THE INFLUENCE OF INDIRECT EFFECTS OF LARGE HERBIVORES ON THE LIFE HISTORY AND POPULATION DYNAMICS OF AN UNPALATABLE FOREST HERB SPECIES

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A main goal of evolutionary ecology is to understand how the biotic and abiotic variables with which a species interacts may influence its life history and population dynamics. Herbivores can dramatically affect both the demography and life history evolution of their prey. However, herbivory may also indirectly affect the biotic and abiotic interactions of neighboring unpalatable plant species. While theory predicts co-occurring unpalatable plant species should benefit from the reduction of neighbors, how the indirect effects of herbivores influence their population dynamics and life history remains largely unexplored. Using white-tailed deer as a model herbivore and *Arisaema triphyllum* as a model unpalatable plant species, I examined the indirect effects of herbivores on the population dynamics and life history traits of unpalatable plant populations. I used a combination of field surveys, experiments, and modeling techniques to determine how indirect effects could influence *Arisaema* population fitness and life history. I found that *Arisaema* exhibited significantly smaller mean size at flowering, lower mean seed number, and expressed increasing male-biased sex ratios as deer browse on a palatable species increased across seven sites in Pennsylvania. Concordant results were found for *Arisaema* and four additional unpalatable species growing in long-term, paired, fenced deer exclusion vs. deer access plots in Virginia. Using a common garden study I found that *Arisaema* from the same Pennsylvania sites had diverged in their relative growth rates and female flowering size threshold, suggesting populations could become locally adapted in response to the indirect effects of deer. I used integral projection models (IPMs) to show that mean *Arisaema* population growth rates (λ) declined with increasing indirect effects of deer largely due to decreased rates of

plants transitioning into and out of larger flowering plant stages. Two populations experiencing the highest deer-mediated indirect effects exhibited λs less than unity, indicating their potential decline. The overabundance of ungulate herbivores is an issue of global concern. My results show that the negative effects of herbivore overabundance can extend to plant species with which herbivores do not directly interact and provides novel insights for both ecologists and conservationists.

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PREFACE

I must thank a number of people because without them this dissertation may not have come to fruition. First is my advisor Dr. Susan Kalisz. The support that Sue has provided me over the course of my doctoral studies has been nothing short of Herculean. Because of her I have learned to be a better scientist and writer and have witnessed what it takes to be a top scientist. Sue invested countless amounts of time and energy in me and I can never thank her enough for that. I would also like to thank my committee for providing supports when I needed. I feel very lucky to have been able to have such well-respected and accomplished scientists to learn from. Dr. Tia-Lynn Ashman, Dr. Steve Tonsor, Dr. Brian, Dr. Steeve Côté, and Dr. Jonathan Pruitt have all given me useful with comments and criticisms through the years that have improved my research. In addition they have been outstanding examples from which I could learn, not only how to do great science, but also to balance life and work. In addition, I am indebted to Dr. William McShea and Dr. Norman Bourg of the Smithsonian Institution National Zoological Park, Conservation and Research Center.

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Finally, I would like to thank all my family. They have encouraged and supported me all along the way. My wife Pam has served as field assistant, photographer, and helped me through this by always believing in me.

1.0 INTRODUCTION

Indirect effects occur when the interaction between one species and another is mediated through a third species. This type of interaction has long been known to exist in nature but the importance of indirect effects within the frameworks of community and evolutionary ecology is only recently considered (Strauss 1991, Facelli 1994, Wootton 1994, Agrawal 2007, Walsh 2013). Indirect effects are now known to produce significant responses in phenotypic traits (Strauss *et al.* 2005), be strong sources of natural selection (Walsh & Reznick 2010), have important roles in community dynamics (Johnson & Stinchcombe 2007), and can even have greater magnitude than direct effects (Peckarsky *et al.* 2008). However, non-trophic indirect effects, the effects of one species on another species as a result of one species' alteration of abiotic components of the community, are still poorly understood (Estes *et al.* 2011, Kefi *et al.* 2012).

The outcomes of indirect effects can be positive or negative. Indirect facilitation is the positive effect of one species on a second species mediated through changes in its interactions by an intermediary (third) species (Brooker *et al.* 2008). Within a plant community, an intermediary plant species can indirectly facilitate a beneficiary species if the intermediary relieves competition between the beneficiary and a neighbor plant species (Lawlor 1979, Levine 2000, Callaway 2007). Indirect facilitative effects resulting from such multiple competitive interactions (Lawlor 1979) have been experimentally demonstrated in terrestrial plant systems (e.g. Miller 1994, Levine 2000) and may be especially common in species-rich communities (Brooker *et al*.

2008). Neighbor species identity within a community may also alter the magnitude of indirect effects. Such associational resistance occurs when a species receives fewer attacks due to the presence of unpalatable or non-prey neighbor species (Andow 1991). In contrast to indirect facilitation, species that share the same habitat with a favored prey species may experience associational susceptibility and experience increased predation (White & Whitham 2000).

Across trophic levels, herbivores can indirectly facilitate some plant species by modifying the balance between positive and negative interactions with co-occurring plant species (Graff *et al*. 2007, Alberti *et al*. 2008, Crain 2008). Specifically, herbivores alter the context for plant interactions by removing palatable plant biomass, which can effectively reduce palatable species' competitive ability (Louda *et al*. 1990) or induce their production of costly defenses (Agrawal *et al*. 2006). This can cause competitive release of co-occurring unpalatable species that may already make large investments in defense. In addition to indirect facilitative effects, herbivores alter the abiotic conditions of a community and affect plant species with which they do not consume. For example, herbivore removal of leaf biomass of target species can increase the light availability for non-target plants (Jacquemyn *et al.,* 2003), while their excrement or carcass decomposition can increase soil resources (Wardle *et al.,* 2001). Negative effects of herbivores include interruption of above- and belowground linkages between plants and soil resources through reduced leaf litter inputs (Wardle *et al.,* 2001) and increased soil compaction (Vavra *et al.,* 2007) that can limit nutrient flow to plant roots (Gass & Binkley, 2011). These non-trophic indirect effects can be as powerful as trophic indirect effects and may alter selection on plant traits (Kefi *et al.* 2012).

In this dissertation I examine how the indirect effects associated with activities of large generalist herbivores affect the ecological and evolutionary trajectories of unpalatable forest herb

species. Overabundant white-tailed deer (*Odocoileus virginianus*) browsing on temperate forest herbs is a contemporary and near ubiquitous interaction in eastern North America that can generate both direct and indirect effects on plant species. For my thesis research, I focus on the large generalist herbivore, white-tailed deer, and a common and unpalatable forest herb, *Arisaema triphyllum*. *Arisaema* is one of several forest herbs demonstrated to be generally unpalatable by deer but this species is unique in that it exhibits size-dependent sex switching. To understand how indirect effects of deer can impact *Arisaema* population dynamics and life history evolution I use a combination of observational field studies, deer-exclusion/deer-access paired plot experiments, and a common garden experiment. My research provides a unique perspective on the global phenomenon of overabundant and irrupting herbivores by demonstrating how indirect effects of herbivores can cascade through abiotic pathways to negatively affect unpalatable plant species.

