CHICAGO STATE UNIVERSITY

A METAPOPULATION APPROACH TO EXAMINING THE EFFECT OF

RESTORATIONS ON POPULATION VIABILITY IN THE INDIANA DUNES.

A Thesis presented to the Faculty of the Department of Biological Sciences in Partial

Fulfillment of the Requirements of the Degree Masters of Science in Biological Sciences

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**Approval Sheet**

We have examined this thesis manuscript and we verify that it meets the program and university

requirements for the degree of

# Master of Science in Biological Sciences

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I am grateful for my parents who were always supportive of my school career especially science projects. Last but not least, I want to thank my husband JP, for his encouragement and confidence in everything I do.

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**Abstract**

To increase metapopulation viability, new populations of *Cirsium pitcheri,* a federal threatened dune plant with metapopulation dynamics, were introduced to the Indiana Dunes National Lakeshore in 1994. To determine the degree to which addition of reintroduced populations affect *C. pitcheri* metapopulation viability at Indiana Dunes, I used 23 years of demographic data to quantitatively predict persistence rates using matrix models that simulate the progression of the metapopulation with and without the addition of reintroduced populations. I also used simulations to project how many populations are needed for the metapopulation to persist for 50 years. I compared the vital rates (survival, growth and fecundity) between: natural and reintroduced populations within the metapopulation via life-table response experiments (LTRE) in order to assess demographic responses on population growth rate ($\lambda$). I also used elasticity analysis to determine whether natural or reintroduced populations have a greater contribution to the metapopulation growth rate. I expect that Indiana Dunes' *C. pitcheri* metapopulation viability will improve with the addition of reintroduced populations as compared to without the addition of reintroductions.

Matrix model simulations indicated that reintroductions decreased the probability of extinction of the Indiana Dunes' *C. pitcheri* metapopulation though only by a few years and additional populations would not yield a significant increase in population viability. LTRE analyses suggest that population type, native or reintroduced, has no significant bearing on the contribution on the growth rate with each individual populations' dynamics influenced by differences in their life histories and habitat. Positive contributions of growth transitions to larger plants and negative contributions of

fecundity are the driving factors that have the greatest impacts on the overall metapopulation growth rate. Elasticity analysis of the contributions of the different vital rates to $\lambda$ shows strong linear relationships between growth and fecundity with population growth rates. In contrast stasis has an inverse relationship with population.

These analyses aid management decisions through the determination of the number of reintroductions required and how each population improves the metapopulation viability. Overall, the addition of two *C.pitcheri* populations to Indiana Dunes' metapopulation has improved the viability of the species from a metapopulation perspective, albeit not by much. Time and effort that would be spent increasing the number of populations will not result in any significant improvement in viability. I suggest effort might be better spent trying to improve the populations already established. Fecundity is a driving factor in the viability of this monocarpic species, mitigated by seed predation, seedling survival and germination success.  However, there is an upper limit on the contribution fecundity can make to the growth rate of this species. *C. pitcheri* must spend the majority of its life growing to a large enough size to flower; therefore, growth of plants is essential. Management actions can best improve Indiana Dunes' metapopulation of *C. pitcheri* by promoting growth of plants, reducing time spent in stasis and improving fecundity and seedling survivorship.

**Specific Aims**

1. To what degree does the addition of reintroduced populations increase the metapopulation viability of *C. pitcheri?*

2. Is there a difference between the vital rates of the native and reintroduced *C. pitcheri* populations?

3. How do differences in life history strategies of *C. pitcheri* populations contribute to the population growth rate?

**Chapter I. Introduction**

**Restorations**

Reintroductions of rare plant species are still relatively new with little information available to guide the design and quantitative analysis of such experiments (Bell et al., 2002). Past plant restorations have primarily focused on technical aspects of introductions such as habitat choice, management, and planting methods (Colas et al., 2008). Every restoration attempt is unique and can be grouped into one of three basic categories (Bottin et al., 2007): reintroductions, enhancements, or introductions. Reintroductions are the creation of a population where the species was previously located, whereas an introduction is the creation of a new population where the species has never been previously reported. Enhancements are the addition of individuals to an existing population to improve viability by increasing population size and/or genetic diversity. Preliminary studies are needed to match environmental characteristics of the restoration sites and the needs of the species, as well as have sufficient population size and genetic variation to avoid demographic stochasticity, the Allee effect and inbreeding depression (Bottin et al., 2007).

Few studies have compared reintroduced populations with their natural counterparts. Colas et al. (2008) conducted a ten-year demographic study of two experimentally introduced and six natural populations of *Centaurea corymbosa* by constructing stage-structured matrix population models and comparing asymptotic growth rates, vital rates and contributions to the difference in the population growth rates between populations. The results indicated that introduced populations had higher survival than natural populations that had higher fecundity.

**Metapopulations**

Metapopulations are collections of separate but potentially interacting populations separated by discrete gaps in habitats and characterized by gene flow between them. Many plant populations and metapopulations are threatened by a variety of factors, some of which are associated with human actions, e.g. habitat degradation and the introduction of invasive species (U.S. Fish and Wildlife, 2002). Most studies involving metapopulations tend to involve animals, with only a few limited studies dedicated to plants. The basis of metapopulation theory links landscape processes with population dynamics, where local species populations live in suitable habitats that are surrounded by unfavorable habitats with a balance of extinctions and colonizations (Schtickzelle, Boulenge & Baguette, 2002; McEachern, Bowles & Pavlovic, 1994).

There are several characteristics that allow the identification of plant metapopulations including seed and pollen dispersal permitting gene flow across landscapes to patches of organisms where the number, size, growth and fates of individuals are influenced partially by uncorrelated space and time disturbances (U.S. Fish and Wildlife, 2002). Habitat fragmentation has become one of the most important threats to plant population viability with smaller population sizes and restricted exchange of pollen and seeds (U.S. Fish and Wildlife, 2002). Persistence of a metapopulation depends on three factors: colonization rates must equal or exceed extinction rates, local environment events must act independently on populations and there must be spatial variation in demographic processes (McEachern et al., 1994). Metapopulation models have the ability to make predictions about the persistence of a system of subpopulations from measurements of area, isolation, and occupancy (presence of species) in order to estimate rates of colonization and extinction (Brigham & Thomas 2003). Correctly identifying species whose survival depends on metapopulation dynamics and using a

metapopulation approach may prove to be an effective method for improving population viability in conservation management and practices.

Menges (2008) proposed that plant restorations that increase the number of populations can serve to produce favorable metapopulation dynamics. From previous studies (Brown, Spector & Wu, 2008; Kirchner, Robert & Colas, 2006), the addition of populations may help to improve a metapopulation's viability but no studies to date confirm that this is true.

### *Cirsium pitcheri*

Pitcher's thistle (*Cirsium pitcheri* (Eaton) Torrey and Gray, Asteraceae) has historically inhabited intermittently stable beaches and open patches in grassland dunes of Great Lakes shorelines. Increasing coastal development and changing habitats has caused a decline in the number of populations throughout most of species' range (McEachern et al. 1994). *C. pitcheri* is a federally threatened species with few populations remaining in Indiana, Michigan, and Wisconsin and has been extirpated from Illinois shorelines (Bowles, Flakne, McEachern & Pavlovic, 1993). There is an approved recovery plan for the purpose of saving *C. pitcheri* from further extirpation; however, the restoration of this disturbance-dependent plant demands further understanding of its natural habitat dynamics, ecological requirements, life history strategies, and responses to natural and anthropogenic disturbance regimes (Bowles et al. 1993). *C. pitcheri* is a monocarpic species that depends on the seed production of a single lifetime flowering episode (Bevill, Louda & Stanforth, 1999; Havens et al. 2012).The viability of *C. pitcheri* populations is greatly affected by seed predation from natural insect enemies, which can be a limiting factor for the survival, growth, and reproduction (Havens et al. 2012)

*C. pitcheri* population dynamics includes wide fluctuations in its population density, with the survival of plants largely impacted by several factors. Rowland & Maun

(2001) suggested that the greatest impact on survival occurs in smaller plants from herbivory (due to the fact that smaller plants must compensate for tissue loss with their underground biomass). Other investigators found that larger individuals are more likely to suffer damage from herbivory than smaller size classes because they are easier to locate (Girdler & Radtke, 2006). Aside from herbivory, other factors affecting *C. pitcheri* mortality include insect infestation, sand burial, species competition and bare area percentage. Sand dunes are fragile systems that are subjected to both natural and human-caused disturbances impacting seedling recruitment and distribution (D'Ullisse & Maun, 1996; Emery & Rudgers, 2007).

Gauthier et al. (2010), determined that *C. pitcheri* populations have low levels of genetic diversity overall that may be the result of low dispersal rates between populations, high levels of inbreeding and population differentiation. The low success of population establishment from introduced seeds as compared to seedling transplantations prompted Hamze and Jolls (2000) to study the seed ecology of *C. pitcheri* in an effort to aid reintroduction efforts. They conducted an *ex situ* study of the conditions that are required for breaking seed dormancy as well as the effect of light, seed mass, and burial depth on germination success. Their results showed that seed burial and minimum light produced the greatest success stimulating seed germination.

The key to a successful conservation strategy for *C. pitcheri* may therefore be to facilitate metapopulation dynamics by establishing new populations and analyzing local spatial patterns in the existing populations as a way to enhance restoration efforts (Girdler & Radtke 2006). Pitcher's thistle recovery plans (Bowles et al. 1993; McEachern et al. 1994; U.S. Fish and Wildlife 2002) have been developed in order to provide guidelines to help identify, protect, inform, survey, and restore the remaining populations of *C. pitcheri*. Population viability analyses have the potential to provide crucial information to

aid conservation efforts through the process of projection modeling, life table response experiments, and elasticity analysis.

I will describe the results of efforts to increase the population viability of five populations of Indiana Dunes National Lakeshore and State Park *C. pitcheri* using a metapopulation approach by addressing the following specific aims or research questions:

1. To what degree does the addition of reintroduced populations increase the metapopulation viability of *C. pitcheri?*

2. Is there a difference between the vital rates of the native and reintroduced *C. pitcheri* populations?

3. How do differences in life history strategies of *C. pitcheri* populations contribute to the population growth rate?

**Chapter II. Population Viability Analysis**

**Background**

Population Viability Analysis (PVA) has an important role in defining and measuring the success of threatened plants as well as contributing to the emerging science of designing methods to analyze demographic monitoring data (Bell et al., 2003). The most common approach to PVAs for plants is the use of population matrix models to represent population dynamics as well as vital rates such as growth, stasis and fecundity (Damman & Cain 1998; Garcia 2008; Machinski, Baggs, Quintana-Ascencio & Menges, 2006). Matrix models are then used to create graphical representations of current and future trends in the population growth rate ($\lambda$). Crone et al. (2011) identifies over 400 published studies that successfully demonstrate the use of matrix models as a way to guide the understanding and management of plant populations by assessing population status and extinction risk. With matrix models it is possible to estimate median time to extinction (MTE), the average time it will take for a population to go extinct as well as the probability of extinction ($P_E$), the cumulative extinction risk of a population at a particular time period (Damman & Cain, 1998). Demographic models allow for an in depth assessment of the current fates of the individuals of a population from emergence to death, that can then be used to develop future conservation, recovery and management strategies, and identify those areas of a species' life history that are the most vulnerable (Caswell, 2001).

I sought to determine the degree to which the addition of reintroduced populations increases the Indiana Dunes' *C. pitcheri* metapopulation viability. I expected that the reintroduced populations of *C. pitcheri* have improved the population growth rate of Indiana Dunes' metapopulation because an increased number of local populations will increase the number of potentially reproductive individuals in the metapopulation. The addition of two populations will also decrease the probability that stochastic processes

will affect all populations simultaneously, resulting in a higher probability of the species persistence over a greater length of time. The use of projection matrices is a common approach to quantitatively predict the probability of persistence ($P_P$) or extinction ($P_E$) and median time to extinction (MTE) (Schwartz, 2003).

**Methods**

**Study Site**

The study sites (Fig.1) are located along the southern tip of Lake Michigan in the Indiana Dunes National Lakeshore and Indiana Dunes State Park near Porter, Indiana. This study incorporated up to 23 years of demographic data from the native and reintroduced populations which have been monitored every year since 1988 except for 1995 and 1996. The five study sites consist of three native populations which are known as State Park Big Blowout (SPBB), Miller High Dunes (MIHI) and West Beach (WEBE) where 1000 m$^2$ fixed plots were created in 1988. The reintroduced sites, Ogden Dunes East (ODEAST, 150 m$^2$) and Ogden Dunes West (ODWEST, 225 m$^2$), were created in 1994 using 1800 seeds each through the process of broadcast and burial at 1 cm deep (U.S. Fish and Wildlife 2002). McEachern  (1992) calculated the succession index for each population site as the weighted average of American marram beach grass (*Ammophila breviligulata)*, sand reed *(Calamovifa longifolosa)* and little bluestem (*Andropogon scoparius*) (Fig.2). Each year, monitors identified and tagged each *C. pitcheri* plant, recording its location from a central stake as well as size (root crown diameter), class (flowering plant, juvenile or seedling), mortality, and number of flowering heads. The mean, standard deviation and range of plant population abundances are as follows State Park Big Blowout ($\bar{x}$ =33.43±*SD* 29.91, range=1-84), Miller High Dunes ($\bar{x}$=95.30±*SD* 20.94, range=36-211), West Beach ($\bar{x}$=160.21±*SD* 158.96,
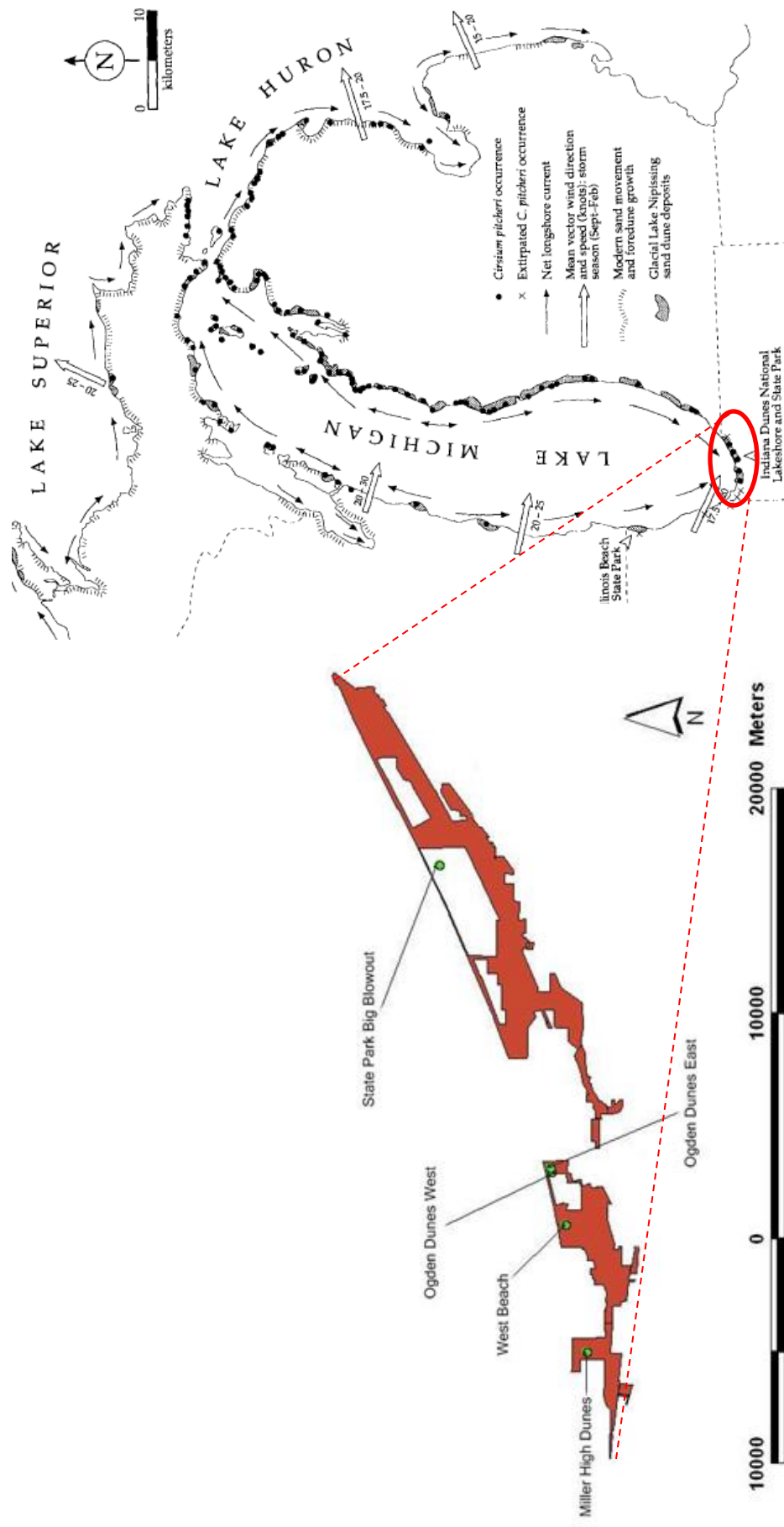
**Figure 1.** Map of *Cirsium pitcheri* survey sites at Indiana Dunes National Lakeshore and range map.(Adapted from McEachern et al 2004).
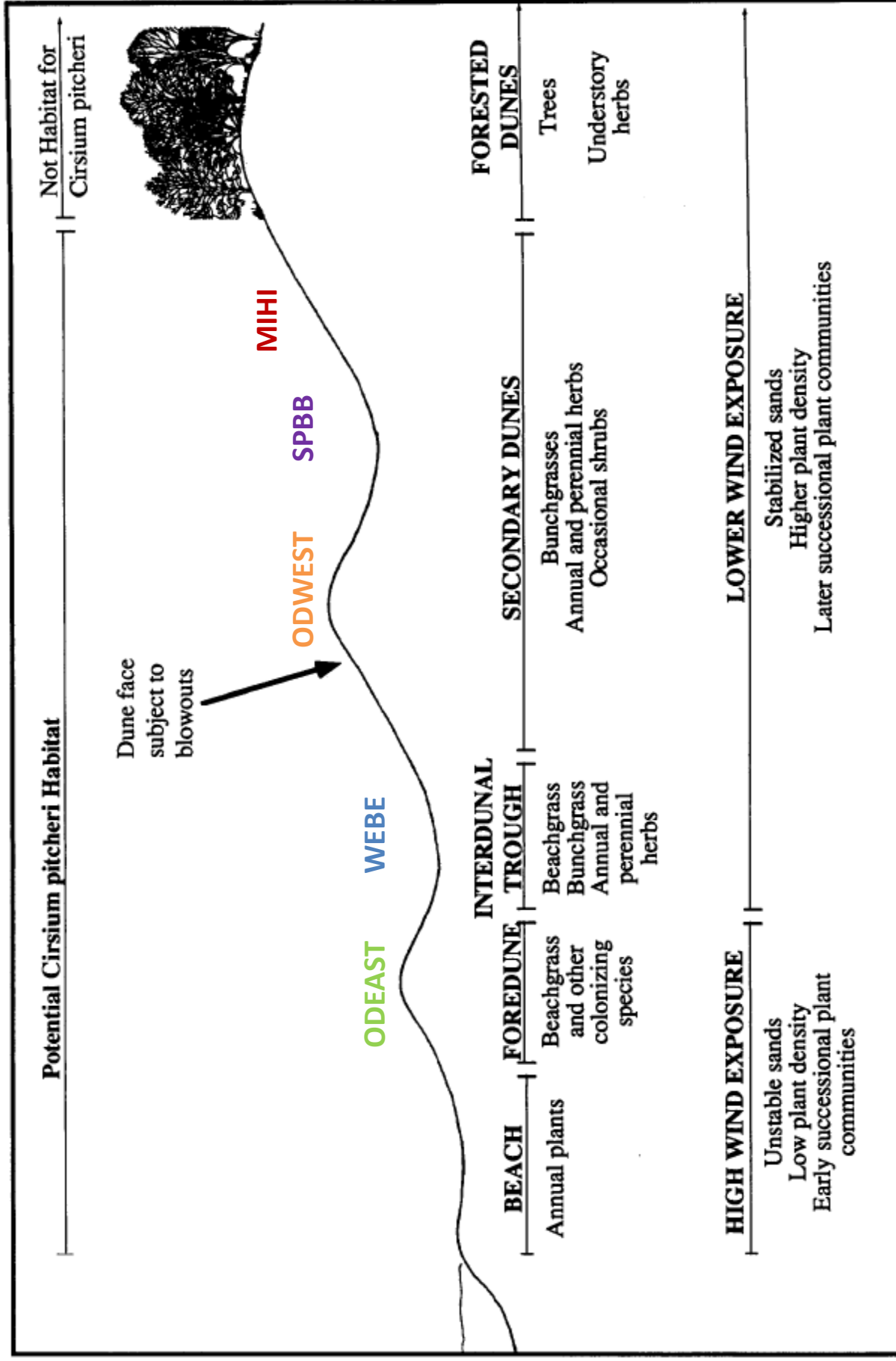
**Figure 2.** Indiana Dunes *Cirsium pitcheri* study populations overlaid according to current habitat and succession index onto generalized dune landscape . (Adapted from McEachern 1992) Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).

range=28-554), Ogden Dunes East ($\bar{x}$=65.71±*SD* 54.33, range=47-108), Ogden Dunes

West ($\bar{x}$=84.57±*SD* 46.66, range=2-195).

**Plant Stage/Size Classification**

I assigned each plant to a stage class based upon root crown diameter size using

the Moloney Algorithm, which determines cutoffs for size classes based on the size

which has the smallest combined sample error (error caused by observing a subset of a

population instead of the whole population) and distribution error (a measure of the

deviation of the sample population from the expected value) (Moloney, 1986). I used a

different method to determine the lower size limit of the pre-flowering class for each

population by comparing observed and expected numbers of flowering plants and non-

flowering plants along a range of test diameters (mm).  The expected number of plants in

each category was determined by placing those plants under the test cutoff diameter in

the non-flowering category and those plants at or above the test diameters as flowering

plants. I chose the pre-flowering lower size limit, using the test diameter value with the

maximum percentage of correct predictions.   The six stage-size classes are as follows;

Seedlings, J1 (Small Juvenile), J2 (Medium Juvenile), J3 (Large Juvenile), J4 (Pre-

Flowering) and A (Flowering) (Table 1).

**Projection Matrix Construction**

Following Caswell (2001), I created 87 population projection matrices from the

demographic monitoring data, where matrix **A** is a function of the size classes (**n**) where

**n** is a vector of size class abundances for the time interval of one year (*t*).

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

Matrix elements ($a_{ij}$) are defined as the transitions from size class *j* to size class *i* during a

one year interval creating matrices that resemble Table 2, where transition frequency

values vary between 0 and 1. These frequencies are obtained by dividing the number of

**Table 1**. Stage classes and Moloney size class (mm) for each of the five Indiana Dunes *Cirsium pitcheri* populations. Miller High(MIHI), Ogden Dunes East(ODEAST), Ogden Dunes West (ODWEST), State Park Big Blowout(SPBB), West Beach (WEBE)

| Populations | Stage-Size Classes | | | | | |
|---|---|---|---|---|---|---|
| | S | J1 | J2 | J3 | J4 | A |
| MIHI | 1st year | <3.7 | 3.8-5.6 | 5.7-10.0 | >10.0 | Flowering |
| ODEAST | 1st year | <4.4 | 4.5-7.2 | 7.3-12 | >12.0 | Flowering |
| ODWEST | 1st year | <4.5 | 4.6-7.0 | 7.1-12.0 | >12.0 | Flowering |
| SPBB | 1st year | <4.3 | 4.4-5.5 | 5.6-9.0 | >9.0 | Flowering |
| WEBE | 1st year | <4.0 | 4.1-7.0 | 7.1-15.0 | >15.0 | Flowering |

Seedling (S), Small Juvenile (J1), Medium Juvenile (J2), Large Juvenile (J3), Pre-flowering (J4), Adult (A)

**Table 2.** Projection matrix of possible transitions of *Cirsium pitcheri* stage-size classes[a] where matrix elements[b] ($a_{ij}$) 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($F_{ij}$)

| $t+1$ | $t$ | | | | | |
|---|---|---|---|---|---|---|
| | 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] Size classes defined for each population in Table 1
[b] $j$ is the current year $t$ and $i$ is the year $t+1$

plants that move from one stage at time (*t*) to another stage at time (*t* + 1) by the total

number of plants in that column. Each frequency corresponds to the growth of plants to

larger size classes (G), stasis of plants in their same classes (S) as well as regression of

plants to smaller size classes (R) (Fig. 3). Fecundity values can exceed 1, calculated by

dividing the number of seedlings from (*t*+1) by the number of flowering plants of the

previous year (*t*). The 87 matrices created for the five populations included 21 matrices

each for Miller High Dunes, State Park Big Blowout and West Beach, 13 matrices for

Ogden Dunes East and 11 matrices for Ogden Dunes West. Though the restorations

started in 1994, each plant was not tagged and recorded until 1999 for Ogden Dunes East

and 2000 for Ogden Dunes West therefore complete matrices were not able to be

completed before then.


