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Contributed Paper

Effects of life history and reproduction on recruitment time lags in reintroductions of rare plants

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Abstract: *Reintroductions are important components of conservation and recovery programs for rare plant species, but their long-term success rates are poorly understood. Previous reviews of plant reintroductions focused on short-term (e.g., ≤3 years) survival and flowering of founder individuals rather than on benchmarks of intergenerational persistence, such as seedling recruitment. However, short-term metrics may obscure outcomes because the unique demographic properties of reintroductions, including small size and unstable stage structure, could create lags in population growth. We used time-to-event analysis on a database of unusually well-monitored and long-term (4–28 years) reintroductions of 27 rare plant species to test whether life-history traits and population characteristics of reintroductions create time-lagged responses in seedling recruitment (i.e., recruitment time lags [RTLs]), an important benchmark of success and indicator of persistence in reintroduced populations. Recruitment time lags were highly variable among reintroductions, ranging from <1 to 17 years after installation. Recruitment patterns matched predictions from life-history theory with short-lived species (fast species) exhibiting consistently shorter and less variable RTLs than long-lived species (slow species). Long RTLs occurred in long-lived herbs, especially in grasslands, whereas short RTLs occurred in short-lived subtropical woody plants and annual herbs. Across plant life histories, as reproductive adult abundance increased, RTLs decreased. Highly variable RTLs were observed in species with multiple*

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reintroduction events, suggesting local processes are just as important as life-history strategy in determining reintroduction outcomes. Time lags in restoration outcomes highlight the need to scale success benchmarks in reintroduction monitoring programs with plant life-history strategies and the unique demographic properties of restored populations. Drawing conclusions on the long-term success of plant reintroduction programs is premature given that demographic processes in species with slow life-histories take decades to unfold.

Keywords: life-history theory, population dynamics, rare species, seedling recruitment, species recovery, survival analysis, translocation

Efectos de la Historia de Vida y la Reproducción sobre las Demoras en el Tiempo de Reclutamiento en la Reintroducción de Plantas Raras

Resumen: *Las reintroducciones son componentes importantes de los programas de conservación y recuperación de especies raras de plantas, pero las tasas de éxito a largo plazo cuentan con muy poco entendimiento. Las revisiones previas de las reintroducciones de plantas se han enfocado en la supervivencia a corto plazo (p. ej.: ≤ 3 años) y en el florecimiento de individuos fundadores en lugar de enfocarse en puntos de referencia para la persistencia inter-generacional, como el reclutamiento de plántulas. Sin embargo, las medidas a corto plazo pueden ocultar los resultados ya que las propiedades demográficas únicas de las reintroducciones, incluyendo el menor tamaño y la estructura inestable de estadio, podrían crear demoras en el crecimiento poblacional. Usamos un análisis de tiempo-para-evento en una base de datos de reintroducciones inusualmente bien monitoreadas y de largo plazo (4–28 años) de 27 especies raras de plantas para probar si los atributos de la historia de vida y las características poblacionales de la reintroducción crean respuestas con demoras temporales en el reclutamiento de plántulas (es decir, demoras temporales en el reclutamiento), un punto de referencia importante para el éxito y un indicador de la persistencia en poblaciones reintroducidas. Las demoras temporales de reclutamiento (RTLs, en inglés) fueron muy variables entre las reintroducciones, abarcando desde <1 hasta 17 años después de la instalación. Los patrones de reclutamiento se acoplaron a las predicciones de la teoría de historias de vida, donde las especies de vida corta (especies rápidas) exhibieron RTLs consistentemente más cortas y menos variables que las especies de vida larga (especies lentas). Las RTLs largas ocurrieron en hierbas de vida larga, especialmente en los pastizales, mientras que las RTLs cortas ocurrieron en plantas leñosas subtropicales de vida corta y en hierbas anuales. En todas las historias de vida de las plantas, conforme incrementó la abundancia de adultos reproductivos, las RTLs disminuyeron. Se observaron RTLs altamente variables en las especies con eventos de reintroducción múltiples, lo que sugiere que los procesos locales son igual de importantes que la estrategia de historia de vida para determinar los resultados de las reintroducciones. Las demoras temporales en los resultados de restauración resaltan la necesidad de poner a escala los puntos de referencia de éxito en los programas de monitoreo de reintroducciones que tengan estrategias de historia de vida de las plantas y las propiedades demográficas únicas de las poblaciones restauradas. La obtención de conclusiones sobre el éxito a largo plazo de los programas de reintroducción de plantas es algo prematuro ya que los procesos demográficos de especies con historias de vida lentas tardan décadas en desarrollarse.*

Palabras Clave: análisis de supervivencia, dinámicas poblacionales, especies raras, reclutamiento de plántulas, recuperación de especies, reubicación, teoría de historias de vida