In Chapter 2 I establish that, contrary to ecological theory, unpalatable forest herb species experience no benefit from the browse of palatable neighbors. In collaboration with Dr. William McShea and Dr. Norman Bourg at the Smithsonian Institution National Zoological Park, Conservation and Research Center, and Dr. Susan Kalisz at the University of Pittsburgh we used a combination of observational studies and experimental deer exclusion plots and found that plant life history traits important to demography declined in association with increased deer browse levels or deer exclusion. Soil quality was negatively affected by deer via high soil compaction (measured as penetration resistance) and low leaf litter depth suggesting a potential mechanism for the indirect effects of deer. This work is published in *Ecology* (Heckel *et al.* 2010).

In Chapter 3 I build upon the results detailed in Chapter 2 and use a common garden experiment to test the extent to which the observed shifts in *Arisaema* life history traits across populations represent local adaptation or phenotypic plasticity. I transplanted *Arisaema* from sites that displayed a gradient of deer browse levels and grew them in a common garden for five years. Using the garden data I evaluate divergence among populations in a set of life history traits: flowering and sex switch thresholds, relative growth rate, biomass allocation, and asexual reproduction. In agreement with life history theory, plants from populations with greatest deer impacts transition to female at a smaller size and have the highest relative growth rate compared to low deer impact sites. This work was conducted with Dr. Susan Kalisz.

In Chapter 4 I evaluate the demographic consequences of indirect effects of deer on *Arisaema* population dynamics. I use integral projection models (IPMs) to estimate population growth rates, λ, as well as elasticities and sensitivities, for six western PA *Arisaema* populations that experience a gradient deer impacts. Working with Dr. Susan Kalisz, I use the results from the IPMs to demonstrate that the negative effects of herbivore outbreaks and overabundance can extend even to plant species with which herbivores do not directly interact. These results have important implications for basic ecologists as well as conservationists and land mangers where deer are overabundant.

In Chapter 5 I synthesize the findings of all my data Chapters. I detail how the results presented therein yield important knowledge that can help to fill gaps in our current understanding of the ecological and evolutionary importance of indirect effects. In addition, I identify areas for future research of indirect effects on the evolutionary ecology of populations.

2.0 NON-CONSUMPTIVE EFFECTS OF A GENERALIST UNGULATE HERBIVORE DRIVE UNPALATABLE FOREST HERBS DECLINE

2.1 INTRODUCTION

Herbivores are key drivers of their individual prey plant's performance (reviewed in Gurevitch et al. 2000, Morris et al. 2007) that can profoundly affect the composition and function of plant populations and communities (reviewed in Huntly 1991, Strauss and Agrawal 1999). The effect of herbivores on co-occurring unpalatable plant species is less clear. Unpalatable or non-browsed species are predicted to benefit from herbivores if consumption of palatable neighbors by herbivores causes competitive release (Rooney and Waller 2003) and high levels of herbivory can favor increased abundances of unbrowsed species as palatable prey plants are lost from the community (Graff *et al.* 2007). Conversely, if the herbivores are large mammals, their non-consumptive effects can create unfavorable conditions for both palatable and unpalatable plant growth. These include direct effects like trampling (reviewed in Persson *et al.* 2000) or indirect influences via decreased soil fertility (Olofsson and Oksanen 2002, Bakker et al. 2004), degraded soil quality (Wardle *et al.* 2001), and potentially increased exotic species abundance (Vavra et al. 2007). The extent to which unpalatable plants benefit from herbivores depends upon how the herbivores affect local abiotic and biotic contexts, which can vary over space and time (Wilson and Nisbet 1997; Graff et al. 2007; Alberti et al. 2008; Crain 2008).

White-tailed deer (*Odocoileus virginianus* Zimmerman; henceforth deer) are generalist herbivores that consume a wide array of palatable species and have clear detrimental effects for palatable plant populations (reviewed in Rooney and Waller 2003, Côté et al. 2004). In forests experiencing high deer densities, dramatic drops in both the abundance and population stability of browsed species are observed (e.g. Anderson and Loucks 1979, McGraw and Furedi 2005, Knight et al. 2009a), which can lead to greater proportions of unpalatable plant species within the community (Anderson and Loucks 1979, Horsley et al. 2003, Royo and Carson 2006). Indeed, a recent large scale study suggests that unpalatable and non-native species are the beneficiaries of long-term increases in deer activity (Wiegman and Waller 2006). Deer densities in eastern North American forests have increased dramatically over the past fifty years (McShea et al. 1997), however, at a local scale, deer use of forest habitats can vary substantially (DeCalesta and Stout 1997). Currently, deer impose a wide range of browse levels across the forested landscapes of North America, presenting an ideal system for assessing generalist herbivore effects on unpalatable plant species.

Here we test for non-consumptive costs and benefits to unpalatable forest herbs in sites used by deer for forage. We define "unpalatable" as plant species that are typically not browsed because they are either less preferred by deer or contain defensive chemicals. We acknowledge that deer avoidance of unpalatable plants can vary in time and space depending on the local availability of preferred forage species, which can result in consumption of previously avoided species (e.g. Ruhren and Handel 2000). In this study, we use a combination of data from natural populations and replicated long-term deer exclusion experiments to quantify if unpalatable plant species experience benefits or costs from deer browsing. Specifically, to estimate effects on unpalatable plant demography, we quantify individual demographic traits of one focal

unpalatable species, *Arisaema triphyllum* [L.] Schott (Araceae; hereafter *Arisaema*), in multiple natural beech-maple forest sites that differ in mean annual levels of deer browse on a co-occurring palatable species (*Trillium grandiflorum*). Second, to quantify the effects on unpalatable plants in general, we assess individual plant size of five unpalatable species, including *Arisaema*, growing within paired long-term deer exclusion/deer access plots. In both natural sites and experimental plots we document deer avoidance of these unpalatable species. Finally, because large browsers are known to alter abiotic conditions important for plant growth, we tested the hypothesis that deer negatively affect abiotic conditions in the natural sites and experimental plots.

2.2 MATERIALS AND METHODS

2.2.1 Study system

Natural sites: In 2005, we established seven sites in Crawford County, Pennsylvania, USA (41° 39' 25" N, 080° 25' 23" W) that were well separated (2 – 42 km) and where *Arisaema* and *Trillium* co-occur for use in the current study (Appendix A). In each of the seven sites we established a 50x50m study plot that we censused annually. Winter deer density estimates in this area of PA range from 4 to 18 deer km^{-2} over the last decade (Wallingford and Grund 2003) and historically have not exceeded 30 deer km^{-2} (Redding 1995). Sale of Dibble Hill in 2006 resulted in only one year of data for that site.