**Model Validation**

In order to validate population projections, I created mean transition matrices and

standard deviation matrices using the matrices from the years 2000-2006 for each of the

five populations as these were the first six years in which all five populations had

complete mean and standard deviation matrices and allowed a remaining six years to

compare the projections to actual data. I used Ramas Metapop *v. 4.0* (Akcakaya, 2002) to

project  population abundances six years into the future with the model parameters of

demographic stochasticity, lognormal environmental stochasticity to reduce truncation

bias, no density dependent effects, no dispersal (because habitat fragmentation prevent

this), quasi-extinction level of zero and 1000 replications. I used 2006 observed values of

abundance and stage distribution in each population for initial values for the first year of

the model. Projected abundances were than compared to observed abundances to

**Figure 3.** Life cycle diagram of Indiana Dunes *C. pitcheri* Metapopulation. Colors indicate transitions as represented by matrix. Red-Regression, Orange-Stasis, Green-Growth, Purple-Fecundity. Size of blue ellipses is an indication of the abundance of plants in each stage.
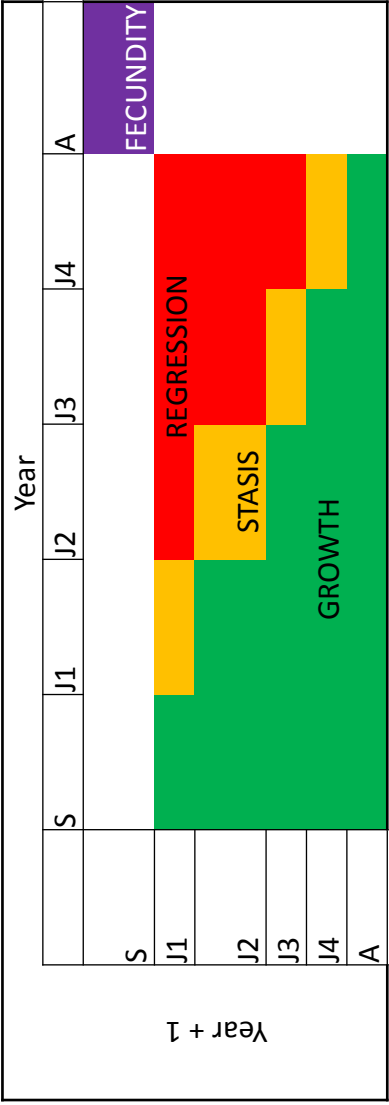
determine whether the observed values fell within the 95% confidence intervals of the projected values.

**Metapopulation Viability Analysis**

I created mean matrices with standard deviations using all of the data collected for each population to project 50 years (starting from 2012) using the same parameters as above. The initial 2012 observed abundances were used to estimate the cumulative probability of extinction throughout the years in order to find the median time to extinction (MTE) as well as 5% threshold of extinction probability. I determined the probability of extinction for each of the populations separately, for the three native populations combined (MIHI, WEBE, SPBB), the addition of each of the two reintroduced populations singly to the native populations and finally the whole metapopulation consisting of all five populations. To determine the degree to which the introduction of more populations will affect extinction probability, I simulated the creation of new reintroduced populations with 1800 seeds: the number of seeds that were used to start each of the original two reintroductions in 1994. The mean and standard deviation matrices of the two reintroduced populations were used as predictors of the behavior of populations introduced in a habitat at a similar successional stage. Two scenarios are presented: the addition of populations similar to Ogden Dunes East (an early-successional habitat) and Ogden Dunes West (a mid-successional habitat). I gradually increased the number of populations added (in increments of 1 up to 10, then 5 up to 50 and finally 10 up to 100 populations) in order to determine how many populations would be needed to increase metapopulation viability for 50 years without additional human intervention. I also simulated the one time enhancement of the existing populations with 1800 seeds in order to determine how enhancements compared to the introduction of new populations.

**Results**

The growth rate of the five *C. pitcheri* populations varied from year to year (Appendix A1). The growth rates of each population were normally distributed and the analysis of variance (ANOVA) showed that the growth rates differed among the populations, ($F_{(4,80)}$=5.903, *p*=0.000). State Park Big Blowout (0.448 ± *SD*=0.481) had the lowest mean population growth rate yet it was not significantly different from Ogden Dune West (0.756 ± *SD*=0.306) (Fig. 4). Ogden Dunes East (0.960 ± *SD*=0.188) had the greatest mean λ though it is not significantly different from Miller High Dunes (0.902± *SD*=0.277), Ogden Dunes West or West Beach (0.787 ± *SD*=0.347). Population projection trends tend to follow the same trajectory from 2006-2012 as the observed abundances with Miller High Dunes, Ogden Dunes East and Ogden Dunes West abundances falling within the 95 % confidence intervals for at least some years; however, State Park Big Blowout and West Beach projections were significantly lower than the observed abundances (Fig 5 and 6). The observed abundances fall within the maximum projected simulation abundance values for all of the years of West Beach and the first three years of State Park Big Blowout with maximum points not shown exceeding axis range values (Fig. 6).

The probability of extinction varied among the five populations with State Park Big Blowout having a faster rate of extinction and Miller High Dunes having the slowest rate of extinction. Miller High Dunes has the highest median time to extinction (MTE) of 14.3 years and State Park Big Blowout has the lowest MTE of 4.2 years (Fig. 7). West Beach, Ogden Dunes West and Ogden Dunes East, respectively had MTE of 7.1 years, 6.1 years and 11.9 years (Fig. 7). The addition of the reintroductions increased the MTE of the metapopulation (Fig 8). The three native populations had a metapopulation MTE of 15.6 years, the addition of ODWEST to the native populations had a MTE of 16.0 years;
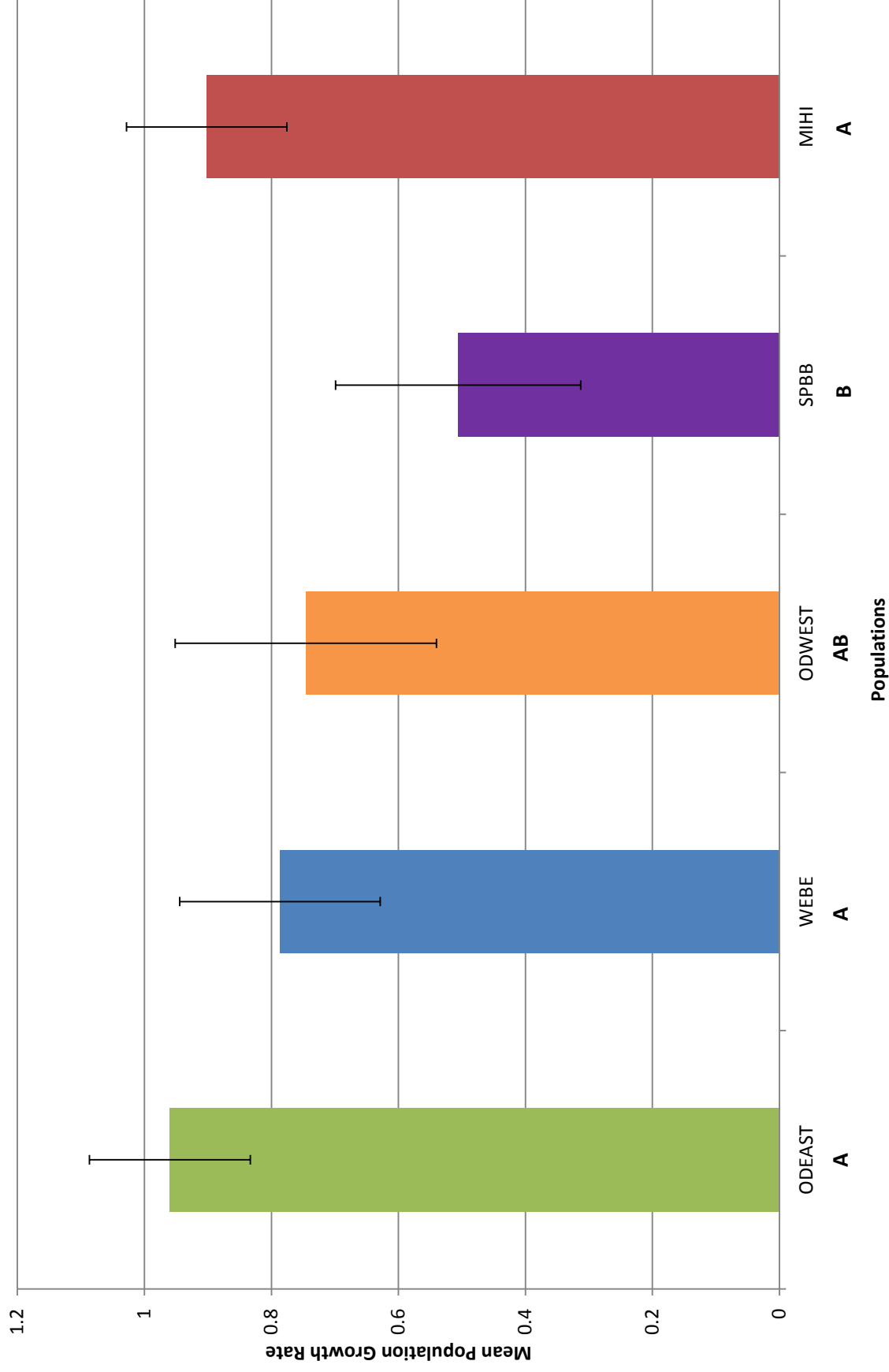
**Figure 4.** Mean population growth rates (λ) of the five *Cirsium pitcheri* populations with 95% CI. Groups sharing common letters are not significantly different from each other based on Tukey HSD multiple comparisons with α=0.05. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).

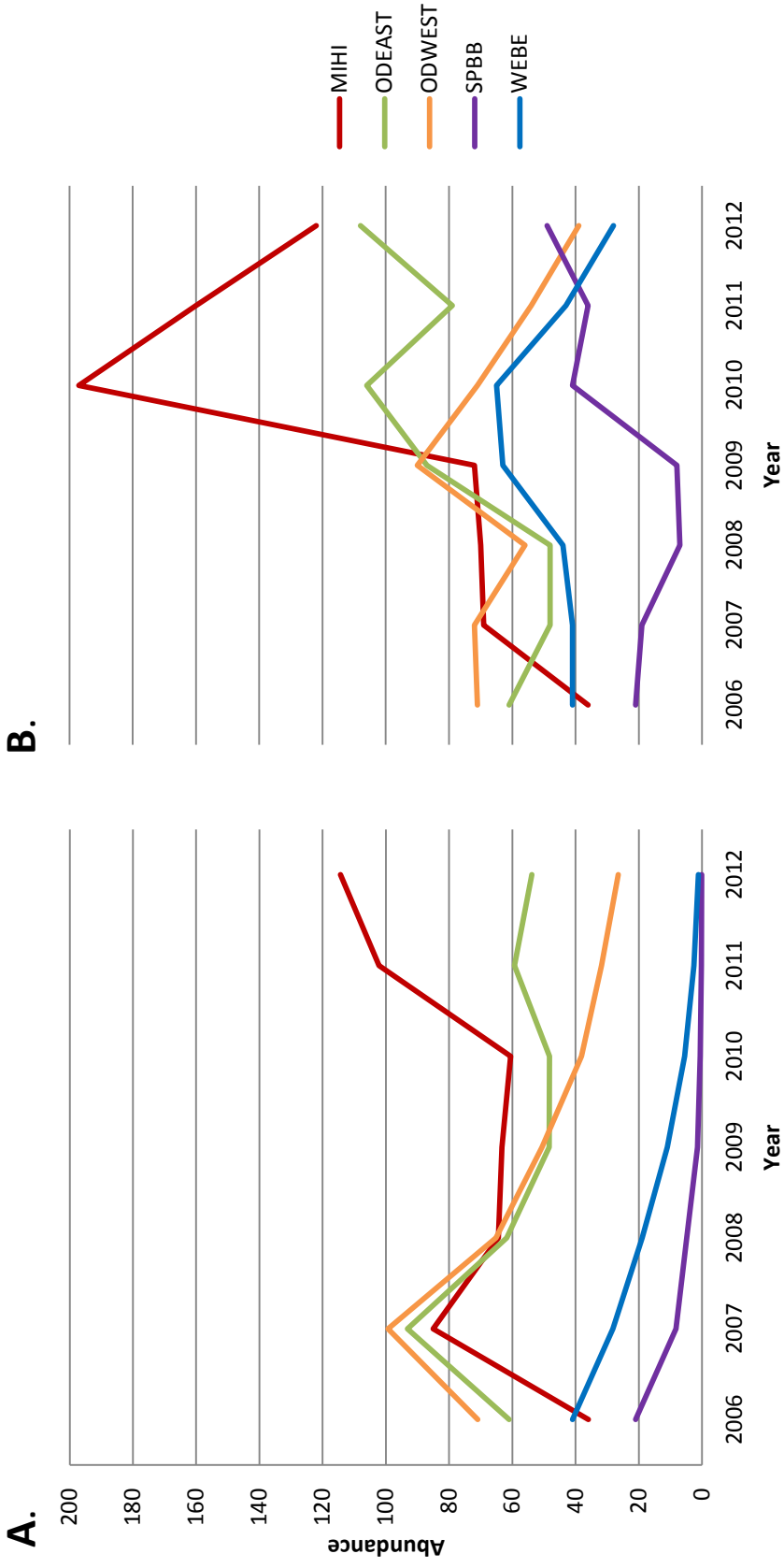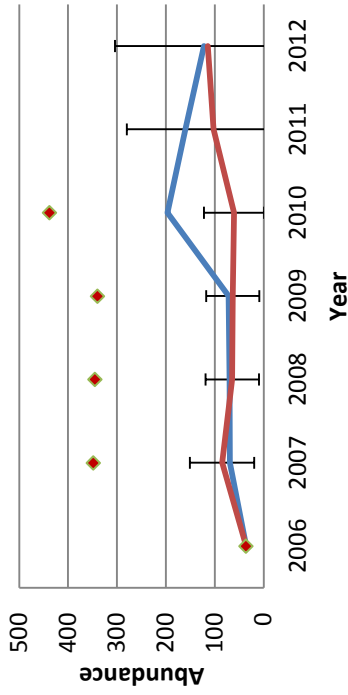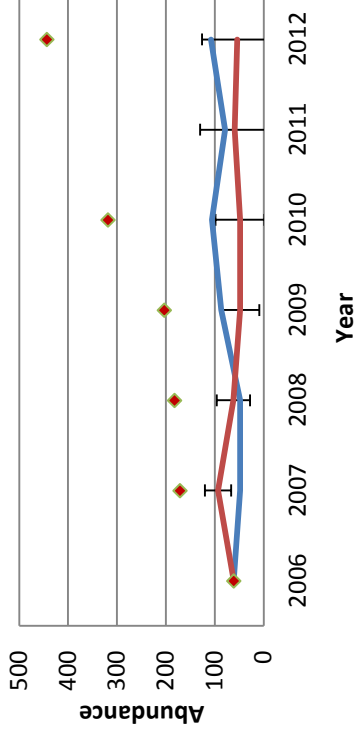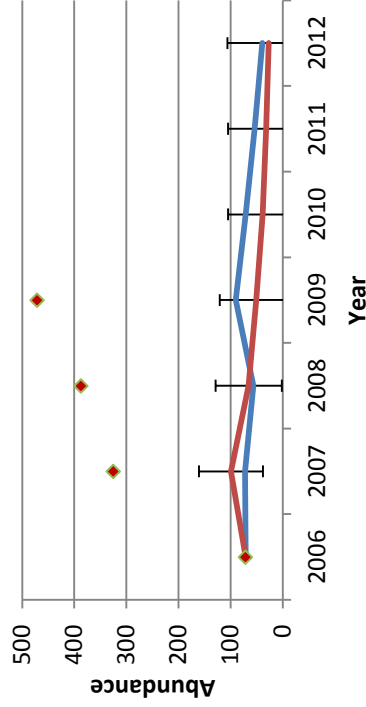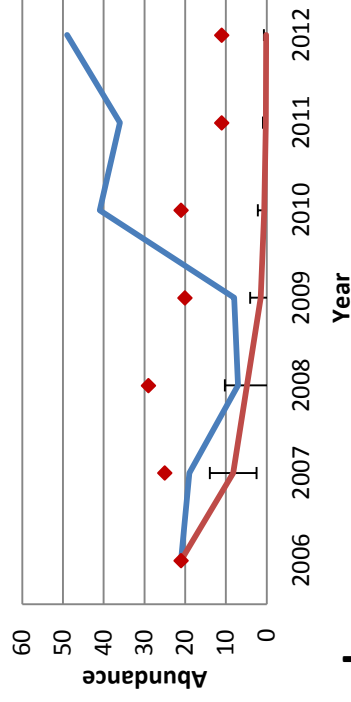**Figure 5 (A)** Mean *Cirsium pitcheri* population abundance projection 6 years into future using mean matrices and SD matrices from 2000-2006. **(B)** Mean observed population Abundances for years 2006-2012. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
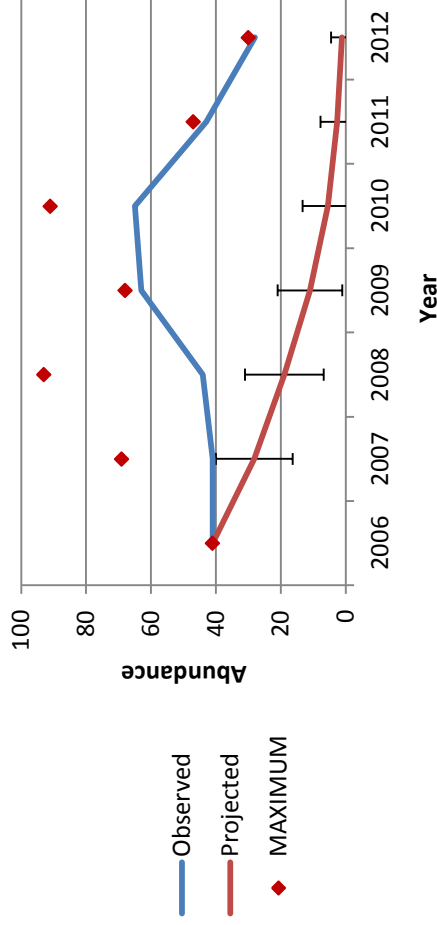
**Figure 6.** Observed vs. Projected abundances for 5 populations in Indiana Dunes *Cirsium pitcheri* metapopulation with projected 95% CI of mean and maximum values at each time step. Maximum values not shown exceed axis range.
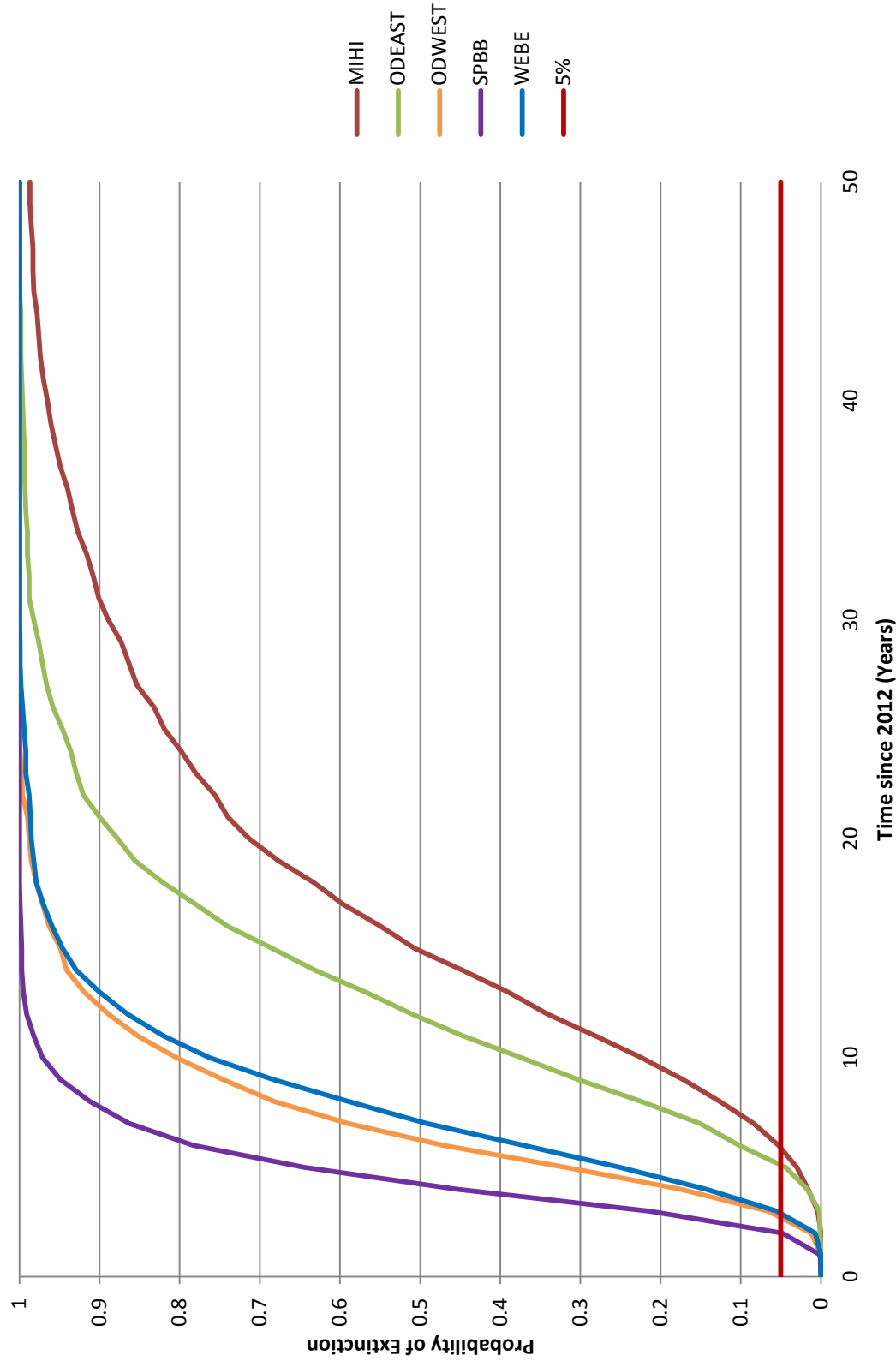
**Figure 7**. Cumulative Probability of Extinction since 2012 for 5 populations of *Cirsium pitcheri* within the Indiana Dunes Metapopulation. Median Time to Extinction lies at 50% probability. 5% line indicates threshold of acceptable extinction threat. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
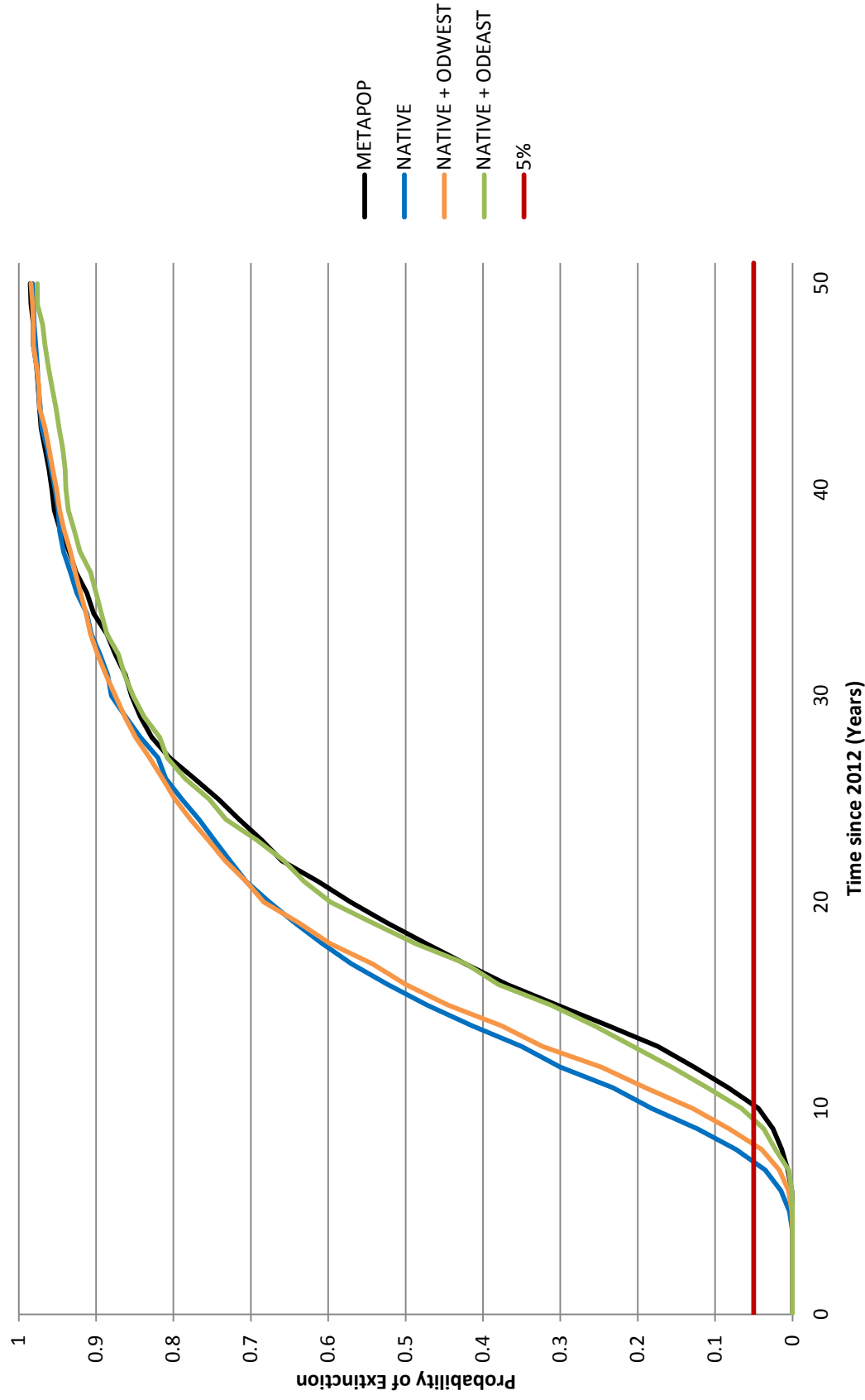
**Figure 8.** Probability of Extinction comparison of population Native (without reintroductions), Native + Ogden Dunes West (ODWEST), Native + Ogden Dunes East (ODEAST) and Metapopulation (METAPOP) with both native and reintroduction populations. Median Time to Extinction lies at 50% probability. 5% line indicates threshold of acceptable extinction threat.

the addition of ODEAST to the native populations had a MTE of 18.3 years and the overall metapopulation all five subpopulation had a MTE of 18.6 years (Fig 8). Increasing the number of populations to the metapopulation by introducing populations similar to Ogden Dunes East gradually increased the number of years the probability of extinction remained below the threshold of 5%. On average it would take 10 years for the probability of extinction to rise above 5% whereas the addition of one population resulted in an increase to 13 years, two populations resulted in 16.5 years, five populations resulted in 20 years, 50 populations resulted in 35 years and 100 population results in 40 years before the population exceeds the 5% extinction threshold (Fig. 9).