摘要: *重引入是稀有植物保护和恢复计划的一个重要组成部分, 但其长期的成功率仍不得而知。对植物重引入已有的综述主要关注引入个体短期 (如三年内) 的存活和开花情况, 而不是以其跨代续存 (如幼苗更新) 为基准。然而, 短期指标可能会掩盖真实结果, 因为重引入物种有独特的种群统计特征, 包括小种群和不稳定的阶段结构, 可能导致种群增长存在滞后。我们用时间-事件分析法, 对开展了非常好的监测的 27 种长期 (4 – 28年) 重引入植物的监测数据进行分析, 检验了重引入物种的生活史特性和种群特征是否会导致幼苗更新存在时间滞后响应 (即更新时滞) , 这是重引入成功与否的重要基准, 也是重引入种群续存的一项指标。不同的重引入物种更新时滞 (recruitment time lags, RTL) 差异很大, 变化范围从栽种后不到一年到长达十七年。更新模式与生活史理论预测结果相吻合, 即相比于寿命长 (生长慢) 的物种, 寿命短 (生长快) 的物种RTL都更短、变异也更小。寿命长的草本植物RTL长, 特别是草原上的物种, 而寿命短的亚热带木本植物及一年生草本植物RTL则较短。在植物整个生活史中, RTL随着可繁殖成体的数量增加而下降。有多次重引入事件的物种RTL变异较大, 这表明局部过程与生活史策略在决定重引入结果上同等重要。恢复结果时滞效应的存在强调了利用恢复种群的植物生活史策略及特殊的种群统计特征来衡量重引入监测项目成功与否的必要性。鉴于生活史慢的物种可能需要几十年的时间来完成种群统计过程, 对植物重引入项目的长期成功下定论尚为时过早。***【翻译: 胡怡思; 审校: 聂永刚】***

关键词: 生活史理论, 幼苗更新, 物种迁移, 种群动态, 稀有物种, 生存分析, 物种恢复

Introduction

Given the alarming rates at which species are rare and require human assistance for recovery, conservation reintroduction or the intentional movement and release of an organism inside its native range is now increasingly practiced to enhance species survival (Seddon et al. 2007; Godefroid et al. 2011). Although hundreds of rare plant species worldwide are now in conservation reintroduction programs (Guerrant 2012), long-term success rates remain elusive because many published studies base success on short-term (≤3 years) demographic performance (e.g., survival and reproduction) of the founder population (Menges 2008; Godefroid et al. 2011; Dalrymple 2012; but see Drayton & Primack 2012). Although short-term metrics are important initial indicators of success, they are weakly correlated with future growth and viability because conditions that promote establishment can differ from those required for long-term persistence and viability (Armstrong & Seddon 2008). Barriers to understanding long-term persistence of reintroduced plant populations have included short funding cycles, nonstandardized monitoring protocols, and lack of centralized data repositories (Godefroid & Vanderborght 2011; Maschinski et al. 2012).

Seedling recruitment is an important success benchmark in reintroduction programs as it demonstrates that founder individuals produced viable offspring and a recipient site can potentially support a self-sustaining population (Primack 1996; Menges 2008; IUCN/SSC 2013). Despite its importance for determining population growth and abundance, seedling recruitment remains underreported in reintroduction programs and recent reviews suggest only a moderate proportion (30–40%) of reintroductions ever reach this benchmark (Godefroid et al. 2011; Dalrymple 2012; Guerrant 2013). However, previous reviews of reintroductions did not examine how different plant life histories might shape the timing of demographic events across space and time. For example, long-lived perennials may require over 30 years after reintroduction to recruit seedlings, whereas an annual herb may recruit within just a few years. Drawing conclusions on reintroduction outcomes based on short-term metrics could be misleading without accounting for the time scale at which demographic events occur across a species life cycle (Albrecht et al. 2011; Seddon et al. 2014).

Time lags in population establishment and growth are frequently reported in plant invasions (Larkin 2012), and there are reasons to expect similar demographic lags in plant reintroductions. First, episodic seedling recruitment is common in plants. Lags of more than a decade occur between recruitment events in natural populations of perennials (Inghe & Tamm 1985), a life-history type disproportionately represented in rare plant reintroductions (Dalrymple 2012; Guerrant 2012). Second, the fast–slow continuum framework of classic life-history theory (Stearns 1992) predicts that trade-offs in demographic schedules (e.g., survival and reproduction) constrain plant life-history strategies and influence population dynamics (Franco & Silvertown 1996; Burns et al. 2010; Salguero-Gómez et al. 2016). This framework that predicts the importance of recruitment for maintaining population growth is inversely proportional to life span; trade-offs in survival, growth, and reproduction determine the relative importance of seedling recruitment for plant population growth (Franco & Silvertown 2004). Third, along with life-history strategy, reproductive traits (mating system, seed dispersal, and seed production) could further influence the degree and magnitude of recruitment limitation in plant populations (Clark et al. 2007).