Deer exclusion experiments: The long-term paired four-hectare deer exclusion/deer access plots were erected in 1990 and maintained since that time (McShea 2000). Plots are located near Front Royal, VA, USA (38° 55' 05" N, 078° 11' 41" W) at the Smithsonian's Conservation and Research Center (CRC) and in the adjacent Shenandoah National Park [Matthews Arm (MA)

and Keyser's Ridge (KR) sites] and are separated by 2 - 21km. The deer exclusion plots are surrounded by 2.4m high combination of woven and high tensile wire fencing that allow all other animals to freely enter the plots. Average deer density at the CRC in 2007 was 33 deer km^{-2} (19-56 deer km^{-2} 95% C.L.) based on distance sampling methods (McShea unpub. data) and match estimates across the past 18 years at the CRC (McShea unpub. data) and the Shenandoah National Park (R. Gubler, pers. comm.).

2.2.2 Quantifying deer browse intensity in natural sites:

We used deer browse of *Trillium grandiflorum* [Michx.] Salisb. (Liliaceae; hereafter *Trillium*) an established phyto-indicator of deer browse (Anderson 1994, Augustine and Jordan 1998, Augustine and DeCalesta 2003, Kirschbaum and Anacker 2005) as our index of deer browse intensity. Each year for three years (2005-2007), we sampled *Trillium* populations within three parallel 1x50m transects that originated from a random location along one side of the 50x50m study plots. In each transect we counted all stems of *Trillium* and recorded their stage (flowering or non-flowering) and browse status. Deer browse on *Trillium* results in a stem devoid of leaves with a cut parallel to the ground, which is distinct from lagomorphs and rodents browse that cut stems at a 45° angle (Augustine and Jordan 1998). We calculated deer browse intensity at each site as the proportion of all *Trillium* stems that were browsed by deer across the three transects. The annual percent *Trillium* browsed in our study sites (2005-2007) ranged from 0 to 25% and were similar in magnitude to Trillium browse data collected at the same sites (Knight 2003). Thus, we calculated a six year *Trillium* browse average for each natural site by averaging the three years of data (1999-2001) published in Knight (2003) with the 2005-2007 data from this study. Since large browsing ungulate herbivores' effects on plant community composition may

be evidenced only after many years (e.g. Wiegman and Waller 2006), we used this long-term average in all subsequent analyses.

2.2.3 Focal species:

We chose *Arisaema* as the focal unpalatable species for detailed demographic study in the natural sites because it is a long-lived widespread understory perennial that expresses discrete gender stages (Bierzychudek 1982). Individual *Arisaema* plants typically progress from vegetative to flowering (Figure 1.1 A&B) and from male to female (Figure 1.1 C&D) with increasing size. An individual's gender can switch across seasons as it grows (male→female) or shrinks (female→male) in size (Bierzychudek 1982). This size-dependent gender switching allows us to quantify important changes in reproduction that are would be less obvious in hermaphroditic species. In the deer exclusion paired plots (CRC, KR, MA) we measured size of *Arisaema* and additional unpalatable plants as available: *Actaea racemosa* (Ranunculaceae, black bugbane), *Osmorhiza claytonii*, (Apiaceae, Clayton's sweetroot), *Podophyllum peltatum* (Berberidaceae, Mayapple), Botrychium *virginianum* (Ophioglossaceae, rattlesnake fern). An ongoing, large-scale study in the CRC includes deer browse estimates for three of these species and supports their classification as plants that deer avoid [# stems : % stems browsed—*Arisaema* 343: 0.006%; *Actaea* 120: 0%, *Botrychium* 35: 0.008%; no data for *Podophyllum* or *Osmorhiza* (Bourg and McShea, unpublished data)].

2.2.4 Testing the effects of deer on *Arisaema's* demographic traits:

In April 2005, all flowering *Arisaema* plants in the 50x50m plots were permanently tagged (N flowering/ site = 27-35). We excavated plants outside the plots and found that stem diameter at ground level can be used as a proxy estimate for biomass (Appendix B). In April at each site we annually estimated biomass of all tagged flowering plants in our 50x50m study plots (2005-2007) and we counted and estimated biomass of all the non-flowering plants in three 1x50m transects (2005-2006; N total/ site =214-424) to estimate density. Annually we determined the gender of each flowering plant in our plots and calculated sex ratio at each site as the proportion of the flowering plants that were male. Finally, each year we assessed deer browse of *Arisaema* as the number of deer browsed or otherwise damaged stems across all *Arisaema* individuals surveyed (N=9746).

2.2.5 Female reproductive success:

For each female identified in our censuses, we counted the number of flowers, fruits and the number of seeds/fruit in July 2005 and 2007. We calculated fruit set = [#fruits/#flowers]. We used these data to estimate *Arisaema*'s seed rain m^{-2} at each site each year:

$$seed\ rain = \frac{(\#\,\text{females})(\text{mean}\ \#\,\text{fruits/female})(\text{mean}\ \#\,\text{seeds/fruit})}{\text{sample area}}$$

and calculated the two year mean seed rain for each site.

To examine the relationship between browse level in the natural sites and *Arisaema* demographic traits, we regressed mean flowering plant biomass, sex ratio, and seed rain m^{-2} on

the mean annual *Trillium* browse level for the natural sites. We used site means for biomass and sex ratios because regression of these variables on browse levels did not differ in slopes among years (PROC GLM year*browse history P>0.70). We compared fruit set among sites in 2005 and 2007 using ANOVA; 2005 data were square root transformed to make the variances equal.

2.2.6 Testing the effects of deer on unpalatable plant species size:

Due to the patchy distribution of the focal unpalatable species within the experimental plots, we first identified sampling areas within the paired deer exclusion/deer access plots where the five focal unpalatable species occurred and that were matched for aspect and slope of terrain, distance from the fence, and understory and canopy cover. One 1x50m transect was marked in each sampling area. Every meter, we selected individuals of the focal species closest to the meter mark and measured each for size. If a focal species was not found at that distance, we moved one meter down the transect. This process was repeated until 30-46 plants/transect were measured for each species in each plot. Not all focal species co-occurred at each site (Appendix C). To estimate size of the focal species, we measured stem diameter at the soil surface. For *Osmorhiza* and *Actaea,* we also measured plant height since Webster and Parker (2000) found height of those species to be an estimator of deer browse intensity.

At each site, we determined the effect of deer exclusion on plant size by calculating the log response ratio, *L*, (Hedges et al. 1999, Gurevitch and Hedges 2001). We calculated *L* for each species at each site (CRC, KR, and MA) as $L = \ln(R) = \ln(\bar{X}_E) - \ln(\bar{X}_A)$ where $\bar{X}_E$ is the mean species size in deer exclusion plots and $\bar{X}_A$ is the mean species size of in deer access plots. We used a mixed-model analysis to calculate the across site mean effect sizes for each species,

$\bar{L}^*$, under the assumption of random variation in effect size at different sites. Mixed model analysis incorporates the within species across site pooled variances to produce a total variance in effect size for each species (Hedges et al. 1999). To determine if deer exclusion had a *general* effect on unpalatable species sizes we calculated the grand mean effect size across all species, $\bar{\bar{L}}^*$.