The addition of one population similar to Ogden Dunes West resulted in an increase to 12 years from a timeframe of 10 years before the population crossed the 5% threshold of extinction. Similar increases of two populations resulted in 14 years to the 5% extinction threshold, five populations resulted in 18 years, 50 populations resulted in 31 years and 100 populations resulted in 35 years (Fig. 10).

In contrast to reintroductions where a new population is established where no plants have been previously reported, enhancements are the addition of seeds or plants to existing populations (Bottin et al., 2007). A simulated one-time enhancement of 1800 seeds to existing populations with the exception of State Park Big Blowout improved the Indiana Dunes' metapopulation viability by increasing the time the metapopulation is below the 5% threshold of extinction as well as the increasing MTE (Fig. 11 and 12). The enhancement of Ogden Dunes East, Ogden Dunes West or West Beach increased the MTE to 21 years from 18 years whereas the enhancement of Miller High Dunes increased the MTE to 23 years.  There is no change in the metapopulation viability with the enhancement of State Park Big Blowout.
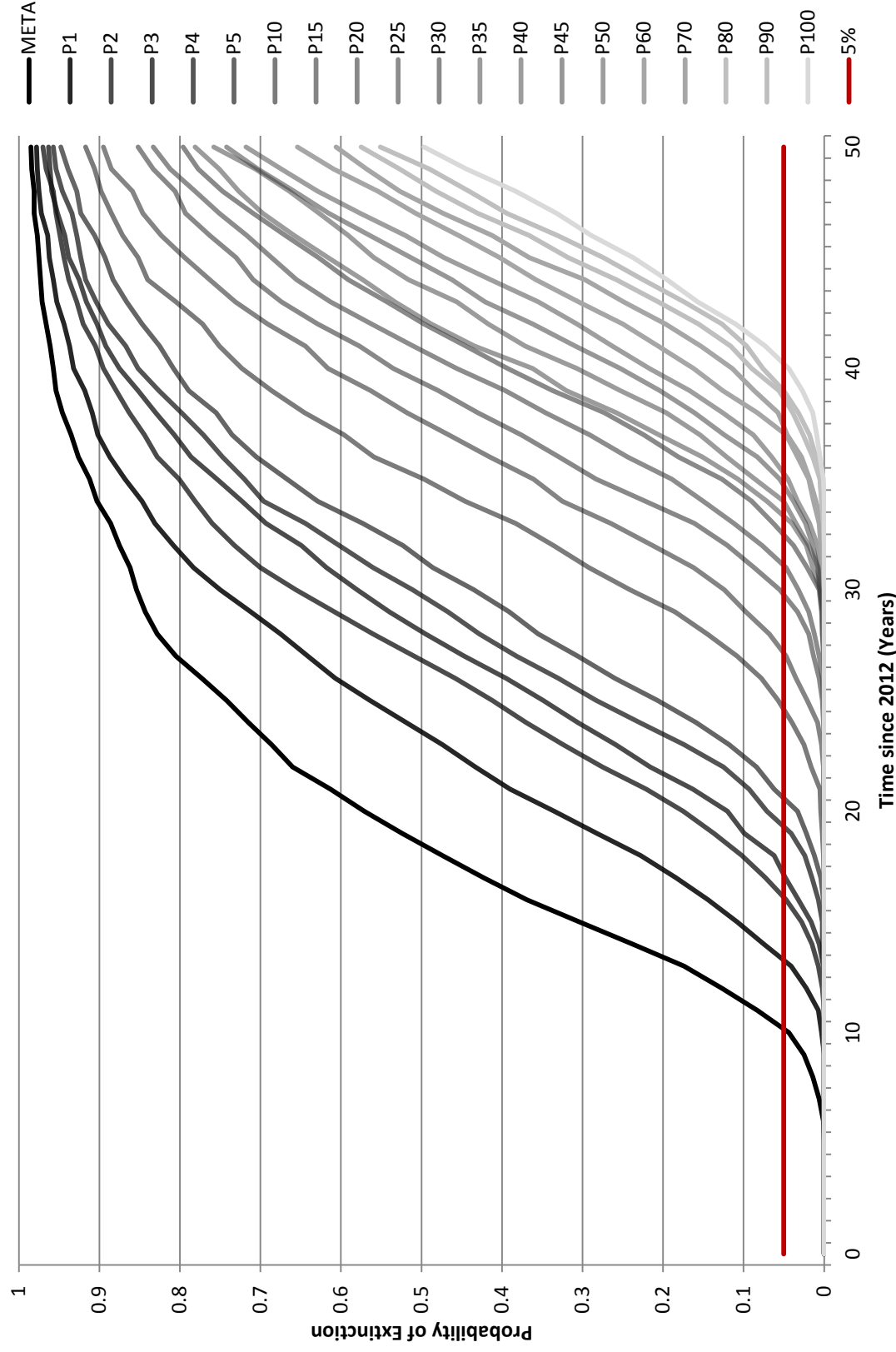
**Figure 9.** Probability of Extinction comparison of the addition of reintroduced *Cirsium pitcheri* populations to the Indiana Dunes Metapopulation started with 1800 seeds using Ogden Dunes East matrices. (P1-100 represents the number of populations added). Median Time to Extinction lies at 50% probability. 5% line indicates threshold of acceptable extinction threat.
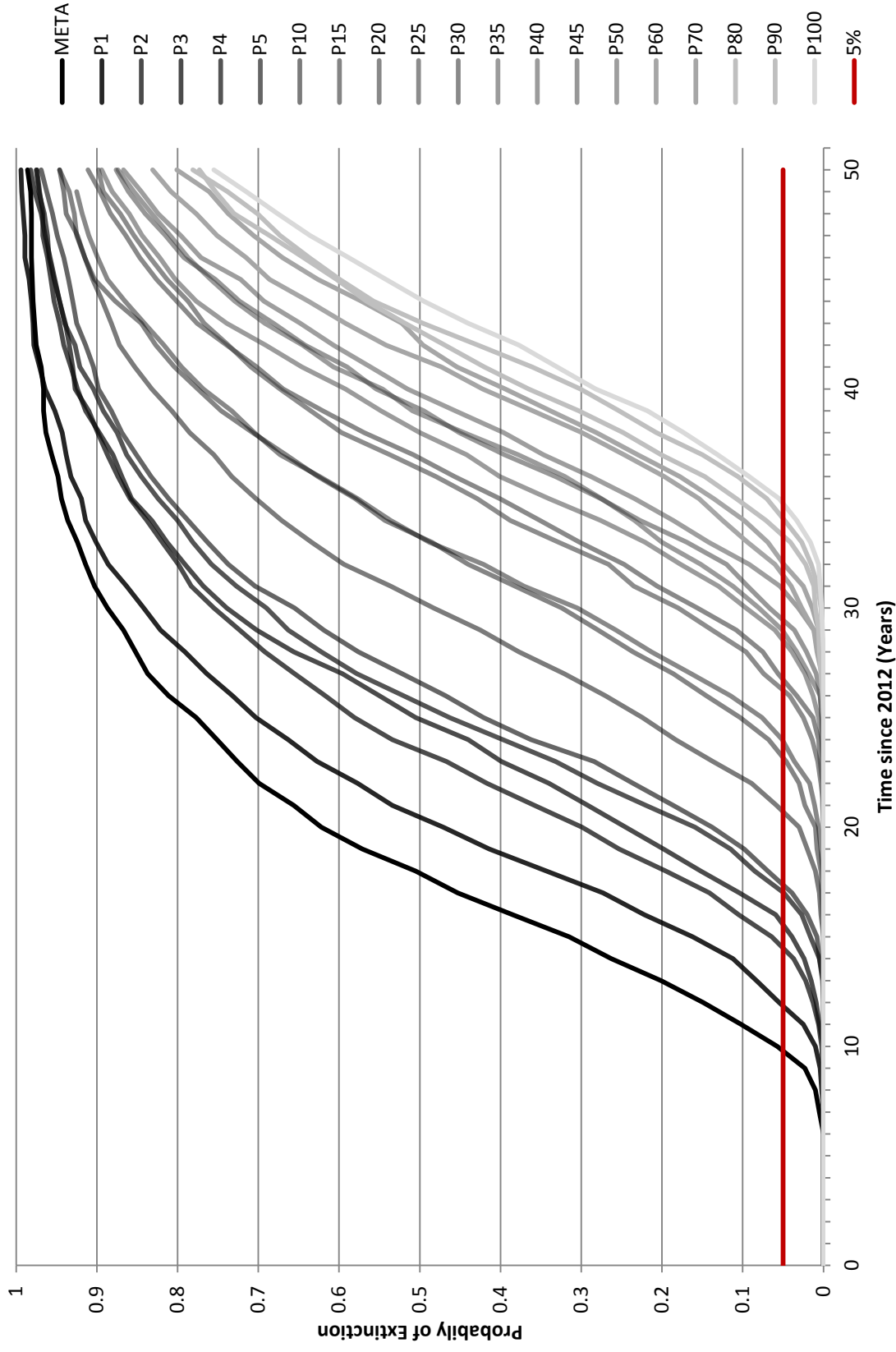
**Figure 10.** Probability of Extinction comparison of the addition of reintroduced *Cirsium pitcheri* populations to the Indiana Dunes Metapopulation started with 1800 seeds using Ogden Dunes West matrices. (P1-100 represents the number of populations added). Median Time to Extinction lies at 50% probability. 5% line indicates threshold of acceptable extinction threat.
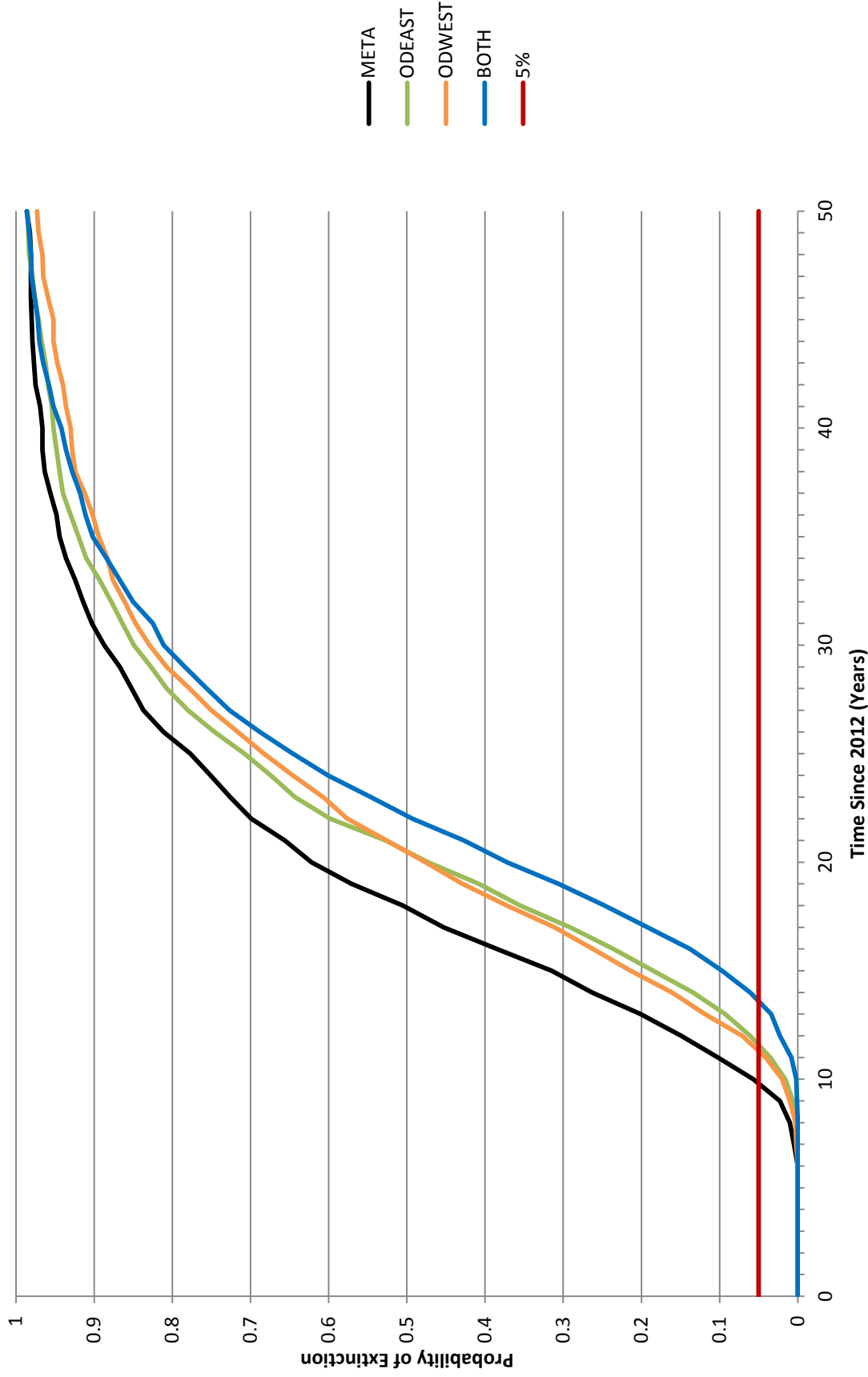
**Figure 11.** Probability of Extinction comparison of the addition of 1800 seed to reintroduced *Cirsium pitcheri* populations Ogden Dunes East (ODEAST) and Ogden Dunes West (ODWEST) to the Indiana Dunes Metapopulation. Median Time to Extinction lies at 50% probability. 5% line indicates threshold of acceptable extinction threat.
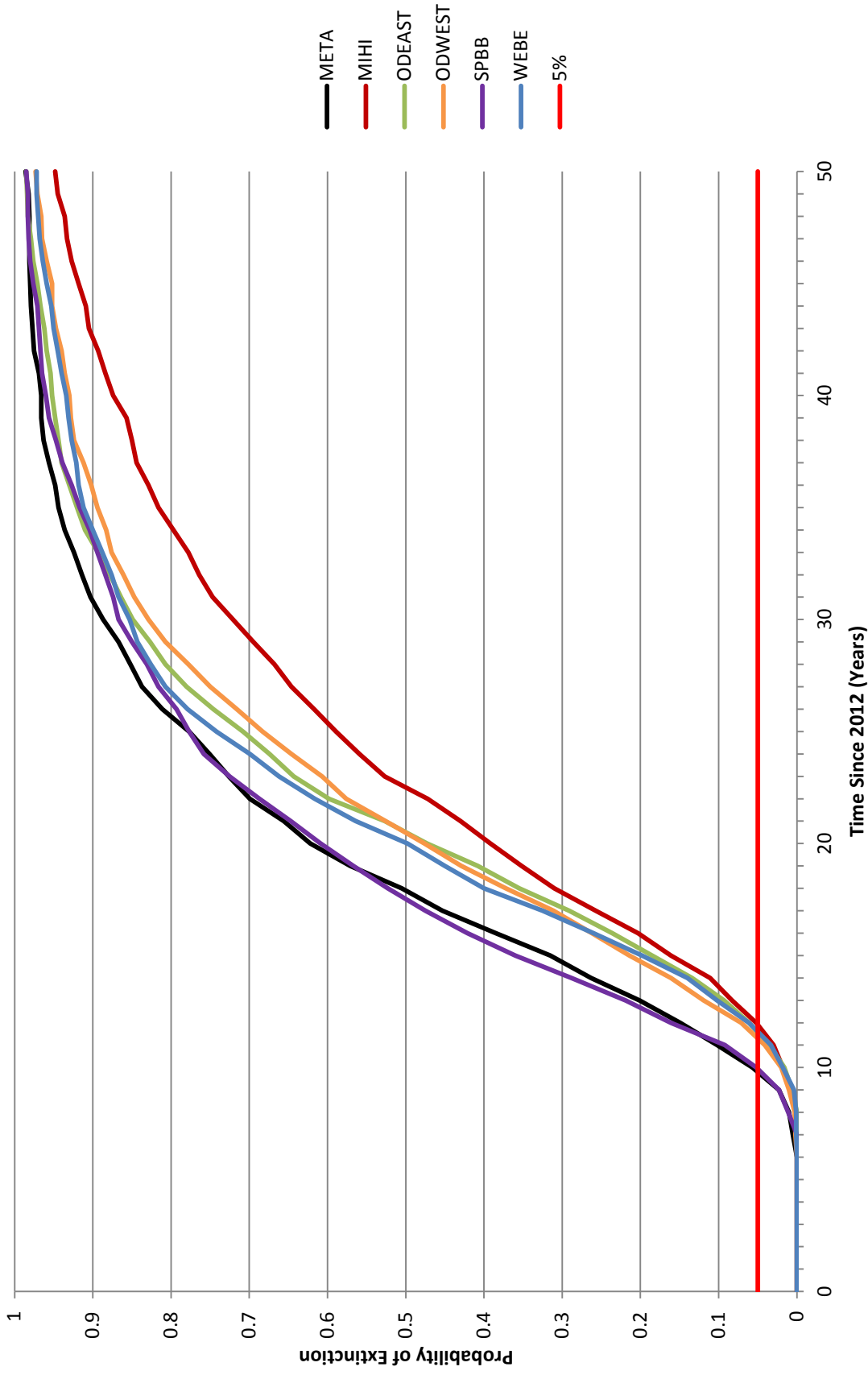
**Figure 12.** Probability of Extinction comparison of the addition of 1800 *Cirsium pitcheri* seeds to each of the five populations of the Indiana Dunes Metapopulation separately. Median Time to Extinction lies at 50% probability. 5% line indicates threshold of acceptable extinction threat. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).

**Discussion**

The addition of two *C. pitcheri* populations to the Indiana Dunes improved the viability of the species from a metapopulation perspective. The general consensus from the results is that all five populations are declining though the rates at which they are doing so varies. State Park Big Blowout had the lowest mean finite growth rate, resulting in the inability to make complete matrices for several of the latter years due to an insufficient number of plants and lack of representation of all 6 size classes. Observations from the site show that since 1988 this species has migrated outside of the boundaries of the fixed plot; nevertheless, monitors have tagged and recorded all plants up to 50 meters from the borders since 2008. *C. pitcheri* plants are poor dispersers with seeds falling within a 1 meter of the parent plants (McEachern, 1992); therefore I believe that the inclusion of the plants from out of the plot area demonstrates that the data from this site is a true representation of the entire population.

Ogden Dunes East had the highest mean finite growth rate, which was not surprising given the fact that *C. pitcheri* is thought to be favored in early successional dune habitats such as Ogden Dunes East (McEachern, 1992). However, Miller High Dunes growth rate is not significantly different form Ogden Dunes East yet it is on the opposite end of the successional index, ranking a little bit later than State Park Big Blowout. None of the five populations are very stable, with their growth rates spiking and declining erratically over the years. This coincides with previous observations of *C. pitcheri* exhibiting large yearly variability in density from variable seed establishment and juvenile survival (Rowland & Maun, 2001). Demographic stochasticity or chance events resulting in random differences between years, could be affecting the populations of Indiana Dunes, increasing the risk of extinction because of the small size of the populations (Boyce, 1992).Other contributing factors are herbivory and anthropogenic impacts. Herbivory is known to increase the time spent in the juvenile stages of the life

cycle due to the necessity to replace lost plant tissue. The extended time to reach flowering size can increase mortality risks from increase time spent exposed to environmental stresses (Rowland & Maun, 2001). Anthropogenic impacts include the altering of the habitat by recreational use, especially at the study site of the Indiana Dunes as well as accelerated erosion of Lake Michigan shorelines through the construction of offshore structures (McEachern et al., 1994).

A key question in population viability analyses is whether a population can persist on its own and for how long without intervention. I choose to model the five populations as a metapopulation in order to determine how long it would take for the entire species to be extirpated from this Indiana Dunes' metapopulation, but first it was necessary to determine whether my model would be reliable because there are many criticisms on the accuracy of PVAs (Coulson, Mace, Hudson & Possingham, 2001; Crone et al. 2011). Validation such as using earlier data and comparing it with data from latter years, can demonstrate the reliability of a model. Similar to Brook et al. (2000), I validated my model by dividing my data set in half using the first half of the data to model and compare with the last half. I used the first six matrices as the parameterization period to predict the population abundances for a forecast period of last 6 years in order to get an estimate on whether I should include density dependence, demographic stochastic and dispersal in the model. The purpose was to try to get projected abundance as close as possible to observed abundances with minimum confidence intervals.

The model turned out to be very simple, most likely because of the small population sizes (<200). I was able to parameterize the model with no density dependence effects since competition is not a factor. As stated before, all the populations exhibited seemingly random growth rates from year to year, so demographic stochasticity was included as well. Since *C. pitcheri* plants are poor dispersers and the length of time it would take for plants to migrate between populations would extend the project period, I

chose to not include dispersal as part of my model. I chose an extinction threshold of zero, to ensure that no plants remained in the population before it is considered extinct. This model (e.g., no demographic stochasticity, density dependence included, etc.), resulted in the closest prediction of population abundances as compared to other models, therefore this was the model chosen to proceed with my analysis.

The model tended to underestimate the abundances of each population, but the only significant differences were with State Park Big Blowout and West Beach. I attribute this to the quality of the matrices from 2000-2006, that were used for parameterization. The data used in this study is considered high quality with detailed yearly observations of each plant over a lengthy period of time and acceptable for PVAs. However, it is possible that the State Park Big Blowout population did not adhere to the criteria that the observation period should be similar to the future period in terms of vital rates for a PVA to be accurate and valid (Coulson et al., 2001). State Park Big Blow had a few years where the matrices consisted of all zeros due to the fact that some years did not have enough plants to create complete matrices. Therefore those matrices were not included as part of the mean and standard deviation matrices in an effort to reduce underestimation. The State Park Big Blowout population saw an increase from the year 2009 onward which coincided with the increased area in which the plants were monitored. I don't believe the model should be invalidated on the basis of State Park Big Blowout alone. West Beach observed abundances did not fall between the confidence intervals of the projected, the possible reason being that the parameterization period showed decreasing population growth rates but started to rise during the forecast period, a violation of modeling assumptions..

Population viability analyses are and will continue to be useful in conservation biology, by providing insight into management application, though caution must be used when modeling, since models are a simplified version of a very complex world (Reed et

al., 2002). By using cumulative probability of extinction, I was able to determine the trajectory of each population and determine which population is more at risk of going extinct sooner and therefore more in need of management. It is hardly a surprise that State Park Big Blowout has the greatest risk of extinction, though the time frame in which that is to occur is unexpected. In two years, the population will have exceeded the acceptable extinction threat threshold, with its extinction probability rising sharply.  The other populations are not that far behind with the last population, Miller High Dunes crossing that threshold six years from now. Looking at these populations independently provides just another perspective into the comparison of each individual population; however, the main objective is to determine whether the addition of the two reintroduced population had an effect on the metapopulation and to what degree.

Using only the three native populations as a reference point as to how the metapopulation would have behaved without the addition of the reintroduction, it is clear that the reintroductions had an impact in increasing the probability of persistence, albeit only increasing the time spent below the 5% threshold by a few years.  From this it is obvious that the two populations Ogden Dunes East and Ogden Dunes West contribute differently to the metapopulation, resulting in additional questions. For example, how many populations would this population need to increase the viability and keep the threat of extinction below 5% for 50 or 100 years?

I performed a few analyses from a management perspective in order to determine the different ways the viability of Indiana Dunes' *C. pitcheri* can be improved. Introducing new populations similar to either reintroduction would result in increased persistence of the Indiana Dunes' metapopulation. There are some problems with this approach such as finding the habitat to start these populations and harvesting enough seeds due to the observation of levels of fecundity for this species. For me to suggest that adding 100 new populations in a habitat similar to Ogden Dunes East with a startup of

1800 seeds a piece as a strategy to ensure that this population would persist for the next 40 years is unthinkable since that would require 100 suitable sites at an early successional stage as well as 180,000 seeds. The same goes for Ogden Dunes West though the number of years the metapopulation is projected to remain below the 5% threshold of extinction decreases to about 35 years.  The biggest increase in viability occurs with the first few introductions, before it becomes fruitless where the time and effort of adding new populations does not show any significant improvement in metapopulation viability. Therefore I suggest that instead of adding new populations, effort might be better spent trying to protect the populations already established. Viability can be improved through enhancement of existing populations resulting in a similar improvement as adding new populations, without the added work of procuring suitable habitat for a new population. The question then becomes, should we enhance the native population as a way to improve their viability and coincidently the contribution to the overall metapopulation viability?

Putting aside the issue as to whether it is correct to enhance native populations by introducing seed sources from other populations, I would recommend that if there were resources that allowed one population to be supplemented with additional seed, that it be Miller High Dunes because that one site has the potential to increase viability just as much as adding seeds to both reintroduction sites. Of course enhancing the populations with seeds is assuming that low fecundity is the main reason these populations are declining. In order to make informed management decisions, it is essential to perform more than one type of population viability analysis since conservation actions require time, money and effort and therefore management decisions must be based upon knowing the pros and cons of all possible scenarios. To my knowledge there have been few studies that involve plant restorations (Bladow, 2010; Bottin el al., 2007; Bowles et al., 1993) and even fewer that have compared restorations to their native counterparts (Bell et al

2003; Colas et al. 2008); and I found none that have examined whether adding restorations to a population that exhibits metapopulation dynamics such as *C. pitcheri* would improve the metapopulation viability.

