

Population-specific life histories contribute to metapopulation viability

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Citation: Halsey, S. J., T. J. Bell, K. McEachern, and N. B. Pavlovic. 2016. Population-specific life histories contribute to metapopulation viability. *Ecosphere* 7(11):e01536. 10.1002/ecs2.1536

Abstract. Restoration efforts can be improved by understanding how variations in life-history traits occur within populations of the same species living in different environments. This can be done by first understanding the demographic responses of natural occurring populations. Population viability analysis continues to be useful to species management and conservation with sensitivity analysis aiding in the understanding of population dynamics. In this study, using life-table response experiments and elasticity analyses, we investigated how population-specific life-history demographic responses contributed to the metapopulation viability of the Federally threatened Pitcher's thistle (*Cirsium pitcheri*). Specifically, we tested the following hypotheses: (1) Subpopulations occupying different environments within a metapopulation have independent demographic responses and (2) advancing succession results in a shift from a demographic response focused on growth and fecundity to one dominated by stasis. Our results showed that reintroductions had a positive contribution to the metapopulation growth rate as compared to native populations which had a negative contribution. We found no difference in succession on the contribution to metapopulation viability. In addition, we identified distinct population-specific contributions to metapopulation viability and were able to associate specific life-history demographic responses. For example, the positive impact of Miller High Dunes population on the metapopulation growth rate resulted from high growth contributions, whereas increased time of plant in stasis for the State Park Big Blowout population resulted in negative contributions. A greater understanding of how separate populations respond in their corresponding environment may ultimately lead to more effective management strategies aimed at reducing extinction risk. We propose the continued use of sensitivity analyses to evaluate population-specific demographic influences on metapopulation viability. In understanding the underlying causes of the projected extinction probabilities of each population and identifying broad-scale contributions of different populations to the metapopulation, the process of pinpointing target populations is simplified. More detailed analyses can then be applied to the target populations to increase population viability and consequently metapopulation viability. Based on our research, we suggest that the best approach to improve the overall metapopulation viability is to manage the contributions to population growth for each population separately.

Key words: demographic responses; elasticity analysis; life-table response experiments; Pitcher's thistle; restorations.

Received 19 August 2016; accepted 24 August 2016. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Variation in demographic responses can occur within populations of the same species living in different environments (Caswell et al. 1999, Coulson et al. 2005). At any given instance, species inhabit spatially and temporally heterogeneous habitats that allow variation in growth, survival, and reproduction to occur (Alexander et al. 2012). Demography is a product of local conditions over space and time as a result of interactions with local environments such as habitat type (Burns et al. 2013). Therefore, the relationship between habitat and population dynamics can be best understood by long-term studies that consider multiple habitat types with demographic data that encompass the entire life cycle of a species (Pardini et al. 2015). Understanding how different environments within metapopulations influence local population demographic responses can improve restoration efforts.

Restoration is often used as the last resort to bolster biological diversity and population viability when habitat protections and other management strategies fail (White 1996); however, the restoration efforts of rare plant species often occur with little information available to guide such actions (Bell et al. 2002). Plant restorations have primarily focused on technical aspects such as habitat choice and planting methods in efforts to match environmental characteristics of sites, with few studies comparing restorations with the natural counterparts (Freville and Silvertown 2005, Colas et al. 2008). However, it is useful to understand the demographic responses of natural occurring populations in order to appropriately apply restoration efforts.

Restorations can simulate colonization events, in cases where habitat connectivity via dispersal has been lost in metapopulations. Increasing the number of populations should increase the probability of species persistence over time because of reduced likelihood of all populations going extinct (Colas et al. 2008, Menges 2008). Increased longevity of restored populations now provides long-term demographic data that conservation biologists can use to evaluate successes in relation to conservation management goals. Previous studies (Kirchner et al. 2006, Brown et al. 2008) speculated that the addition of populations may improve metapopulation viability and Halsey

et al. (2015) demonstrated that the reintroduction of two plant populations increased metapopulation viability through increased median time to extinction. In addition, enhancement of existing populations improved population growth rates, while reducing the management effort it would take to create new populations. For a species with metapopulation dynamics, using restorations to improve metapopulation viability is an effective method and will likely become more commonplace and useful with ongoing and future restorations.

Population viability analyses (PVA) are useful planning tools (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. Popular approaches to PVA include matrix models and integral projection models which can be used to analyze population dynamics and identify trends in population growth rate (λ) (Easterling et al. 2000, Caswell 2001). In addition to PVA, sensitivity analyses aid in the understanding of population dynamics (Damman and Cain 1998, Maschinski et al. 2006, Garcia 2008). Sensitivity analyses can identify underlying vital rates that should be targets of management efforts in an attempt to improve population viability (Crouse et al. 1987, Heppell 1998, Morris and Doak 2002). Life-table response experiments (LTRE) investigate the response of a population to changes in vital rates by decomposing observed differences in λ into contributions made by each vital rate (Caswell 2001, Freville and Silvertown 2005). In contrast, elasticity analysis evaluates how hypothetical changes in vital rates would alter λ . Elasticities assume linear relationships where proportional changes in elasticities result in a proportional change in λ (Morris and Doak 2002).

