保护成功指标的相对重要性,发现不同时间段和不同成功指标的迁地保护结果驱动因素各不相同。管理技术对实现生命周期基准和短期种群趋势的影响最大,而位点属

性和物种特征对种群续存和长期趋势更为重要。具体来说,奠基者数量多可以增加下一代繁殖和种群补充的潜力,而栖息地质量下降和物种外植种子产量低则分别会导致灭绝风险增加和潜在的长期繁殖输出减少。我们还发现了一些最重要的驱动因素之间发现了新的相互作用,例如种子产量高的物种下一代种群补充的概率会增加,但只有在奠基者数量多的时候才存在这种关系。通过改进技术或通过早期干预及管理解决位点的问题,可以克服植物迁地保护中主要的障碍,因此我们建议将长期监测与适应性管理相结合,以帮助迁地保护计划取得长期成效。【翻译:胡怡思;审校:聂永刚】

关键词: 重引入, 出苗, 物种恢复, 种群恢复, 受威胁物种, 濒危物种

INTRODUCTION

Reintroductions and other types of conservation translocations are an established method to reduce the extinction risk of rare plants when in situ conservation measures fail to adequately protect and recover a species (Maschinski & Haskins, 2012; Maunder, 1992). They involve the intentional and planned movement of plants or plant propagules from one place to another either to augment an existing population or to establish a new population (IUCN/SSC, 2013). The use of translocations as a conservation tool has increased significantly in recent decades (Armstrong et al., 2019), and as threats to biodiversity intensify due to rapid anthropogenic climate change, habitat degradation, and the spread of invasive species and diseases (Díaz et al., 2019), further increases are expected (Swan et al., 2018). Yet, despite their growing popularity, translocations can be risky (Novak et al., 2021) and expensive (Fenu et al., 2019) and are less certain of a beneficial outcome than in situ management actions (Zimmer et al., 2019).

Global syntheses of plant translocations indicate mixed success rates, with short-term survival, flowering, and fruiting rates generally being quite low (Dalrymple et al., 2012; Godefroid et al., 2011). Poor performance has prompted several investigations into the factors influencing translocation success (Albrecht & Maschinski, 2012; Godefroid et al., 2011; Liu et al., 2015; Menges, 2008; Silcock et al., 2019). However, many published studies base success on a few short-term performance measures of the founder population (Menges, 2008), which can be misleading when trying to infer future growth and viability because factors that promote establishment may differ from those required for long-term persistence (Iles et al., 2016). Additionally, slow-maturing and long-lived plants require a much longer term perspective on success because it may take decades for the outplanted individuals to become reproductive (e.g., Menges et al., 2016) and even longer to reach a second generation (Albrecht et al., 2019). Consequently, the success of a plant translocation depends on the adopted definition, the period within which the evaluation is applied, and the life history of the focal species (Drayton & Primack, 2012).

A diverse array of factors can influence translocation outcomes, and they can be broadly grouped into three categories: site attributes, management techniques, and species' traits (Kaye, 2009). Site attributes, such as soil type, species composition, and physical habitat structure, are often evaluated

based on their apparent similarity with local natural populations (Holl & Hayes, 2006; Osborne & Seddon, 2012; Turner & McGraw, 2015). Because poor physical habitat quality and unsuitable environmental conditions rank as the most commonly reported causes of project failure (Godefroid et al., 2011; Silcock et al., 2019), relying on similarities to present conditions of a species occurrence may be insufficient for translocation planning. Management techniques, such as increasing the number of founders and the life stage of transplants, have led to increases in survival and attainment of reproduction and next-generation recruitment of seedlings (Liu et al., 2015; Silcock et al., 2019; Whitehead et al., 2023). Less attention has been given to the influence of life-history traits on translocation outcomes given the short time scales reported for many plant translocations (Albrecht et al., 2019). Ultimately, complex interactions between multiple factors likely drive translocation outcomes, but previous syntheses are limited to a small number of variables, often analyzed in isolation.

Because plants have different limiting factors at different life stages, the relative importance of site attributes, management techniques, and species' traits should vary depending on the success metric under consideration (Young et al., 2005). However, most preceding syntheses analyzed variable importance for attaining metrics associated with the reproductive niche of the founder individuals, such as the occurrence of flowering or fruiting (Dalrymple et al., 2012; Godefroid et al., 2011; Liu et al., 2015; Reiter et al., 2016; but see Silcock et al., 2019). Evaluations of these metrics have yielded valuable insight and have an advantage over intergenerational metrics (such as next-generation recruitment) in that sample sizes and analyses are less constrained by the short average monitoring length (3 years [Dalrymple et al., 2012]) of plant translocations. However, this bias toward metrics associated with the founder individuals, combined with the frequent decision to bypass early life stages by planting ex situ grown transplants (Albrecht & Maschinski, 2012), means relative understanding of the factors governing the recruitment niche and the development of the second generation, which have been shown to limit population growth (Clark et al., 2007), is poor.

We assembled a large data set of well-monitored and well-documented rare plant translocations in the United States to identify the most important site attributes, management techniques, and species' traits for six metrics of translocation success. These metrics, which represent key life-cycle

benchmarks and indications of a population's health and reproductive potential (Maschinski & Albrecht, 2017), include population persistence, next-generation recruitment, next-generation maturity, overall population size, and the short- (≤ 6 years) and long-term (> 6 years) reproductive population size. By considering both short- and long-term indicators of population performance across a broad range of species, sites, and ecosystems, we aimed to gain comprehensive insights into the most influential drivers of rare plant translocation success.

METHODS

Data collection

We assembled a data set on the translocations of rare plant species in the United States as part of an ongoing effort by the Center for Plant Conservation (CPC) to develop a standardized repository and continually expanding database of long-term rare plant translocations (<https://saveplants.org/reintroduction-database/>). Our data collation efforts included all categories of conservation-motivated translocations defined by the International Union for Conservation of Nature: reinforcements, reintroductions, and conservation introductions within and beyond a focal species' indigenous range (IUCN/SSC, 2013). Projects conducted for commercial purposes or with no clear conservation-related objective were excluded. We focused only on translocations of globally or regionally rare plant taxa according to the NatureServe conservation status system, which assigns conservation ranks on a 1–5 numerical scale (from most vulnerable to most secure, G/T1 to G/T5) to organisms distributed in North America.