Differences in population characteristics, such as the initial founder and propagule size, planting technique, and microhabitat, often differ among sites and could explain why some species establish and persist at some locations but not others (Guerrant 1996; Menges 2008; Godefroid et al. 2011; Albrecht & Maschinski 2012). For example, previous studies show that using larger founder sizes and propagule stages increased establishment and survival rates in rare plant reintroductions (Godefroid et al. 2011; Albrecht & Maschinski 2012; but see Liu et al. 2015); thus, founder population structure could potentially influence recruitment rates and persistence. Alternatively, failure to recruit offspring could simply reflect low habitat quality for seeds and seedlings. Because plant reintroductions often bypass early life-history stages by using ex situ grown transplants (Albrecht & Maschinski 2012), which often have a broader ecological niche than seeds or seedlings, reintroduction sites may support the survival of founder individuals but not next-generation seedlings (Young et al. 2005). Thus, identifying factors that influence seedling recruitment rates may help better predict the combinations of species traits and ecological contexts that might underlie long-term reintroduction success.

We explored how life-history traits and population characteristics influenced the probability and timing of seedling recruitment (i.e., recruitment time lag [RTL]) in an unusually well-monitored and long-term (4–28 years) data set on rare plant reintroductions. We focused on species traits with demonstrated implications for seedling recruitment, specifically traits related to life span, reproductive output, and factors known to influence recruitment limitation in plant populations, including those under control of restoration practitioners (initial founder size and propagule stage). We developed specific hypotheses on how these variables may influence RTLs (Table 1).

Table 1. Traits and population characteristics used to test for differences in recruitment time lags (RTLs) among reintroductions of rare plant species.

Trait or characteristic	*Relevance to seedling recruitment*	*Hypothesized difference in RTL*
Life history (life span and growth form)	life-history trade-offs: earlier maturation and greater reproductive output in fast relative to slow species (Salguero-Gómez et al. 2016); woody plants often have longer life spans relative to herbs (Ehrlén & Lehtilä 2002) and depend less on recruitment for population growth (Franco & Silvertown 2004)	slow woody > fast woody slow herb < slow woody slow herb > fast herb fast herb < fast woody fast herb < slow woody slow herb > fast woody
Mating system (selfers vs. outcrossers)	influences seed production and fecundity: self-compatible species less reproductively constrained in newly established populations (Baker 1955); obligate outcrossers more prone to pollination failure (Knight et al. 2005) and to mate and genetic limitations in reproduction than selfers (Busch & Schoen 2008)	selfers < outcrossers
Seed dispersal (short vs. long)	negative trade-offs of dispersal ability with local seedling recruitment (Eriksson 2000)	short < long
Seed production (low vs. high)	recruitment limited by seed availability: trade-offs in seed size and production means stronger seed producers produce smaller seeds with a greater chance of persisting in the soil and reaching safe sites (Westoby et al. 2002; Clark et al. 2007)	low > high
Adult shade tolerance (tolerant vs. intolerant)	disturbance-dependent species with light requirement often more seed limited than species without disturbance-dependent reproduction (Clark et al. 2007)	shade-tolerant adults < shade-intolerant adults
Initial founder size (continuous)	influences population survival, future densities, and ability to overcome effects of small population size (Guerrant 1996)	RTL decreases as founder size increases
Founder propagule stage (reproductive vs. nonreproductive)	determines rate of population growth and demographic processes (Guerrant 1996)	reproductive < nonreproductive
Reproductive adult abundance (continuous)	recruitment in plant populations limited by fecundity and reproductive output (Clark et al. 1998)	RTL decreases as reproductive adults increase
Habitat	delayed reproduction and lower total fecundity in grasslands and savannas relative to forests, deserts, and shrublands (Burns et al. 2010)	forests < savanna, shrubland, and scrub, ≤ grasslands, outcrops, and dune

Methods

Data Collection

To quantify RTLs, we used data in the Center for Plant Conservation International Reintroduction Registry (CPCIRR), which includes monitoring data for 145 rare plant reintroduction events mainly in North America (Guerrant 2012). We defined a reintroduction event as the outplanting of propagules of a rare plant species to a unique site over 1 or multiple years. To minimize spatial nonindependence among multiple reintroductions of the same species, we summed across experimental treatments within a site and confirmed with study authors whether multiple reintroduction sites were spatially independent. To minimize differences in methodology, we restricted our analysis to reintroductions conducted by conservation organizations in the Center for Plant Conservation network, which usually follow a common protocol (Falk et al. 1996; Maschinski et al. 2012). Because previous reviews focused largely on short-term (≤ 3 years) metrics of survival and fecundity (Godefroid et al. 2011), we focused on longer-term reintroductions and restricted the data set to reintroduced populations that had persisted ≥ 4 years and were confirmed extant as of 2012 (when data were collected); focal species that reached sexual maturity at the reintroduction site; and reintroductions that explicitly reported whether seedling recruitment occurred or not. In total, these selection criteria yielded 66 reintroduction events initiated from 1984 to 2007 that represented 27 plant species across a broad range of life forms and habitats (Supporting Information). Reintroduction events had an average time since outplanting of 10.45 years (SD 5.79); some were established over 20 years ago (e.g., *Potentilla robbinsiana* [Supporting Information]). A majority (91%) of cases were reintroductions (previously occupied sites) or introductions (previously unoccupied sites), whereas the remaining were augmentations. We included only augmentations in which the origin of seedlings could be differentiated between reintroduced individuals and existing plants at the site.