Building upon reinforced ideas that restorations can facilitate and improve viability of a species dependent on metapopulation dynamics for persistence (Halsey et al. 2015), we sought to further understand individual population dynamics and subsequent influences on metapopulation persistence through the use of both retrospective (LTRE) and prospective (elasticities) analyses (Bottin et al. 2007). We investigated how population-specific life-history demographic responses (growth, stasis, regression, and fecundity) contributed to the metapopulation viability.

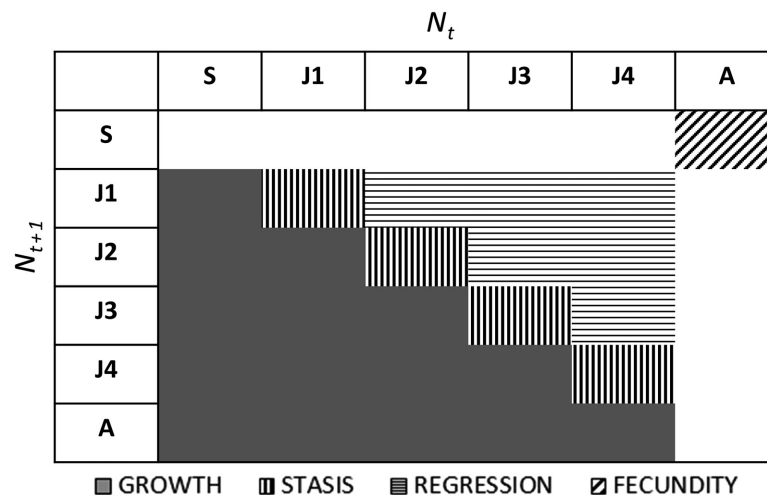


Fig. 1. Generalized transition matrix for *Cirsium pitcheri*, grouping transitions of plants from six stage classes (seedling [S], juvenile [J], and adult [A]) into growth, stasis, regression, and fecundity regions.

We specifically tested the following hypotheses using long-term data collected on the demography of the Federally threatened Pitcher's thistle (*Cirsium pitcheri*): (1) Subpopulations occupying different environments within a metapopulation have independent demographic responses and (2) advanced succession results in a shift from a demographic response focusing on growth and fecundity to one dominated by stasis. A better understanding of the underlying influences on population-specific dynamics will allow for efficient use of resources by managers to improve restoration efforts in metapopulations.

METHODS

Study species and system

Cirsium pitcheri is a Federal threatened dune thistle inhabiting intermittently stable beach and grassland dunes of the western Great Lakes shorelines (Harrison 1988). It is dependent on sand dynamics to create its preferred habitat with greater than 50% bare sand (Loveless 1984, McEachern 1992). At the Indiana Dunes, northwest aspects are favorable habitats because of northwest winds from late fall storms (McEachern 1992). This monocarpic species depends on the seed production of a single lifetime flowering episode with plants generally remaining in the juvenile, prereproductive stage for 4–8 yr. Seed predation and herbivory from native and

introduced insect enemies can severely reduce fecundity (Bevill et al. 1999, Havens et al. 2012). Passive dispersal results in individual seeds falling within 1 m of the parent plant; long-distance dispersal is uncommon, but can occur through mechanisms such as wind, waves, or birds (Loveless 1984, Keddy and Keddy 1984). *C. pitcheri* has a stage-size population structure with seedlings (first year), juveniles, and flowering adults (Fig. 1). The six stage-size classes are as follows: S (Seedlings), J1 (Small Juvenile), J2 (Medium Juvenile), J3 (Large Juvenile), J4 (Preflowering), and A (Flowering) (as described in Halsey et al. 2015) using root crown diameter to divide juveniles due to high correlation with growth and survival (Loveless 1984, McEachern 1992).

Field sampling

The five study populations are located in blowouts within the narrow linear dunes stretching for 35 km along the southern tip of Lake Michigan in the Indiana Dunes National Lakeshore (INDU) and Indiana Dunes State Park (IDSP) between Gary and Michigan City, Indiana. Miller High Dunes (MIHI, INDU, Lake County), West Beach (WEBE, INDU, Porter County), and State Park Big Blowout (SPBB, IDSP, Porter County) are native populations where a single 1000-m² fixed demographic monitoring plot was created in 1988 (McEachern 1992; Table 1). This interconnected

Table 1. Description of the five Indiana Dunes study sites with size, population type, and succession stage.

Site name	Size (m ²)	Type	Succession	Distance from Lake Michigan (m)
Miller High Dunes	1000	Native	Late	517
West Beach	1000	Native	Early	334
State Park Big Blowout	1000	Native	Late	400
Ogden Dunes East	150	Restoration	Early	187
Ogden Dunes West	225	Restoration	Mid	158

system is surrounded by beach, forest, and urban development, with large blowouts extending about 1 km inland. The five populations in this study have an average distance of 3.3 ± 1.3 km, interspersed with occupied (but not sampled) and potential habitat.