The data we analyzed were collected directly from individuals involved in translocations rather than the scientific literature, which can be biased toward the most successful plant translocations (Godefroid et al., 2011). We used a three-step approach to assemble our data set (see Appendix S1). First, we disseminated an electronic survey (June 2016) via multiple listserves (e.g., Center for Plant Conservation and Plant Conservation Alliance) to identify participants willing to contribute data on rare plant translocations. Second, we circulated a survey via REDCap (research electronic data capture), a secure and freely available web-based application (<https://www.project-redcap.org/>), to individuals who agreed to participate in step 1. Finally, we supplemented our REDCap data set with projects that met our criteria described above from CPC's original Reintroduction Registry, which included data from published and unpublished translocation projects (Guerrant, 2012).

Our approach to data collection resulted in the contribution of projects from a variety of organizations, including federal, state, and local governments, botanical gardens, research institutes, nonprofit organization, indigenous groups, and private individuals. We use the term *practitioner* as an umbrella term to encompass the diverse range of groups and individuals involved in the practice of rare plant translocation.

Each data point in the REDCap data set represents a unique translocation project defined as the outplanting of plant propag-

ules of a single species over a single or multiple years at the same site or in multiple locations (< 1 km apart) within a single site (Appendix S1). In cases where a species was translocated to multiple locations or sites, contributors were asked to decide whether they qualified as a single or separate translocation project based on their familiarity and knowledge of the species and translocation sites. We provided two rules of thumb: a spatial proximity rule (adapted from NatureServe's 2004 Habitat-based Plant Element Occurrence Delimitation Guidelines) and an experimental treatments rule. With spatial proximity, distinct units that are < 1 km apart are collapsed into a single translocation project; those that are 1–10 km apart are considered single or separate projects, depending on the species biology, project goals, and habitat; and those that are > 10 km apart are considered separate translocation projects. With experimental treatments, all experimental treatments at a site are collapsed into a single translocation project unless they can be considered separate translocation projects based on the spatial proximity rule.

After cleaning and processing (Appendix S1), our final data set consisted of 275 translocation projects, involving 127 taxa from 21 distinct orders (see Appendix S2 for list of translocated taxa). A majority of translocations were of taxa that were imperiled or critically imperiled (83%) at the global level according to NatureServe conservation statuses and occurred within a taxon's indigenous range (98%). We did not conduct a comprehensive compilation of all rare plant translocations in the United States. Rather, we assembled a broadly representative data set of well-documented and monitored translocations spanning varied geography (23 states, including Hawaii), life forms (50% forbs, 41% woody plants, 5% cacti, 3% ferns, 1% graminoids), and ecosystems (41% forest, 21% savanna and shrub-steppe, 12% herbaceous wetlands, 11% upland grassland). Due to their low representation in the data set, translocations of ferns, graminoids, and cacti were combined with the two dominant life-form categories (ferns and graminoids with forbs to form perennial herbs and cacti with woody plants to form woody plants and cacti) (Table 1).

Metrics of translocation success

We initially evaluated translocation success across six metrics, one focused on population persistence, three focused on the attainment of life-cycle benchmarks (reproductive maturity, next-generation recruitment, and next-generation maturity), and two derived from population censuses (population size and reproductive population size) (Appendix S1). To evaluate population persistence, we grouped all extinct populations with populations containing < 50 individuals and a decreasing population trend, based on the assumption that these populations have too few individuals surviving to result in a viable population without further augmentation (Silcock et al., 2019). The threshold of 50 is based on a minimum viable effective population size rule in which 50 individuals are assumed to represent the absolute minimum number of plants required to prevent inbreeding depression (Jamieson & Allendorf, 2012).

TABLE 1 Predictor variables included in the random forest models to analyze benchmarks of success in rare plant translocations.

Variable	Type	Levels or observed ranges
Site attribute		
Habitat quality (preplanting)	Categorical	excellent, good, poor, or fair
Habitat quality change (between preplanting and most recent assessment) ^a	Categorical	positive, negative, no change
Ecosystem type	Categorical	forest, herbaceous wetland, savanna & shrub-steppe, sparsely vegetated, upland grassland, upland shrub land, woody wetlands or riparian
Number of obstacles ^a	Categorical	0, 1, >1
Number of threats (preplanting) ^a	Categorical	0, 1, 2–4, >4
Change in number of threats ^a	Categorical	increasing, decreasing, no change
Management technique		
ln(founder size) ^b	Continuous	0.693–10.389 (original range: 2–32,500)
Founder relatedness	Categorical	bulk collection, maternal lines separated
Management interventions (preplanting) ^a	Categorical	0, 1–3, >3
Management interventions (postplanting) ^a	Categorical	0, 1–3, >3
sqrt(monitored length)	Continuous	0–6.782 (original range: 0–46)
Number of outplanting years	Categorical	single, 2–5, >5
Number of source populations	Binary	single, multiple
Number of subsites	Binary	single site, multiple subsites
Project type	Categorical	assisted colonization, introduction (to indigenous range), reinforcement, reintroduction
Propagule type	Categorical	seeds, seedlings, adults, mixed
Traits		
Clonal reproduction	Categorical	strongly clonal, clonal, weakly clonal, none
Dispersal mode	Categorical	animals: high mobility, low mobility; plants: wind or water, other mode, no obvious agent
Disturbance dependency	Categorical	frequent disturbances, infrequent disturbances, none
Life form	Binary	perennial herbs, woody plants & cacti
Life span	Categorical	2–10 years, 11–50 years
Light requirement for reproduction	Categorical	high, low, none
Mating system	Categorical	autogamously selfing, obligately outcrossing, mixed mating
Order ^c	Categorical	Apiales, Asparagales, Asterales, Brassicales, Caryophyllales, Ericales, Fabales, Gentianales, Lamiales, Liliales, Malpighiales, Malvales, Poales, Polypodiales, Ranunculales, Rosales, Sapindales, Solanales
Pollination mode	Binary	insect, other modes
Conservation status ^c	Categorical	G/T1, G/T2, G/T3, G/T4, G/T5
Reproductive frequency	Categorical	iteroparous, semelparous
Seed production rate (number of seeds per plant)	Binary	<100, ≥100
Seed size	Categorical	small (<1 mg), medium (1–500 mg), large (>500 mg)

^aDerived from existing variables either by summing and categorizing multiple selection questions or by calculating a change between two related variables. See Appendix S1 for methodology behind each modified variable.