To model the probability and timing of seedling recruitment, we scored 2 outcomes for each reintroduction event: presence or absence of recruitment and, if recruitment occurred, the number of years between the year of first flowering (i.e., when sexual maturity was reached) and the first year seedling recruitment occurred. We used the 2 outcomes as the response variable for all subsequent survival analyses (see below), and the response variable consisted of a start time (i.e., the year of first flowering) and an event time (i.e., the first year seedling recruitment was observed, if it occurred). We refer to the time between year of first flowering and year seedlings were first observed as the *RTL*.

To determine how plant life histories and population characteristics influenced recruitment, we collected information on 9 predictor variables for each reintroduction (Table 1). We compiled information on the 5 species traits from online databases, CPCIRR, peer-reviewed and gray literature, and queries of species authorities (Supporting Information). Initially, we screened a large pool of plant reproductive traits (e.g., seed mass and seed-bank formation) to include in the data set, but data were either unavailable or unknown in a majority of cases. Because continuous trait values (e.g., life span) remain unknown for most rare plants (Schmidt et al. 2012), we collapsed traits into noncontinuous categories when necessary to avoid small sample sizes. To create a life-history trait, we combined growth form and life span by categorizing each species as herb or woody plant (including subshrubs, succulents, and suffrutescents) and as short-lived (≤ 5 years on average, fast species) or long-lived (>5 years on average, slow species). Population characteristics including initial founder size (total number of propagules outplanted at a site over time), founder propagule stage (reproductive vs. nonreproductive; the latter includes seeds), and reproductive adult abundance at last census were documented from the CPCIRR and supplemented by authors of the study when necessary. We also classified the reintroduction habitat type as open grassland, rock outcrop, or dune; savannah, shrubland, or scrub; or forest.

Data Analyses

To explore the influence of species traits, habitat, and population characteristics on RTL, we used a 2-step approach. We first parameterized a series of mixed-effects Cox regression models (hereafter COXMEs) separately for each of the 9 predictors (Table 1) with the *coxme* package in R (Therneau 2015). Second, to test whether interactions among traits, population characteristics, and habitat influenced RTLs, we used a nonparametric multivariate approach because small sample sizes and correlated predictors precluded testing for higher-order interactions with COXMEs.

We used the COXMEs to examine whether predictors increased or decreased the risk of seedling recruitment occurring over time. We assigned reintroductions that flowered but failed to recruit as right-censored observations because recruitment beyond the last observation year (2012) remains uncertain. For all COXMEs, we calculated the hazard ratios (95% CI), which represents the likelihood of seedling recruitment occurring per unit change in a continuous variable or how much more or less likely a reintroduced population is to experience seedling recruitment at a given level of a categorical variable.

In each COXME, we accounted for 2 potential sources of nonindependence: multiple reintroductions of the same species and phylogenetic relatedness. To account for a positive correlation among multiple reintroduction locations with the same species, we used species as a random intercept. To account for phylogenetic relatedness between species, we used a phylogenetic variance–covariance matrix (Supporting Information). Although our data set showed no phylogenetic signal, we report results from the correlated random effects models to account for nonindependence of species with multiple reintroductions and to minimize the influence of reintroductions with large deviations from the population average (Supporting Information).

To explore the combined relative importance and interaction of predictors on RTLs, in a second analysis, we used nonparametric tree-based methods. Unlike the COXMEs, tree-based methods lack distributional assumptions and minimize overfitting with small data sets and many predictors (Strobl et al. 2007; Strobl et al. 2008). To evaluate the combined relative importance of all predictors on time to recruitment, we implemented a random forest analysis in the R package *party* (Hothorn et al. 2006; Strobl et al. 2007; Strobl et al. 2008), which constructs a large number of conditional inference trees that predict relative importance of predictor variables with and without the variable in the model (Strobl et al. 2008). We calculated the relative variable importance by dividing each value by the maximum variable importance value (Cochran-Biederman et al. 2015). To explore higher-order interactions between the most important predictors, we created a single conditional inference tree (*party*) by using all observations in the data. Due to strong collinearity among the species traits (Supporting Information), we reduced the number of traits to orthogonal axes with multiple correspondence analysis (MCA) in the R package *FactoMineR* (Le et al. 2017). We used the first 3 MCA dimensions as predictors in all the above nonparametric tree-based analyses. These 3 MCA dimensions were uncorrelated and explained 70.3% of the cumulative variation in species traits. Mating system loaded moderately on MCA1 ($\eta^2 = 0.59$); seed production ($\eta^2 = 0.5$) and the life-form (herb vs. woody) component of life history ($\eta^2 = 0.69$) loaded on MCA2; and the life span (short- vs. long-lived) component of life history ($\eta^2 = 0.88$) loaded strongly on MCA3 (hereafter life span) (Supporting Information). All statistical analyses were performed in R 3.3.3 (R Development Core Team 2015).