2.2.7 Testing the effects of deer on abiotic site quality:

Natural sites: In 2005, we measured leaf litter depth at 10 locations along each of three transects in all study plots (N=30/plot). We measured three abiotic variables (light, soil moisture and soil penetration resistance) in six natural sites in the 50x50m plots. To ensure uniformity of sampling conditions, all measurements were taken between July 18 and 23 2006 when temperatures were seasonal and skies were clear with no rain events. Between 11am and 1pm on sampling dates, we quantified the amount of light reaching the soil surface (µmol s^{-1} m^{-2}) using a Li-Cor Quantum sensor and Li-1000 data logger (Li-Cor Biosciences) at five points at 10m intervals along three parallel transects evenly spaced within the study plot (N=15/plot). We determined soil moisture at five points at 10m intervals along two parallel transects evenly spaced within the study plot (N=10 points/plot) using a soil moisture probe (Lincoln Soil Moisture Meter, Forestry Suppliers Inc.). Finally, we measured soil penetration resistance (MPa), a key metric of soil compaction using a cone penetrometer (Field Scout SC-900, Spectrum Technologies). Because the corms and roots of *Arisaema* in our natural sites are found within the top 15 cm of soil, we measured soil penetration resistance at all natural sites to a depth of 15 cm, sampling 100 points at 5m intervals on a grid across the entire 50x50m study plot.

We tested for differences in individual abiotic variables among sites (Appendix E), then created a multivariate descriptor of abiotic site quality using principal components analysis (PCA) (Sokal and Rohlf 1995). Factors loaded into the PCA were mean values of the variables light level, soil moisture, soil penetration resistance at 15cm, and leaf litter depth for each site (Appendix F, Table F1). We regressed the site-specific PC1 and PC2 scores on mean browse level using bivariate regression.

To determine if mean browse level, density of flowering *Trillium*, density of *Arisaema*, or soil quality (PC1) were significant predictors of *Arisaema* demographic variables we used backward stepwise regression (Sokal and Rohlf 1995). The model procedure included all quadratic and interaction terms.

Experimental sites: To determine if deer access increased soil compaction relative to the 18 year deer exclusion plots, we measured soil penetration resistance to a depth of 10cm in each of the paired experimental plots used for plant size analysis (CRC, KR, MA) plus a fourth plot in Shenandoah National Park [Hilltop (HT)] between June 4-6, 2008 under uniformly dry and sunny conditions. This depth profile was necessarily shallower than our natural sites because bedrock was often encountered at 10cm depth. We sampled 25 points at 15m intervals on a grid centered on the plant sampling transect in each plot. Data were analyzed using two-way MANOVA (PROC GLM) (Appendix F, Table F2).

All statistical analyses conducted as part of this study were performed using MATLAB (v. R2006a, The Mathworks, Inc., 2006) or SAS ® software, JMP IN 5.1 or SAS Version 9.2 of the SAS System for Windows®.

2.3 RESULTS

2.3.1 Effects of deer on unpalatable plant species demographic traits:

Across the three years of this study and seven natural sites, deer browse of *Arisaema* was a rare event that did not differ among sites. Only 0.6% of our 9746 censused *Arisaema* stems showed evidence of deer browse and only 0.3% showed any other sign of damage. These data validate *Arisaema*'s status as an unpalatable, unbrowsed species. In contrast, *Trillium* in these same sites was regularly browsed and sites exhibited a gradient in their six-year average browse level on *Trillium* (means range from 2.2% to 22.4% Fig. 2.2A). The extreme ends of this gradient (DZ = low; TW = high) were significantly different (t-test: t=-2.9, df=5, P=0.04; Fig. 2A).

We found a significant negative relationship between the average *Arisaema* flowering plant biomass and browse level on *Trillium* across the seven natural sites (Figure 2.2B). We also found a significant positive relationship between browse level and male-biased sex ratios (Figure 2.2C), likely due to *Arisaema's* size dependent gender expression. In the three populations with highest browse levels, >80% of the flowering plants were male. Fruit set/flower differed among sites in 2005 (range: 13-44 fruits/flower; ANOVA: $F_{5,95}$=2.5; P=0.04) but not in 2007 (range: 14–32 fruits/flower; ANOVA: $F_{4,26}$=0.3; P=0.89). Fruit set differences in 2005 were not correlated with site differences in browse level, but were in 2007. While the two-year mean seed rain was low for all populations (range: 0-0.38 seeds m^{-2}), it declined significantly as browse level on *Trillium* increased (Figure 2.2D). Females were rare in highly browsed sites and in one instance (TW 2005) totally absent. The number of flowering *Arisaema* stems did not differ across years within sites (ANOVA: $F_{5,16}$=1.9; P=0.18).

Results from the backward stepwise regression of PC1, PC2, *Arisaema* density/site, *Trillium* density/site, and deer browse level indicate that browse level was the sole or strongest predictor of all *Arisaema* demographic metrics (Appendix F). Deer browse of *Trillium* predicted a decline in *Arisaema* plant biomass, a decline in seed rain m^{-2} and an increase in the proportion of males. In addition, flowering *Trillium* density was a significant predictor of *Arisaema* flowering plant biomass decline (Appendix F).

2.3.2 Effects of deer on unpalatable plant species size:

All five unpalatable focal species were significantly larger in the deer exclusion plots relative to the deer access plots (Appendix D). The grand mean effect size of deer exclusion on plant size across all unpalatable focal species was strong and significantly greater than zero ($\bar{\bar{L}}^*$=0.41 ± 0.11 95% C.L; Appendix D).

2.3.3 Effects of deer on abiotic site quality*:*

Deer effects on abiotic characteristics of natural sites: There were significant differences among sites found for all abiotic variables, however no clear pattern related to mean herbivory levels emerged (Appendix F, Table F1). In the PCA, the first two eigenvectors combined to explain 87% of the variance among sites. PC1 (eigenvalue = 2.4) explains 59% of the variance and is positively correlated with soil penetration resistance (eigenvector = 0.58) and litter depth (eigenvector = 0.60). PC2 (eigenvalue = 1.1) explains 28% of the variance and is correlated positively with light level (eigenvector = 0.74) and negatively with soil moisture (eigenvector = -

0.62). PC1 decreased with increasing *Trillium* browse level (P=0.07), signifying that high browse sites had more compacted soils with less litter than low browse sites (Figure 2.2E). PC2 and browse level were not correlated (P>0.90).

Deer effects on soil compaction in paired plots: In the paired experimental plots we found deer exclusion treatment, site, and their interaction all had significant effects on soil penetration resistance (Appendix F, Table F2). Soils exhibited significantly higher penetration resistance in the deer access plots relative to deer exclusion plots (P>0.05; Appendix F). High compaction in deer access plots required 4 - 145% more force to penetrate soils than in the paired deer exclusion plots.