^bNumber of founder individuals.

^cObtained independently from NatureServe. Conservation status extracted at the taxonomic level at which the focal taxon was reported in the REDCap survey (i.e., G, ranks for full species; T, ranks for subspecies and varieties).

We also split the two population census metrics into projects with short- (≤ 6 years) and long-term (> 6 years) monitoring lengths because the importance of certain factors in determining changes in population size may vary across different time frames (Bialic-Murphy et al., 2022).

When analyzing variable importance for each of the success metrics, we excluded reinforcements ($n = 72$) because it was unclear whether the observations of life-cycle benchmarks or the results of censuses were due to outplanted individuals or naturally occurring plants. We also excluded annuals ($n = 14$)

and the longest lived species (>50 year life spans) ($n = 33$) due to highly imbalanced cases in the response variables and reduced model performance (see “Caveats” below).

Predictor Variables

We focused on 29 predictors of translocation success and classified all predictor variables into one of three categories: site attributes, management techniques, or species’ traits (Table 1). Site attributes describe characteristics of the location where the species was translocated; management techniques describe characteristics specific to an individual translocation event and largely under the control of practitioners; and species’ traits describe characteristics of the species translocated. Although we considered the relative effects of each predictor variable separately, we classified predictors into three categories to facilitate synthesis and aid in the identification of generalities that influence different metrics of translocation success. To prepare the data for analyses, we modified the levels of some predictors by collapsing levels with very low frequencies. We created new variables by summing and categorizing multiple selection questions or by calculating a change between two related variables (Table 1; Appendix S1). We also transformed the two continuous variables, founder size (natural log) and monitoring length (square root), to improve model performance (by reducing effects of skewed distributions on variable selection) and to enhance the visualization of model outputs (Zheng & Casari, 2018).

Analyses

To quantify the relative importance of predictor variables for each metric of translocation success, we used the random forest algorithm. When compared with classical parametric methods, such as logistic regression, random forests offer some advantages, such as their robustness to missing information, effectiveness at detecting patterns in high-dimensional data (i.e., when the ratio of the number of cases to number of predictors is low), ability to reveal complex interactions and nonlinear relationships, and capacity to handle multiclass classification problems (Strobl et al., 2009). Because our data set was characterized by a substantial amount of missing data, a large number of mostly categorical predictors, and multiple response variables with more than two classes (e.g., population size and reproductive population size), random forest offered a valuable approach for which comparable parametric methods would have been less appropriate (Strobl et al., 2007).

Because random forests constructed from individual classification trees are biased toward selecting variables with more categories over variables with only a few, we used unbiased conditional inference trees drawn without replacement (Hothorn et al., 2006), as recommended in Strobl et al. (2007). To identify the most influential predictor variables for each metric of translocation success, we generated variable importance values with the `varimp` function in the `party` package 1.3-10 (Hothorn et al., 2022) in R 4.2.0 (R Core Team, 2022), which calculates

importance by comparing model prediction accuracy before and after permutation of each predictor (Strobl et al., 2008); large decreases in model accuracy after permutation indicate greater importance.

Random forests were run in two phases. In the first phase, random forest analysis was run as a filter to exclude unimportant variables that made little contribution to the model. These models were run with 10,000 trees and eight randomly chosen predictors tested at each node (`mtry = 8`); default values were retained for all other parameters of the `cforest` function. We applied Strobl et al.’s (2009) approach to variable exclusion. We removed all variables with importance values that were negative, zero, or had a small positive value that was within the same range of the negative values because these variables provide less information than random variables. In the second phase of random forest analysis, we ran models with only the selected variables from phase 1 and kept the default settings for function `cforest` but not for `ntree` (`ntree = 10,000`). Variable importance values of the most important predictors in each model were relativized for presentation.

We used the `partial_dependence` function in the `edarf` package 1.1.1 in R to estimate partial variable effects for the most important predictors (Jones & Linder, 2016). Partial dependence shows how the predicted outcome changes with respect to a single predictor variable, whereas all other predictors in the model are held constant. We produced partial dependence plots to visualize and interpret the relationship between each important predictor variable and the associated response variable. Determining which predictors were the most important from each of the phase 2 models was done by assessing the size of the steps in the variable importance plots (Holmes et al., 2015). Although strongly correlated predictors can affect the interpretation of variable importance through the unpredictable inflation or deflation of other closely associated predictors (Biau & Scornet, 2016), we did not find any significant pairwise correlations or associations between predictor variables that might affect final interpretation (Appendix S1).

To identify potential interactions between the most important predictors, we computed classification trees with the `cree` function from the `partykit` package 1.2-16 (Hothorn & Zeileis, 2015). This function uses recursive partitioning to create a classification tree and identifies the predictor variable and split point (or variable levels) that maximize the statistical association between the predictor and the response at each node of the tree. Statistical significance ($\alpha = 0.05$) indicates that the null hypothesis of independence between the predictor and the response can be rejected. Interactions are represented by nodes in the tree where multiple predictors are involved in the split. This approach avoids overfitting and a selection bias toward covariates with many possible splits, which are common features in other recursive partitioning methods (Strobl et al., 2009).

We evaluated the classification performance of our random forest models with the area under the curve (AUC) of the receiver operating characteristic (ROC) and generalized for multiclass classifications when response variables consisted of more than two classes (Hand & Till, 2001). The value of AUC

ranges from 0.50, for discrimination that is no better than random, to 1.00, for perfect discrimination (Hanley & McNeil, 1982). We considered models with an AUC of ≥ 0.70 to have at least acceptable levels of discrimination capacity (Hosmer et al., 2013). Random forest models for reproductive maturity and short-term population size (≤ 6 years) did not meet our AUC threshold and were consequently excluded from variable importance analyses (model AUC scores in Appendix S3).