**Chapter III.  Life Table Response Experiments**

**Background**

Life Table Response Experiments (LTRE) are an additional method for examining PVA and  used to investigate how a population responds to changes by decomposing the population growth rates ($\lambda$) into contributions made by each vital rate(growth, stasis & fecundity) of a species (Frevile & Silvertown, 2005). For example, Jacquemyn, Brys, Davision, Tuljapakar & Jongejans (2011) applied vital rate LTRE analysis to two populations of the perennial grassland herb *Primuta veris* in order to investigate the effects of herbivory on population dynamics and assess the contributions of mean vital rates, variances, and correlations to the population growth rate ($\lambda$). The results showed the effect of low fecundity or seed production was balanced by stasis or population maintenance (Jacquemyn et al., 2011). LTRE can also show yearly comparisons between populations such as Mondragon's (2009) analysis of the orchid *Guarianthe aurantica*, which found that $\lambda$ was slightly higher in 2005-2006 than 2004-2005 because of positive contributions of stasis of individuals for the 2005-2006 transition year as compared to 2004-2005. LTRE's are effective in understanding population dynamics and are best used in context with other PVA methods such as projection matrices and modeling.

My second specific aim is to determine if there is a difference between the vital rates of natural and reintroduced populations of *C. pitcheri*. Determining the difference between the vital rates of natural and reintroduced populations of *C. pitcheri* in Indiana Dunes will allow for an explanation of how the vital rates among the populations contributed to the metapopulation growth rate ($\lambda_M$). In plants, LTRE analyses have been used to assess demographic future responses of treatments as well as allow the dissection of how $\lambda$ varies with changes in different vital rates and decomposing the variations in $\lambda$ into contributions from multiple demographic rates. Few comparisons have been made

between multiple populations of the same species living in contrasting environments (Fréville & Silvertown, 2005).

**Methods**

In order to determine if there is a difference between the vital rates of the natural and reintroduced populations, I conducted life-table response experiments (LTRE) using the POPBIO package (Stubben & Milligan 2007) in R 2.15.2, a free software programming language and software environment for statistical computing and graphics ( R Code Team 2012). I 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. Following Caswell (2001), the growth rate of each population ($\lambda^{(m)}$) is expanded as a function of the $a_{ij}$ around $\mathbf{A}^{(r)}$ where the terms in the summation (Eq.1) are the contributions of $a_{ij}$ to the effect on lambda ($\lambda$) of the different populations on the metapopulation growth rate. Contributions ($\mathbf{C}^{(m)}$) are produced from the Hadamard product; a binary operation that produces a matrix, where each element ($ij$) is the product of the element ($ij$) of two matrices of the same dimension: the matrix of differences ($\mathbf{D}^{(m)}$) and the sensitivity matrix ($\mathbf{S_A}^{\dagger}$) (Eq. 2). The matrix of differences ($\mathbf{D}^{(m)}$) is the difference between the treatment matrix and the reference matrix (Eq. 3). Sensitivities ($\mathbf{S_A}^{\dagger}$) of $\lambda$ to changes in $a_{ij}$ are evaluated relative to a matrix that is midway between $\mathbf{A}^{(m)}$ and $\mathbf{A}^{(r)}$ (Eq. 4 and Eq. 5).

$$\lambda^m \approx \lambda^r + \sum_{i,j}\left(a_{ij}^{(m)} - a_{ij}^{(r)}\right)\frac{\partial\lambda}{\partial a_{ij}}\bigg|_{A^{\dagger}} \quad m=1,\ldots,N \qquad \text{(Eq. 1)}$$

$$\mathbf{C}^{(m)} = \mathbf{D}^{(m)} \circ \mathbf{S}_{A^{\dagger}} \qquad m=1,\ldots,N \qquad \text{(Eq. 2)}$$

$$\mathbf{D}^{(m)} = \mathbf{A}^{(m)} - \mathbf{A}^{(r)} \qquad m=1,\ldots,N \qquad \text{(Eq. 3)}$$

$$S_{A^\dagger} = \left(\frac{\partial \lambda}{\partial a_{ij}}\right) \hspace{4cm} \text{(Eq. 4)}$$

$$A^\dagger = \left(A^{(m)} + A^{(r)}\right)/2 \hspace{2cm} m=1,\dots,N \hspace{2cm} \text{(Eq. 5).}$$

I performed LTRE of the population types Native and Reintroduced by dividing the matrices with respect to their population type with 63 matrices categorized as Native (SPBB, MIHI, WEBE) and 24 matrices categorized as Reintroduced (ODEAST, ODWEST). Once the source effects were calculated, I compared the population types using randomization without replacement of the matrices into either category of "Native" or "Reintroduced" with 1000 replications in order to calculate 95% confidence intervals and $p$ values in order to determine whether each population source effect was different from each other. Finding no difference between the population types, I repeated this randomization procedure using each of the five populations separately in order to determine if there was any difference in the source effects of each separate population. The source effects were further divided into each contribution of the 36 transition elements of the matrix with the significance of the each transition determined using randomization. The matrix elements were also summed with respect to the combination of vital rates that make up growth, stasis, fecundity or regression in order to decompose how each aspect of the life history contributed to the population growth rate of each population.

I performed a Bivariate Correlation to determine whether there was a correlation between the LTRE year contributions to the metapopulation growth rate ($\lambda_M$) and weather variables such as monthly temperature (mean, minimum, maximum), total monthly precipitation and total snowfall. Since demographic data was collected in June of each year, the years of each transition matrix is viewed as cycling from July (of the previous year $t$) to June (of the current year $t+1$) therefore weather data was arranged to mimic this

pattern for each particular matrix. Normality assumptions were met and Pearson's two-tailed correlation was used at $\alpha=0.05$.

**Results**

Reintroductions had a positive contribution to the metapopulation growth rate ($\lambda_M$) as compared to the negative contribution of the native populations; however, neither of these contributions were significantly different from the pooled metapopulation (Fig. 13, $p>0.05$). Miller High Dunes had a significantly positive contribution (0.10, $p<0.001$) on $\lambda_M$ whereas State Park Big Blowout had a significantly negative contribution (-0.27, $p<0.001$) on the $\lambda_M$ (Fig. 14). Ogden Dunes East, Ogden Dunes West and West Beach did not differ significantly from each other in their contributions to the Indiana Dunes' metapopulation growth rate. The contribution of each matrix element of Indiana Dunes' metapopulation varied in its contribution to the overall metapopulation growth rate (Appendix B1) Only a portion of the matrix transition elements were significant in their contribution to lambda (Fig 15). State Park Big Blowout's adult-seedling (A-S) transition had the greatest significantly negative contribution to $\lambda_M$ (Fig. 15). Other significant negative contributions for SPBB included seedlings to medium juveniles (S-J2), small juveniles to medium juveniles (J1-J2), stasis of medium and large juvenile (J2-J2 and J3-J3), growth of medium juvenile to adults ( J3-A) and retrogression of pre-flowering plant to medium and large juveniles ( J4-J2 and J4-J3). Positive significant contributions of State Park Big Blowout vital rates to $\lambda_M$ include transitions of seedling to large juveniles (S-J3), small juveniles to pre-flowering (J1-J4) and large juvenile to pre-flowering (J3-J4).

Miller High Dunes had several significantly positive contributions such as growth of seedlings to medium juveniles (S-J2), medium juveniles and large juveniles to pre-flowering (J2-J4, J3-J4). Ogden Dunes East had both positive (S-J2, J1-J2, J3-A, J4-A) and negative significant contributions (J1-J1, J2-J1, J2-J2 and J3-J3) to $\lambda_M$.   West
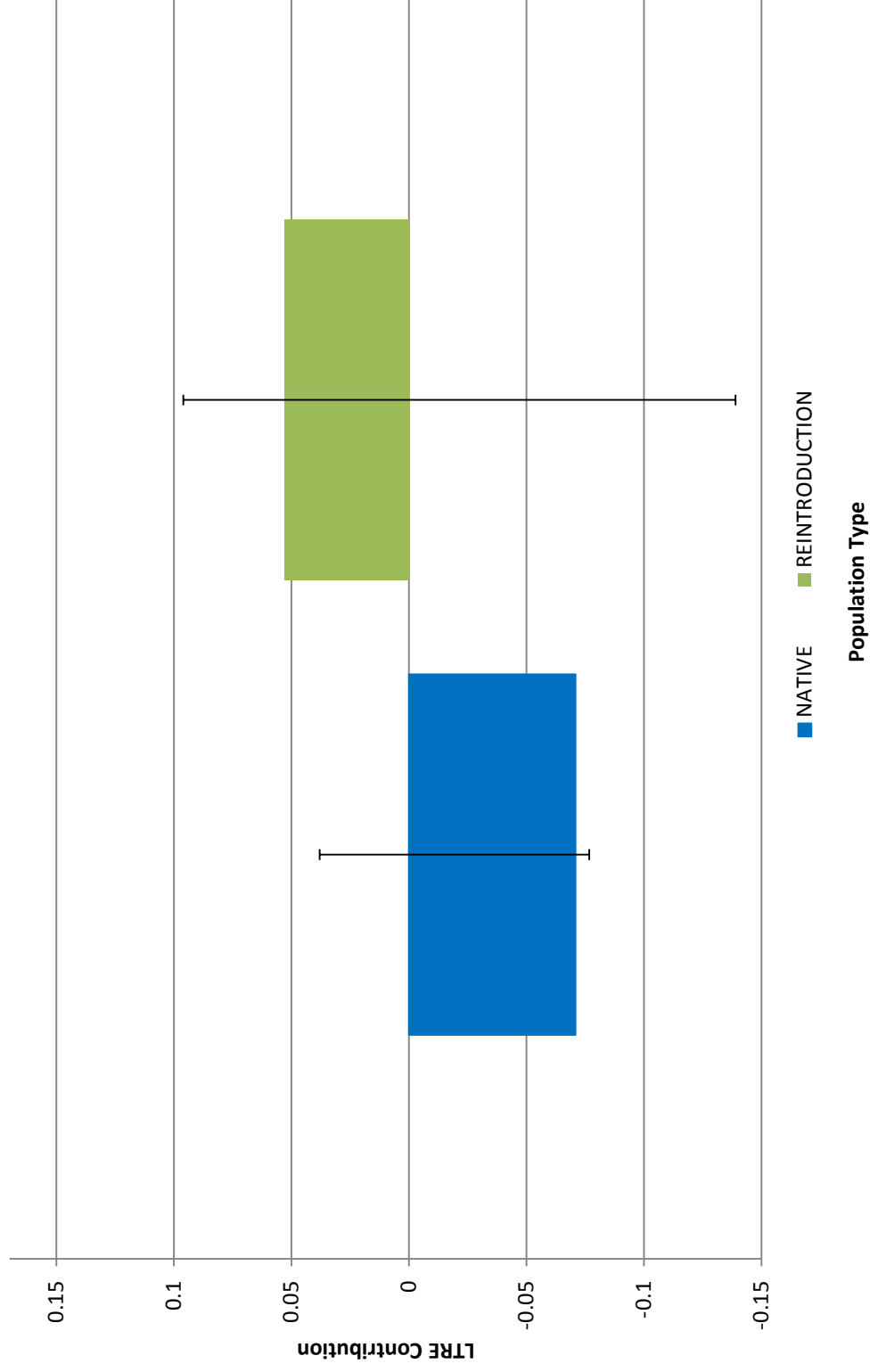
**Figure 13.** LTRE contributions of each population type's effect on Indiana Dunes *Cirsium pitcheri* metapopulation growth rate ($\lambda_M$). with 95% CI. Native *p*=0.07 & Reintroduction *p*= 0.22
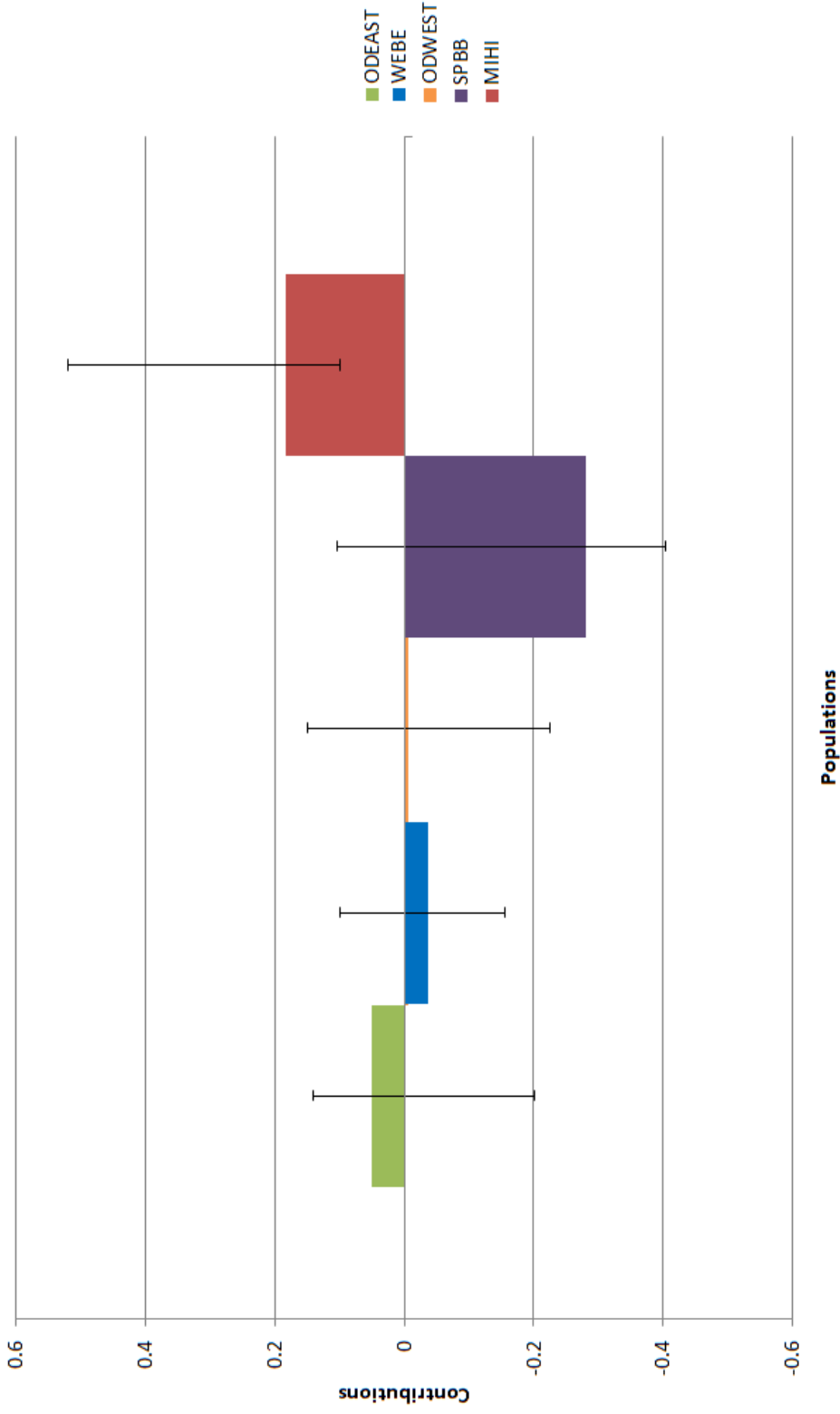
**Figure 14.** LTRE contribution of each population's effect on Indiana Dunes *Cirsium pitcheri* Metapopulation growth rate ($\lambda_M$) with 95% CI. Ogden Dunes East (ODEAST) *p*=0.316, West Beach (WEBE) *p*=0.98 Ogden Dunes West (ODWEST) *p*=0.81, State Park Big Blowout (*SPBB*) *p*< 0.001, Miller High Dunes (MIHI) *p*<-0.001.
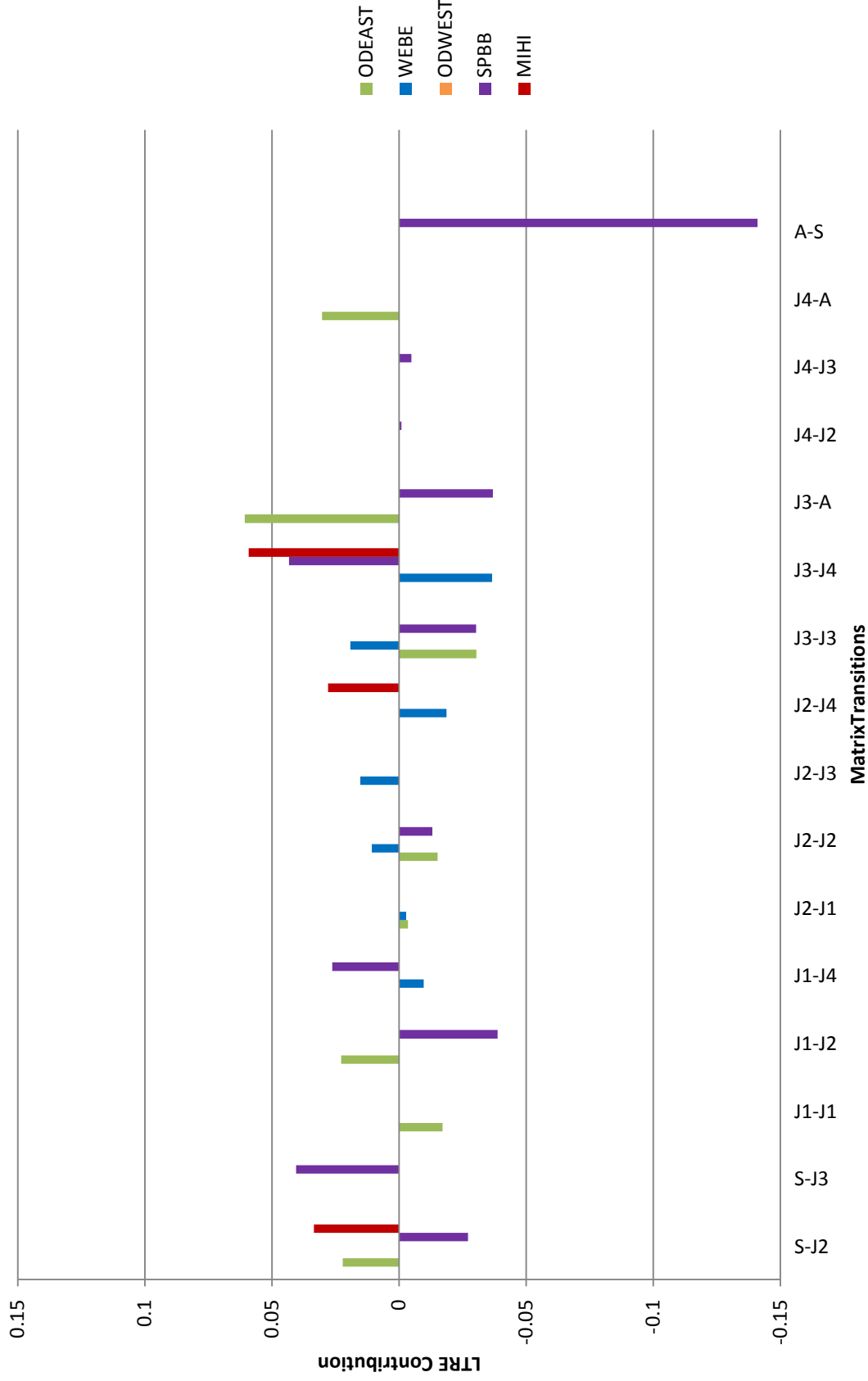
**Figure 15.** LTRE decomposition of contribution of matrix elements with significant effect ($p<0.05$) of each of the five populations on the Indiana Dunes *Cirsium pitcheri* Metapopulation growth rate($\lambda_M$). Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).

Beach also had both positive (J2-J2, J2-J3 and J3-J3) and negative (J1-J4, J2-J1, J2-J4 andJ3-J4) significant contributions to $\lambda_M$. Ogden Dunes West did not have any significant contributions on $\lambda_M$ from the matrix elements. Growth of plants contributed positively to ($\lambda_M$) in Miller High Dunes and Ogden Dunes East whereas growth contributed negatively in Ogden Dunes West, State Park Big Blowout and West Beach (Fig. 16). Stasis contributed negatively in all populations except West Beach (Fig. 16). State Park Big Blowout was the only population that contributed negatively to ($\lambda_M$), Ogden Dunes West had the greatest positive contribution of fecundity followed by Miller High Dunes. The contribution of regression was negligible compared to the other vital rates with Miller High Dunes and Ogden West having positive contributions and Ogden Dunes East, State Park Big Blowout and West Beach having negative contributions.

Year had an effect on the ($\lambda_M$), that was correlated with the mean ($r=0.477$, $p=0.034$) and minimum ($r=0.0551$, $p=0.012$) temperature in May with high peaks in temperature corresponding to greater positive contributions to ($\lambda_M$) and low peaks in temperature in corresponding to greater negative contributions (Fig. 17).

**Discussion**

Population type, Native or Reintroduced had no bearing on the type of contribution (positive or negative) on the Indiana Dunes' metapopulation growth rate. Each individual population's dynamics seemed to be influenced by differences in their life histories that contributed to the population growth rate ($\lambda$). Most notably, State Park Big Blowout had a significant negative contribution to the metapopulation growth rate $\lambda_M$. Through further decomposition of the underlying vital rates, I determined that a decrease in fecundity was responsible for the negative contribution. These small differences (Appendix B5) in fecundity had a disproportionally larger contribution to the $\lambda_M$ than the other population populations. This may be attributed to the fact that low fecundity matrix elements have a greater negative impact on population growth rates as
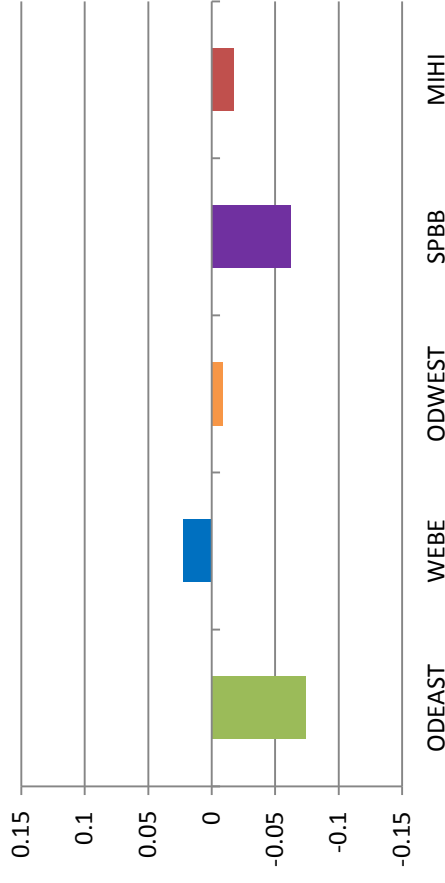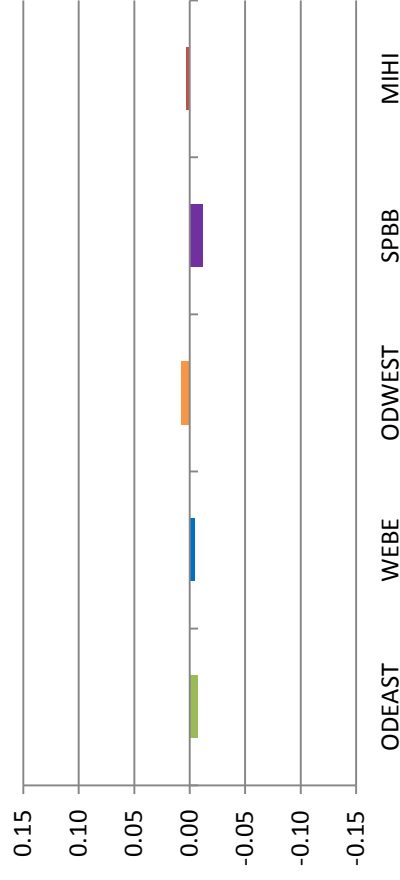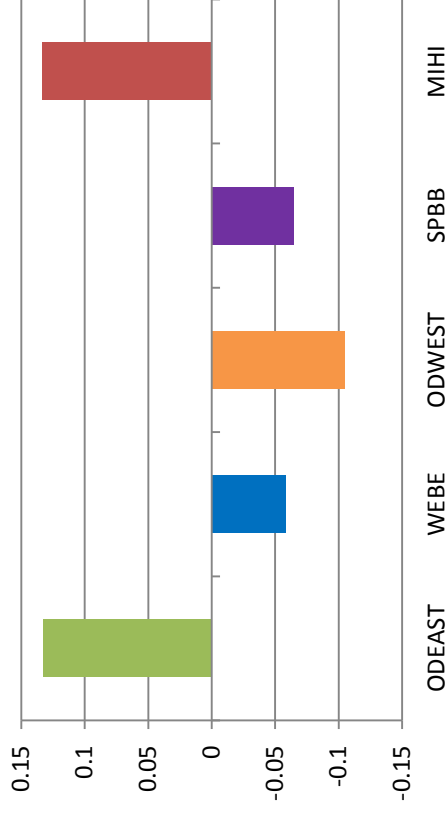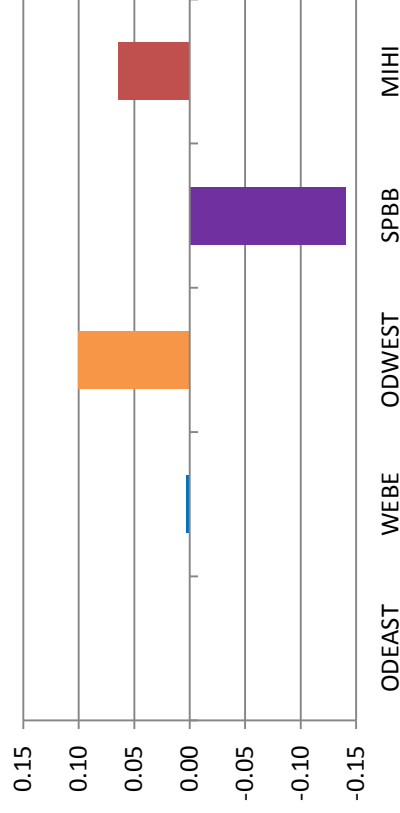
**Figure 16.** LTRE contributions of summed matrix elements in respect to vital rates of each of the 5 populations on the Indiana Dunes *Cirsium pitcheri* Metapopulation growth rate ($\lambda_M$). Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
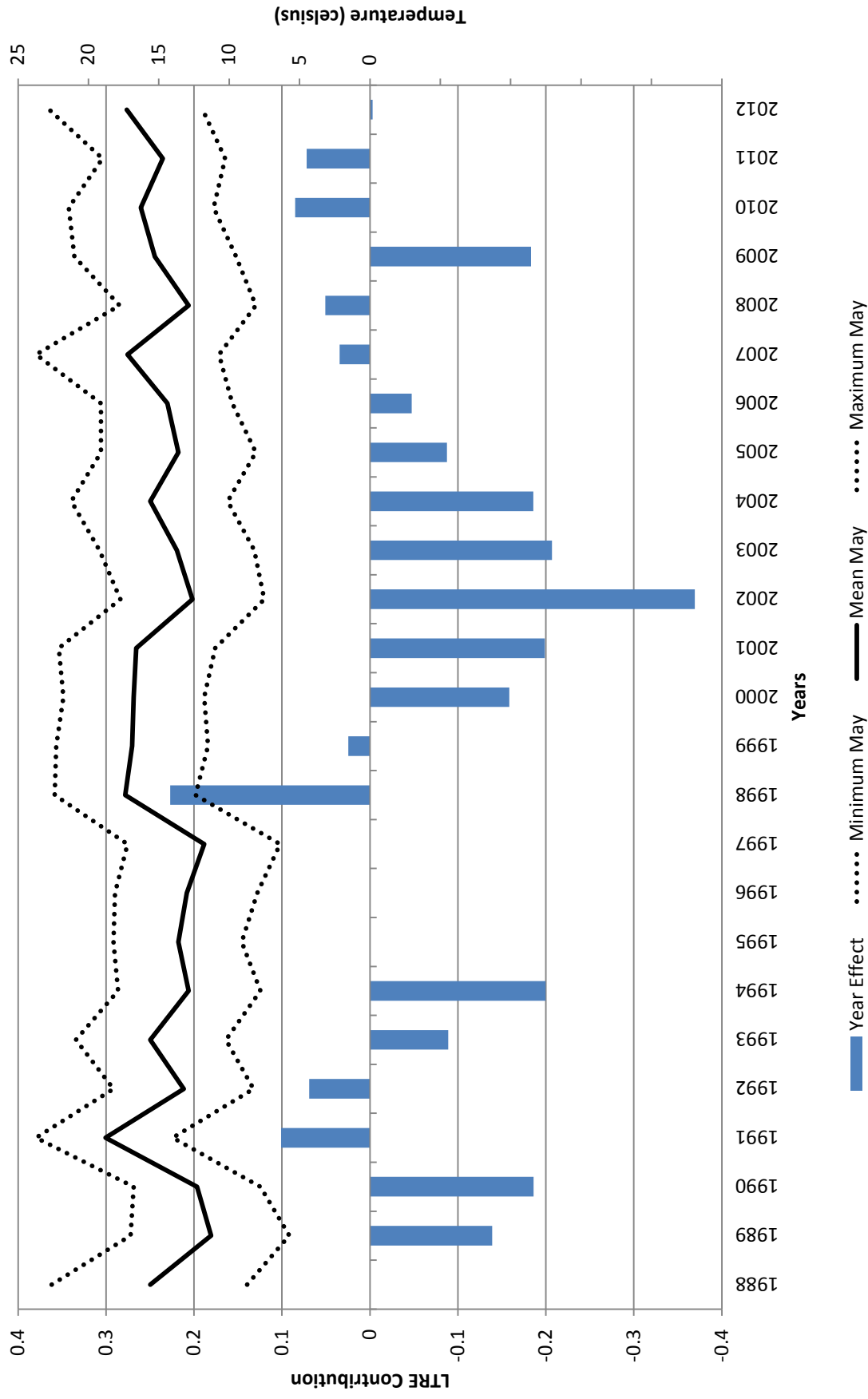
**Figure 17**. LTRE contribution of each year's effect on all five populations of *Cirsium pitcheri* on the Indiana Dunes Metapopulation growth rate (λ). Correlation with Mean May Temperature (C) (*r=0.477, p=0.034*) and Minimum May Temperature (C) (*r=0.551, p=0.012*) retrieved from NOAA.