In 1994, two restoration sites in INDU, Porter County, Ogden Dunes east (ODEAST) and Ogden Dunes West (ODWEST) were created through methods of seed broadcasting and burial at 1 cm deep (U.S. Fish and Wildlife Service 2002). Community successional states can be characterized by the relative abundance of three dominant beach grasses (*Ammophila breviligulata*, *Calamovilfa longifolia*, *Schizachyrium scoparium*) which have different tolerances for sand movement (Cowles 1899, Olson 1958). We calculated succession indices (SI) for each site ("Succession" in Table 1) as the weighted ratio cover where w_i is the weighting factor for species i (early, $w_{A. brev} = 1$; mid, $w_{C. long} = 2$; late, $w_{S. scop} = 3$) and a_i is the relative cover for species i (McEachern 1992; Eq. 1):

$$SI = \frac{\sum (w_i a_i)}{\sum a_i}. \quad (1)$$

The restoration sites are closest to Lake Michigan whereas the existing population demographic plots are further inland (Table 1). Ogden Dunes East and West Beach are more dominated by *Ammophila* and *Calamovilfa* and have active microblowouts. Ogden Dunes West is primarily dominated by *Schizachyrium*, but also has an active microblowout on the north side toward the lake. The south two-thirds of the plot are stabilized. Both Big Blowout and Miller Dunes plots are furthest from the lake but are very different in their conditions. While these two demographic plots are classified as late successional, Big Blowout is very stable, with fixed patches of *Schizachyrium* on a constant slope without

microblowouts. In contrast, Miller High Dunes also has patches of *Schizachyrium*, but these are interrupted by microblowouts in part created as a result of variation in slope and aspect.

We sampled native populations annually from 1988 through 2012, with the exception of 1997–1998. The restored populations were sampled annually from 1999 through 2012. Each year, we identified and tagged each *C. pitcheri* plant, recording their location, survival, root crown diameter (except for seedlings), and stage class (seedling, juvenile, or flowering plant).

Matrix construction

Following Caswell (2001), we used the demographic monitoring data to create population projection matrices for each population; native (1988–2012, $n = 21$) and restoration (1999–2012, $n = 13$). In total, there are 63 matrices for native populations and 26 restoration matrices.

LTRE

We conducted life-table response experiments (LTRE) using the LTRE function in the POPBIO package (Stubben and Milligan 2007) in R 3.1.1 (R Core Team 2014). We used a fixed one-way design to examine the effects of each population measured as a deviation from the growth rate of a reference matrix which is the overall metapopulation matrix calculated from the data of all five populations.

We performed LTRE on the population types, native and reintroduced, by dividing the matrices with respect to their population type with a total of 63 matrices categorized as native (SPBB, MIHI, WEBE) and 26 matrices categorized as reintroduced (ODEAST, ODWEST). We used randomization of matrices without replacement with 1000 replications to determine differences between native and reintroduced populations as well as individual populations. Contributions were further divided into contributions of the 36

transition elements of the matrix and summed with respect to a combination of transitions that are associated with growth, stasis, fecundity, and regression as indicated in Fig. 1. We define “growth” as the progress of plants from one size to a larger size class, “stasis” as no transition between size classes, “regression” as the transition to a smaller size classes, and “fecundity” as the per capita average of seedlings produce from flowering plants.

Elasticities

We performed elasticity analysis on each matrix using `eigen.analysis` function in the POPBIO package (Stubben and Milligan 2007), summing the elements of the elasticity matrix with respect to the growth, stasis, and fecundity regions as indicated in Fig. 1. Regression (a state where plants are smaller the following year) is included as part of stasis (i.e., no growth) as it does not fit in with either growth or fecundity categories. There were six State Park Big Blowout matrices (years = 01–02, 02–03, 03–04, 05–06, 07–08, 09–10) where the populations had a population growth rate (λ) of zero as well as elasticity values of zero so they were excluded from all elasticity analyses. We suspect this was due to low population abundance and a lack of representation of plants in all stages to allow for the development of complete matrices and therefore elasticity values. All values were then plotted on a triplot to show the general trend of each population elastic contribution to the population growth rate. Linear regression was used to determine the relationship between elasticity values and population growth rates. Analysis of variance was used to determine differences in the elastic contributions (growth, regression, stasis, and fecundity) of λ between the populations using the different transition years as replications.

RESULTS

LTRE

Reintroductions had a positive contribution to the metapopulation growth rate (λ_M) as compared to native populations which had a negative contribution (note: gray shading in Fig. 2); however, neither of these contributions were significantly different from the pooled metapopulation ($P = 0.060$, $P = 0.596$ respectively,

Fig. 2b). Miller High Dunes had a significant positive contribution ($P < 0.001$) on λ_M , whereas State Park Big Blowout had a significant negative contribution ($P < 0.001$) on the λ_M . West Beach, Ogden Dunes West, and Ogden Dunes East did not differ significantly in their contributions to the Indiana Dunes’ metapopulation growth rate ($P = 0.980$, $P = 0.810$, $P = 0.316$, respectively, Fig. 2b).

Growth of plants significantly contributed positively to (λ_M) in Miller High Dunes ($P = 0.002$) and Ogden Dunes East ($P = 0.028$) whereas growth was negative in Ogden Dunes West, State Park Big Blowout, and West Beach albeit this negative contribution was not significant ($P = 0.258$, $P = 0.122$, $P = 0.204$, respectively, Fig. 3b). Stasis had a significant negative contribution in all populations ($P < 0.001$) except West Beach (Fig. 3b). State Park Big Blowout was the only population whose fecundity contributed negatively to (λ_M) ($P < 0.001$). While Ogden Dunes West had the greatest positive contribution ($P = 0.15$) of fecundity followed by Miller High Dunes ($P = 0.17$), neither of these were significant. The contribution of regression was negligible and non-significant compared to the other summed transitions.