RESULTS

Summary of the full data set

At the time of data collection, translocation projects had been monitored for an average of 7.9 years (median = 6, min–max = 1–46, $n = 275$) since outplanting. Reproductive maturity occurred in 80% of populations, whereas next-generation recruitment was recorded in 53% of populations that reached maturity (43% of total), and next-generation maturity occurred in 50% of populations that recruited (21% of total) (Appendix S1). At the most recent monitoring event, the majority of translocated populations remained extant with ≥ 50 individuals present and a stable or increasing population (71%). The size of extant populations tended to be medium (51–500, 55%) or small (1–50, 31%), rather than large (>500 , 14%), at the most recent census. Most extant populations had a small number of reproductive individuals present (1–50, 41%), one-third had a medium-to-large number (>50 , 32%), and the remainder had no reproductive individuals present (27%).

Predictors of translocation success

Predictors associated with management techniques had the largest influence on population persistence and the two life-cycle benchmarks (Figure 1a–c). Large founder population sizes reduced the probability of extinction (Figure 2a) and increased the probability of recruitment success (Figure 2d). Next-generation maturity was best detected when monitoring lasted longer (Figure 2e). The introduction of propagules from a single-source population rather than multiple populations and outplanting across multiple subsites rather than a single subsite also increased the probability of attaining next-generation maturity. Site attributes, such as the change in habitat quality and the habitat quality before outplanting, influenced population persistence. A poor or fair baseline habitat quality or a negative change in quality increased the probability of extinction (Figure 2b,c). However, classification tree analysis showed that extinction probabilities at sites with negative changes in habitat quality could be reduced to levels more comparable with stable or increasing habitat conditions when the founder size exceeded 112 ($\ln = 4.718$) individuals (Figure 3a).

Founder size also ranked highly in models of census-derived metrics, such as population size and the number of reproductive individuals recorded within 6 years of outplanting (Figure 1d,e). Increasing the founder size increased the probability of estab-

lishing medium- and large-sized populations (Figure 4a) and increased the number of reproductive individuals in the short term (≤ 6 years) (Figure 4d). However, founder size was less influential for long-term metrics, such as next-generation maturity (Figure 1c), population size at >6 years (Appendix S3), and the number of reproductive individuals at >6 years (Figure 1f). In the two long-term census metrics, site-level variables, such as the number of threats at the time of outplanting and the change in habitat quality, were more important. A higher relative number of threats at outplanting (two or more) reduced reproductive population sizes, and negative changes in habitat quality reduced the overall population size (Figure 4e; Appendix S3).

Trait-related variables tended to influence census-derived metrics more than life-cycle benchmarks when considered independently (Figure 1). However, classification tree analysis revealed an interactive effect between seed production rate and founder size for next-generation recruitment, indicating that even with a substantial number of founders (>119 , $\ln = 4.779$), recruitment rates were three times lower in species with low seed production (Figure 3b). Population sizes were largest in taxa with 2- to 10-year life spans, and variation in population size was much greater for taxa with life spans of 11–50 years (Figure 4b; Appendix S3). In the short term (≤ 6 years), populations of woody plants and cacti were most likely to be represented by a medium- to large-sized number of reproductive individuals, whereas perennial herbs were most likely to have small reproductive populations (Figure 4c). Herb translocations often required very large founder sizes (>550 , $\ln = 6.310$) to establish a reproductive population within 6 years (Figure 3c). Over time frames of >6 years, translocations of taxa with comparatively higher seed production rates (≥ 100 per plant) resulted in larger reproductive populations than less fecund taxa (<100 seeds per plant) (Figure 4f).

DISCUSSION

We assembled a large data set on translocations of rare plant species in the United States that spanned multiple life forms (herbaceous to woody), biomes (tropical to temperate), and ecosystems (forest to grassland), and averaged much longer time frames than previous syntheses of plant translocations (nearly 8 years compared with 3–5 years in Dalrymple et al., 2012, Liu et al., 2015; Reiter et al., 2016; though see Silcock et al., 2019). Our results demonstrated how the relative importance of site, technique, and species' traits vary across different life-cycle benchmarks and population metrics in rare plant translocations. Additionally, we uncovered novel interactions among these factors that highlight the most important barriers to creating viable populations of translocated rare plant species.

Site attributes

Habitat quality is a fundamental driver of translocation success in plants globally (Godefroid et al., 2011). Consistent with this, low-quality habitat at the time of outplanting was one of