compared to the other matrix elements (Jacquemyn et al., 2001; Freville & Silvertown 2005).

Following Caswell (2001), I interpreted from my conclusions in the previous paragraph that State Park Big Blowout's effects on the Indiana Dunes' metapopulation is due more to the effects of reduced fecundity than any other vital rate. Since *C. pitcheri* is a monocarpic perennial that flowers only once, it is not surprising that fecundity can be a driving factor in the viability of this species. In order to improve the viability, I suggest that the focus should be directed toward improving fecundity and survival of seedlings. There are factors that can affect fecundity such as seed predation, herbivory and low germination success. Over the years researchers have found increased infestation of *C. pitcheri* seed heads by two weevil species (*Larinus planus and Rhinocyllus conicus),* which can reduce the seeds in a seed head by 95% (Havens et al., 2012; Bell et al., 2003) Seed head consumption of flowering plants by the eastern white tailed deer (*Odocoileus virginianus*) and subsequent LTRE analysis of the effects of deer herbivory on American ginseng (*Panax quinquefolius)* population dynamics found that deer herbivory decreases $\lambda$ through a decrease in fecundity (Farrington, Muzika, Drees & Knight, 2008). Further studies must be done to quantify whether seed predation and herbivory is the actual cause behind low fecundity in State Park Big Blowout, before a management plan can be put into action to prevent this such as netting or caging of flowering plants.

At the other end of the spectrum, Miller High Dunes had a significant positive contribution to the metapopulation growth rate, which was a result of a combination of positive contributions from growth and fecundity. There was a slightly larger proportion of growth's positive contribution to $\lambda_M$ as compared to the difference between Miller High Dunes and the pooled metapopulation but this was not as pronounced as the negative difference and contributions. For the Indiana Dunes' *C. pitcheri* metapopulation, negative differences of growth, stasis, fecundity and regression tended to lead to greater

effects on the 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 a the same proportional contribution as its differences.

There is great variability from year to year among the population growth rates of each population with some years very good and others poor. The LTRE I performed to decompose the population effects on the metapopulation used mean matrices of 23 years of data which  obscured how the individual matrices (years) contributed to the metapopulation. There was a year effect with 60% of the years contributing negatively to the $\lambda_M$. The differences between these years correlated to the mean and minimum May temperature suggesting that temperature played an important role during the time that the plants are reappearing at the beginning of the growing season with mean temperatures around and above 15°C having positive effects on $\lambda_M$. There doesn't seem to be a significant correlation with rainfall at any point throughout the years on the metapopulation growth rate.

By incorporating LTRE analysis with modeling, there is a greater understanding of the underlying causes of the projected extinction probabilities of each population. Since populations of the same species can differ in demographic structures when occupying distinct habitats, vital rates and ultimately persistence can vary. LTRE identifies the ways in which populations differ so as to allow appropriate management actions to take place (Davidson et al., 2010).  For example, using what was learned from State Park Big Blowout and following the Coulson et al. (2001) warning about modeling only being useful when past data (parameterization period) are similar to the future (forecast period), one can manipulate the data in order to determine what would happen if fecundity were to increase or any other vital rates.  This allows for a fairly simple way to

determine whether or not a particular management method would actually improve viability or be ineffective. LTRE has given insight into how each of the five populations of *C. pitcheri* within the Indiana Dunes' metapopulation compare with each other as well as explain how these difference contributed to the overall metapopulation viability.

**Chapter IV. Elasticity Analysis**

**Background**

Elasticity analysis of contributions of different life stages to population growth can help guide management applications by measuring the relative effect of small changes to the matrix elements that represent a particular transition in the life cycle (growth, stasis, and fecundity) (Bell et al., 2003). Elasticities allow comparisons between populations by looking at the variation between different populations of the same species (Silvertown et al., 1996). Caswell (2001) warns that contributions must be interpreted carefully since $\lambda$ is not actually composed of independent contributions of each matrix element. This means that each elasticity value depends on the others. For example without stasis or survival, both fecundity and growth would be non-existent and vice versa. All stages of the plant life cycle are important to the survival of the species but these methods help give a better understanding as to the factors that contribute to the growth of a population in order to make restorations possible. In contrast to LTRE which is retrospective analysis looking at matrices and asking how much the variance of the matrix elements contribute to the variance in $\lambda$; elasticity analyses are a prospective type of analysis allowing one to see, based on past observations, how the contributions of certain vital rates would affect the population growth rate when they change (Caswell, 2001).

The last specific aim is to determine which population type; natural or reintroduced has the greatest contribution to the metapopulation growth rate. The determination of contributions of the two population types to the metapopulation growth rate will allow for the identification of why reintroductions have an effect on metapopulation viability, if any. Elasticity analysis of contributions of different life stages to $\lambda$ can help guide management applications and differentiate approaches used for plants with different life strategies (Bell et al., 2003). In order to determine which

population type, reintroduced or natural, has the greatest contribution, elasticities will be used for the first time as a way to determine which population type has a greater contribution to the metapopulation growth rate in much the same way that elasticities are used in order to determine which vital rates has a greater contribution to a single metapopulation growth rate.

**Methods**

Elasticities allow comparisons between populations by measuring the relative effects on the growth rate to small changes of the vital rates such as growth, stasis and fecundity (Silvertown et al., 1996). According to Caswell (2001), the elasticity ($e_{ij}$) of the population growth rate ($\lambda$) with respect to the matrix element ($a_{ij}$) is

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}}$$

Where

$$\sum_{ij} e_{ij} = \sum_{ij}\frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} = 1$$

I performed elasticity analysis on each matrix using POPTOOLS in Microsoft Excel (2010), summing the elements of the elasticity matrix with respect to the growth, stasis and fecundity regions as indicated in Fig. 3. Regression is included as part of stasis. There were 6 State Park Big Blowout matrices (years=01-02,02-03,03-04,05-06,07-08,09-10) where the populations had a $\lambda$ of zero as well as elasticity values of zero so they were excluded from all elasticity analyses. All values were then plotted on a triplot to show the general trend of each population elastic contributions to the population growth rate. I plotted the finite growth rate of each matrix as a function of its respective elasticity value in order to determine the relationship through the use of linear regression. Lastly, in order to determine if there was a difference in the elastic contributions of $\lambda$ between the populations, I performed an Analysis of Variance (ANOVA) of the four elasticities (Growth, Regression, Stasis, and Fecundity) using the different transition

years as replications. I used Tukey HSD or Tamhane multiple comparisons depending on whether or not variances were equal.

**Results**

Growth, stasis and fecundity varied throughout the populations as well as among the years of the populations. Indiana Dunes' populations plotted on a triplot showed that the majority of contributions to the finite population growth rate ($\lambda$) were a result of greater contributions of growth elasticity values compared to stasis and fecundity (Fig. 18). All Indiana Dunes' populations were along the similar fecundity axis between 5-15%, but varied in where they fell along the stasis and growth axis (Appendix C1). Miller High Dunes showed variability in the contributions of stasis and growth to lambda with contributions of fecundity being relatively constant between 10-20% (Appendix C2). Growth and stasis appeared to trade off, as growth elasticities increased, stasis decreased and vice versa. Ogden Dunes East points tended to cluster together on the triplot indicating that this population had a relativity stable life history strategy in which growth of plants contributed between 65-80% to lambda, whereas stasis was between 5-15% and fecundity contributes between 20-30% (Appendix C2). Ogden Dunes West shared a similar trend as Miller High Dunes with fecundity contribution ranging from 0-20% and growth and stasis trading off (Appendix C4). Most contributions to low $\lambda$ of State Park Big Blowout resulted from high stasis elasticities, fecundity values around 0% and growth between 0-30% (Appendix C5). The few State Park Big Blowout points with 20-30% fecundity contribution had a marked increase in lambdas resulting in one point indicating population growth at ($\lambda$=1.44, Appendix C5). West Beach shared a trend similar to that of Miller High Dunes with the fecundity contributions concentrated between 0-20% and with tradeoff of growth and stasis contributions (Appendix C6). Increases in $\lambda$ are associated with increased fecundity elasticities and decreased stasis
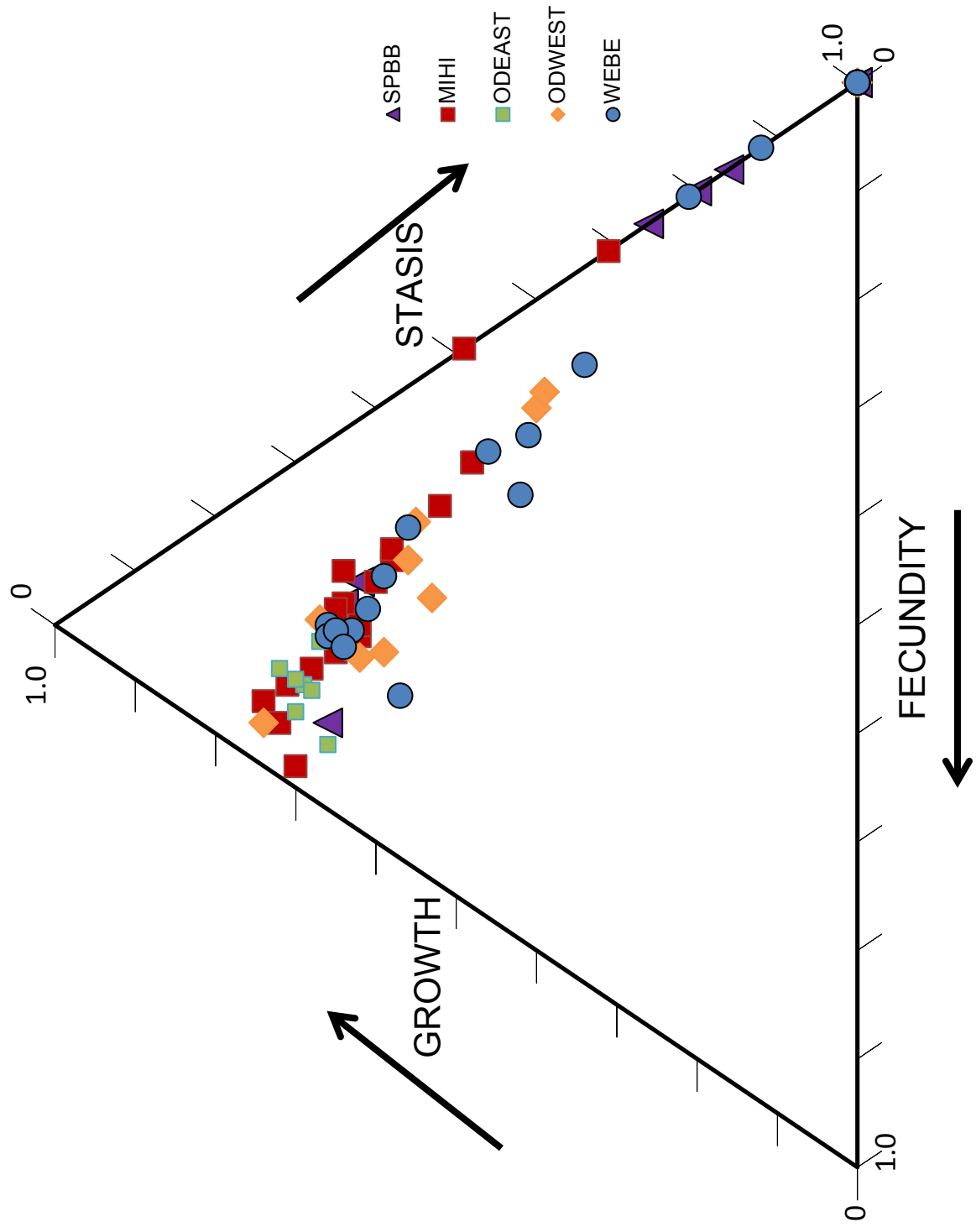
**Figure 18.** Triplot showing the five Indiana Dunes *Cirsium pitcheri* Metapopulation and elasticity values. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).

elasticities (Appendix C7). There was no clear relationship between succession stages and elasticity values (Appendix C8).

There was a linear trend between growth elasticities and their corresponding $\lambda$. State Park Big Blowout had the strongest relationship with increases in contributions of growth resulting in higher $\lambda$ (Fig. 19, $R^2=0.656$, $p<0.001$). Miller High Dunes and Ogden Dunes West had moderately positive relationships between growth elasticities and $\lambda$ (Fig. 19, $R^2=0.37$, $p=0.003$; $R^2=0.459$, $p=0.022$). West Beach also showed a positive yet weak relationship between growth and $\lambda$ ($R^2=0.144$, $p=0.09$). Ogden Dunes East showed no relationship between growth and $\lambda$ ($R^2=0.066$, $p=0.445$). Figure 20 shows that there was a moderate inverse relationship between stasis and $\lambda$ for Miller High ($R^2=0.449$, $p=0.001$) and Ogden Dunes West ($R^2=0.489$, $p=0.017$) and a nonsignificant inverse relationship for State Park Big Blowout ($R^2=0.009$, $p=0.680$) and West Beach ($R^2=0.1556$, $p=0.077$). Ogden Dunes East had a positive yet nonsignificant relationship between stasis and $\lambda$ ($R^2=0.019$, $p=0.681$). Fecundity showed positive relationships for all Indiana Dunes' populations with increased fecundity contributions resulting in increased $\lambda$ (Fig. 21). 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 $\lambda$.

An analysis of variance showed that the growth elasticities differed significantly between the populations, ($F_{(4,80)}=22.987$, $p<0.001$). Post Hoc analysis with $\alpha=0.05$ indicated that State Park Big Blowout ($0.121\pm SD=0.229$) had the lowest mean growth elasticity but was not significantly different from West Beach ($0.391 \pm SD=0.268$) (Fig. 22, $p>0.05$). Ogden Dunes East ($0.960 \pm SD=0.187$) had the greatest mean growth elasticity; however, it is not significantly different from Miller High Dunes ($0.902 \pm$

**Figure 19.** Scatter plots of growth rates of each population of *Cirsium pitcheri* within the Indiana Dunes Metapopulation as a function of elasticity values of growth. Lines represent linear trend with p-values of slope. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
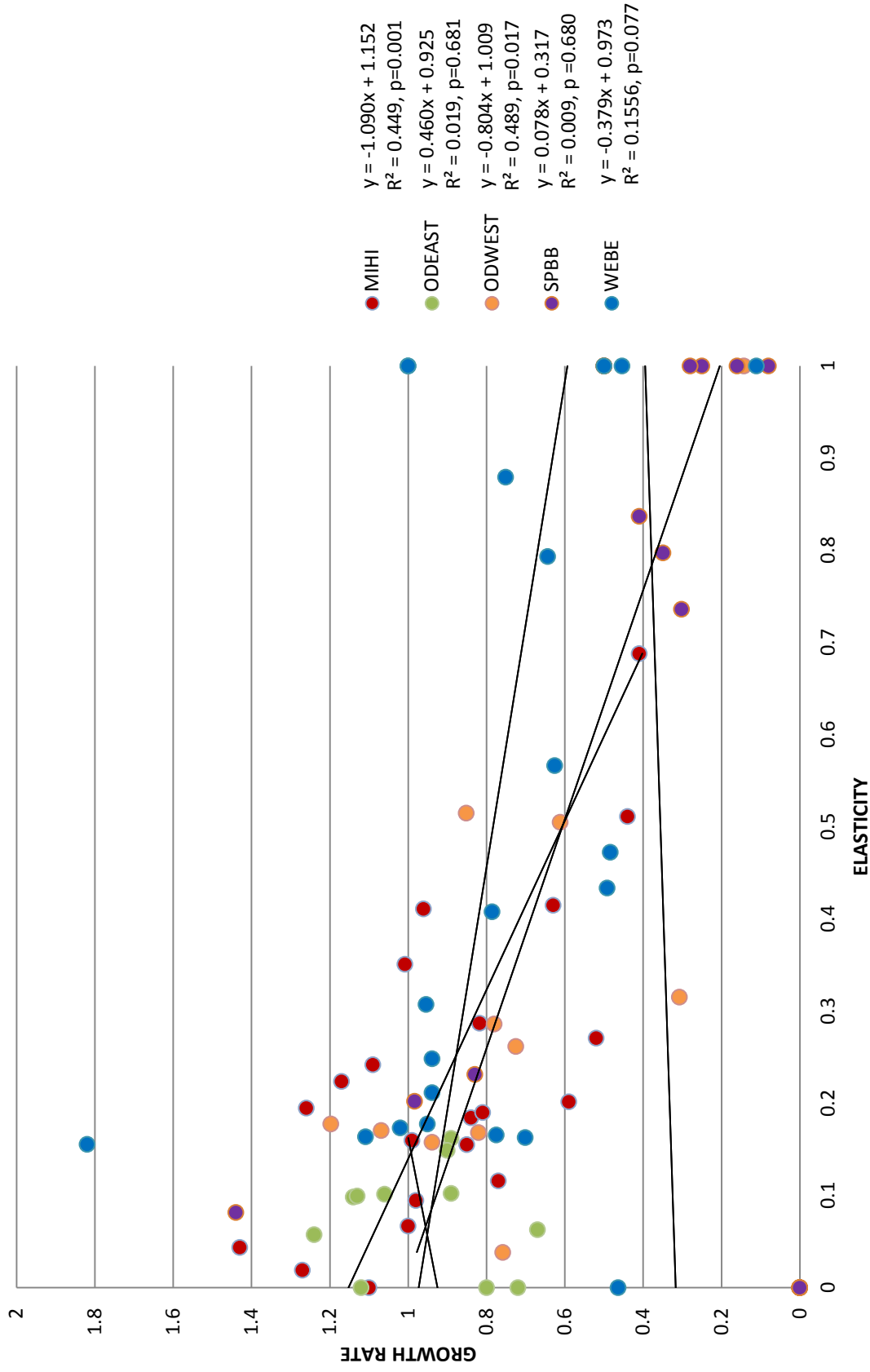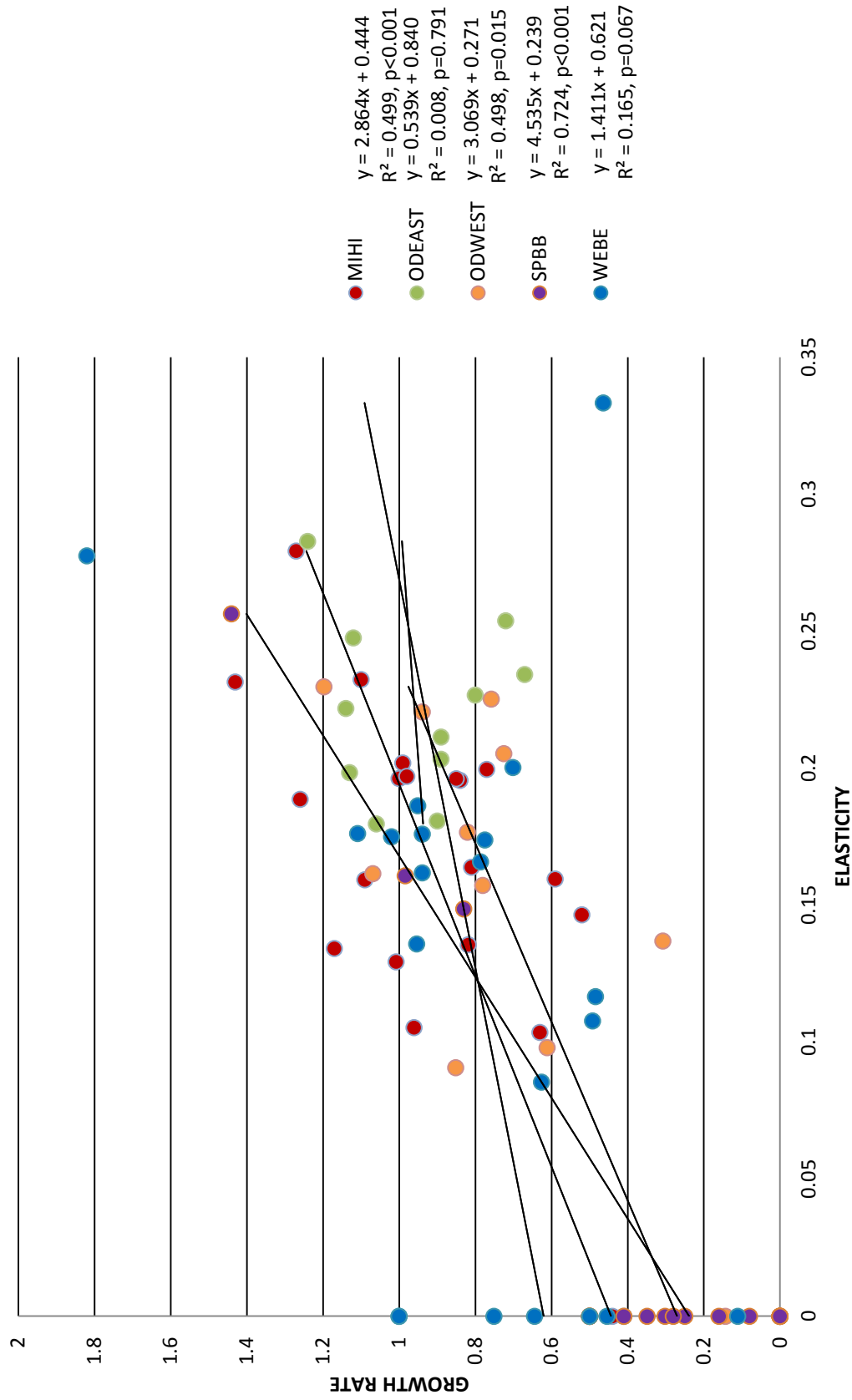
**Figure 20.** Scatter plots of growth rates of each population of *Cirsium pitcheri* within the Indiana Dunes Metapopulation as a function of elasticity values of stasis . Lines represent linear trend with p-values of slope. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).

