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RESEARCH ARTICLE

Comparison of reintroduction and enhancement effects on metapopulation viability

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Metapopulation viability depends upon a balance of extinction and colonization of local habitats by a species. Mechanisms that can affect this balance include physical characteristics related to natural processes (e.g. succession) as well as anthropogenic actions. Plant restorations can help to produce favorable metapopulation dynamics and consequently increase viability; however, to date no studies confirm this is true. Population viability analysis (PVA) allows for the use of empirical data to generate theoretical future projections in the form of median time to extinction and probability of extinction. In turn, PVAs can inform and aid the development of conservation, recovery, and management plans. Pitcher's thistle (*Cirsium pitcheri*) is a dune endemic that exhibited metapopulation dynamics. We projected viability of three natural and two restored populations with demographic data spanning 15–23 years to determine the degree the addition of reintroduced population affects metapopulation viability. The models were validated by comparing observed and projected abundances and adjusting parameters associated with demographic and environmental stochasticity to improve model performance. Our chosen model correctly predicted yearly population abundance for 60% of the population-years. Using that model, 50-year projections showed that the addition of reintroductions increases metapopulation viability. The reintroduction that simulated population performance in early-successional habitats had the maximum benefit. In situ enhancements of existing populations proved to be equally effective. This study shows that restorations can facilitate and improve metapopulation viability of species dependent on metapopulation dynamics for survival with long-term persistence of *C. pitcheri* in Indiana likely to depend on continued active management.

Key words: active management, metapopulation dynamics, model validation, pitcher's thistle, probability of extinction, restoration

Implications for Practice

- Early successional habitat would be the better choice when attempting to restore a population of *Cirsium pitcheri*.
- Largest increase in viability occurs with the first few introductions.
- Effort might be better spent improving, protecting and increasing growth of the populations already established.
- Use of on-site seed-production nurseries to propagate seeds might be the best strategy to enhance and expand existing struggling populations.
- Management will always be needed to replace the colonization functions in a metapopulation whose habitat connectivity is now lost until it can be restored.

Introduction

Metapopulations are collections of local populations separated by gaps in habitats, characterized by immigration and emigration of individuals among populations as well the extirpation of local populations balanced with colonization of unoccupied habitat. The persistence of a metapopulation depends on three factors: colonization rates must equal or exceed extinction rates, local events must happen independently, and there must be spatial variation in demographic processes (Goodman 1987). In metapopulations, the regional presence of a species is facilitated by landscape processes (e.g. disturbance events) that are linked with population dynamics which create malleable mosaics of both suitable and unfavorable habitats (Hanski 1994). As long as there is a balance of extinction and colonization of local populations, metapopulations remain viable. However, many plant populations are threatened by human-caused factors that can interfere with metapopulation processes, such as removal of potential habitat, which can alter migration rates through space and time (McEachern et al. 1994). The few metapopulation empirical studies we found dedicated to plants (e.g. Laine & Hanski 2006; Dornier et al. 2011; Alexander et al. 2012)

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were structured as spatially explicit models estimating colonization and extinction rates from measurements of area, isolation, and occupancy in order to make predictions about the persistence of a system of subpopulations (Brigham & Thomson 2003). Our search yielded no results of papers that reported plant reintroductions as a means to improve the metapopulation viability.

The reintroduction of rare plant species is gaining momentum as there are increasing numbers of long-term datasets to guide the design of quantitative analyses (Menges & Kennedy 2007; Pavlovic & Grundel 2009; Thorpe & Kaye 2011). With increasing longevity of reintroductions, conservation biologists are now able to evaluate successes in relation to conservation management goals. Within metapopulations, introductions or reintroductions that increase the number of populations should serve to produce favorable dynamics (Menges 2008). Previous studies (Kirchner et al. 2006; Brown et al. 2008) speculate that the addition of populations may improve metapopulation's viability; however, we found no empirical studies to confirm that this is true. Similarly, enhancements that improve growth rates in existing populations may increase metapopulation longevity. Restorations are often used as the last resort to bolster biological diversity (White 1996), and population viability when habitat protections and other management strategies fail. For a species with metapopulation dynamics, using a metapopulation approach in restorations may prove to be an effective method for improving long-term persistence. Population viability analysis (PVA) can be a useful planning tool (Menges 2008) for choosing the type and extent of a restoration project, especially when resources such as time, money, propagules, and habitat availability are limited.

PVA has long contributed to the science of demographic analysis (Bell et al. 2003). The most common approach to plant PVA is through the use of matrix models to represent population dynamics and create graphical representations of current and future trends in the population growth rate (λ) (Damman & Cain 1998; Maschinski et al. 2006; Garcia 2008). With matrix models, it is possible to estimate viability measures such as median time to extinction (MTE) and probability of extinction at time ($p_0(t)$) (Groom & Pascual 1998; Pe'er et al. 2013). Demographic monitoring makes it possible to assess fates of individuals in a population from emergence to death and use the results to develop conservation, recovery, and management strategies (Caswell 2001). Crone et al. (2011) identified over 400 published studies that used matrix models to guide the understanding and management of plant populations through the assessment of local population status and extinction risk. To date, no studies have modeled the effect of restorations on viability within a metapopulation context.