Elasticities

Growth, stasis, and fecundity varied throughout the populations as well as among the years of the populations. All Indiana Dunes populations were along the similar fecundity axis between 5% and 30%, but varied in where they fell along the stasis and growth axes (Fig. 4). Miller High Dunes showed variability in the contributions of stasis and growth to λ with contributions of fecundity being relatively constant between 10% and 20%. Ogden Dunes East points tended to cluster together on the triplot with growth contributing 65–80% to λ whereas stasis and fecundity contributing between 5–15% and 20–30%, respectively. Ogden Dunes West shared a similar trend as Miller High Dunes with fecundity contributions ranging from 0% to 20% and growth and stasis between 60–80% and 0–40%, respectively. State Park Big Blowout points tended to cluster around high stasis elasticities with fecundity values close to 0% and growth between 0% and 30%. The few State Park Big Blowout transition years with 15–25% fecundity contributions resulted in population growth

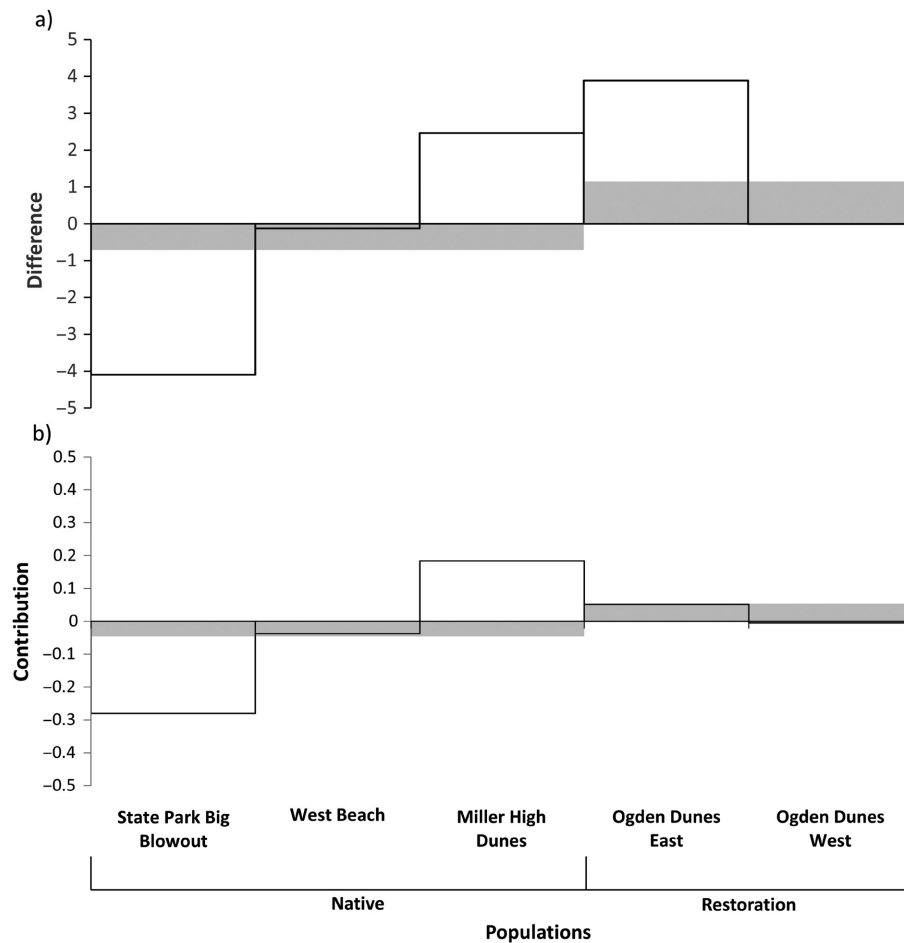


Fig. 2. Population-specific LTRE. (a) Differences in population from pooled metapopulation. (b) Contribution of these differences to (λ_M) . White blocks represent individual populations, and gray blocks represent population type (native, restoration). Native ($P = 0.060$) and Restoration ($P = 0.596$). SPBB ($P < 0.001$), WEBE ($P = 0.981$), MIHI ($P < 0.001$), ODEAST ($P = 0.812$), ODWEST ($P = 0.316$).

rates higher than 0.80. West Beach shared a trend similar to that of Miller High Dunes with the fecundity contributions concentrated between 0% and 20% and with tradeoff of growth and stasis contributions.

For all populations, increases in λ are associated with increased fecundity elasticities and decreased stasis elasticities (Fig. 5). Linear trends occurred with growth elasticities and their corresponding λ (Fig. 5a). State Park Big Blowout had the strongest relationship with increases in contributions of growth resulting in higher λ ($R^2 = 0.656$, $P < 0.001$). Miller High Dunes and Ogden Dunes West had moderately positive relationships between growth elasticities

and λ ($R^2 = 0.37$, $P = 0.003$; $R^2 = 0.459$, $P = 0.022$, respectively). West Beach also showed a positive yet weak relationship between growth and λ ($R^2 = 0.144$, $P = 0.09$). Ogden Dunes East showed no relationship between growth and λ ($R^2 = 0.066$, $P = 0.445$).