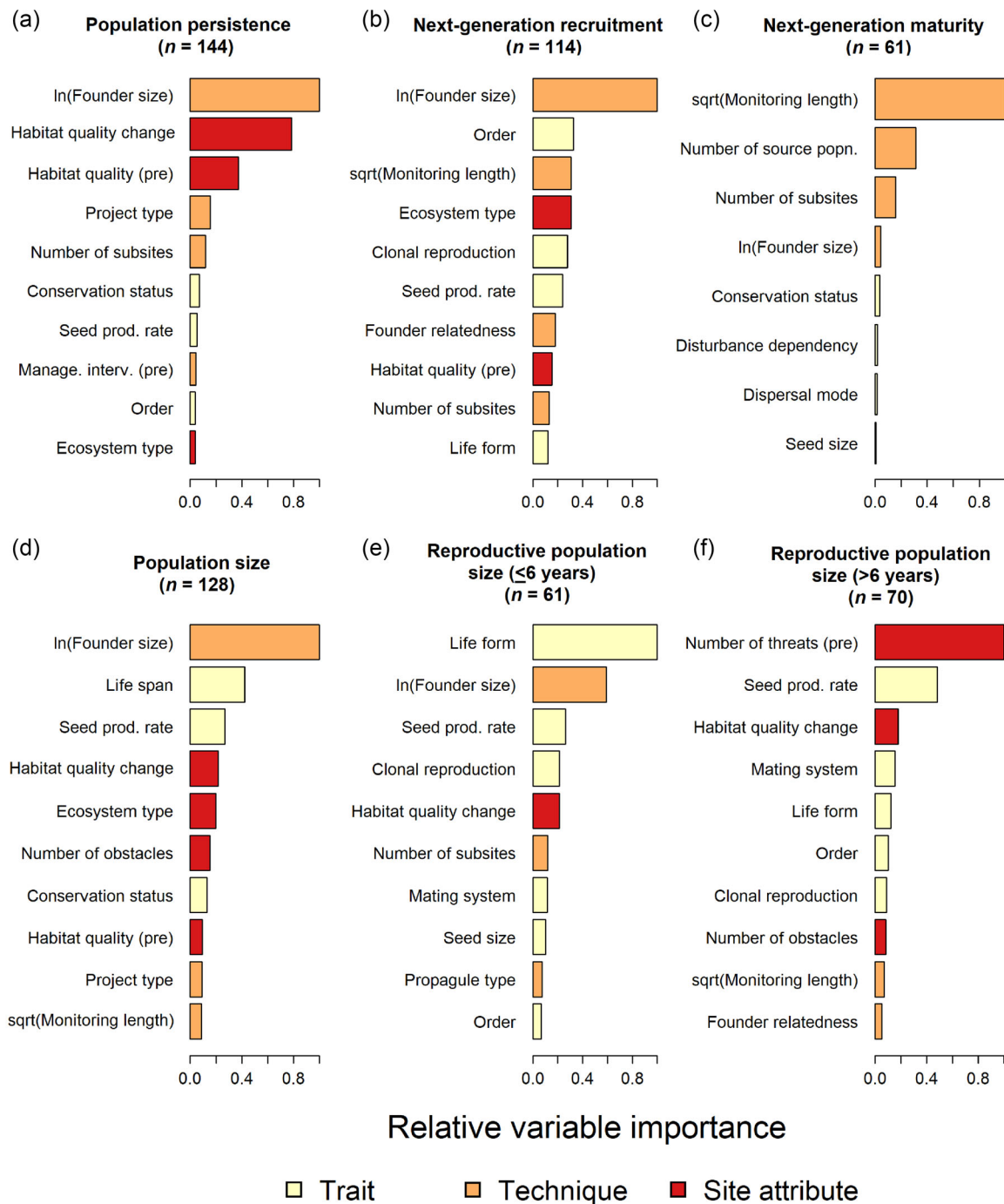


FIGURE 1 Relative variable importance of the 10 or 8 (next-generation maturity) most influential predictors for six metrics of plant translocation success identified using random forest models: (a) population persistence, (b) next-generation recruitment, (c) next-generation maturity, (d) population size, (e) reproductive population size (≤ 6 years), and (f) reproductive population size (> 6 years). Models were fit with data on two life-span categories (2–10 years and 11–50 years). Importance was calculated by comparing model prediction accuracy before and after permutation of each predictor.

the strongest predictors of population extinction in U.S. plant translocations. The typically complex habitat requirements of rare species are sometimes underestimated in translocations. Recipient sites are selected based on subjective judgements of habitat quality (Osborne & Seddon, 2012) or the historical presence of the species, which disregards recent or potential future

changes in environmental conditions (but see Rusconi et al., 2022). Low relative habitat quality prior to outplanting and diminished habitat quality after outplanting emerged as primary barriers to population persistence, supporting this contention. Although a recent review of recipient site selection indicated a shift toward more systematic approaches, such as habitat

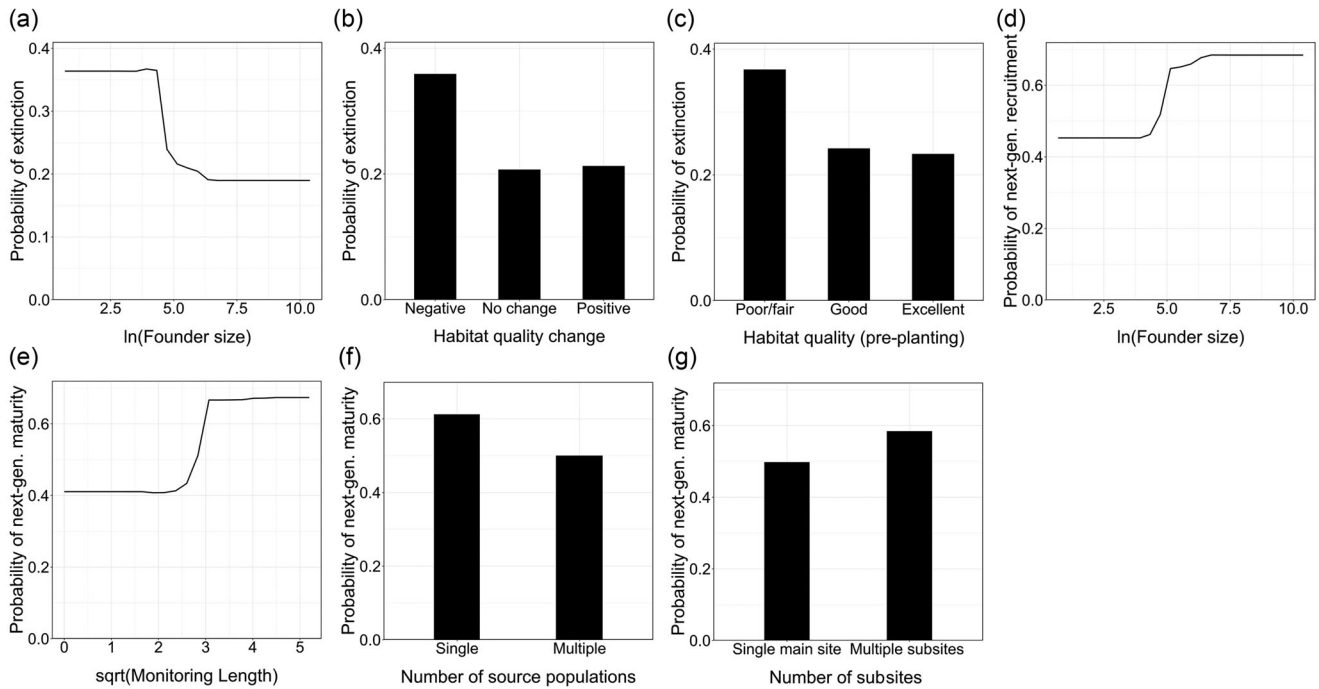


FIGURE 2 Partial dependence of the most influential variables for species with 2–10 and 11–50 year life spans in random forest models on (a–c) population persistence, (d) next-generation recruitment, and (e–g) next-generation maturity (lines or bars, predicted probability of the response class according to all values of a continuous variable or level of a categorical variable). Partial dependence indicates dependence of the dependent variable on the focal predictor variable while controlling for the effects of all the other predictors in the random forest model.

suitability modeling and experimental translocation trials (Stadtmann & Seddon, 2018), our findings suggest that more rigorous selection of high-quality sites and greater attention to changes in habitat quality after outplanting could help reduce the extinction risk of translocated plant populations.