Table 2. Time spans for rare plant reintroductions that achieved seedling recruitment at each level of 7 categorical predictors.

			Mean number of years to seedling recruitment since (SD)	
Factor	*Level*	*n*	*year of outplanting*	*year founders reached maturity*
Life history	slow herb	16	4.938 (2.081)	3.750 (2.295)
	slow woody	14	5.357 (4.326)	2.077 (2.871)
	fast herb	7	1.714 (1.254)	0.714 (1.254)
	fast woody	8	1.125 (0.354)	0.125 (0.354)
Mating system	outcrosser	16	4.875 (4.603)	1.69 (2.701)
	mixed	27	3.444 (2.470)	2.407 (2.469)
Light requirement	shade-tolerant adults	7	3.429 (2.258)	1.167 (0.983)
	shade-intolerant adults	38	3.974 (3.583)	2.263 (2.678)
Dispersal	long distance	9	4.000 (2.449)	2.625 (2.326)
	limited distance	36	3.861 (3.619)	2.000 (2.597)
Seed production	high	25	3.160 (2.392)	1.760 (2.047)
	low	20	4.800 (4.225)	2.579 (3.061)
Propagule stage	reproductive	13	3.385 (1.981)	2.385 (1.981)
	nonreproductive	32	4.094 (3.830)	2.000 (2.757)
Habitat	forest	8	2.889 (2.205)	1.000 (1.000)
	grassland, outcrop, dune	16	4.938 (2.081)	3.750 (2.295)
	savannah, shrubland, scrub	21	3.381 (4.353)	1.238 (2.488)

Results

Of the 66 reintroduced populations in our data set, 45 had seedling recruitment; RTLs varied widely among species, locations, and traits (Table 2). Across all 66 reintroductions, time to recruitment ranged from <1 to 17 years after outplanting with an average time of 3.89 years (SD 3.39). For those reintroductions that flowered but had yet to recruit offspring (*n* = 21), they were on average outplanted 8.75 years ago (SD 5.94). In reintroductions with offspring recruitment, RTLs averaged 2.08 years (SD 2.51). There were lags up to 10 years in some species. Of the 22 species that attained recruitment after reaching reproductive maturity, 73% (*n* = 16) exhibited RTLs ≤1 year in at least 1 reintroduction event; half of these involved slow species. In contrast, only 2 fast species exhibited RTLs >1 year once founders reached reproductive maturity, and only 1 short-lived species failed to recruit offspring after 4 years. Overall, slow species exhibited greater variation in RTLs than fast species (Fig. 1); maximum observed RTLs for slow species were over 3 times longer than in fast species (3 years). For species (*n* = 7) with ≥3 reintroduction events, RTLs varied widely among locations, especially for slow species (Fig. 1).

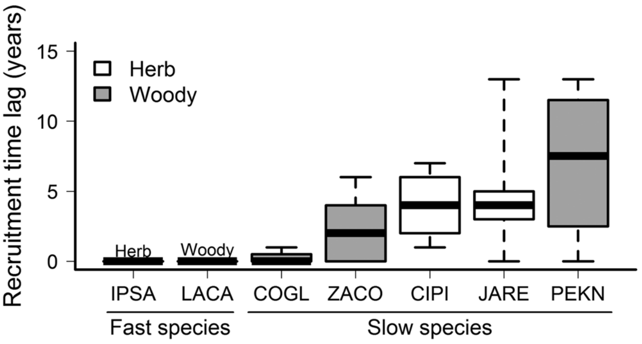

Figure 1. Variation in recruitment time lags in rare plants with multiple (≥3) reintroduction events (bars, maximum and minimum; dashed lines, 25th and 75th percentiles; middle line, median; IPSA, Ipomopsis sancti-spiritus, n = *3; LACA, Lantana canescens,* n = *3; COGL, Conradina glabra,* n = *3; ZACO, Zanthoxylum coriaceum,* n = *5; CIPI, Cirsium pitcheri,* n = *4; JARE, Jacquemontia reclinata,* n = *13; PEKN, Pediocactus knowltonii,* n = *4).*