Inverse relationships occurred with stasis (includes regression of plants to smaller size) elasticities and population growth rate for four of the five populations (Fig. 5b). Miller High Dunes and Ogden Dunes West have a moderate relationship ($R^2 = 0.449$, $P = 0.001$; $R^2 = 0.489$, $P = 0.017$). In contrast, relationships between State Park Big Blowout and West Beach are non-significant ($R^2 = 0.009$, $P = 0.680$; $R^2 = 0.1556$,

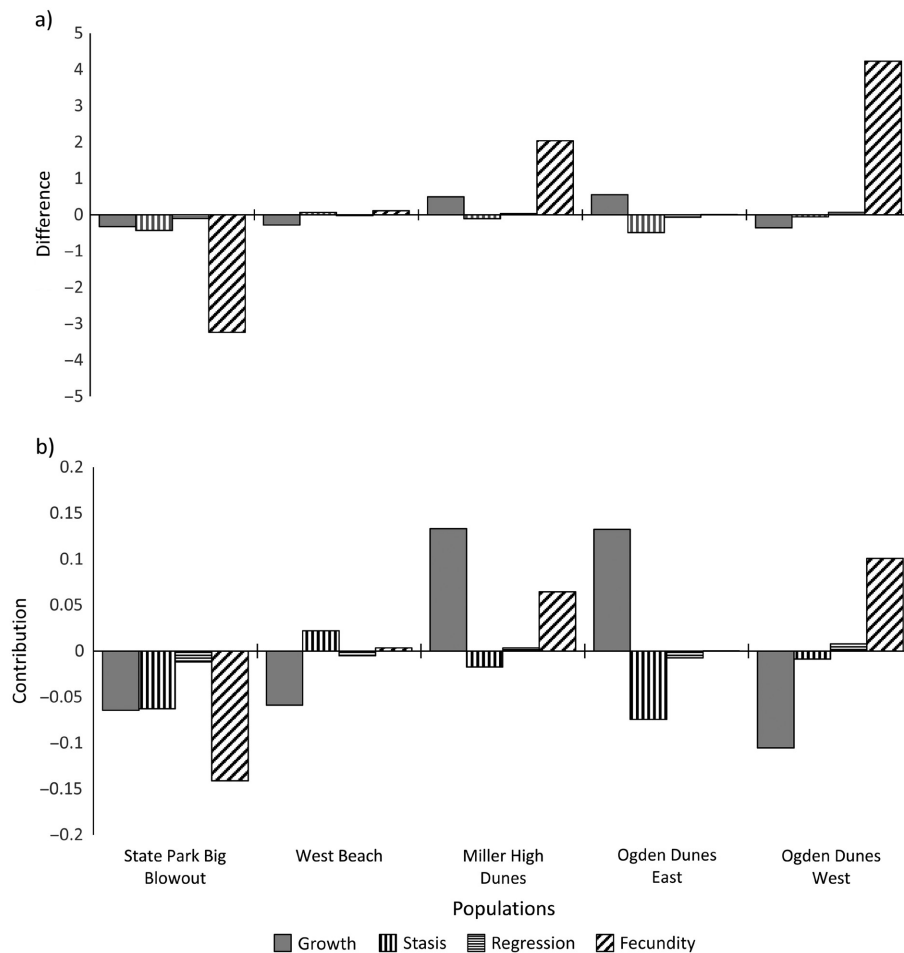


Fig. 3. Summed matrix elements representing growth, stasis, regression, and fecundity for each Indiana Dunes *Cirsium pitcheri* population. (a) Differences of populations from pooled metapopulation. (b) Contribution of these differences to (λM).

$P = 0.077$). Ogden Dunes East, however, had a positive yet non-significant relationship between stasis and λ ($R^2 = 0.019$, $P = 0.681$).

Fecundity showed positive relationships for all Indiana Dunes' populations with increased fecundity contributions resulting in increased λ (Fig. 5c). State Park Big Blowout ($R^2 = 0.724$, $P < 0.001$) had the strongest relationship, Miller High Dunes ($R^2 = 0.499$, $P < 0.001$) and Ogden Dunes West ($R^2 = 0.498$, $P = 0.015$) had moderate relationships whereas Ogden Dunes East had no relationship ($R^2 = 0.008$, $P = 0.791$) and West Beach ($R^2 = 0.165$, $P = 0.067$) had the weakest relationship between fecundity and λ .

Growth ($F_{4,82} = 16.228$, $P < 0.001$), stasis (including regression) ($F_{4,82} = 6.912$, $P < 0.001$), and

fecundity ($F_{4,82} = 11.045$, $P < 0.001$) elasticities differed significantly between the populations. A post hoc Tukey's HSD with $\alpha = 0.05$ showed that State Park Big Blowout mean growth elasticities differed significantly from Miller High Dunes, Ogden Dunes East, Ogden Dunes West, and West Beach (Fig. 6a). Miller High Dunes growth also differed significantly from West Beach. Ogden Dunes East stasis elasticities differed significantly from West Beach and State Park Big Blowout, with State Park Big Blowout also differing significantly from Miller High dunes (Fig. 6b). State Park Big Blowout fecundity elasticity differed significantly from Miller High Dunes, Ogden Dunes West, and West Beach (Fig. 6c).