In this study, we evaluated the impact that restorations have had on metapopulation viability. We used *Cirsium pitcheri* (Pitcher's thistle [Eaton] Torrey and Gray, Asteraceae) as our model species because it exhibits metapopulation dynamics (McEachern 1992). We used a high-quality 23-year demographic dataset with detailed observations of each plant (Ellis et al. 2012) in both native and reintroduced populations at the southern tip of Lake Michigan in Indiana. First we evaluated which model parameters accurately portrayed the local population dynamics, comparing projected population sizes with observed. Second we used the most accurate model to project 50 years into the future to determine *C. pitcheri* regional viability in Indiana with and without reintroductions into habitats of different successional stages. Because *C. pitcheri* colonizes open dune habitats, we expected the early-successional reintroduction to lead to a greater increase in regional viability. Finally, we addressed management questions regarding the number and type of restorations necessary to reduce extinction risk for 50 years. We chose to follow the DAC-PVA protocol in an effort to provide a comprehensive reporting of our model design concepts (Pe'er et al. 2013).

Methods

Organism

Cirsium pitcheri is a federal threatened dune thistle inhabiting intermittently stable beach and grassland dunes of the western Great Lakes shorelines (Harrison 1988). Although *C. pitcheri* colonizes open spaces, it persists and declines slowly as vegetation closes in, inhabiting a variety of successional stages within the highly dynamic dune systems (McEachern 1992). This monocarpic species has a mixed mating system, and depends on the seed production of a single lifetime flowering episode for population growth. Plants generally remain in the juvenile, pre-reproductive stage for 4–8 years, making long-term protection of habitats and plants from disturbance especially critical for population growth. Fecundity is greatly affected by seed predation and herbivory from native and introduced insect enemies (Bevill et al. 1999; Havens et al. 2012). *Cirsium pitcheri* is dependent on periodic landscape disturbances related to fluctuating lake levels to maintain a mosaic of open habitats on beaches and dunes (McEachern 1992). Dispersal is generally via individual seeds that fall within 1 m of the parent plant. However, they can occasionally disperse several meters when entire seed heads blow and roll with the wind, or when seeds are carried by birds. *Cirsium pitcheri* has a size-stage population structure with seedlings (first year), juveniles and flowering adults. Root crown diameter is significantly correlated with growth and survival (McEachern 1992) and was used to divide juveniles into three size classes (Moloney 1986). A fourth pre-flowering class was indicated by the threshold size with the greatest probability of flowering the following year (Table S1, Supporting Information). The six stage-size classes are as follows: S (seedlings), J1 (small juvenile), J2 (medium juvenile), J3 (large juvenile), J4 (pre-flowering) and A (flowering) (Fig. 1).

Study System

The study populations are located along the southern tip of Lake Michigan in the Indiana Dunes National Lakeshore and Indiana Dunes State Park near Porter, Indiana (Fig. S2). This is a system of narrow linear dunes that stretch along the beach for about 35 km at the southern tip of Lake Michigan, interconnecting a

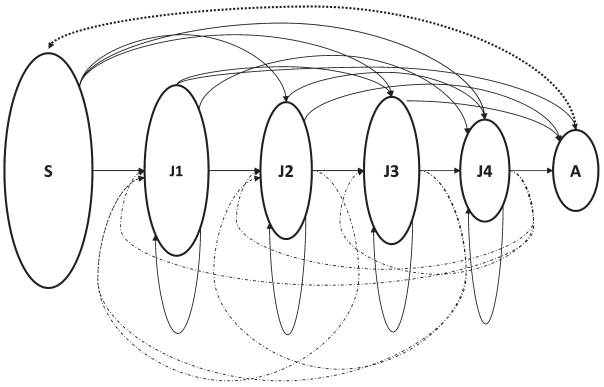

Figure 1. Life cycle diagram of the Indiana Dunes *Cirsium pitcheri* pooled over five populations. Arrows indicate direction of transitions. Size of ellipses is an indication of the relative abundance of plants in each stage, S (seedlings), J1 (small juvenile), J2 (medium juvenile), J3 (large juvenile), J4 (pre-flowering), and A (flowering).

system of large blowouts where wind has pushed sand inland to form isolated dune fields surrounded by forest. The beach dunes are only intermittently available, eroding away about every 60 years during climate-driven high stands of Lake Michigan (Larsen 1985; Thompson 1989) and rebuilding again as lake levels recede. The massive blowouts, separated by distances averaging 3.3 ± 1.3 km (median of 3 km), extend inland as much as 1 km and are maintained as a mosaic of open grassland habitat by persistent northwest winds.