In the single-predictor COXMEs, reintroductions with greater founder sizes and reproductive adult abundances had increased likelihood of recruitment (Fig. 2a). Although 27% of reintroductions were founded with reproductively mature transplants, propagule stage did not significantly (*p* = 0.41) influence RTLs (Fig. 2a). Reproductive traits that significantly (all *p* values <0.05) influenced RTLs include life history, dispersal ability, mating system, and seed production. Overall, short life spans, self-compatible mating systems, localized seed dispersal, and high seed production reduced RTLs (Figs. 2b & 2c). On average, recruitment took >3 years longer after outplanting in slow relative to fast species (Table 2). Slow herbs experienced significantly longer RTLs than fast herbs (*p* = 0.01) and fast woody plants (*p* < 0.0001) (Fig. 2b). In contrast, slow herbs and slow woodies had similar RTLs (*p* = 0.34) (Fig. 2b). Among woody plants, slow species exhibited significantly longer RTLs than fast species (*p* < 0.01). Habitat also significantly (*p* < 0.0001) influenced RTLs (Fig. 2d). Grasslands, outcrops, or dunes species, which were entirely comprised of slow herbs, took on average 2 years longer to recruit seedlings relative to other habitats (Table 2).

Figure 2. Hazard ratios from single-predictor mixed-effects Cox regression models showing the effects of (a) population characteristics, (b) life history, (c) reproductive traits, and (d) habitat on recruitment time lags in rare plant reintroductions. Hazard ratio >1 indicates the baseline category has a greater likelihood of recruitment (i.e., shorter recruitment lag times) or, in the case of a continuous variable, the likelihood of recruitment increases with each unit change in the predictor variable (vice versa for a hazard ratio <1) (${}^{*}p < 0.05$, ${}^{**}p < 0.01$, ${}^{***}p < 0.001$). For multiple comparisons among life-history levels, p-value adjustments were made with the Tukey method.

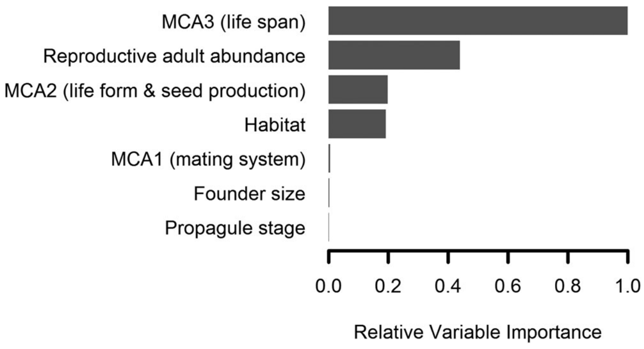

Figure 3. Relative importance of variables on recruitment time lags based on random forest analysis. Species traits were reduced to 3 independent dimensions with multiple correspondence analysis (MCA) to minimize collinearity among predictors.

Life span (MCA3), reproductive adult abundance, and life-form and seed production axes (MCA2) ranked as the top 3 most important predictors of RTL, respectively (Fig 3). Other significant predictors (e.g., dispersal ability and initial founder size) in single-predictor models were relatively less important in the presence of other predictors (Fig 3). The conditional inference tree analysis illustrates interactions and pathways that lead to different RTLs (Fig. 4). The most important primary split in the conditional inference tree occurred with reproductive adult abundance at last census. Reintroductions with <24 adults at last census had longer RTLs relative to those with >24 reproductive adults. Each branch was then further split by species life span; fast species experienced shorter RTLs than slow species on both branches.

Discussion

Restoring persistent populations that are resilient to environmental change will require understanding the factors that influence demographic processes beyond population establishment. By quantifying the timing and drivers of recruitment from founder individuals, rather than just their short-term survival and fecundity, we have explored a very relevant measure of reintroduction success and presented realistic timescales for setting demographic benchmarks. Using data on rare plant reintroductions across an array of habitats, life histories, and restoration techniques, we observed substantial variation (ranging from <1 to over 17 years after outplanting) in RTLs and detected significant effects of life-history variation and population characteristics on RTLs. These trends were consistent across multiple analyses with a relatively small data set.

Extending plant life-history theory to rare plant reintroductions, we predicted recruitment rates would correlate with life span (Table 1). At one end of the life-span continuum, we observed consistently fast recruitment times (≤1 year) across short-lived species,