2.4 DISCUSSION

Our results clearly show that unpalatable plant species do not generally benefit from deer browsing on co-occurring palatable species. *Arisaema* vital rates are correlated with increasing deer browse level on *Trillium.* Where deer browse levels were highest *Arisaema* had smaller individual plant size (Figure 2.2B), male biased sex ratios (Figure 2.2C) and low seed rain m^{-2} (Figure 2.2D). Importantly, these negative trends documented for our *Arisaema* populations are surprisingly similar in magnitude and direction to those of deer browsed palatable species (Anderson 1994, Knight 2003, McGraw and Furedi 2005). *Arisaema's* demographic responses are not caused by herbivory by deer or any other herbivore. Deer browse of *Arisaema* was rare in both our natural (0.6%) and experimental (0.006%) study sites. Thus, the demographic trait declines observed here cannot be attributed to *Arisaema's* associational susceptibility with *Trillium* (*sensu* White and Whitham 2000). Data from our deer exclusion experiments conclusively implicate deer as indirect causal agents of *Arisaema's* declines and support the

results from our natural sites. The significantly smaller plant size of all five unpalatable species in deer access plots relative to deer exclusion plots suggests this decline may be a widespread phenomenon wherever white-tailed deer or other ungulate overbrowsing occurs (e.g. Webster and Parker 2000).

High rates of ungulate herbivory on palatable forest perennial herbs invert the natural stage progression from vegetative to flowering because herbivory can halt or reverse their biomass accumulation (Augustine and DeCalesta 2003, Knight 2003). In *Trillium* spp., deer browse results in smaller average plant size, a reduced proportion of flowering plants, and declining populations [i.e. $\lambda < 1$] (Lubbers and Lechowicz 1989, Anderson 1994, Knight 2003). Across 12 *Trillium* populations deer drove the significant negative relationship between λ and herbivory level (Knight et al. 2009a). Similarly, a viability analysis of 36 deer-browsed populations of American ginseng (*Panax quinquefolius* L.) revealed that 80% of these populations had >99% chance of extinction within 100 years (McGraw and Furedi 2005). For both of these studies, loss of population viability was driven by deer mediated declines in individual plant stage and size. The fact that our unpalatable species were significantly smaller in experimental deer access relative to the exclusion plots (Appendix D) suggests that these species will also exhibit population decline if non-browsing deer effects are sustained.

Another aspect of decline is seen in the *Arisaema* population sex ratios. The sex ratios of our study populations are exceptionally male biased; they overlap with only the upper 14% of the sex ratios distribution derived from a survey of 74 *Arisaema* populations (reviewed in Richardson and Clay 2001). Because the smallest flowering *Arisaema* plants within a population are male, declines in average flowering plant size with increasing browse level at a site likely drive the observed highly skewed sex ratios. Size effects on gender allocation can be expected

for non-gender diphasic species, too. For example, in two *Trillium* species, the largest plants within each population had the highest proportional allocation to female function while the smallest plants allocated more to male function (Wright and Barrett 1999). Reductions in plant size and thus declines in female function (Figure 2.2B & 2.2D) may be a cryptic but widespread outcome for plants in forests with persistent high ungulate browse levels. In addition, the low absolute number of *Arisaema* females in our study populations translates directly into low seed rain (Figure 2.2D) and low recruitment potential. Although population growth rate is more sensitive to changes in adult survival than it is to changes in recruitment and early stage class survival (Pfister 1998), populations with no seedling recruitment are obviously non-sustaining and more vulnerable to stochastic extinction (Kery *et al.* 2000).

2.4.1 Negative indirect effects of deer on unpalatable species

Several factors related and unrelated to deer that we did not measure could also contribute to the observed unpalatable species performance declines. For example, loss of palatable species cover by browsing is known to increase drought stress (Yates et al. 2000) and percentage bare ground (Knight et al. 2009b), and foraging activities of deer may increase physical disturbances of soil (Vavra et al. 2007). Aboveground activities of ungulate browsers and anthropogenic disturbances due to logging, agricultural, or recreational use of forest sites can all contribute to decreased soil quality. The presence of exotic earthworms that can increase soil compaction, decrease understory vegetation and fine root density (Hale et al. 2005). We acknowledge that some or all of these other effects may operate to shape plant population and community dynamics in temperate forests.

Our experimental paired plot data provide clear evidence of negative indirect of effects of deer on unpalatable plant species. However, the mechanism for these indirect effects is unknown. The analyses of abiotic characteristics provide clues about one potential mechanism for indirect negative effects of deer. The significantly higher levels of soil penetration resistance in deer access vs. deer exclusion experiments (P=0.014; Appendix F, Table F2) conclusively show that deer browse negatively affects soil quality and supports the PCA results (Figure 2.2E). In the analysis of natural site abiotic variables, values of PC1 decreased with increasing herbivory levels, suggesting a relationship between soil penetration resistance and leaf litter depth on plant demographic traits.

2.4.2 General relationships between ungulates, soil compaction and plant growth

Trampling of forest and grassland habitat by domestic or wild ungulates is known to cause soil pore collapse and directly increase soil compaction (Cumming and Cumming 2003, Vavra et al. 2007). Ungulate herbivores can also indirectly affect soil compaction because their browsing causes the loss of vegetation cover (Wardle et al. 2001), and reduces both leaf litter deposition and new fine root growth of browsed species (Sharrow 2007). These losses can increase water run-off and soil erosion, resulting in increased compaction, decreased available water capacity and decreased nutrient availability (Cumming and Cumming 2003, Sharrow 2007). Soil compaction can directly reduce plant growth (Godefroid and Koedam 2004) and decrease seedling establishment (Bassett et al. 2005, Kyle et al. 2007). Bassett et al. (2005) found both the number and size of native woody seedlings significantly declined with increasing forest soil

compaction. We found that soil compaction in deer access plots was between 4 - 145% more compacted than paired deer exclusion plots.

Soil compaction caused by deer has the potential to modify the interaction between plant species and their soil mutualists. Arbuscular mycorrhizal fungi (AMF) are vitally important for soil resource uptake of most forest perennial herbs and woody plants (Brundrett and Kendrick 1988, van der Heijden et al. 2008). Browsing by overabundant ungulates is linked to declines in abundance and function of soil mycorrhizae (Rossow et al. 1997) and decreases in the colonization rate of roots by beneficial AMF as a result of declining soil pore size (Waltert *et al.* 2002). Nadian et al. (1997) found reduced hyphal growth in compacted soils because compacted soils have soil pore size < 3µm, which is smaller than most hyphae's diameter (5-20µm in diameter). Finally, compaction can have long-term effects— soil compaction levels beyond the tolerances for plant growth or seedling establishment can persist for up to 30 years in forested areas retired from livestock grazing (Bassett et al. 2005, Sharrow 2007). The relationship between deer browse level and soil compaction observed in our study suggests that the diminished size of *Arisaema* and the other unpalatable species in the presence of deer are likely attributable, at least in part, to these direct and indirect effects on plant growth mediated by deer via the soil environment.