Historically, *C. pitcheri* inhabited the blowouts and the intermittent linear dunes that connected them. During low lake levels, beach foredunes formed and were colonized by dispersal from blowout populations, allowing beach populations to function as periodic conduits for gene flow among blowouts. With urban, recreational and industrial development beginning in the mid-1800s (Moore 1959), dispersal pathways along the beach were cut off, blocking natural colonization that drove *C. pitcheri* metapopulation dynamics in the past. Hence, metapopulation functions allowing gene flow and rejuvenation of blowout populations from foredunes no longer exist and must be replaced by management actions.

Field Methods

This study used demographic data from three native populations in different stages of dune succession (sensu Cowles 1899; Olson 1958), one each from State Park Big Blowout, Miller High Dunes, and West Beach as well as two reintroduced populations at Ogden Dunes. A single 1000 m^2 fixed demographic monitoring plot was created at each native site in 1988 (McEachern 1992) with succession stage calculated as the weight ratio of cover of three beach grasses characteristic of early, mid- and late-successional sites. In 1994, *C. pitcheri* seeds were planted in two reintroduction sites using methods of both broadcasting and burial at 1 cm deep, at Ogden Dunes East (150 m^2) and Ogden Dunes West (225 m^2), respectively (U.S. Fish and Wildlife Service 2002). In our choice of restoration sites, we sought places that varied in successional stages and were infrequently visited by visitors to Indiana Dunes National Lakeshore. At each site we identified and tagged each *C. pitcheri* plant, recording location, survival, root crown diameter, and stage class (flowering plant, juvenile, or seedling). The native populations were sampled annually from 1988 through 2012, except in 1997–1998. The reintroduction populations were sampled annually from 1999 to 2012. Generally, the native populations were not manipulated in any way for recovery. However, in 2009 we bagged seed heads at Miller and Big Blowout to protect them from American goldfinch (*Spinus tristis*) predation for the growing season, then un-bagged and planted their seeds directly within a meter of the parent plant at the end of the growing season.

Modeling Approach

We evaluated whether regional metapopulation viability is improved through the addition of one to two reintroduced populations. We evaluated alternative population models (Brook et al. 2000) for each of the five populations and chose the model with the best predictive accuracy by comparing observed and predicted population abundances based on both quantitative estimates of mean square error (MSE) and theoretical assumptions of the species population dynamics (Crone et al. 2011). Using the model with the best predictive accuracy, we determined the degree to which the addition of reintroduced populations increased metapopulation persistence. The native populations alone were used as a baseline scenario and compared with scenarios including both actual and simulated reintroductions. Local occupancy of populations was used to estimate extinction risk and time to extinction. We also evaluated future management implications of population enhancement with varying numbers of seeds. We modeled metapopulation viability using RAMAS Metapop *v4.0* (Akcakaya 2002), which simulates a metapopulation's future growth or risk of decline.

Model Construction

Density Dependence. Density-dependent mortality occurs when limits on resources based on the density of the affected population are the cause of changes in individual performance and population growth rates (Morris & Doak 2002). In the Indiana *C. pitcheri* populations, there is no density dependence because the populations are not large enough (<200) and are not growing fast enough to be limited by environmental resources (Girdler & Radtke 2006).

Environmental Stochasticity. Environmental stochasticity is modeled by random fluctuations in stage-specific fecundity, survival, or carrying capacity (F, S, K), which can change population demographic characteristics in an unpredictable fashion. RAMAS Metapop replaces the constant parameters of F, S, K with random variables, which are estimated from the mean and standard deviation of past observations. RAMAS allows for either normal or lognormal distributions; the latter can be used to prevent truncation of the vital rates that could

have resulted in either over or underestimations of the extinction risks (Akcakaya 2002).

Demographic Stochasticity. We observed annual variation in the number of individuals and population growth rates even when the vital rates remained constant. To account for this we included demographic stochasticity by allowing the model to sample survivors from a binomial distribution and the number of offspring from a Poisson distribution (Akcakaya 1991).

Movement and Dispersal. We did not include dispersal among populations as part of our model because dispersal between these populations is unlikely to occur within the time frame of our model. The beach dunes and blowouts are so interrupted by development and recreational use that dispersal along the beaches and into blowouts is unlikely. Further, we do not include the colonization of unoccupied habitat because in more than two decades we have observed only two colonization events on a newly formed beach dune from an inland population; however, this has not resulted in established populations. Roads, towns, and steel mills have blocked longer distance dispersal between the nearest blowouts. Instead, the addition of reintroduced populations to the model simulated the colonization of new populations within the metapopulation context.