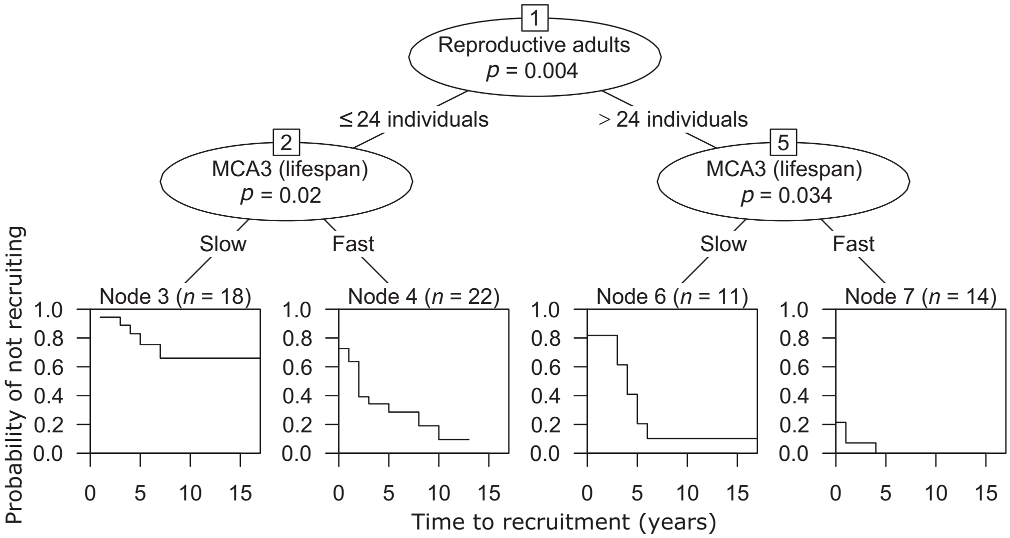

*Figure 4. Interactive effect between the 2 most important predictors (reproductive adult abundance and life span) of recruitment time lags in rare plant reintroductions. From the top (node 1), the tree shows reproductive adult abundance is the predictor with the strongest association with time to recruitment and makes a binary split of observations based on a threshold number of reproductive adults observed at last census. Axis 3 (life span) from the MCA (multiple correspondence analysis) is the predictor with the strongest association with time to recruitment in both nodes along this split (nodes 2 and 5). These splits then produce 4 nodes spanning a time-to-recruitment continuum (range: delayed recruitment [>15 years] at node 3 to accelerated recruitment [<4 years] at node 7) (*n*, number of reintroduction events in each terminal node).*

which allocate a greater proportion of resources toward growth and reproduction, maintain short prereproductive periods, and can rapidly recruit offspring when environmental conditions are suitable (Franco & Silvertown 2004; Salguero-Gómez et al. 2016). Although short-lived plants frequently delay germination and form persistent soil seed banks until environmental conditions become favorable (Rees 1997; Venable 2007; but see Ehrlén & Lehtilä 2002), once founders reached reproductive maturity, recruitment lags of >1 year seldom occurred, suggesting environments were favorable for population growth and recruitment in the reintroductions we considered. In contrast, the variable and delayed offspring recruitment observed in reintroductions of slow species was consistent with their life-history strategy of maintaining long prereproductive periods and spreading reproduction over many years (Franco & Silvertown 1996; Salguero-Gómez et al. 2016).

Short-lived plants are predicted to have greater sexual reproduction rates than longer-lived species (García et al. 2008; Salguero-Gómez et al. 2016), and this can be partly determined by differences in their reproductive traits. For example, self-compatibility should be more frequent in short-lived species because it ensures high seed production and reduces the risk of reproductive failure (Ehrlén & Lehtilä 2002). In our study, however, mating system was relatively less important in explaining patterns of recruitment among opposing life spans because short-lived species were approximately evenly represented by herbaceous and woody growth forms (mostly suffrutescents) and consisted of species with highly variable mating systems and seed production rates. Alternatively, the consistently short RTLs in fast species could be linked to the population dynamics expressed in certain combinations of habitat types and growth forms (Salguero-Gómez 2016; Salguero-Gómez et al. 2016). In our data set, most short-lived species were heliophytes of pyrogenic subtropical shrublands or savannas, where reintroductions are often coupled with habitat restoration, such as prescribed fire and exotic species or woody encroachment removal (Possley et al. 2008; Peterson et al. 2013). These postdisturbance environments are known to promote high growth rates and seedling recruitment in short-lived species and species dependent on high light levels (Menges & Quintana-Ascencio 2004). The short-lived species represented in our sample were also predominantly reintroduced as seedlings rather than seeds, which may have allowed them to grow more rapidly and produce greater numbers of offspring despite small founder sizes and unstable stage structures relative to longer-lived, slow-growing species (Guerrant 1996; Deredec & Courchamp 2007; Iles et al. 2016). Additional research on short-lived species in arid and grassland systems, which were poorly represented in our data set, could shed more light on the importance of habitat on RTL.