Our results contrast with other studies that appear to demonstrate benefits to unpalatable species in heavily browsed forests (Anderson and Loucks 1979, Horsley et al. 2003, Wiegman and Waller 2006). We can think of several reasons why increases in unpalatable species abundance can appear at first glance to benefit from deer. First, high levels of deer browse force an immediate and automatic increase in the relative abundance of unpalatable species as the abundance of browsed, palatable species decline. However, our data suggest that an initial

positive response by unpalatable species can reverse and become a negative response if high deer browse levels are sustained. Second, unlike our measures of individual plant performance, the above studies use indirect metrics of species performance (i.e. percent cover or relative abundance). These indirect measures are known to be poor predictors of population viability because the long life spans of forest perennial species create time-delays (Colling and Matthies 2006) that obscure the detection of diminished performance with habitat quality declines. Third, our data and that of Knight et al. (2009b) reveal that high levels of deer herbivory in a site alter the soil environment, which can negate the positive effects of ungulate herbivores. Indeed, Michalet et al. (2006) argue that positive interactions can be nullified when stress or disturbance reach extreme levels, such as those created by overabundant deer.

2.4.3 Conclusions

The success of unpalatable species found in other studies that estimated abundance or percent cover (e.g. Anderson and Loucks 1979, Horsley et al. 2003, Wiegman and Waller 2006) may be evidence of the ghost of past benefits from deer. Recent studies document that the outcome of past transient negative interactions, like interspecific competition (Miller et al. 2009) or granivory (Howe and Brown 2001), can significantly change the trajectory of community composition via the suppression of competitive subordinates or palatable species. The implications of our data are that even unpalatable species populations will decline through indirect negative effects of overabundant deer. Ungulate herbivores are drivers of palatable plant community change worldwide (Côté et al. 2004, Royo and Carson 2006, Vavra et al. 2007), but mechanistic studies of their interactions with unpalatable species have not been previously examined in depth. We expect that sustained browsing pressure will eventually result in

environmental decline, the indirect positive effects of browsers on unpalatable species will be overwhelmed by direct and indirect negative effects of browsers, and both palatable and unpalatable species in forest communities could exhibit performance declines. A general loss of native forest understory biodiversity is a likely outcome if current deer browse levels remain constant or increase.

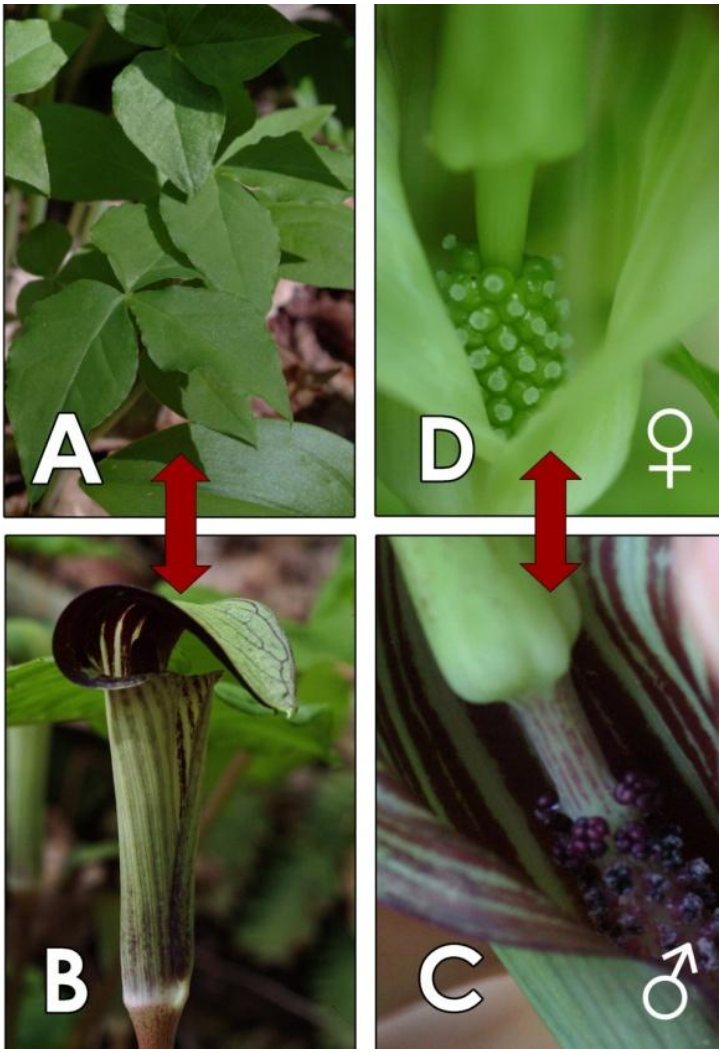

Figure 2.1. The stage and gender of an *Arisaema triphyllum* plant can switch between growing seasons, as a function of plant size. Arrows indicate the direction of possible switches. (A) The smallest individuals are vegetative. (B) When an individual reaches a population specific threshold size for reproduction, it produces an inflorescence. (C) Small reproductive plants bear only male flowers. (D) Larger reproductive plants bear only female flowers

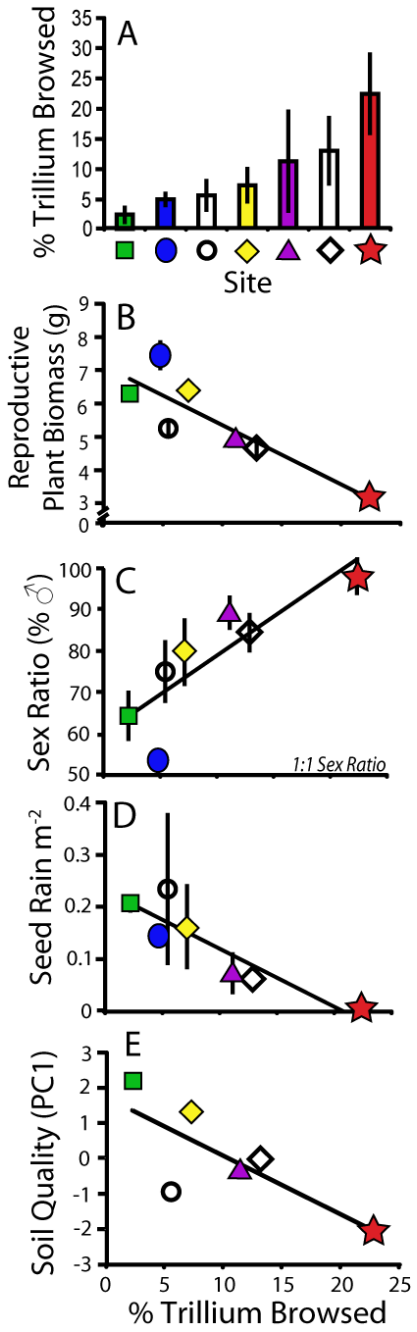

Figure 2.2. Average flowering plant size, population sex ratio, seed rain m-2 of *Arisaema triphyllum* and soil quality are significantly related to mean % deer browse of co-occurring *Trillium*. (A) Six-year site averages of % *Trillium* browsed for seven PA sites ■=Deezik Creek, ●=Dibble Hill, ▲=Ellis Road, ○=Wallace Woods, ♦=Woodcock Lake, ◊=Fox Road, ★=Tryon