Model Application

Matrix Creation. Using demographic monitoring data, we followed Caswell (2001) and created yearly population projection matrices 1988–2012 ($n = 22$) for each of the native population and 1999–2012 ($n = 13$) reintroduction populations. The matrix A is a function of the size classes (n) where n is a vector of size class abundances for the time interval of 1 year (t) (Equation 1).

$$n(t+1) = \mathrm{An}(t) \tag{1}$$

Matrix elements (a_{ij}) are defined as the transitions from size class j to size class i during a 1-year interval (Table 1), where transition frequency values vary between 0 and 1. We calculated the deterministic population growth rate (λ) as the dominant eigenvalue (Caswell 2001) for each projection matrix and conducted an analysis of variance (ANOVA) in to order to determine differences between the mean population growth rates.

Initialization and Input Data. The model required mean and standard deviation (SD) matrices, initial abundances, and stage distributions for each population. Each population was initially occupied with the number of individuals and abundance distribution of the six stages in accordance with the actual field observation data collected during the year projections started. We utilized constraints, as the transition frequencies of each matrix column are percentages so as not to exceed 1. We also specified the number of replications, time steps and extinction threshold.

Model Outputs. RAMAS Metapop gives deterministic measures such as population size (N) and finite rate of increase (λ). We were also able to extract stochastic measures that incorporate variability such as the distribution of extinction times and cumulative probability of extinction with standard deviations and 95% confidence intervals (Akcakaya 2002). The outputs of comparison were $p_{0.05}(t)$, the time at which the probability of extinction reaches the 5% acceptable level of extinction risk, and metapopulation median time to extinction ($\mathrm{MTE}_{(\mathrm{M})}$) (Thompson 1991).

Parameterization, Calibration, and Validation. The data used to parameterize the model in the calibration and validation phases included mean and SD matrices created from 6 years (2000–2006) of data for each of the five populations. We used 1,000 replications and projected 6 years into the future. In order to determine the best model, we compared the observed population abundance for the years 2007–2012 to the projected abundances. We used MSE of the 30 observed and projected values (five populations and 6 years) to determine the "best fit model" of 12 models for the entire metapopulation based on the varying parameter combinations. MSE is essentially the mean of the squared differences between the projected and observed population abundance. Because most of the 12 models did not differ significantly from each other in MSE based on 95% confidence intervals (Fig. S2), we chose the parameters for the projection model that best fit our understanding of the population dynamics of *C. pitcheri* (McEachern 1992; Bowles et al. 1993; McEachern et al. 1994). The projection model included the following parameters: demographic stochasticity, lognormal distribution of environmental stochasticity, uncorrelated fluctuations among populations and uncorrelated fecundity, survival and carrying capacity. This model did not include density dependence, catastrophes, migration, dispersal, or management actions.

Projections. RAMAS Metapop predicts population trends based on the assumption that the observation period is similar to the future period in terms of vital rates (Crone et al. 2013). We used all 23 (native) and 14 (reintroduced) years of demographic data to construct mean and SD matrices and projected 50 years in to the future, assuming no changes in the habitat or land use during the projection period as the managing agencies have committed to the current level of dune conservation in perpetuity. We used a quasi-extinction level of zero, with initial abundance equivalent to 2012 observed abundances. We compared the baseline scenario (native population only) to models with the addition of the reintroduced populations to determine the extent to which reintroduced populations affect viability. Subsequent management scenarios were simulated. We first simulated the addition of up to 100 reintroduced populations based on matrices created from data of the two field reintroductions to determine the number of populations of a particular succession type needed to reduce metapopulation extinction probability to less than 5% for 50 years. Second, we simulated the addition of 450–1800 seeds (enhancements) to existing populations to evaluate the effect a one-time enhancement would have on current populations and metapopulation viability.

Table 1. Projection matrix of possible transitions of *Cirsium pitcheri* stage-size classes where matrix elements[a] (a_{ij}) are defined as the probability of surviving and growing to the next size class (G_{ij}), the probability of surviving and staying in the same size class (S_{ij}), the probability of surviving and regressing to a small size class (R_{ij}) and fecundity (F_{ij}).

	T					
$t+1$	*S*	*J1*	*J2*	*J3*	*J4*	*A*
S	0	0	0	0	0	F_{16}
J1	G_{21}	S_{22}	R_{23}	R_{24}	R_{25}	0
J2	G_{31}	G_{32}	S_{33}	R_{34}	R_{35}	0
J3	G_{41}	G_{42}	G_{43}	S_{44}	R_{45}	0
J4	G_{51}	G_{52}	G_{53}	G_{54}	S_{55}	0
A	G_{61}	G_{62}	G_{63}	G_{64}	G_{65}	0

A, flowering; J1, small juvenile; J2, medium juvenile; J3, large juvenile; J4, pre-flowering, S, seedlings.
[a] j is the current year t and i is the year $t+1$.