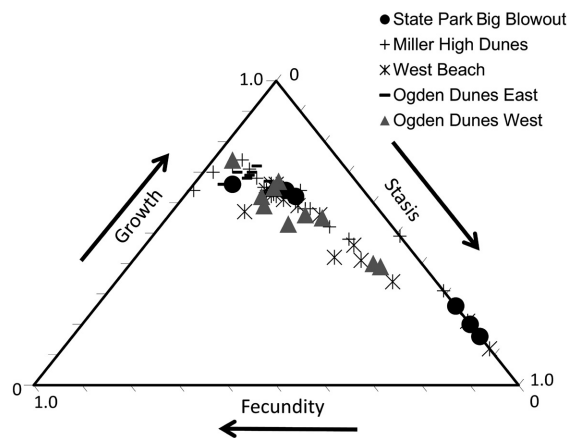


Fig. 4. Triplot of growth, stasis, and fecundity transition groups for each Indiana Dunes *Cirsium pitcheri* transition matrix.

DISCUSSION

All things being equal, increasing the number of populations should increase the probability of species persistence over time (Colas et al. 2008, Menges 2008). However, populations of the same species living in different environments can vary in demographic rates and population growth (Coulson et al. 2005). Demography is a product of local conditions, dependent upon local interaction with habitat, competition, and predators (Burns et al. 2013). Therefore, a greater understanding of how separate populations respond in their corresponding environment will ultimately lead to more effective strategies aimed at reducing extinction risk (Schemske et al. 1994, Bruna and Oli 2005). We proposed utilizing both retrospective and prospective approaches to evaluate how population-specific demographic responses influence metapopulation viability.

Retrospective analyses such as LTRE allow for the decomposition of observed differences between populations to assess actual contributions to the population growth rate (λ) (Caswell 2000). In this study, neither population type, native or reintroduced, had a significant effect on the type of contribution (positive or negative) to the Indiana Dunes metapopulation growth rate (λ_M). Each individual population's dynamics seems to be influenced by differences in life-history responses. Most notably, State Park Big Blowout had a significant negative contribution

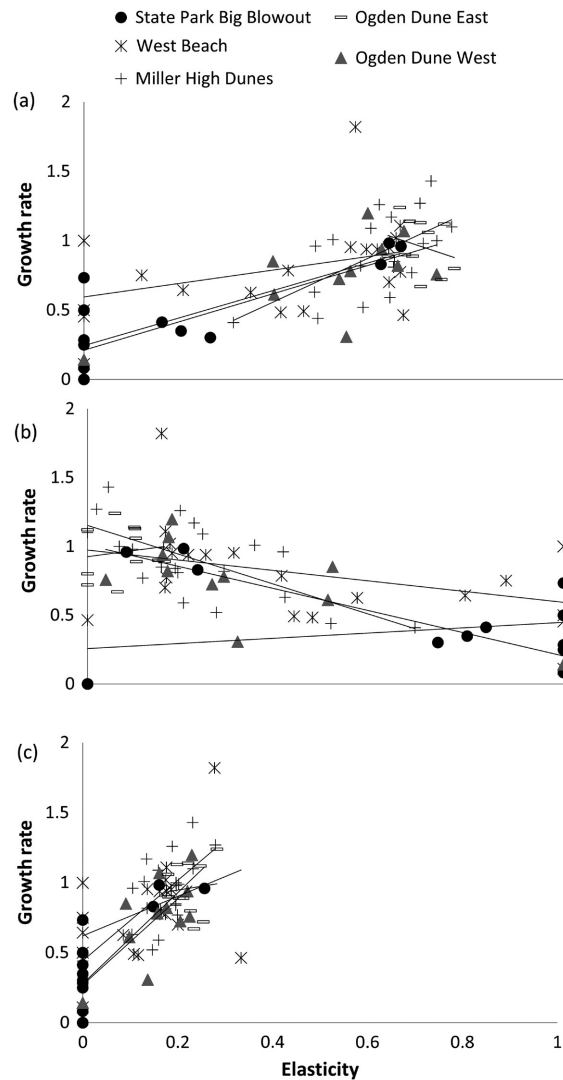


Fig. 5. Population growth rates as a function of elasticity values (a) growth, (b) stasis, and (c) fecundity for Indiana Dunes populations of *Cirsium pitcheri*. Lines represent linear trend separately for each population.

to λ_M . Through further decomposition of the underlying matrix transitions, decreased fecundity was found to be the main contributor. Small differences in fecundity had a disproportionately larger contribution to the λ_M as compared to other matrix elements, similar findings have been reported in previous studies (Jacquemyn et al. 2001, Freville and Silvertown 2005). Because *C. pitcheri* is a monocarpic perennial that flowers only once, it is not surprising that fecundity is a