Weber Woods. (B-E) Relationship of *A. triphyllum* demographic metrics and soil quality with % *Trillium* browse: (B) Mean mass of *A. triphyllum* flowering individuals ($y = -0.18x + 7.1$, $r^2 = 0.76$, $F_{1,6}=16.0$, $P<0.01$); (C) Proportion of male *A. triphyllum* ($y=1.90x +60.2$, $r^2=0.72$, $F_{1,6}=13.0$, $P<0.02$). Note: x-axis represents 1:1 sex ratio. (D) Average number of seeds/m^2 ($y= -0.01x + 0.23$, $r^2=0.82$, $F_{1,6}=22.4$, $P<0.01$). (E) Soil quality (PC1) ($y=-0.17x + 1.7$, $r^2=0.59$, $F_{1,5}=5.84$, $P=0.07$). Error bars depict ±1 SE. Note: fresh weight and sex ratio means based on 3 years of data except Dibble Hill (1 yr.). Seed rain means for two years except Dibble Hill (1 yr.).

3.0 LIFE HISTORY TRAIT DIVERGENCE AMONG POPULATIONS OF AN UNPALATABLE SPECIES REVEALS STRONG NON-TROPHIC INDIRECT EFFECTS OF AN ABUNDANT HERBIVORE

3.1 INTRODUCTION

Indirect interactions among many species in a community rather than pair-wise direct interactions are increasingly acknowledged as driving phenotypic evolution in nature (Strauss, 1991; Miller & Travis, 1996; Strauss & Irwin, 2004; Strauss *et al.*, 2005). Indirect effects occur when multiple species influence the density or phenotypic traits of a co-occurring species or when such species interactions alter abiotic conditions that influence the fitness of a co-occurring species. Indirect interactions are ubiquitous in nature (reviewed in Peckarsky *et al.*, 2008). Yet, few studies focus on evolutionary aspects of indirect effects (e.g. Walsh & Reznick, 2010; Lau, 2012). Since indirect effects can be of greater magnitude and/or opposite sign to direct effects (Abrams & Rowe, 1996; Peckarsky *et al.*, 2008), experimental studies are critically needed to expand our understanding of species' evolutionary responses to indirect effects (Johnson & Stinchcombe, 2007; Walsh, 2013).

Evolutionary responses to indirect effects are primarily examined from the perspective of either how trophic, or consumer-prey interactions (i.e. density- and trait-mediated indirect

effects; reviewed in Walsh, 2013) affect a third species, or how the biotic and abiotic resources available to a third species are altered (Kefi *et al.,* 2012). While an evolutionary role of indirect effects in communities has been considered since Darwin (1859), experimental studies detailing species' evolutionary responses to indirect effects are few and recent (Johnson & Stinchcombe, 2007; Walsh, 2013). Studies that examine non-trophic indirect effects to date typically address interaction modifications (e.g. pollination and competition) with far fewer examining indirect environmental modification (reviewed in Kefi *et al.,* 2012).

The direct and indirect effects of large grazing herbivores can exert strong selective pressure on plant communities (McNaughton, 1984; Didiano *et al.,* 2014). The strength of interaction between plant species and these large herbivores and the type of effect— direct or indirect— can vary with the herbivore's feeding preferences (Rooney & Waller, 2003; Thompson, 2005). When effects of herbivores on their target plants are large in magnitude, they can affect co-occurring non-target plant evolution through both indirect and non-trophic pathways (Turley *et al.,* 2013), which can either ameliorate or increase biotic and abiotic stresses on non-target plant species. For example, ungulate herbivore removal of leaf biomass of target species can increase the light availability for non-target plants (Jacquemyn *et al.,* 2003), while their excrement or carcass decomposition can increase soil resources (Wardle *et al.,* 2001). Negative effects of ungulates include interruption of above- and belowground linkages between plants and soil resources through reduced leaf litter inputs (Wardle *et al.,* 2001) and increased soil compaction (Vavra *et al.,* 2007) that can limit nutrient flow (Gass & Binkley, 2011). Altered physical and chemical soil properties can interfere with soil microbiological properties and inhibit beneficial fungi's growth (Gass & Binkley, 2011; Kardol *et al.,* 2014). Thus, non-trophic indirect effects of herbivores can modify target and non-target plant species' access to crucial

resources, their level of abiotic stress, and the flow of biomass and matter through an ecosystem. When these effects are chronic, they may ultimately alter the direction and magnitude of selection on life history traits of non-target plants (Kefi *et al.*,2012), driving local adaptation, phenotypic plasticity, or both.

Plant populations that experience stressful, low-resource environments like those generated by herbivore-driven indirect effects (IE) described above are expected to exhibit reduced growth rate and biomass accumulation (Chapin III *et al.*, 1993) and face constraints on allocation among important plant life history functions (Stearns & Koella, 1986; Weiner *et al.*, 2009). Three types of life history responses could be expected. First, phenotypic plasticity to local environmental conditions can drive among-populations differences in life history traits (Sultan, 2000) including size at reproduction (Stearns & Koella, 1986; Salguero-Gomez & Casper, 2010). For flowering plants growing in low-resource environments, adaptive plasticity in growth rate is predicted to result in decreased size at flowering (Stearns & Koella, 1986; Sibly and Calow, 1989; Bonser & Aarssen, 2009). Second, the evolution of lower threshold sizes for reproduction can be driven by higher rates of per capita mortality under stressful conditions (Kozlowski & Uchmanski, 1987; Bonser & Aarssen, 2009). Third, shifts in resource allocation patterns can evolve in response to local conditions. Stressful abiotic environments created by indirect effects may favor increased allocation to storage and decreased allocation to asexual or sexual reproduction due to the positive effects of storage on survival (Ryser & Eek, 2000; Freschet *et al.*, 2013). In addition, stressful environments associated with indirect effects may favor higher allocation to asexual reproduction if sexual reproduction is relatively more costly (Olejniczak, 2001). Thus, populations experiencing stressful environments may either adapt or

respond plastically in the expression of life history traits, ultimately affecting local lifetime fitness (Stearns & Crandall, 1981).