Results

Local Population Model Validation

The model version chosen for projection had a MSE of 2,629 and based on 95% confidence intervals was not significantly different from nine of the other models. MSE of the two remaining models ranged from 10,000 to 32,000 (S3), differing significantly from the chosen model. Population projection trends from 2007 to 2012 for the chosen model tended to follow the same trajectory as the observed abundances (Fig. 2). Miller High Dunes, Ogden Dunes East, and Ogden Dunes West abundances fell within the 95% confidence intervals for 88% of the years. However, State Park Big Blowout and West Beach projections were significantly lower than the observed abundances for 80% of the years. Observed abundances fell within the maximum projected simulation abundance values for all of the years of West Beach and the first 3 years of State Park Big Blowout.

The growth rates (λ) of the five *Cirsium pitcheri* populations (Table 2) varied from year to year and differed significantly between the populations ($F_{[4,80]} = 5.903$, $p = 0.000$). Miller High Dunes was the only population with a pooled λ greater than 1.0. The two introduced populations hovered slightly below 1.0, while West Beach and Big Blowout showed much lower pooled λ over all 23 years. In agreement with population growth rates, we found that Miller High Dunes had the highest MTE whereas State Park Big Blowout had the lowest MTE.

Metapopulation Viability Model

The $MTE_{(M)}$ predicted by the metapopulation model baseline using three native populations was 15.6 years (Table 2). The addition of mid-successional Ogden Dunes West to the baseline management scenario of the three native populations resulted in an increase in $MTE_{(M)}$ of approximately 0.4 years. In comparison, the addition of early-successional Ogden Dunes East, resulted in an increase in $MTE_{(M)}$ of approximately 2.7 years. The current management scenario including all five populations (three native and two reintroductions) has increased $MTE_{(M)}$ 3 years. We found that alternative scenarios that increased the number of populations in the metapopulation increased the number of years the probability of extinction remained below the threshold of 5%. Introductions to early-successional habitats showed a more gradual increase compared to mid-successional habitats (Fig. 3). Enhancement of any of the five populations individually, with 450–1800 seeds also increased overall Indiana Dunes $MTE_{(M)}$ and $p_{0.05}(t)$ compared with the native-only baseline scenario. With the exception of State Park Big Blowout, such enhancements also increased overall Indiana Dunes $MTE_{(M)}$ and more than doubled $p_{0.05}(t)$ over the model including native and restored populations.

Discussion

For three of the five populations, our models predicted abundances throughout the forecast period with a high degree of confidence. For State Park Big Blowout, we attribute the lack of accurate prediction capability to small population size coupled with a short parameterization period (2000–2006). Additionally, in 2009 we bagged mature seed heads to prevent goldfinch predation in mid-summer, and then harvested and planted the seeds within a 1 m radius of the parent plant in late summer which accounts for the big increase in observed abundance at Big Blowout. At West Beach there was a high amount of foot traffic in the early years that declined after establishment of a signed trail system in 2003. These provide good examples of how potential source errors can be related to inaccurate matrix projections as well as the importance of the assumption that parameterization years must be similar to projection years (Coulson et al. 2001). We are confident that using all 23 (native) and 14 (reintroduced) years of data in our final model improves the ability of our model to accurately project metapopulation viability.

In highly fragmented or disturbed systems, reintroductions can simulate colonization events and increase metapopulation persistence (Menges 2008). Our results confirm that successfully established reintroductions can increase the viability of a metapopulation. Additionally, this study shows that enhancement of existing populations, effectively increasing local fecundity, can extend projected length of metapopulation persistence by as many or more years as reintroductions. In landscapes managed for holistic recovery, both of these actions could give a metapopulation more time and opportunity to successfully