**Figure 21.** Scatter plots of growth rates of each population of *Cirsium pitcheri* within the Indiana Dunes Metapopulation as a function of elasticity values of fecundity. Lines represent linear trend with p-values of slope. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
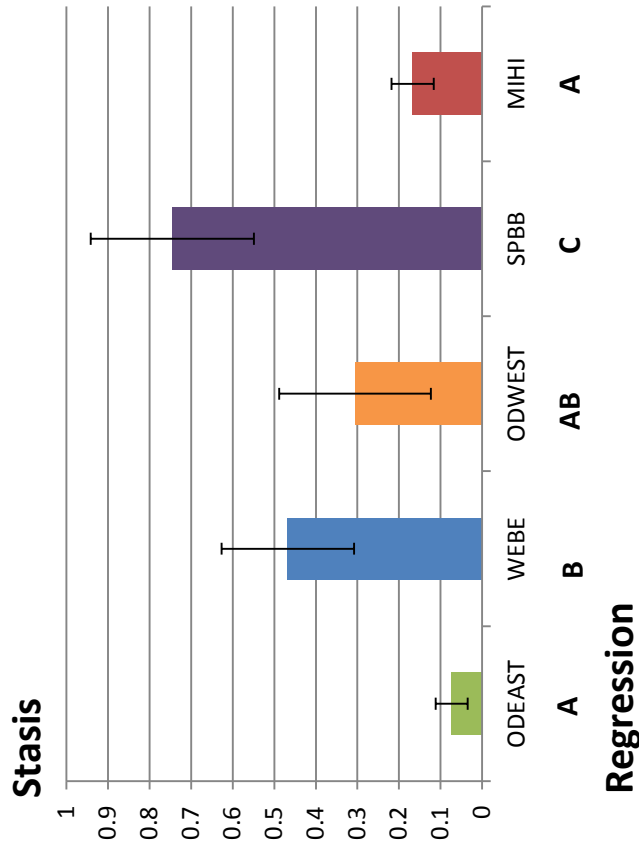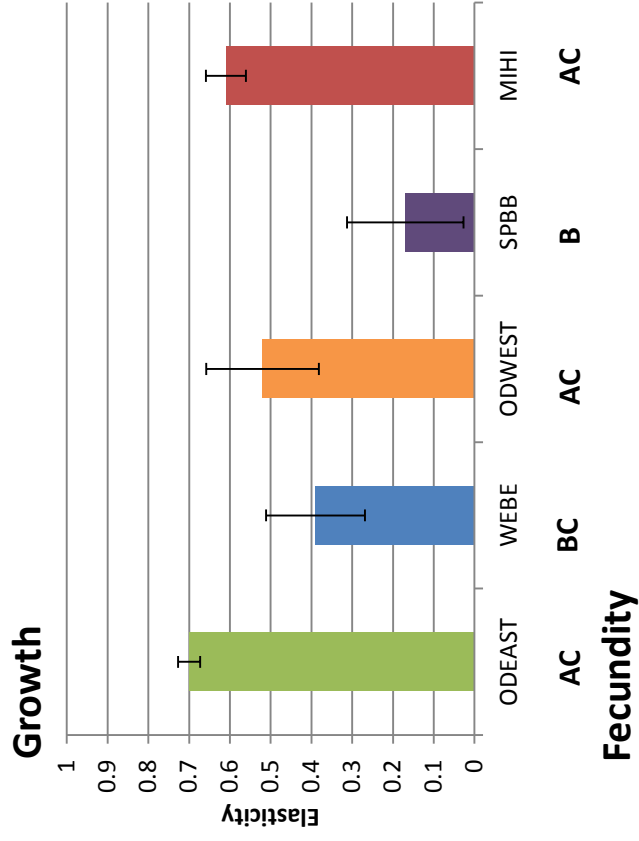
**Figure 22.** Mean elasticity values of the five populations with 95% CI. Groups sharing common letters are not significantly different from each other based on Tukey HSD/Tamhane multiple comparisons with α=0.05. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).

*SD*=0.277) and Ogden Dunes West (0.749 ± *SD*=0.390).

An analysis of variance showed that the stasis elasticities were significant different, ($F_{(4,80)}$=6.676, *p*=0.000) with Ogden Dunes East (0.074 ± *SD*=0.057) having the lowest mean stasis elasticity despite it not being significant different from Miller High Dunes (0.167 ± *SD*=0.112) or Ogden Dunes West (0.518 ± *SD*=0.201) (Fig 22). State Park Big Blowout (0.533 ± *SD*=0.455) had the highest mean stasis elasticity; yet it was not significantly different from Ogden Dunes West and West Beach (0.468 ± *SD*=0.349).

An analysis of variance showed that the fecundity elasticities were also significantly different from each other, ($F_{(4,80)}$=15.126, *p*=0.000)(Fig. 22). State Park Big Blowout (0.027± *SD*=0.070) had the lowest mean fecundity; however, it was not significantly different from West Beach (0.117± *SD*=0.099). Ogden Dunes East (0.222 ± *SD*=0.032) had the greatest mean fecundity elasticity yet it was not significantly different from Miller High Dunes (0.159 ± *SD*=0.068), Ogden Dunes West (0.155 ± *SD*=0.070) or West Beach. There was no significant difference in the regression elasticities between either of the five populations,($F_{(4,80)}$=1.375, *p*=0.250)(Fig 22).

**Discussion**

There was a clear relationship between elasticity values representing growth, stasis and fecundity with population growth rates (λ) reaffirming the Morris and Doak (2002) assumption of a linear relationship between the proportional change in λ and vital rates. In *C. pitcheri* 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. Franco and Silvertown (2004) point out that elasticities do not cleanly separate the contributions of the vital rates and therefore the elasticity values of growth, fecundity and survival are actually a combination of vital rates. An example would be that for a plant to grow it must also survive, therefore a matrix transition representing growth represents survival as

well. *C. pitcheri* is a monocarpic species that must grow large enough to maximize its reproductive capabilities once before dying. Thus, higher contributions of stasis tend to lower the population growth rate because it is not only essential for *C. pitcheri* to survive, but growth is important.

Since elasticity values sum to unity (De Kroon, Van Groenendael & Ehrlen, 2000), it stands to reason that an increase in one elasticity value such as stasis would result in the subsequent reduction in either of the other two elasticity values of growth and fecundity. In other words, a trade-off must occur, which in the case of State Park Big Blowout leads to devastating consequences such as decreased population size and increased extinction risk. State Park Big Blowouts life history strategy focuses on stasis (survival) at the expense of growth and reproduction implies that there is something about the habitat in which State Park Big Blowout resides that is different from the other populations since there is variation in elasticity patterns among populations of the same species (Silvertown et al., 1996; Oostermeijer, 2003). Unfortunately, the late successional stage of State Park Big Blowout's habitat did not explain why there were high contributions of stasis in the majority of State Park Big Blowouts yearly population growth rates. This is because Miller High Dunes had a higher succession index (McEachern, 1992), yet had a higher growth rate as well as fairly low contributions of stasis and increased growth and fecundity contributions (Appendix C8).

Overall, the five Indiana Dunes' *C. pitcheri* populations varied significantly in their elasticity values with the most notable significant difference being State Park Big Blowout's high elasticity of stasis as compared to the other populations. Population growth rates tended to be higher in Ogden Dunes East and Miller High Dunes with averages of 0.96 and 0.90, though these two populations are declining since their $\lambda$ is lower than one; they are declining at a slower rate than the other populations: West Beach, Ogden Dunes West and State Park Big Blowout. From an elasticity viewpoint,

both of these populations are in the upper area of the triplot, where stasis elasticities are lower and growth elasticities are higher. An unexpected occurrence is Ogden Dunes West where the mean $\lambda$ is fairly low even though it falls in the same vicinity of the triplot of high growth and low elasticity values where Ogden Dunes East and Miller High Dunes have higher $\lambda$. This is explained do to the fact that a single point with a very low $\lambda=0.14$ that could bring the average population growth rate down.

The purpose of performing elasticity analyses in this study was to determine which population type, "Native" or "Reintroduced" had the greatest contribution to the overall metapopulation growth rate ($\lambda_M$). However, the phrasing of that question is more in line with what Life Table Response Experiments determine as far as contribution to the growth rate. What I am able to conclude, using a triplot representation of the mean elasticity values of each of the populations as well as the elasticities of the pooled metapopulation (Appendix C1), is that both of the reintroduced populations:  Ogden Dunes East and Ogden Dunes West as well as the native population of Miller High Dunes had higher contributions of growth and fecundity. This coincides with a higher population growth rate ($\lambda$) while West Beach and State Park Big Blowout had higher values of stasis in effect lowering $\lambda$.

Using elasticities in combination with other types of population viability analysis such as Projection Modeling and Life Table Response Experiments (LTRE), it is possible to understand the dynamics of a population to the point of being able to develop management action plans. In the previous chapter, I performed LTRE and concluded State Park Big Blowout's fecundity or lack thereof contributed negatively to the metapopulation growth rate. Yet I failed to see the extent to which the lack of growth or increased time spent in stasis impacted the population growth rate. I suggested that increasing fecundity of State Park Big Blowout would be greatly help the metapopulation growth rate. However, there appears to be an upper limit on contribution of fecundity

with the highest elasticities at around 30% whereas the growth and stasis elasticities varied from 0-100% in any given transition matrix. Removing the negative contributions of decreased fecundity is likely to help the overall metapopulation. However, since *C. pitcheri* only flowers once in its lifetime, fecundity cannot make a high contribution to the population growth since most of the life cycle of a single plant is devoted to growing until it a large enough to flower or simply surviving until it has resources that will enable it to grow.

Based upon this new evidence, I adjust my recommendation to focusing on the growth of plants as well as fecundity. While fecundity is very important, as it adds new plants to the population, if those plants are unable to growth and survive to the point of reaching maturity, it is futile to have a management plan that is solely dedicated to increasing seed production through the elimination of seed predators and herbivores that attack flowering plants.  In the case of State Park Big Blowout, which I used because it is the most vulnerable population in the Indiana Dunes' metapopulation to extinction, the first step to developing a management plan is to identify the reason why stasis would be contributing more to the λ than growth. I've ruled out succession and possible competition from other plant species based on the fact that Miller High Dunes is higher in the succession index yet is doing immensely better. Rowland and Maun (2001) suggest that a reason for *C. pitcheri*  to remain in the juvenile stage longer is a result of deer herbivory where plants that have been browsed must tap into root reserves (below ground biomass) in order to re-growth above ground tissue. It might be useful to take a closer look at monitoring observation notes to determine the extent to which deer browsing occurred; however, since surveys took place over the course of about one week, it is impossible to know the full extent to which this type of herbivory actually occurred throughout the year.

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 population, it is unrealistic to try to continue to use this method of adding new populations of *C. pitcheri* as a way to improve viability. The best approach using what I learned from performing LTRE and Elasticity analyses 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. The outlook for the Indiana Dunes' metapopulation looks bleak for the near future although with this new information it may possible to reverse the downward direction of the population growth rates and improve the population viability to the point where further human intervention is no longer needed.

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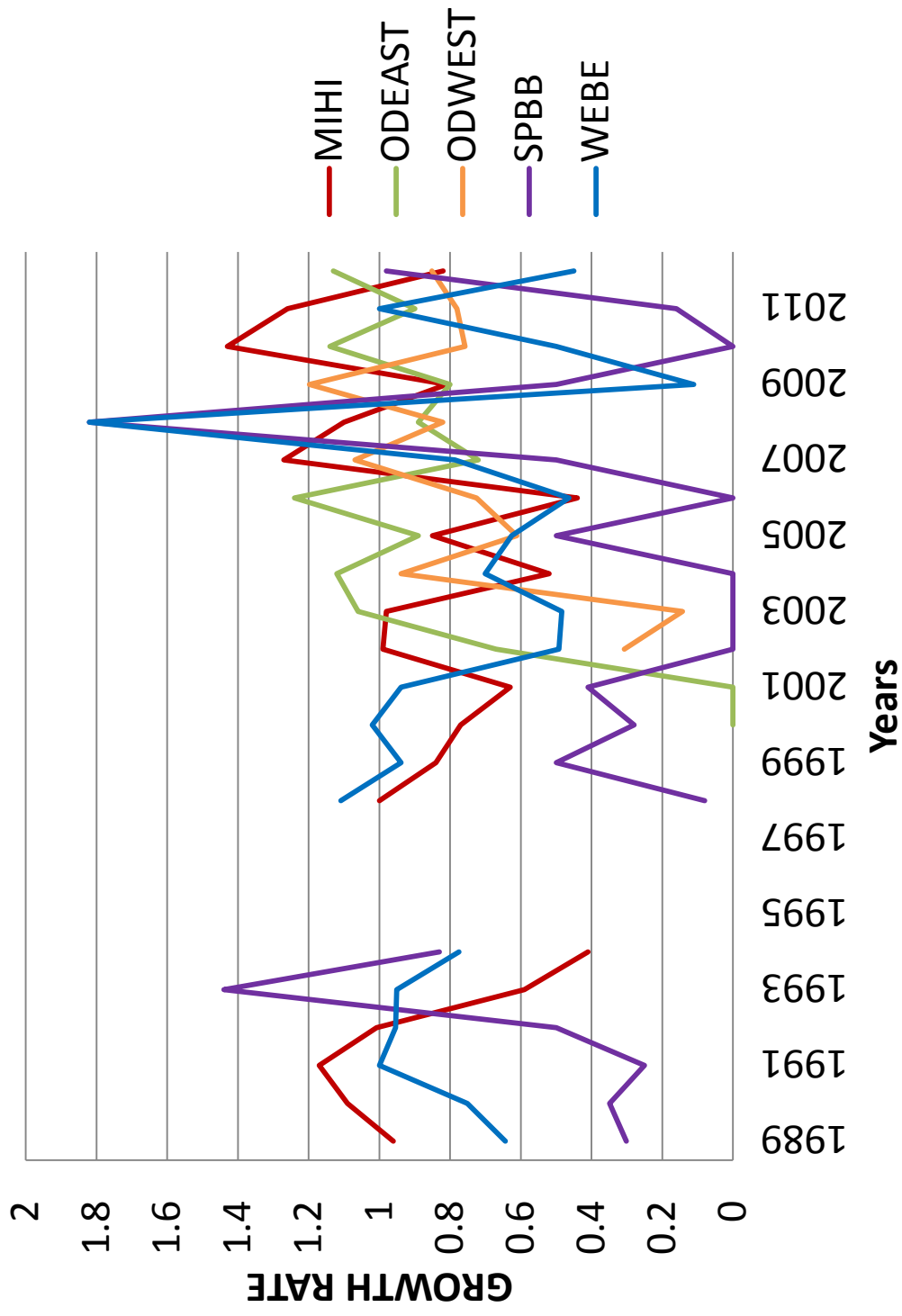
**Appendix A1**. Finite growth rates (λ) varied through out the years for the each population of *Cirsium pitcheri* in the Indiana Dunes Metapopulation. 1995-1996 are years not surveyed. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).

**Appendix A2**. Total population abundances for each of the five Indiana Dunes *Cirsium pitcheri* populations throughout the years. Miller High(MIHI), Ogden Dunes East(ODEAST), Ogden Dunes West (ODWEST), State Park Big Blowout(SPBB), West Beach (WEBE)