Identifying and controlling threats prior to outplanting is a key step for successful translocation (Commander et al., 2018; IUCN/SSC, 2013; Maschinski & Albrecht, 2017). Practitioners in our study reported an average of three threats at the time of outplanting; translocations in Hawaii had almost double (4.1) the number of threats as those in the continental United States (2.3) due to intense anthropogenic pressure from agriculture, invasive species, harvesting, fire, and land conversion (Wilcove et al., 1998). However, the average number of management actions used to control threats was proportionally similar to the number of threats in both regions (Hawaii = 3.9, continental United States = 1.5), which may help explain why the number of threats did not have a significant influence on population persistence.

The number of threats at outplanting was the most influential predictor of the long-term (>6 years) size of the reproductive population. In rare plant translocations, achieving large reproductive population sizes is essential to overcoming reproductive barriers (such as Allee effects and mate limitation) and achieving next-generation seedling recruitment (Albrecht et al., 2019). When no threats or a single threat was observed at the time of outplanting, a medium to large population of reproductive individuals (>50) was the most probable out-

come, whereas when ≥ 2 threats were present, there was roughly the same probability of having zero reproductive individuals. Consequently, practitioners would be well advised to conduct detailed threat assessments during the project planning stage, select recipient locations that have as few threats as possible, and be willing to control threats before and after outplanting (Maschinski & Albrecht, 2017). This may include constructing cages or fences to exclude herbivores (Albrecht & Long, 2019; Monks et al., 2023), protecting plants from recreational activities (Fenu et al., 2016), or changing disturbance regimes, such as fire frequency and intensity (Menges & Quintana-Ascencio, 2004).

Techniques

Best practice guidelines recommend the use of as many founding individuals as is feasible to bolster population growth (Maschinski & Albrecht, 2017). Concordant with this recommendation and results from previous syntheses (Albrecht & Maschinski, 2012; Godefroid et al., 2011; Silcock et al., 2019; Whitehead et al., 2023), founder population size emerged as an important predictor across multiple metrics of translocation success. Larger founder sizes increased the probability of population persistence, the occurrence of next-generation recruitment, the size of the reproductive population within ≤ 6 years, and the attainment of a large (>500 individuals) population size.

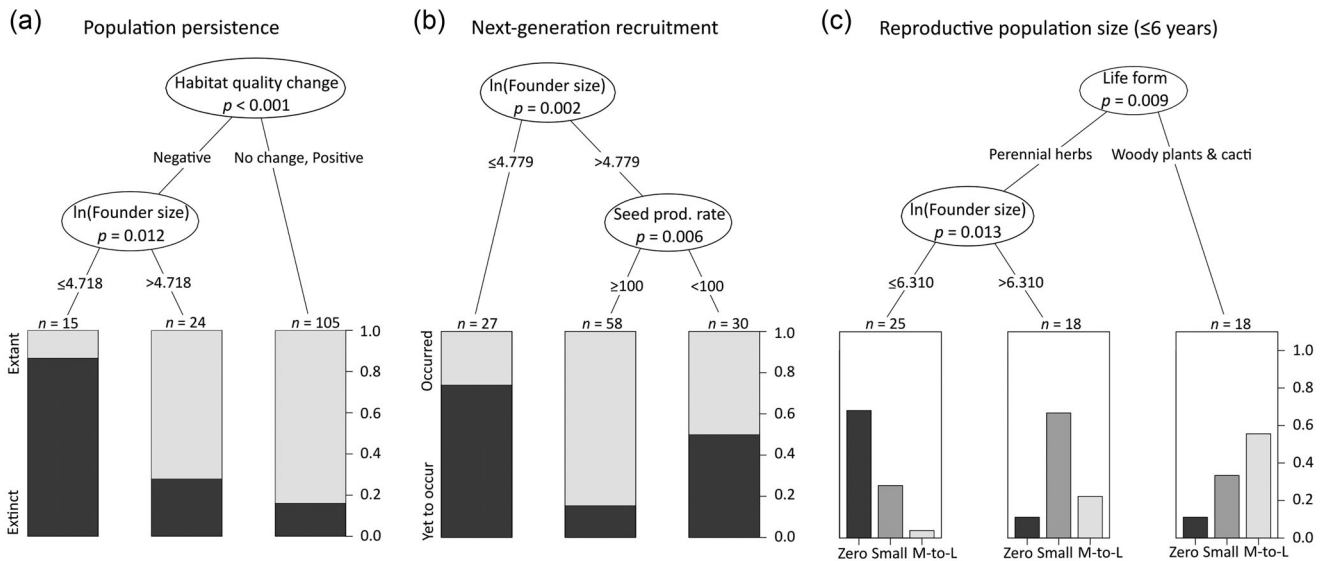


FIGURE 3 Interactive effect of important predictor variables for three metrics of translocation success: (a) population persistence, (b) next-generation recruitment, and (c) short-term reproductive population size (≤ 6 years) (ranges of short-term reproductive population size categories: zero, 0; small, 1–50; M-to-L, medium to large [>50]). Interactive effects are identified using classification tree analysis and are for species with life spans of 2–10 and 11–50 years. Classification tree partitions are based on the lowest statistically significant p value ($\alpha = 0.05$). Categories for each split are shown immediately below the oval displaying the name of the explanatory variable.