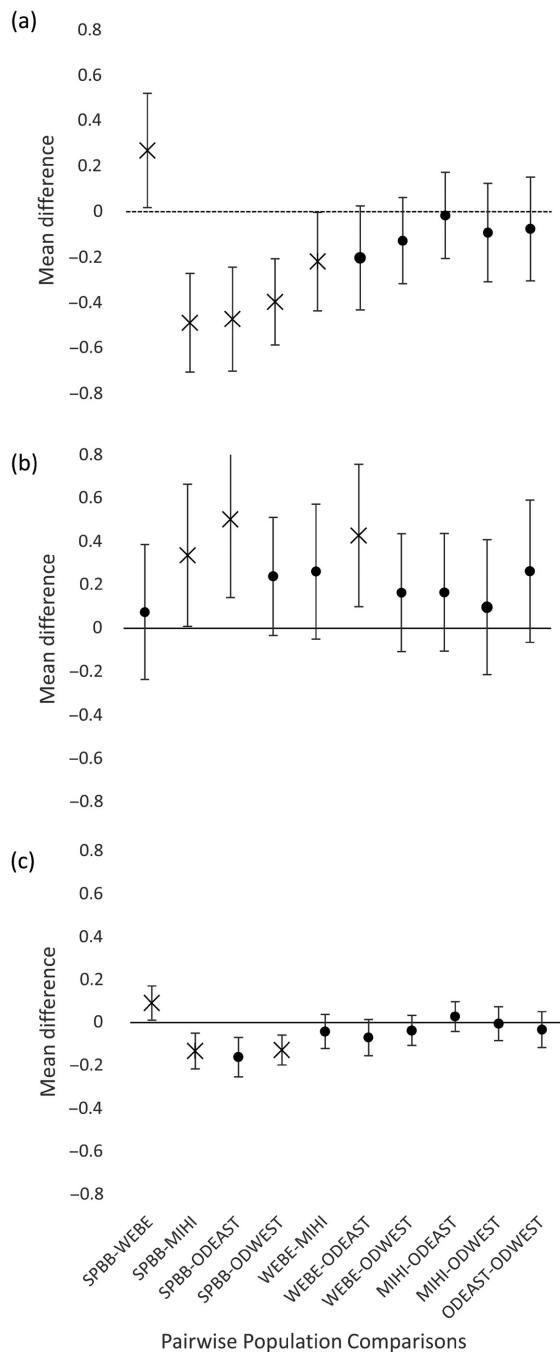


Fig. 6. Mean differences in pairwise comparisons of (a) growth, (b) stasis (including regression), and (c) fecundity elasticity values as determined via post hoc Tukey's HSD. Means indicated with X are significantly different. State Park Big Blowout (SPBB), West Beach (WEBE), Miller High Dunes (MIHI), Ogden Dunes East (ODEAST), Ogden Dunes West (ODWEST).

driving factor in the viability of this species. For the Indiana Dunes' *C. pitcher* metapopulation, negative differences of growth, stasis, fecundity, and regression tended to lead to greater effects on the contribution to population growth rate than their positive counterparts. For example, the negative difference in fecundity for State Park Big Blowout led to a greater negative contribution to the metapopulation growth rate, whereas the positive differences of both Ogden Dunes West and Miller High Dunes contributed about the same proportion as its differences. These results suggest that successional stage or sand dynamics does play a significant role in Pitcher's thistle viability (Loveless 1984, McEachern 1992).

In contrast, prospective approaches such as elasticity analysis, evaluate how hypothetical changes in vital rates would alter λ (Caswell 2001). Elasticities measure the proportional change in λ resulting from a proportional change in a vital rate (de Kroon et al. 1986, Morris and Doak 2002). Overall, the five Indiana Dunes' *C. pitcher* populations varied in their elasticity values with the most noticeable difference being State Park Big Blowout's high values of elasticity for stasis in comparison with the other populations. There are clear relationships between elasticity values representing growth, stasis, and fecundity with population growth rates (λ). In *C. pitcher*, this linear relationship shows that higher growth and fecundity values tend to result in higher λ 's whereas higher stasis values resulted in lower λ 's. Because transition elasticities are actually combinations of vital rates (growth, fecundity, and survival), the contributions of these vital rates to changes in population growth are not clearly separated. However, information about species-specific demographic responses can still be gained from examining elasticities (Franco and Silvertown 2004). For example, *C. pitcher*'s fecundity is the result of growing large enough to maximize its monocarpic reproductive capabilities; thus, higher contributions of stasis tend to lower the population growth rate due to individual *C. pitcher* reproductive values increasing with size.