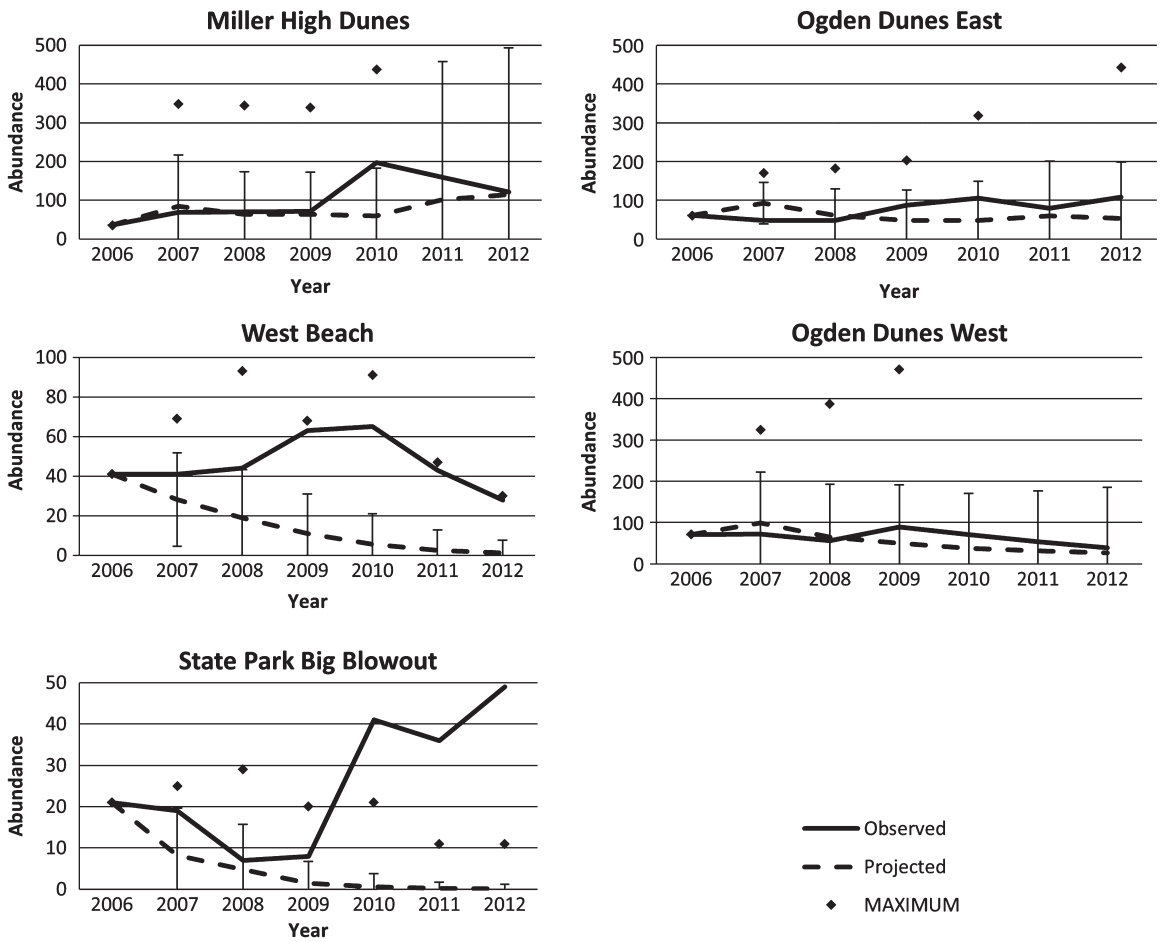

Figure 2. Observed versus projected abundances for five populations in the Indiana Dunes *Cirsium pitcheri* metapopulation with projected 95% CI of mean and maximum values at each time step. Maximum values not shown exceed axis range.

reestablish colonization processes without further human intervention, or allow more time for management activities to restore natural metapopulation dynamics.

For *Cirsium pitcheri* in Indiana, if management actions do not promote natural seed dispersal and establishment in unoccupied habitats, metapopulation processes will not recover. In this case, management will always need to function as the "artificial" dispersal agent at scales appropriate for the species. The choice of which approach to take will certainly depend on local factors, such as the availability of suitable new restoration sites within the metapopulation footprint, the condition of existing populations, management plans for improving landscape connectivity among populations, the ability of management to protect the restoration sites over the long term and existing seed sources for population reintroduction or enhancement.

In Indiana, four of the five sampled populations are declining; thus it is not surprising that the metapopulation is also declining. Bottin et al. (2007) suggests that understanding population dynamics and matching them to environmental habitat characteristics are important to conducting successful restorations. Mimicking poor conditions is not likely to improve viability via enhancement or reintroduction; instead, we need to imitate conditions that are likely to increase viability. For *C. pitcheri*, the early successional reintroduction site was expected to be more favorable for population growth, and our results support that prediction. At the start of the restoration project, the early successional habitat, Ogden Dunes East had 50% greater seedling establishment than Ogden Dunes West. Ogden Dunes East plants grew faster and produced mature adults sooner. Such earlier reproduction, and thus potential for colonization of nearby sites, further increases the value of Ogden Dunes East for metapopulation recovery. Interestingly, habitat successional stage is not the best predictor of population growth at the Miller High Dunes site. This site is situated high on a dune facing directly into the northwest winter winds, which periodically blow open localized patches of sand in the otherwise late-successional vegetation at the forest edge. Here, open sand percentage may have been a better measure of early successional habitat suitability for *C. pitcheri*.

Both Miller and Big Blowout showed immediate increases in population growth after 2009, in response to our harvesting and planting of seed to deter goldfinch predation. Thus, these can now be considered managed populations, where a minor

Table 2. Indiana Dunes National Lakeshore *Cirsium pitcheri* populations successional stages, mean population sizes with standard deviations, 1988–2012 pooled population growth rates (λ), MTE in years and years to 5% probability of extinction ($p_{0.05}$) for each population, metapopulation and the addition of enhancements.