| Years | Populations | | | | |
|---|---|---|---|---|---|
| | MIHI | ODEAST | ODWEST | SPBB | WEBE |
| 1988 | 111 | - | - | 61 | 76 |
| 1989 | 99 | - | - | 46 | 62 |
| 1990 | 90 | - | - | 70 | 54 |
| 1991 | 137 | - | - | 67 | 79 |
| 1992 | 211 | - | - | 79 | 182 |
| 1993 | 124 | - | - | 84 | 138 |
| 1994 | 108 | - | - | 68 | 139 |
| 1995 | - | - | - | - | - |
| 1996 | - | - | - | - | - |
| 1997 | 81 | - | - | 22 | 202 |
| 1998 | 96 | - | - | 21 | 554 |
| 1999 | 75 | 47 | 2 | 23 | 272 |
| 2000 | 69 | 50 | 27 | 19 | 521 |
| 2001 | 53 | 51 | 90 | 7 | 490 |
| 2002 | 67 | 59 | 146 | 3 | 258 |
| 2003 | 63 | 58 | 195 | 1 | 153 |
| 2004 | 45 | 58 | 172 | 7 | 106 |
| 2005 | 37 | 60 | 99 | 7 | 74 |
| 2006 | 36 | 61 | 71 | 21 | 41 |
| 2007 | 69 | 48 | 72 | 19 | 41 |
| 2008 | 70 | 48 | 56 | 7 | 44 |
| 2009 | 72 | 87 | 90 | 8 | 63 |
| 2010 | 197 | 106 | 71 | 41 | 65 |
| 2011 | 160 | 79 | 54 | 39 | 43 |
| 2012 | 122 | 108 | 39 | 49 | 28 |
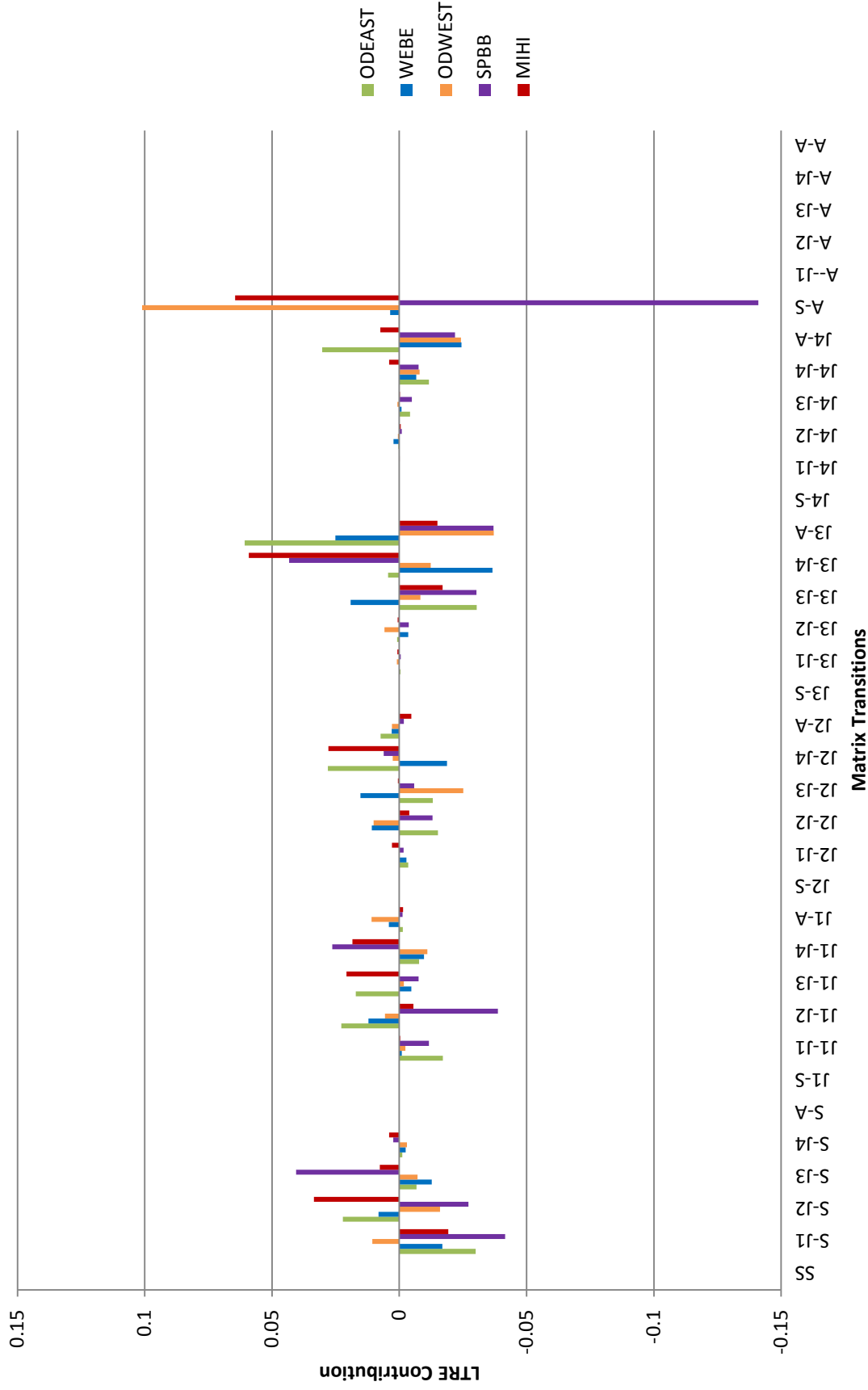
**Appendix B1.** LTRE decomposition of matrix elements of each of 5 populations effect on the Indiana Dunes *Cirsium pitcheri* Metapopulation growth rate ($\lambda_M$). Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
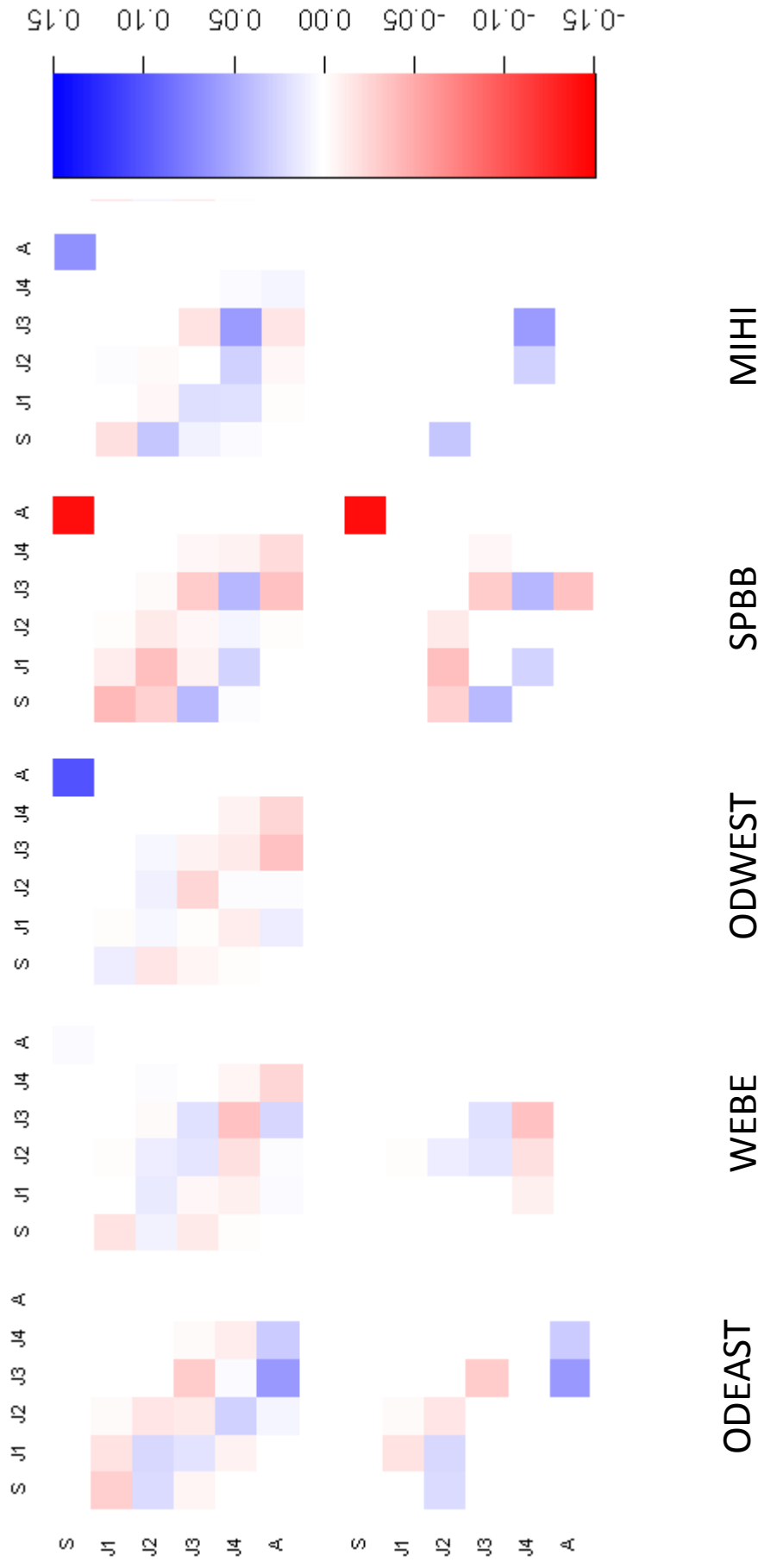
**Appendix B2.** LTRE decomposition of (top) contribution for each matrix element and (bottom) significant contribution for each matrix element (p<0.05) of each of the five populations on the Indiana Dunes *Cirsium pitcheri* Metapopulation growth rate($\lambda_M$). Blue equal positive effects and red equals negative effects along gradient.
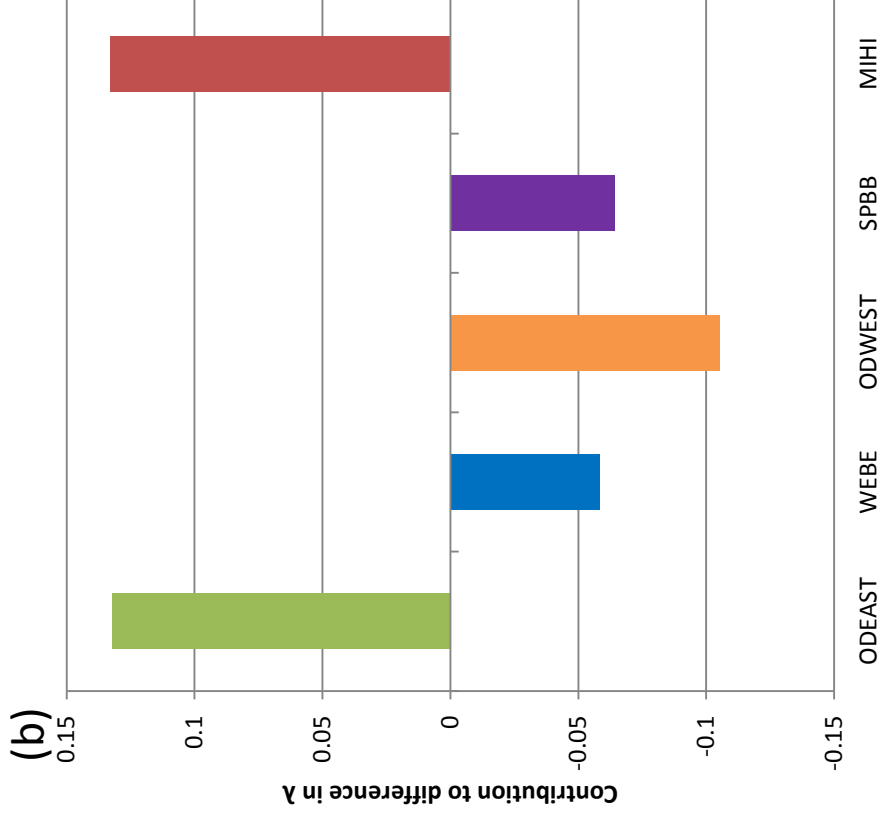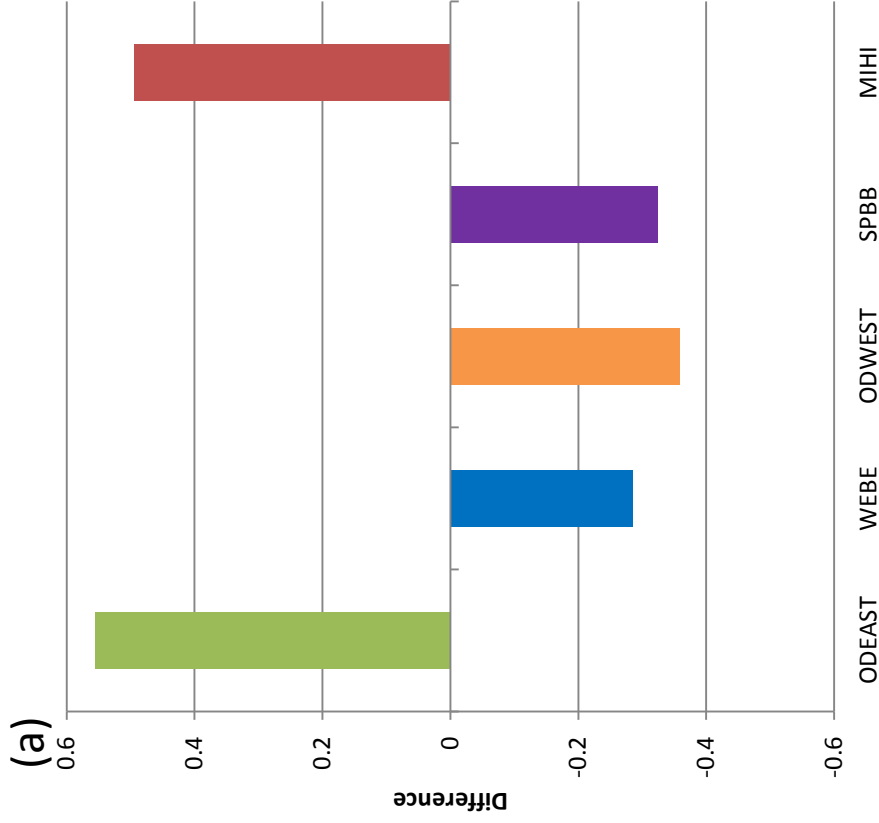
**Appendix B3.** Differences in summed matrix elements that represent growth between populations of Indiana Dunes *Cirsium pitcheri*: (a) difference of population from pooled metapopulation and (b) the contribution of these differences to the differences in $\lambda_M$. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
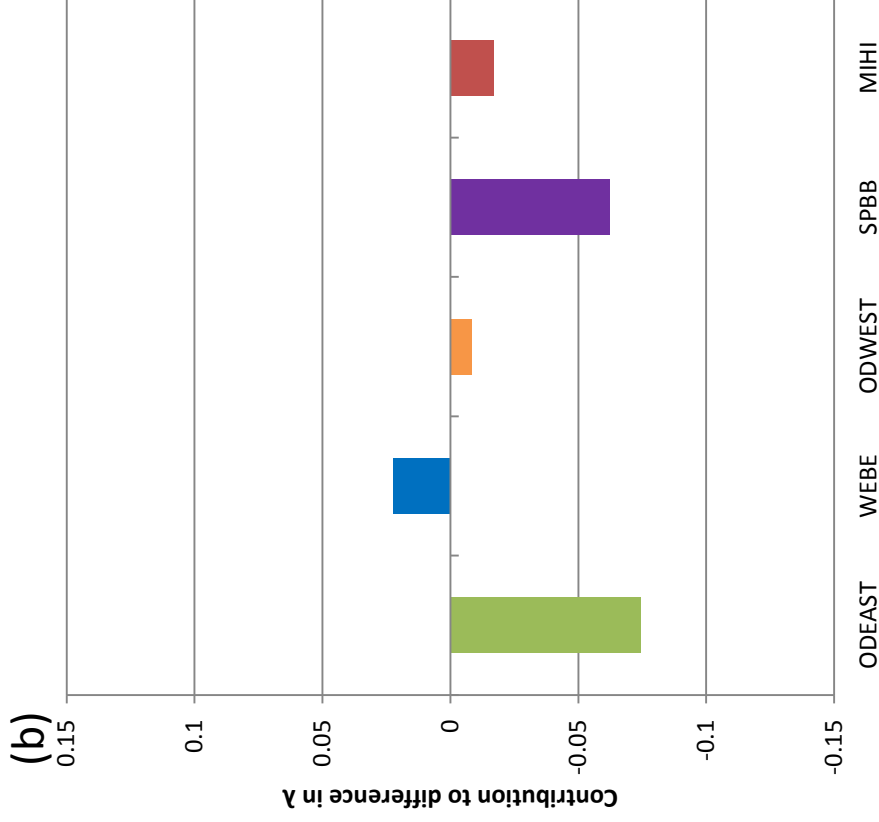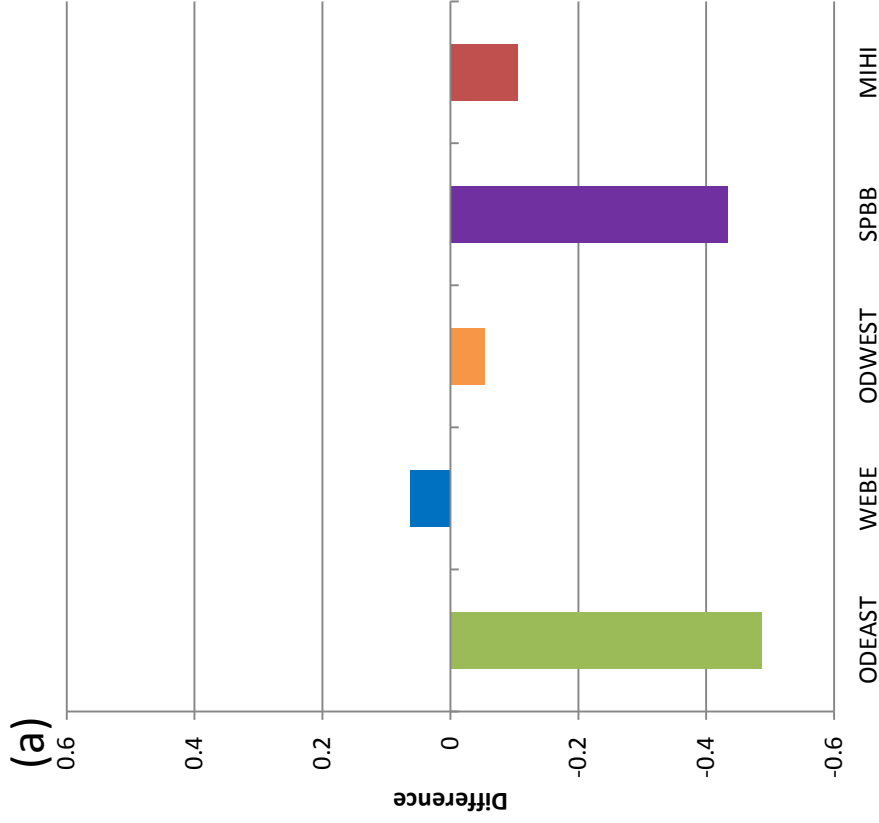
**Appendix B4.** Differences in summed matrix elements that represent stasis between the five populations of Indiana Dunes *Cirsium pitcheri* Metapopulation: (a) difference of population from pooled metapopulation and (b) the contribution of these differences to the differences in $\lambda_M$. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
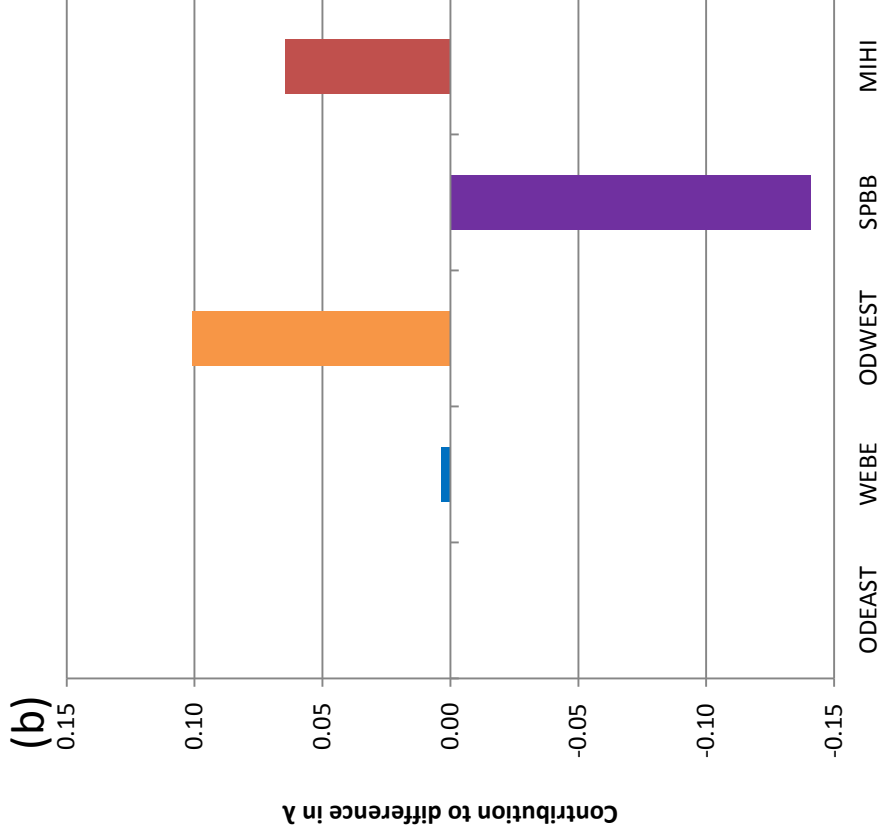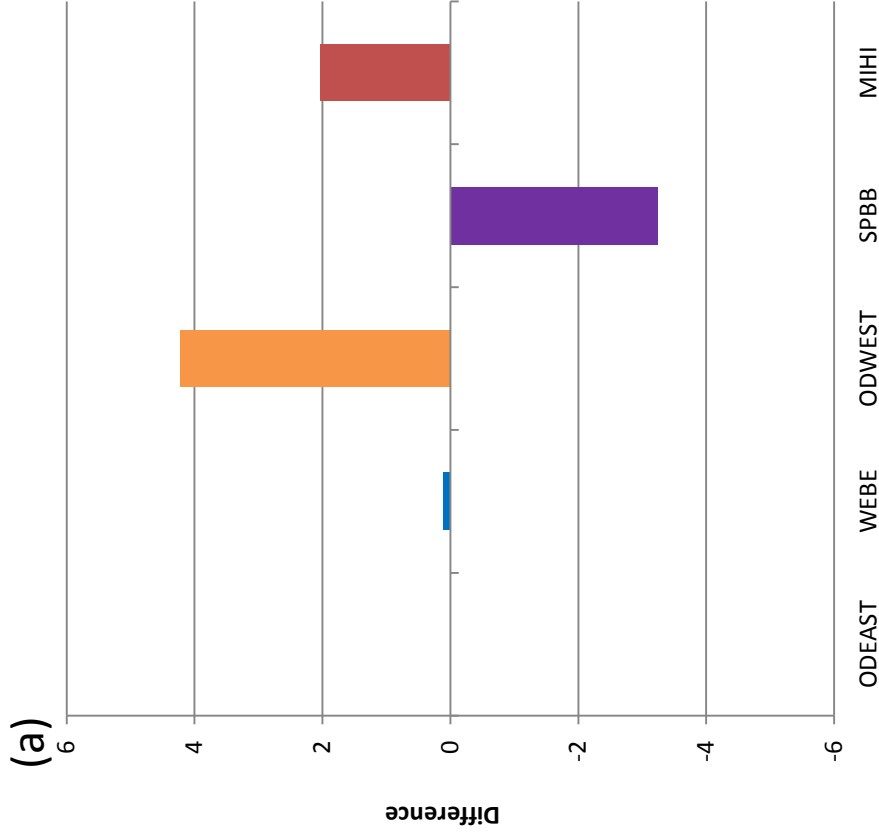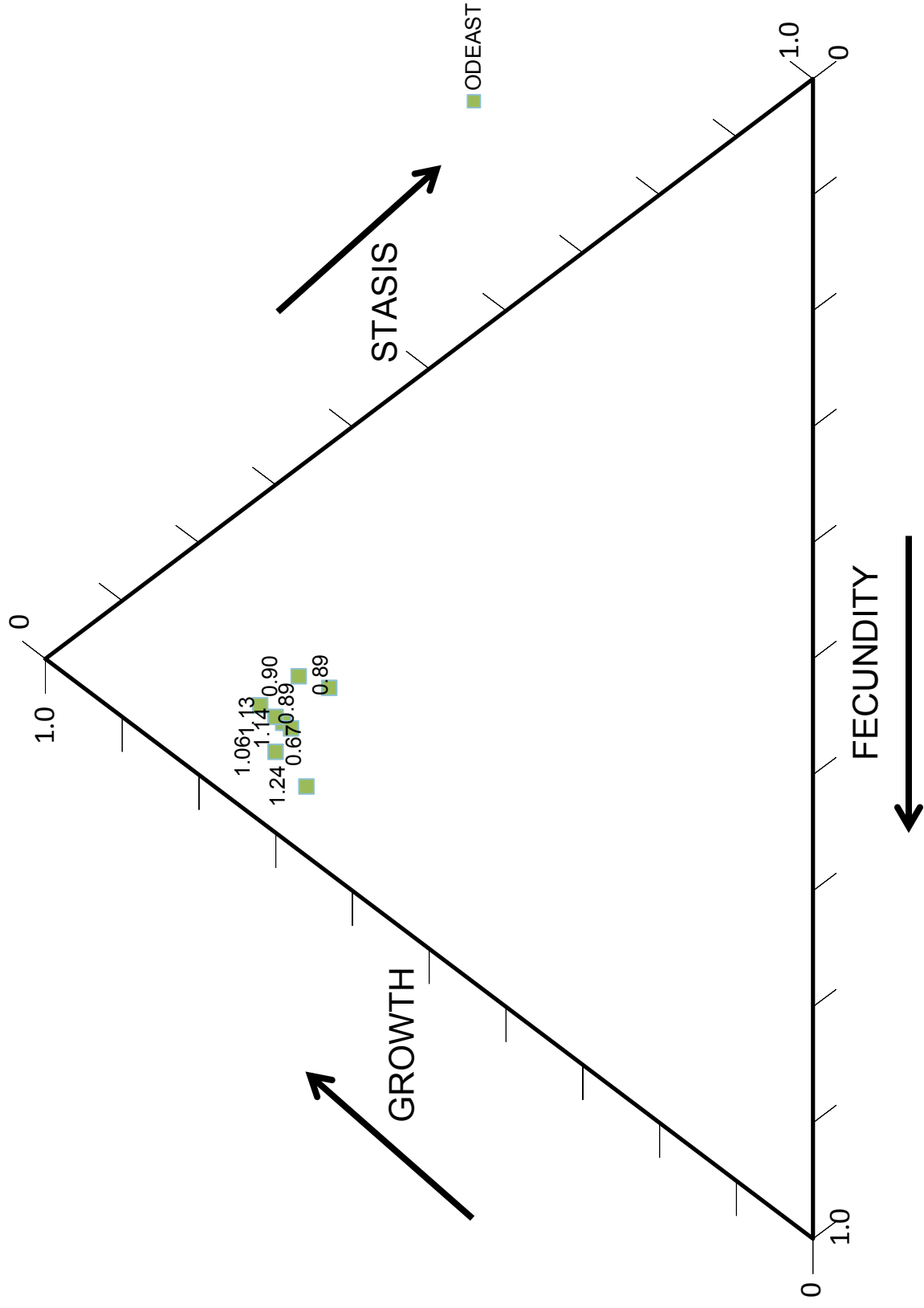
**Appendix B5.** Differences in summed matrix elements that represent fecundity between the five populations of Indiana Dunes *Cirsium pitcheri* Metapopulation:(a) difference of population from pooled metapopulation and (b) the contribution of these differences to the differences in $\lambda_M$. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
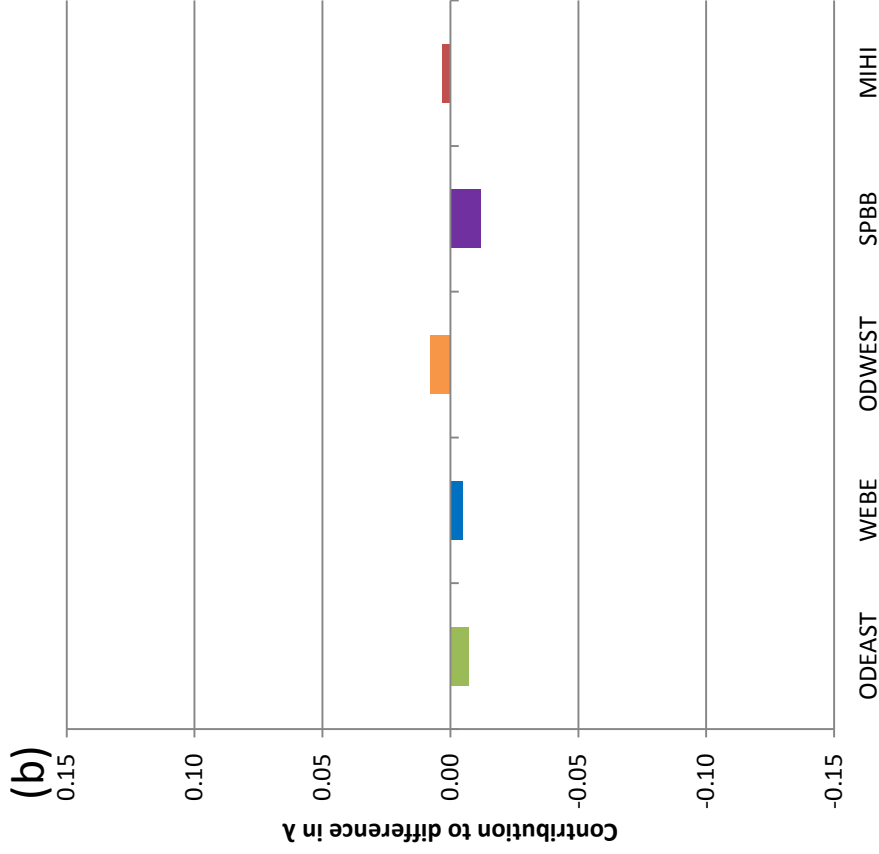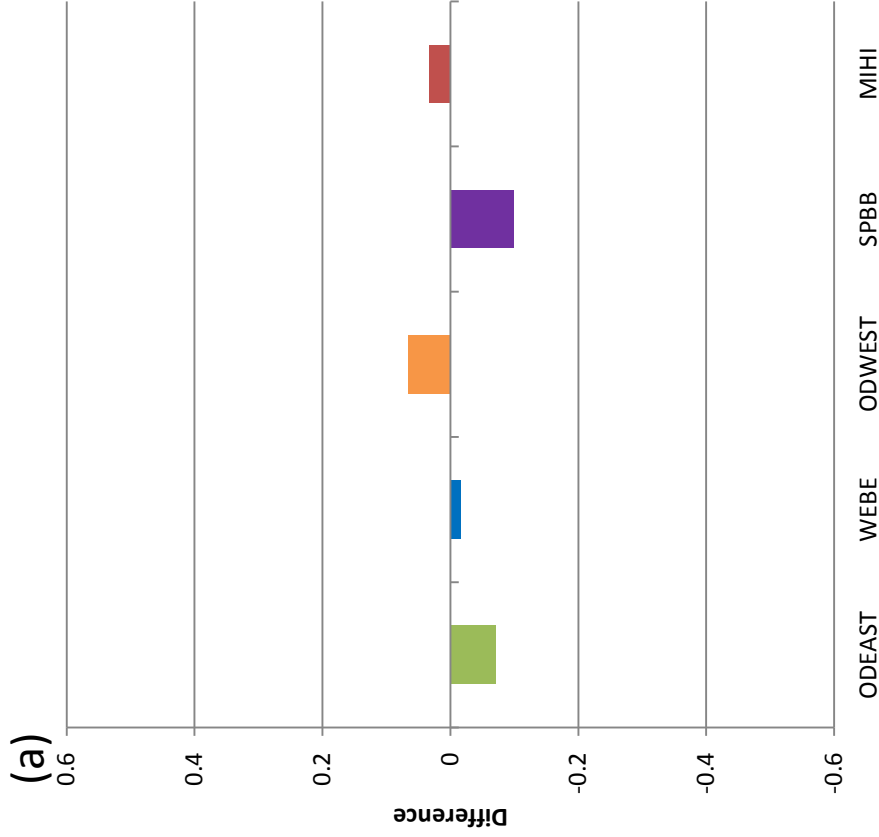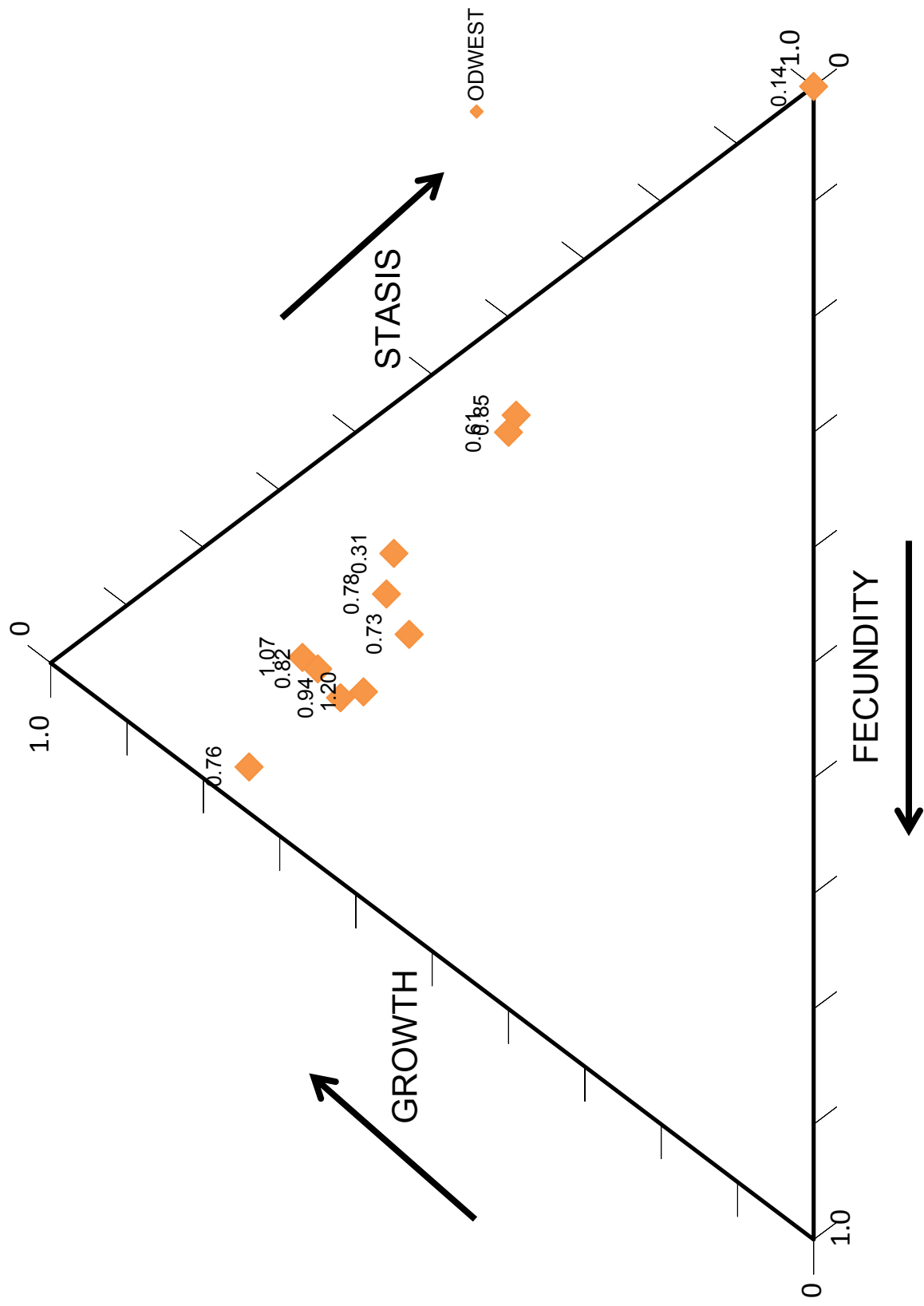
**Appendix B6.** Differences in summed matrix elements that represent regression between the five populations of Indiana Dunes *Cirsium pitcheri* Metapopulation: (a) difference of population from pooled metapopulation and (b) the contribution of these differences to the differences in $\lambda_M$. Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI).
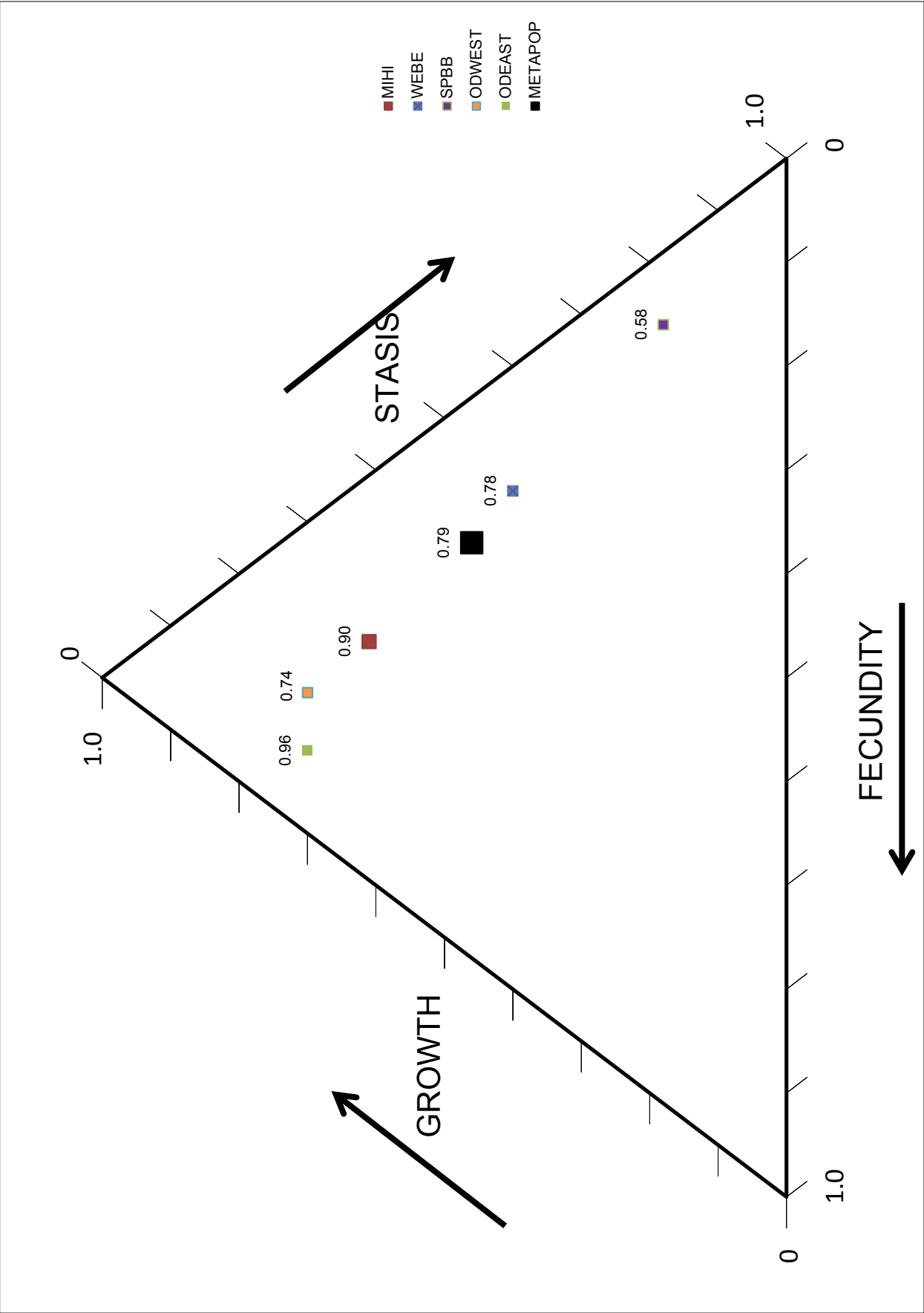
**Appendix C1.** Triplot of mean λ of each *Cirsium pitcheri* population: Ogden Dunes East (ODEAST), West Beach (WEBE), Ogden Dunes West (ODWEST), State Park Big Blowout (SPBB), Miller High Dunes (MIHI) as well as the entire metapopulation (METAPOP).
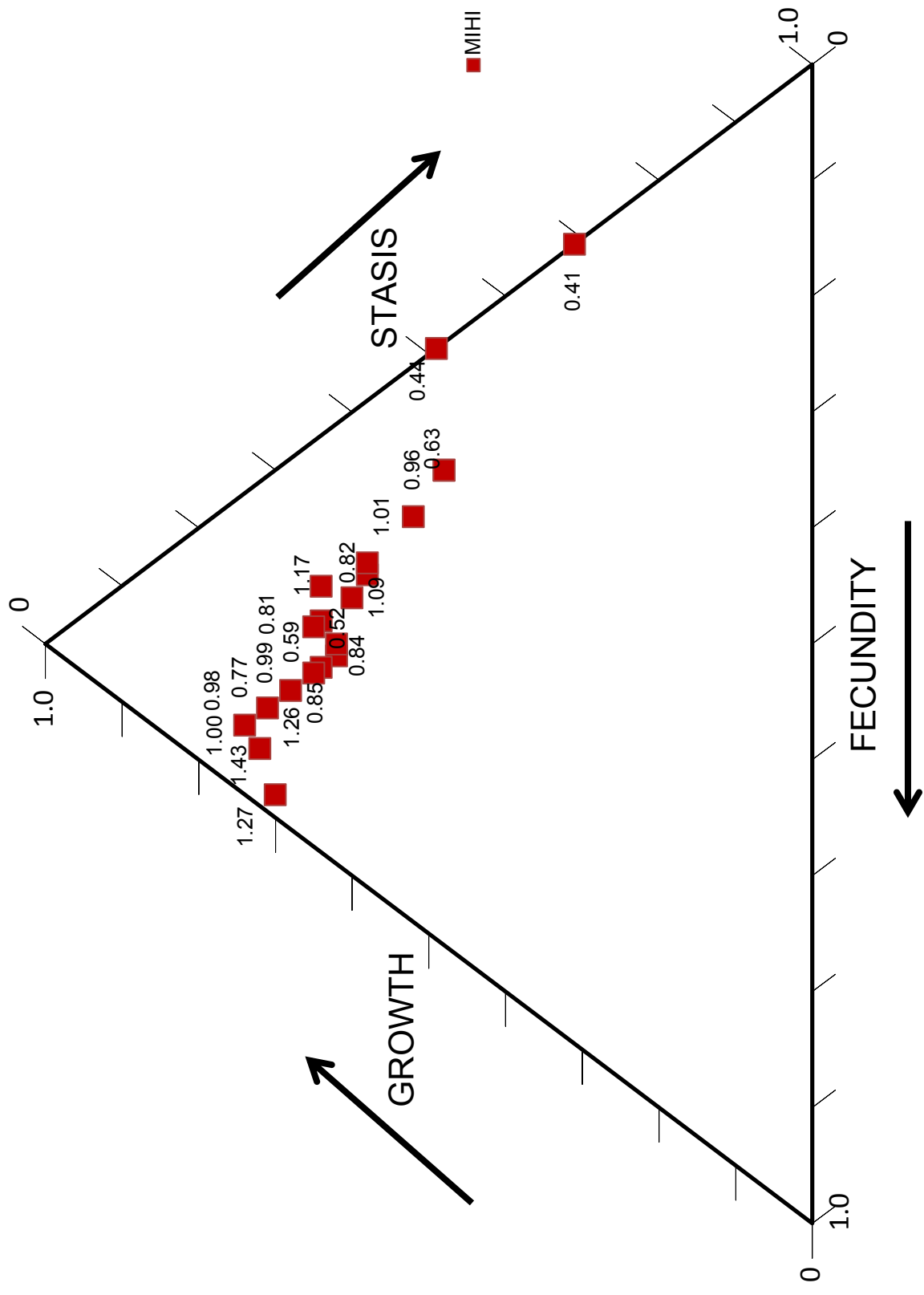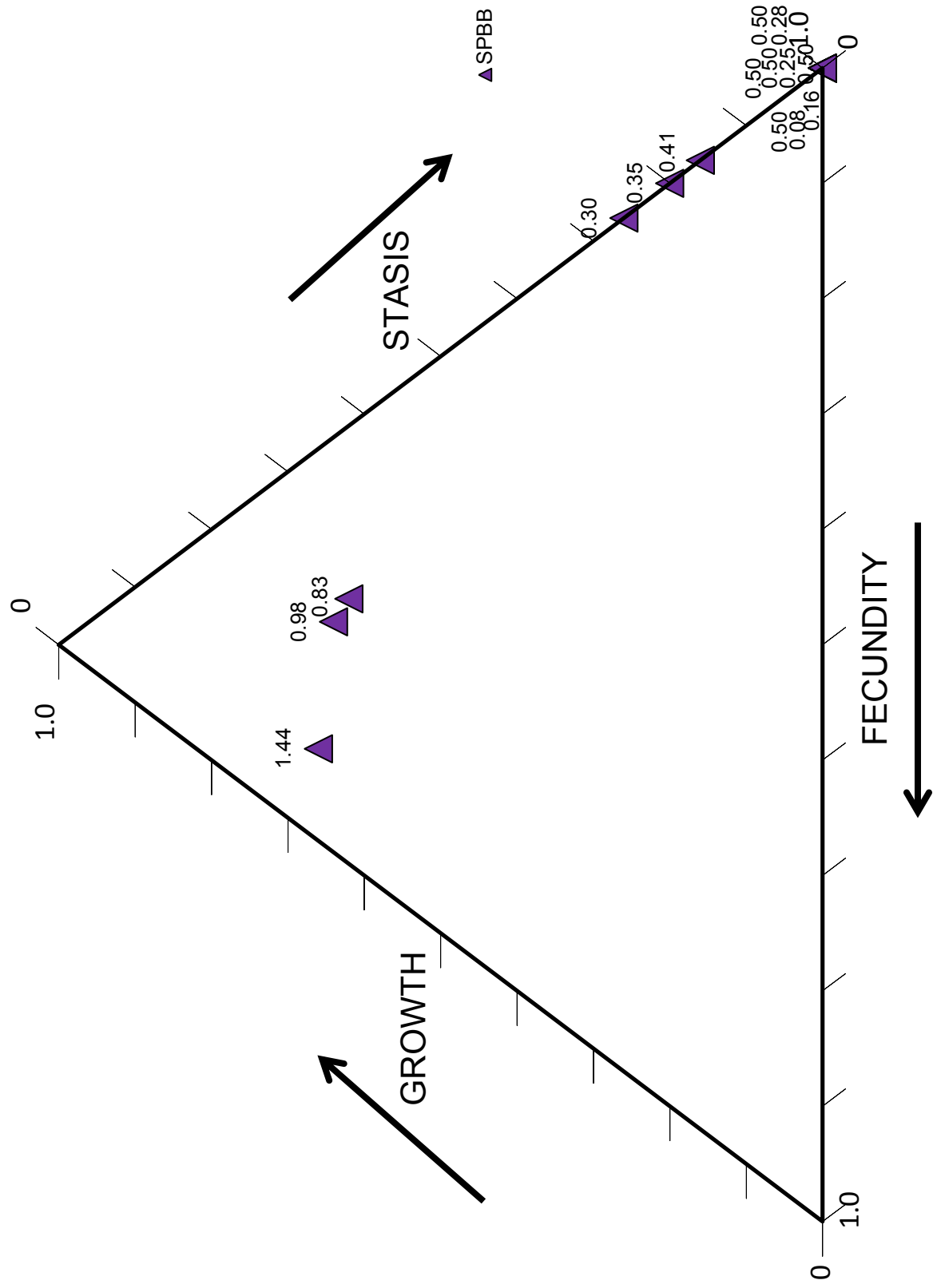
**Appendix C2.** Triplot showing Miller High Dunes *Cirsium pitcheri* population within the Indiana Dunes Metapopulation including population growth rates (λ) of each transition matrix.
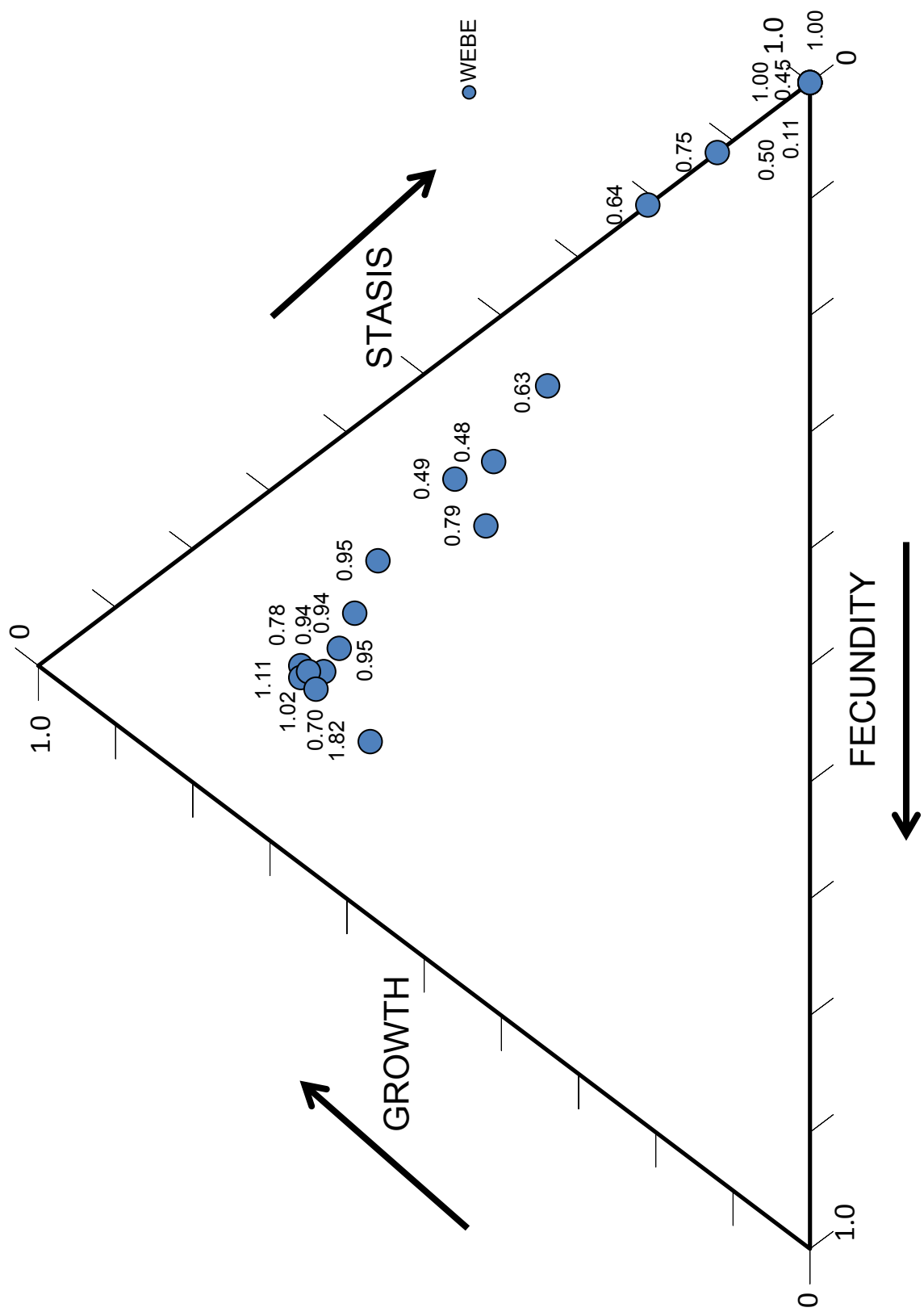
**Appendix C3** . Triplot showing Ogden Dunes East *Cirsium pitcheri* population within the Indiana Dunes Metapopulation including population growth rates (λ) of each transition matrix.