Longer recruitment lags are expected in woodies relative to herbaceous perennials due to their generally longer life spans and delays in reproductive maturity (Table 1). On the one hand, long-lived woodies, such as the subtropical palm *Pseudophoenix sargenti* (Maschinski & Duquesnel 2007), represented a majority (83%) of the reintroductions studied, where delayed sexual maturity precluded offspring recruitment. On the other hand, once founders reached maturity, growth form alone did not accurately predict RTLs, perhaps because plant life histories vary along 2 independent axes (fast–slow continuum and reproductive strategy), which when considered jointly, shows that species with different growth forms can have similar life-history strategies and population dynamics (Salguero-Gómez 2016; Salguero-Gómez et al. 2016). For example, the short-lived subtropical suffrutescents (*Chrysopsis floridana* and *Dicerandra immaculata*) recruited seedlings within the first year after reintroduction (Peterson et al. 2013), similar to reintroductions with annuals and other short-lived herbs. High recruitment rates in these subtropical woodies might, in part, reflect their generally greater rates of iteroparity and net reproduction relative to temperate herbs, especially geophytes (Salguero-Gómez 2016; Salguero-Gómez et al. 2016), which represented a majority of the long-lived herbaceous species in our data set and exhibited much longer RTLs than short-lived woodies. In fact, we observed the longest RTLs in long-lived succulents from arid habitats and perennial herbs of dunes and grasslands, such as *Asclepias meadii*, a rare obligate-outcrossing herb that has yet to recruit offspring nearly 2 decades after reaching reproductive maturity (Bowles et al. 2015). In grassland plants, in particular, trade-offs between delayed reproduction and survival can be correlated with lower lifetime fecundity (Burns et al. 2010), which is consistent with the lower recruitment rates we observed in grassland reintroductions compared with other habitats.

Unlike the consistently short RTLs in fast species, within-species recruitment patterns were highly variable in some longer-lived species. Long-lived species are expected to have low demographic resilience following perturbations (Salguero-Gómez 2016), and several species with variable RTLs were reintroduced to highly stochastic environments, which increases variation in demographic vital rates and population growth (Buckley et al. 2010). For example, population dynamics in the dune-endemic and semelparous perennial herb, *Circium pitcherii*, fluctuate widely across wind-driven successional gradients (Bell et al. 2003), whereas populations of the coastal dune endemic and iteroparous perennial herb, *Jacquemontia reclinata*, are periodically affected by hurricanes (Maschinski et al. 2013). Although our data set was too limited to determine the causes of within-species variation, the large variation in recruitment lags suggests local processes (e.g., competition, herbivory, and disturbance) are just as important as traits and other factors on recruitment. In turn, this may be one reason why founder size and propagule stage were less powerful predictors of recruitment than reproductive adult abundance, which better reflects the suitability of a reintroduction location to support population growth. Indeed, models predict that using larger founder sizes does not increase population viability of reintroductions to low-quality habitat (Knight 2012). Collectively, these results emphasize the importance of using multiple sites and attempts over time to increase the chances that reintroductions occur in locations where a species can maintain high demographic vital rates (Maschinski & Quintana-Ascencio 2016).

Along with variation in plant life histories, seed limitation could limit recruitment if low reproductive adult abundance, mating system, or poor seed production constrains seed availability at reintroduction sites (Young et al. 2005). At low reproductive densities, Allee effects, pollen limitation, or lack of compatible mates can reduce seed production (Table 1), which might potentially delay seedling recruitment by reducing chances that seeds saturate safe sites. Although generally species that were poor seed producers or self-incompatible exhibited longer RTLs than species with high seed production or self-compatibility, respectively, the relative importance of these traits diminished after accounting for life span and reproductive adult abundance, which remained strong predictors in the presence of other variables. These results align with the expectation that increasing population size also increases fitness regardless of life history (Leimu et al. 2006) and suggest that seed limitation caused by low abundance of reproductive adults could represent a fundamental constraint on seedling recruitment in plant reintroductions.

Our synthesis of long-term studies (≥4 years since installation) offers some general lessons for improving reintroduction practice. First, understanding a species life-history strategy can help predict population performance in reintroductions and set appropriate benchmarks. Second, although our data set represents only a subsample of possible traits and life-history combinations, species traits alone are unlikely to explain patterns in reintroduction success. Instead, reintroduction outcomes result from a complex interaction between life-history traits, population characteristics, and habitat. Third, understanding the environmental drivers of population growth and increasing reproductive densities could benefit reintroduction success. Rapid growth and reproduction are key traits for overcoming demographic barriers in recently established populations (Burns et al. 2013; Iles et al. 2016), and poor-quality habitat is considered the leading cause of low success rates in plant reintroductions (Godefroid et al. 2011). Finally, best-practice guidelines advocate that monitoring programs be conceptualized across a series of developmental stages from establishment to persistence, but do not explicitly incorporate how life-history or demographic parameters influence the expected timing of restoration outcomes (Maschinski et al. 2012; IUCN/SSC

2013). Our results emphasize the importance of accounting for time scales and life-history strategies when setting benchmarks across these different stages. Given that delays in reproductive maturity and RTLs often exceed typical monitoring periods reported in the literature, perspectives on reintroduction success could improve over time as demographic processes unfold in longer-lived species.

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Supporting Information

Summary of 66 reintroduction events that satisfied study selection criteria (Appendix S1), description of predictor variables for recruitment time lag analysis (Appendix S2), methods for generating phylogeny of 27 species in 66 reintroduction events with populations that reached sexual maturity (Appendix S3), supplemental methods for comparing fits of models with and without random effects (Appendix S4), association tests between predictor variables (Appendix S5), and multiple correspondence analysis (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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