Elasticities reflect rescaling sensitivity values to allow for unbiased comparisons of the effect of changes in vital rates on population growth rates (Morris and Doak 2002). This scaling results

in elasticities summing to unity (de Kroon et al. 2000), so that an increase in one elasticity value results in the subsequent reduction of other elasticity values. When calculating elasticities, we obtained a value for each of the 36 matrix transitions. By summing these elasticity values in accordance with growth, stasis, and fecundity, we have a useful interpretation of how changes in population-specific demographic responses affect the population growth rate. From a management perspective, this has the potential to direct efforts to either the growth, survival, or reproduction of plant populations. The State Park Big Blowout population seems to have a much different demographic response as compared to the other populations in the metapopulation, with higher values for stasis (survival) at the expense of growth and reproduction. There is a distinct variation in elasticity patterns that imply that the environmental conditions at State Park Big Blowout are different from the other populations (Silvertown et al. 1996, Oostermeijer 2003). The late successional stage of State Park Big Blowout's habitat does not explain the high stasis contributions for the majority of State Park Big Blowout's yearly population growth rates. Succession has advanced further for another population, Miller High Dunes habitat (McEachern 1992), which appears to be doing fine. Miller High Dunes had higher population growth rates as well as relatively low contributions of stasis and higher growth and fecundity contributions. This may be due to the fact that Miller High Dune has more sand movement than State Park Big Blowout. Trees on the high flanks of the State Park Big Blowout prevent northwest winds from reaching the demographic population, and when combined with competition from *Schizachyrium* and the hot microhabitat of the site, this may contribute to the slow growth of the plants.

Understanding population dynamics of species is important to successful management efforts (Bottin et al. 2007). Improving fecundity will add new plants to the population and is likely to improve metapopulation viability. For *Cirsium*, the creation of on-site seed production nurseries may serve to increase fecundity, especially for a population such as State Park Big Blowout; however, there seems to be an upper limit to which fecundity can contribute to the population growth rate. Therefore,

a management plan that is solely dedicated to increasing seed production through the addition of seeds, elimination of seed predators, and (or) herbivores that attack flowering plants may not be sufficient. We suggest that there should also be protection of the existing plants. Because this species is monocarpic, growth is required to reach reproductive size, so we suggest that there be a management focus on maintaining growth and survival of *C. pitcheri*. Fencing off protected sites or individual plants may be effective in reducing deer herbivory. Rowland and Maun (2001) suggest that *C. pitcheri* may remain in a juvenile stage longer as a result of deer herbivory, causing plants that have been browsed use taproot biomass in order to regrow aboveground tissue. It might be useful to determine the extent to which deer browsing occurred; however, as plant surveys take place over the course of about one week each year, it is impossible to know the full extent to which this type of herbivory impacts the species.

CONCLUSION

The addition of the two reintroduced populations improved viability of the Indiana Dunes metapopulation; however, due to the constraints of finding suitable habitat and procuring enough seeds to start additional populations, it is unrealistic to try to continue to use this method of adding new populations of *C. pitcheri* as a way to improve viability (Halsey et al. 2015). Through the incorporation of sensitivity analysis such as LTRE and elasticities in PVA, we have a greater understanding of the underlying causes of the projected extinction probabilities of each population. Populations of the same species can differ in demographic responses when occupying distinct environments; therefore, vital rates and ultimately persistence can vary. LTRE allows us to identify important population differences in demographic responses to environmental conditions so as to allow appropriate management actions to take place for each individual population (Davison et al. 2010). Combined with elasticities, the dynamics of specific population is better understood permitting development of detailed management action plans. For example, for a population with high stasis elasticity

values, the population growth rate could be improved by managing factors that stall plant growth. On the same note, population with low fecundity elasticities may respond better with a management strategy that aims at increasing fecundity (Havens et al. 2012).

Identifying broad-scale contributions of different populations to the metapopulation simplifies the process of identifying populations that need to be targeted for more detailed analysis of population dynamics. In the case of this metapopulation, we were able to identify State Park Big Blowout as most at risk for extinction with sensitivity analysis such as LTRE concluding that fecundity or lack thereof is the perpetrator of negative contribution to λ_M and elasticities identifying the extent to which the lack of growth or increased time spent in stasis impacted the population growth rate.

Population viability analysis continues to be of great use to the management and conservation of species. With increasing long-term data sets, we now have the ability to conduct in-depth evaluations of population dynamics which allow for a better projection for the future. Matrix model projections can be amended to incorporate management efforts such as protections and enhancements (Halsey et al. 2015). From a management perspective, this allows for a fairly simple and efficient way to experiment with different management inputs as a way to determine effectiveness of efforts on viability. Our results confirm the negative effects of successional advancement on Pitcher's thistle viability.

The best approach to improve the overall metapopulation viability is to manage the contributions to population growth for each population separately. This would include promoting growth of plants to larger size classes, reducing time spent in stasis or improving fecundity and seedling survivorship. This may be achieved with active successional management as the shoreline dune processes at the Indiana Dunes have been disrupted (McEachern et al. 1994). The outlook for the Indiana Dunes' metapopulation looks bleak for the near future although with this new information it may be possible to reverse the downward direction of the population growth rates and improve the population viability to the point where further human intervention and management are no longer needed.

ACKNOWLEDGMENTS

Cirsium pitcheri demographic data were collected in collaboration with J. Stumpf and assisted by numerous technicians and volunteers over the years; with funding from National Park Service, U.S. Geological Survey and National Science Foundation award DEB 0516058 to K. Havens, T. Bell, M. Bowles, C. Jolls, and K. McEachern. Population modeling was performed at Chicago State University in collaboration with the Morton Arboretum, with funding from USFWS. We thank the Indiana Dunes National Lakeshore and Indiana Department of Natural Resources for their past and ongoing collaboration on dune management, with enduring commitment to *Cirsium pitcheri* conservation in Indiana. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The funding sources had no role in study design, data collection, analysis, or interpretation.

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