**Appendix C4.** Triplot showing Ogden Dunes West *Cirsium pitcheri* population within the Indiana Dunes Metapopulation including population growth rates (λ) of each transition matrix.

**Appendix C5.** Triplot showing State Park Big Blowout *Cirsium pitcheri* population within the Indiana Dunes Metapopulation including population growth rates (λ) of each transition matrix.

**Appendix C6** . Triplot showing West Beach population with population growth rates of each transition matrix.
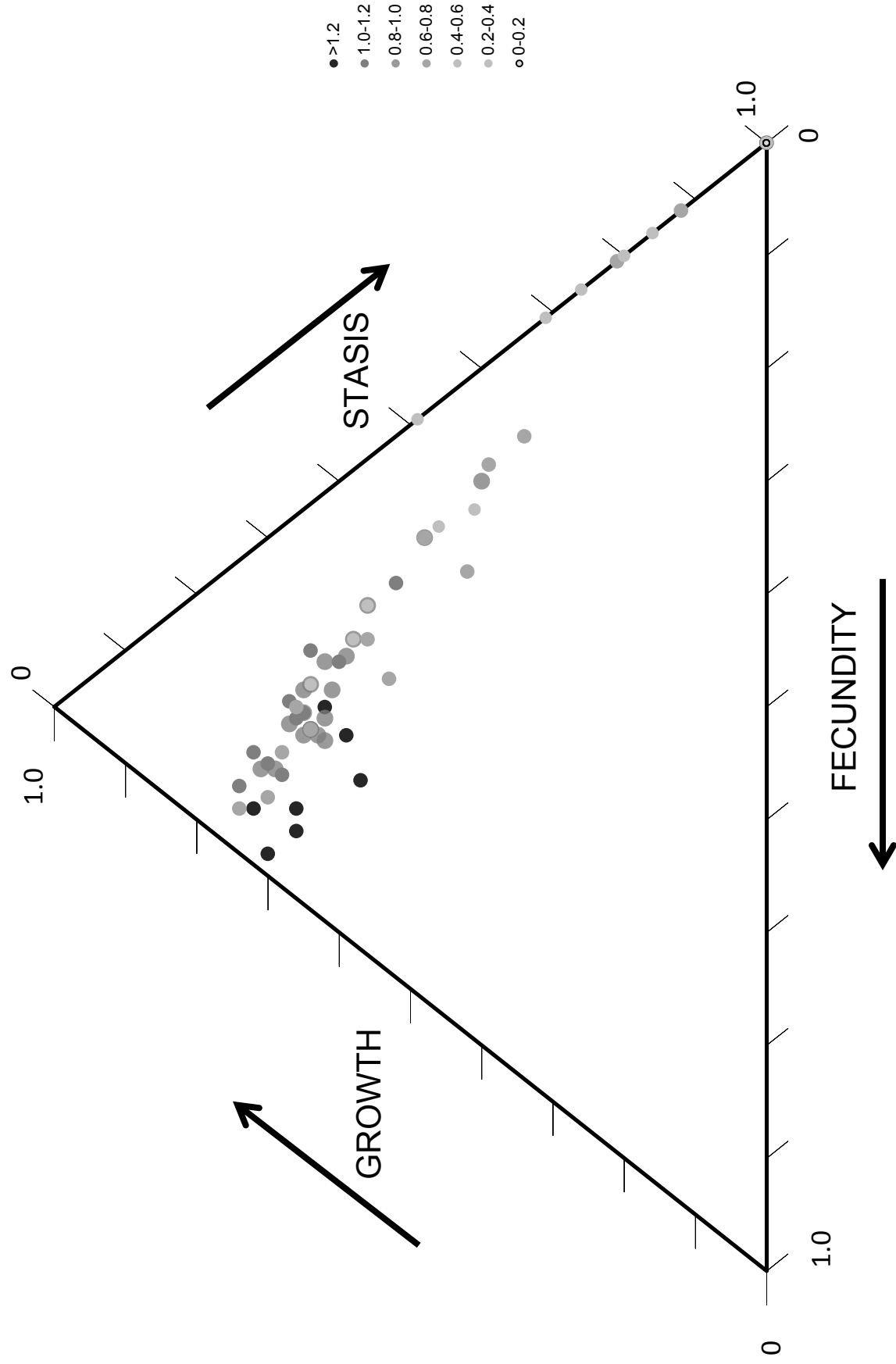
**Appendix C7.** Triplot showing population growth rate (λ) gradient of all five populations of *Cirsium pitcher* within the Indiana Dunes Metapopulation in relation to elasticity values.
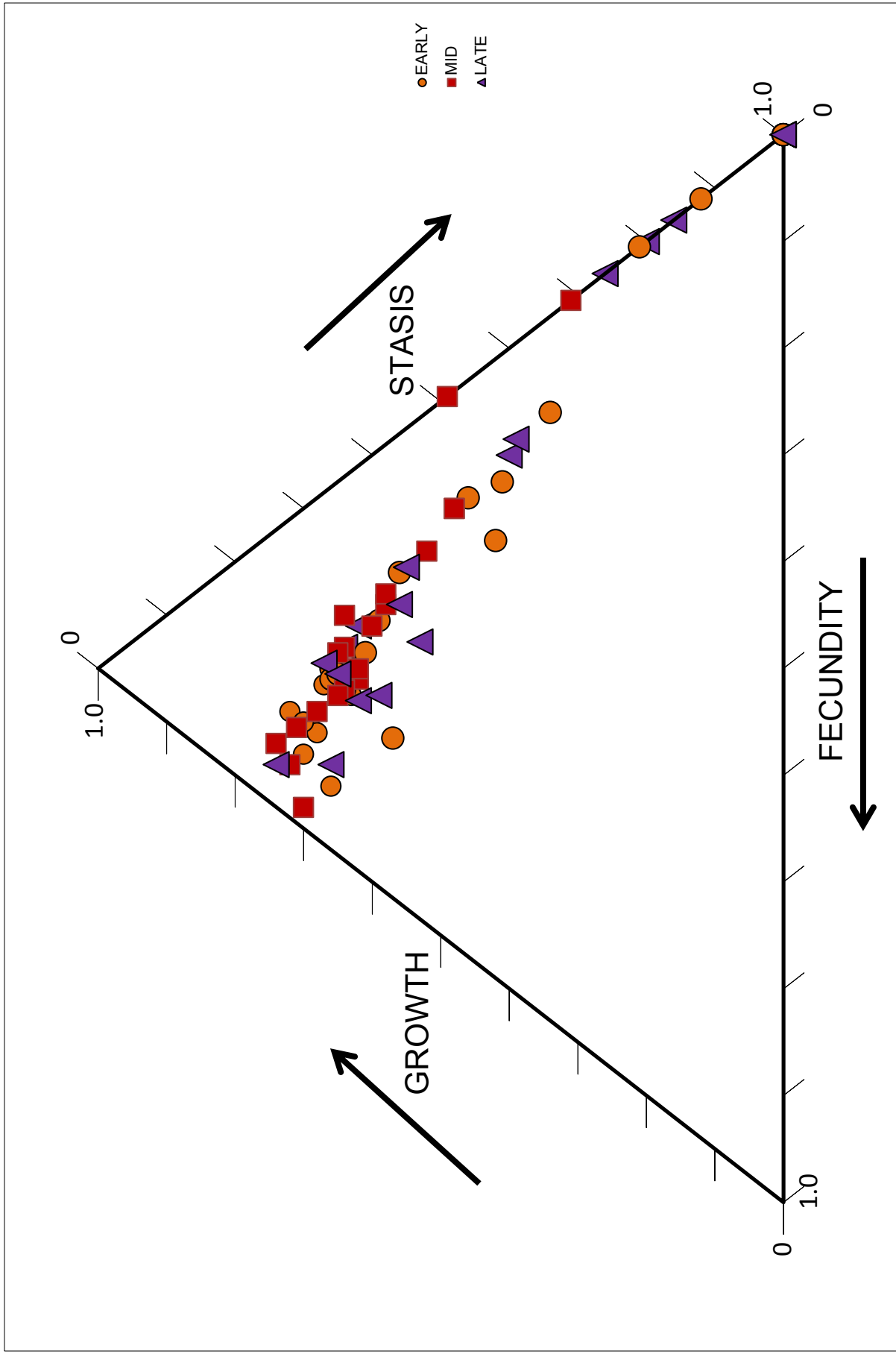
**Appendix C8. T**riplot of each of the five populations of *Cirsium pitcheri* based on successional stage of habitat within the Indiana Dunes Metapopulation.

**Vita**

Samniqueka Joi-Weaver Halsey was born in Detroit, Michigan, on June 25th,
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Nature Museum as well as work as a field assistant in the summer of 2010 with the
University of Colorado. She co-founded CSU's Friends of the Prairie, a student
organization designed to increase awareness of the campuses man-made prairie.

**POSTERS AND PRESENTATIONS**

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Samniqueka J. Halsey, Timothy Bell, Kathyrn McEachern. (2012) "A Metapopulation
    Approach to Examining Population Viability in the Indiana Dunes." Presented to
    Indiana Dunes National Lakeshore Science Conference, Indiana University
    Northwest, Gary, IN.

K.A. Jacobs, S. Kirt, L. Jackson, S. Halsey. "Prairie Education, Research and
    Management at Chicago State University: Poster Presentation at Schulenburg
    Prairie symposium at the Morton Arboretum Lisle IL on September 13-14, 2012.