	Succession Stage	*Mean Population Size (SD)*	*Pooled Population Growth Rate (λ)*	*MTE*	*Time, Approximate 5% Probability of Extinction* $p_{0.05}(t)$
Miller High Dunes	Late	95 (45)	1.1167 (0.87)	14.9	6
West Beach	Middle	160 (155)	0.8834 (0.35)	7.1	2
State Park Big Blowout	Late	33 (26)	0.6483 (0.44)	4.2	2
Ogden Dunes East	Early	65 (20)	0.9719 (0.44)	11.8	5
Ogden Dunes West	Middle	84 (52)	0.9176 (0.59)	6.2	3
NATIVE (baseline)				15.6	7
Native + ODWEST				16.0	8
Native + ODEAST				18.3	9
Native + BOTH				18.6	10
1,800 seeds enhancement					
Miller High Dunes				22.5	12
West Beach				20.0	12
State Park Big Blowout				17.5	10
Ogden Dunes East				20.5	11
Ogden Dunes West				20.5	11
900 seeds enhancement					
Miller High Dunes				21.5	12
West Beach				20.2	11.5
State Park Big Blowout				18.4	10
Ogden Dunes East				21.2	11
Ogden Dunes West				18.8	11
450 seeds enhancement					
Miller High Dunes				20.5	11
West Beach				19.3	11
State Park Big Blowout				18.4	10
Ogden Dunes East				20.2	11.5
Ogden Dunes West				22.1	12

one-time intervention resulted in an upward inflection in population growth rate. This suggests that a mixed recovery strategy involving both reintroductions and enhancements will increase the number of *C. pitcheri* populations and increase individual fecundity for sustained growth and colonization.

The addition of two *C. pitcheri* populations, growing at rates similar to the natural populations, increased the projected time to extinction in Indiana by about 3 years. Whether this is sufficient time for large-scale management efforts to restore connectivity among beach dunes and blowouts is unknown. In addition, for *C. pitcheri* in Indiana, the large number of new populations required to reach a viable level is unrealistic. For example, we estimate that at least 100 reintroductions would be required to prevent the metapopulation from crossing the 5% threshold extinction risk for 35 years. First, there are not 100 suitable habitat sites. Second, *C. pitcheri* fecundity in native populations is too low to sustain high levels of seed harvest (Bowles et al. 1993), and already declining populations would be put at even greater risk of extinction (Menges et al. 2004).

In Indiana, a mixed strategy appears to be the best choice. It is clear that natural dispersal along the beach is not likely where towns, recreation, and industry disrupt natural habitats, so that restoration will have to replace natural dispersal as a means of colonization. The evaluation of "good" early-successional potential habitat will need to involve an assessment of both open sand and indicator species. There must be institutional commitment to protect those new sites from further development over many years, allowing seedling cohorts the 4–8 years required for flowering and seed production. Enhancement of existing populations by protecting seeds from predation and then sowing them has already been shown to improve population growth. Seed for any new restoration or additional enhancement will need to come from on-site seed production nurseries, where locally collected seeds are grown for seed harvesting. Ultimately, persistence of *C. pitcheri* in Indiana depends on active management and long-term commitment to conserving existing populations, maintaining new restorations, and improving landscape connectivity within the remnant natural areas of the beach and dune blowout system.

Limitations

We did not measure dispersal among potential habitats and include them in our model. We believe that the process of dispersal among the Indiana blowouts cannot occur naturally within the projected time period of 50 years because human use has disrupted the dispersal corridors. We also did not model catastrophes due to the inability to correctly estimate the frequency and extent of impact on population dynamics as a result of a lack of sufficient empirical data. An example of a catastrophe that has impacted our site includes a third reintroduction site that was completely buried by nearly a meter of sand the winter