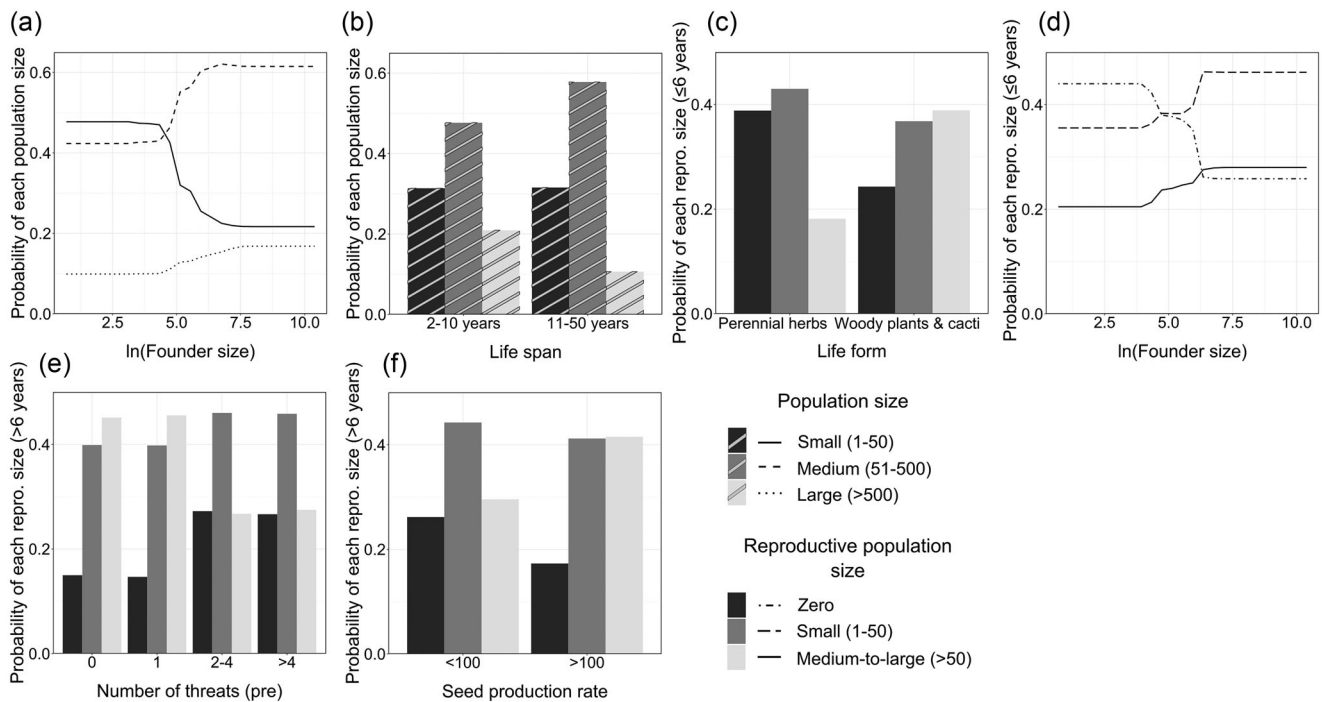


FIGURE 4 Partial dependence of the most influential variables for species with 2–10- and 11–50-year life spans in random forest models on (a, b) population size, (c, d) short-term (≤ 6 years) reproductive population size, and (e, f) long-term (> 6 years) reproductive population size (lines or bars, predicted probability of response class according to all values of a continuous variable, or level of a categorical variable). Partial dependence indicates the dependence of the dependent variable on the focal predictor variable while controlling for the effects of all the other predictors in the random forest model.

Maximizing the number of founder individuals can reduce the risk of loss due to demographic stochasticity (Lande, 1993). In contrast, the introduction of few individuals can limit total genetic diversity, creating a bottleneck and increasing the risk of inbreeding depression and further losses due to genetic drift (Keller et al., 2012), both factors that increase extinction risk (Frankham et al., 2017). We detected a significant interaction between founder size and habitat quality that supports this prediction: small founder sizes (≤ 112) markedly increased the extinction risk of translocated populations in deteriorating habitats, whereas large founder sizes (> 112) resulted in populations that were more resistant to negative changes in habitat quality.

Techniques emerged as the most influential predictors of whether next-generation recruits attained reproductive maturity. Unsurprisingly, this life-cycle benchmark was more likely to be observed in projects with longer monitoring time frames because our data set consisted of perennial species with potentially delayed reproduction. These intergenerational benchmarks may take several decades for long-lived species to attain (Albrecht et al., 2019), highlighting the need for a commitment to long-term monitoring and sustained funding and stakeholder engagement. Although the use of multiple source populations was generally more effective in previous studies (Lesica & Allendorf, 1999; Maschinski et al., 2013; Van Rossum et al., 2020), we found that using a single-source population slightly improved the probability of attaining next-generation maturity. This could be because use of single- versus multiple-source populations is context-specific and depends on the species biology, genetic structure, and goals of the translocation project (Weeks et al., 2011).

Traits

The success of plant translocations is reported to vary widely across species (Dalrymple et al., 2012; Godefroid et al., 2011; Liu et al., 2015), but the role of species' traits in determining translocation outcomes remains unclear. In general, we found that species' traits were better predictors of the population size than life-cycle benchmarks and that taxonomic order was generally not a strong predictor of translocation success. The latter finding suggests that species with shared ancestry may have different translocation outcomes.

Life span and reproductive output, two independent axes of plant life-history strategies that predict demographic performance (Salguero-Gómez et al., 2016), were important predictors of translocation outcomes. Species with short life spans (2–10 years) were more likely to establish large populations compared with long-lived species (11–50 years). Similarly, species that were prolific seed producers were more likely to obtain next-generation recruitment and a large number of reproductive individuals over the long-term compared with species that produce few seeds. These findings are consistent with the prediction that species with short life spans and high reproductive rates have more rapid population growth rates than long-lived species with slow life histories and low reproductive rates (Salguero-Gómez, 2017; Salguero-Gómez et al., 2016). In our data set, most translocations were founded with seedlings

or adult plants as opposed to seeds ($> 90\%$), which can further reduce extinction risk and amplify short-term population growth rates more in short- than long-lived species (Iles et al., 2016). Our results also illustrate how species' traits can interact with techniques to influence translocation outcomes. Species with high seed production were more likely to obtain next-generation recruitment compared with those with low seed production, but only when translocated with large founder sizes. By investing more in seed production, populations with high seed production increase the likelihood of seeds reaching safe sites (Westoby et al., 2002, but see Clark et al., 2007), resulting in higher seedling recruitment rates.

Woody plants and cacti achieved large reproductive population sizes in the short term (≤ 6 years) compared with perennial herbs. Although an interaction between founder size and life form highlighted the very large founder sizes (> 550) required for herb translocations to establish any number of reproductive individuals in the short term, founder sizes in these herb translocations were much larger (median = 322) than in translocations involving woody species (median = 165). There was also little variation in the life spans or the stages of propagules outplanted between the two life forms. Instead, differences in reproductive population sizes may have been driven by life-history factors, such as higher levels of clonal growth in woody species, which may have slowed population declines. Alternatively, biogeographical factors may help explain this variation given that 83% of short-term woody translocations took place in tropical ecosystems of Hawaii, whereas the majority of herb translocations (77%) occurred in temperate habitats of the continental United States. With consistently high temperatures, less seasonality, and greater productivity, tropical environments may allow plants to reach reproductive maturity more rapidly and in greater numbers (Brown, 2014). Given the disproportionately high number of tropical woody species that are extinct or in decline globally (Humphreys et al., 2019), these results hold promise that translocations could promote their future recovery.

Caveats

Time frames that reflect the life history of species are important when evaluating translocation success (Monks et al., 2012). We used the life span of translocated taxa to determine their eligibility for inclusion in our variable importance analysis, retaining species with 2–10 and 11–50 year life spans and excluding annuals and long-lived (> 50 years) species. We preserved life span as a binary predictor (2–10 years, 11–50 years) because our models revealed that shorter life spans were advantageous for establishing larger populations. We excluded annuals and long-lived (> 50 years) species based on extreme imbalances in the ratios of most response classes. For example, despite average monitoring length being relatively long in our sample of translocations (nearly 8 years), just 6% ($n = 2$) of long-lived taxa produced next-generation recruits, whereas every project involving annuals ($n = 14$) attained this benchmark (compared with 62% for all other taxa, $n = 71$). When evaluating the effect of excluding life-span categories on model performance and our interpretations of variable importance, we found that models

run with all life spans mostly had relatively poor discrimination capacity (Appendix S3) and led to the population persistence model falling below our AUC quality control threshold (≥ 0.7) (Hosmer et al., 2013). However, variable importance rankings for the remaining five metrics of success were broadly consistent between models run with (Appendix S4) and without (Figure 1) annuals and long-lived species, especially for the most influential predictor in each model, which changed only for short-term reproductive population size (life span exchanged with founder size). While the most important predictors of translocation success appeared to be consistent across life spans, the success of annual and long-lived species translocations may be less dependent on the predictors identified as important in our analyses. In the case of annuals, although habitat quality and founder size have also proved important for persistence (Holl & Hayes, 2006), field studies suggest that seed bank size and water availability before and after outplanting should also be considered by practitioners (Holl & Hayes, 2006; Pavlik & Espeland, 1998).

The percentage of population extinctions (9%, including annuals and long-lived species) in our data set cannot be directly compared with previous reviews on plant translocations (e.g., Dalrymple et al., 2012; Godefroid et al., 2011). Our survey method depended on responses from practitioners and did not attempt to comprehensively review translocation outcomes in the United States. An underrepresentation of negative results may indicate a reluctance by practitioners to share data on failures, perhaps because of the perceived risks to future funding or potential harm to their reputation or that of their organization. Alternatively, some unsuccessful projects may just be poorly designed and documented. Irrespective of the causes, a lack of data on failed translocations inhibits translocation science and practice by limiting the size and statistical power of future analyses and by preventing practitioners from using that information to devise their own experiments and management plans (Menges, 2008).

Synthesis and recommendations

Plant translocations are complex conservation actions that integrate horticultural, genetic, and ecological dimensions. Understanding the general drivers of translocation outcomes therefore requires the integration of data across many different variables and metrics of translocation success. Our large-scale study demonstrates that the drivers of translocation outcomes vary across different success metrics and change over time: techniques have a greater relative influence on the attainment of life-cycle benchmarks and population persistence, whereas site-level factors and species characteristics have a greater influence on population size and the number of reproductive adults. Although we concentrated on translocation projects in the United States, the diverse range of life forms, biomes, and ecosystems involved indicates the potential applicability of these findings to other regions.

Our study was made possible through the synthesis of translocations with well-designed monitoring programs conducted over long periods, which increased our ability to evaluate

the response of translocated populations to changing habitat conditions and to detect barriers to success that might take years to express (e.g., inbreeding depression in perennial species). Given that most major barriers to plant translocation success involve techniques under practitioner control, site-level changes in habitat quality, or threats that could be mitigated through early intervention, we conclude that integrating a long-term monitoring plan with adaptive management through planned experimentation could increase success rates and reduce extinction risk.

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ACKNOWLEDGMENTS

Our research was supported by Botany in Action Fellowship through Phipps Conservatory; Environmental Securities Technology Certification Program (RC-201201); Florida Endangered Plant Advisory Council; Hawaii Department of Land and Natural Resources Division of Forestry and Wildlife, Napuu Conservation Project; National Fish and Wildlife Foundation; National Park Service; National Science Foundation (DEB-0613611 and DEB-1118702); North American Lily Society; Pacific Cooperative Studies Unit; U.S. Fish and Wildlife Service; and U.S. Geological Survey Ecosystems Mission Area. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank the three anonymous reviewers and the handling editor, whose comments and suggestions contributed to the enhancement of the manuscript.

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SUPPORTING INFORMATION

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

How to cite this article: Bellis, J., Osazuwa-Peters, O., Maschinski, J., Keir, M. J., Parsons, E. W., Kaye, T. N., Kunz, M., Possley, J., Menges, E., Smith, S. A., Roth, D., Brewer, D., Brumback, W., Lange, J. J., Niederer, C., Turner-Skoff, J. B., Bontrager, M., Braham, R., Coppoletta, M., ... Albrecht, M. A. (2024). Identifying predictors of translocation success in rare plant species. *Conservation Biology*, 38, e14190. <https://doi.org/10.1111/cobi.14190>