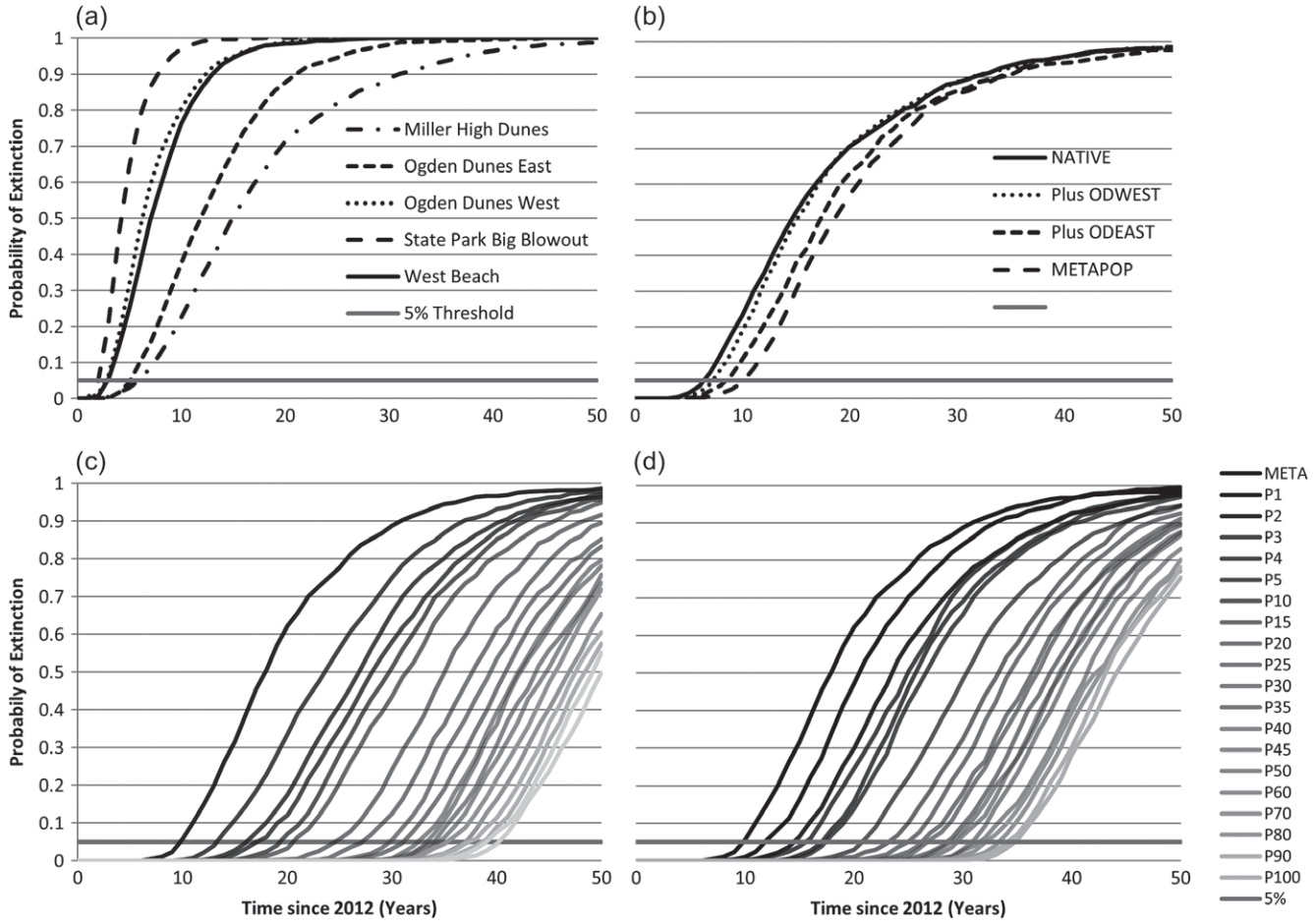

Figure 3. Probability of extinction comparison of (A) Indiana Dunes populations separately (Miller High Dunes, Ogden Dunes East, Ogden Dunes West, State Park Big Blowout, and West Beach). (B) Native (without reintroductions), Native + Ogden Dunes West, Native + Ogden Dunes East and Metapopulation with both native and reintroduction populations. (C) Addition of up to 100 early successional reintroductions (Ogden Dunes East). (D) Addition of 100 mid successional reintroductions (Ogden Dunes West). MTE lies at 50% probability. 5% line indicates threshold of acceptable extinction threat.

following planting. Lastly we did not construct matrix models with correlations, as they are significantly less accurate than models lacking correlation for an Illinois Beach State Park *C. pitcheri* population (Bell et al. 2013).

Outlook

This study reinforces the idea that restorations and enhancements can facilitate and improve metapopulation viability of species dependent on metapopulation dynamics for survival. Based upon previous knowledge, we created *C. pitcheri* reintroductions in habitats identified as meeting the requirements for successful restorations. Populations in early succession habitats, with less vegetation and a greater percentage of open sand, are likely to perform better than populations in later successional stages, with more vegetation and less open sand. Still, it is important to note that these restorations did not improve projected *C. pitcheri* metapopulation longevity in Indiana by a great amount, illustrating the great challenges faced by managers working with species that require large habitats with connectivity among populations and sites. Remaining gaps in knowledge include the spatial movement of *C. pitcheri* through the landscape in response to changes in the community where information on this process may serve to help predict the mechanism of natural new population creation.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Structure of habitat surrounding Lake Michigan, the formation of dune communities, successional stage, and the relative position of five Indiana dunes *Cirsium pitcheri* populations (Adapted from McEachern 1992).

Figure S2. Study populations in reference to potential habitat and located along the southern tip of the Lake Michigan in the Indiana Dunes National Lakeshore and Indiana Dunes State Park near Porter, Indiana.

Table S1. Stage classes and Moloney size class (mm) for each of the five Indiana Dunes *Cirsium pitcheri* populations.

Table S2. Comparison of twelve possible parameter combinations of demographic stochasticity, environment stochasticity and correlations with mean squared error values, standard errors, confidence intervals and ranking.

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