There is mounting evidence that activities of white-tailed deer exert far reaching direct effects and create stressful environments within forest understory communities (Côté *et al.*, 2004, Bressette *et al.* 2012). These herbivores can reduce both the mean size and flowering frequency of their herbaceous prey species (Augustine & deCalesta, 2003; Kirschbaum & Anacker, 2005; Webster *et al.,* 2005). Further, the combination of deer-mediated direct and indirect effects can exert strong selective pressures on life history traits of palatable forest herbs that are their prey and suppress population-level fitness of these species (Rooney & Gross, 2003; McGraw & Furedi, 2005, Knight *et al.*, 2009). Likewise, I recently demonstrated that across seven sites in Pennsylvania indirect effects of deer influenced population-level traits of the unpalatable *Arisaema triphyllum* (L.) Schott (Araceae, Jack-in-the-pulpit, hereafter, *Arisaema*), a species that can switch sex over its lifetime. *Arisaema* exhibited significantly smaller mean size at flowering, lower mean seed number, and expressed increasing male-biased sex ratios as deer browse on a palatable species increased across sites (Heckel *et al.*, 2010). Similar responses were found for *Arisaema* and four additional unpalatable species growing in long-term deer exclusion experiments in Virginia (paired fenced exclusion vs. deer access plots; Heckel *et al.,* 2010), generally supporting IE of deer on unpalatable species. That study also found that soil quality was negatively related to deer interactions with palatable species in both Pennsylvania and Virginia sites; highly browsed PA sites and deer access plots in VA exhibited extremely low soil quality metrics (i.e. drier, more compacted soil with a smaller humus layer) relative to low browse sites or fenced plots. In total, my prior work indicates that sites differ significantly in direct and indirect effects of deer; deer create stressful abiotic conditions where they have strong

interactions with palatable, target species. However, that field study could not test if the observed differences in life history traits among *Arisaema* populations are due to population divergence.

Here I report results from a long-term experiment quantifying the extent to which the observed differences in *Arisaema* life history traits across Pennsylvania populations represent local adaptation or phenotypic plasticity. I employ the classic and powerful common garden approach (Clausen *et al.,* 1947) to explore population differentiation in *Arisaema*. Individuals from six of the Pennsylvania populations studied by Heckel *et al*. (2010) were evaluated for key fitness traits for five growing seasons: growth rate, biomass allocation, size, and sexual and asexual reproductive status. If the life history differences among *Arisaema* populations represent adaptive divergence, then I expect that plants from high stress sites (high deer IE) vs. low stress sites (low deer IE) will: 1) initiate flowering at smaller sizes, 2) express higher growth rates and reach reproductive size earlier, 3) increase allocation to storage, and 4) increase allocation to asexual reproduction. Conversely, if population-level differences in the field are a result of general plastic responses to their local environments, then I expect that all populations will exhibit similar life history responses in the garden environment.

3.2 MATERIALS AND METHODS

3.2.1 Study system

Arisaema triphyllum is a common perennial herb of eastern North American forests that produces calcium oxalate crystals, is highly unpalatable to deer (Bierzychudek, 1982), and is

rarely browsed by deer in my study sites in western Pennsylvania (only 0.6% of 9746 *Arisaema* stems; Heckel *et al.*, 2010). Plants have a belowground bulb-like storage organ, the corm, and a single aboveground stem that bears both leaves and reproductive structures. Reproductive individuals produce a leaf-like spathe surrounding a columnar spadix that bears either male or female flowers. *Arisaema* can reproduce asexually by vegetative side shoots from the corm, termed cormlets (Bierzychudek, 1982).

Arisaema individuals are sequential hermaphrodites. In its first reproductive season an individual typically bears male flowers (Bierzychudek, 1982). In later years, when the individual has grown larger, it switches sex and produces only female flowers. A reproductive plant can switch between male and female flower production throughout its lifetime as it gains (male → female) or loses (female → male) biomass (Vitt *et al.*, 2003). A prior study with *Arisaema* showed that the size of switch to female flowering differed between two populations (Vitt *et al.*, 2003). This result lends preliminary support for the size-advantage hypothesis, which predicts that individuals will switch sex as they increase in size if one sex experiences higher reproductive success when small and lower reproductive success when large, but the opposite is true for the other sex (Ghiselin, 1969). However, the extent to which size at flowering and size at sex switch is the result of local resources and phenotypic plasticity or genetic differences and adaptation remain unclear (Bierzychudek, 1984; Lovett-Doust & Cavers, 1982; Vitt *et al.*, 2003; Heckel *et al.*, 2010).

3.2.2 Estimating indirect effects of deer

All *Arisaema* populations studied by Heckel *et al.* (2010) occur within a 42 km radius in

northwestern PA in mature beech-maple forests that were matched for understory community composition and general abiotic characteristics. Since deer do not eat *Arisaema*, I used the co-occurring, deer-preferred *Trillium* as phyto-indicators for the impacts of deer in my sites (*e.g.* Knight, 2004). For *Trillium*, the proportion of stems browsed (Augustine & Frelich, 1998; Knight, 2003), the proportion of plants flowering (Augustine & deCalesta, 2003), and the size distribution of browsed plant species (Anderson, 1994; Augustine & deCalesta, 2003) are all reliable estimators of deer abundance or impacts on deer-palatable plant populations. Therefore, I quantified these variables for all *Trillium* plants within three, 1x50m transects in each study site (n=6) annually for six years. In each transect I counted all stems of *Trillium* and recorded their flowering and deer browse status (*sensu* Augustine *et al.,* 1998). In 2005 and 2007 I also measured length of the largest leaf of each *Trillium* individual as a size estimate. Following Augustine and deCalesta (2003), I developed deer impact indices for each study site based on these three metrics: the mean percent *Trillium* stems browsed, the mean proportion of flowering *Trillium*, and median *Trillium* leaf length in each site. I ranked each site from lowest (1) to highest (6) based on each metric separately. I then calculated Kendall's coefficient of concordance (Wt) to assess agreement of rankings among the three metrics. My metrics indicate that the six study sites experience consistent ranking in relative deer impact (Wt=0.937, P=0.02). I used the sum of the ranks as an index of the expected amount of deer indirect effects in each site.

3.2.3 Common garden experiment

To quantify the extent to which our *Arisaema* study populations are plastic or have diverged in life history traits due to IE of deer, in May 2006 I initiated a five-year common garden

experiment. I collected 20 non-flowering, ~equal-sized plants from six of the *Arisaema* populations used in Heckel *et al.* (2010) and transported them (N=120 total plants) to the University of Pittsburgh's Pymatuning Laboratory of Ecology Sanctuary Woods site. For each plant I recorded its total wet biomass (henceforth biomass; range: 1.2–3.9 g). I planted each individual into common garden experiment in a randomized location in a 12x12 grid within a 5mx5mx0.2m deep frame filled with soil (Earthgro Brand).

Each spring for the next five years, I recorded stem diameter, flowering status (vegetative, male, or female), and number and stem diameter of all vegetatively-produced cormlets for each individual. In the autumn of 2008 and in subsequent autumns through 2011, once aboveground structures began to senescence, I excavated all the plants, rinsed them with water, blotted them dry, and recorded their total biomass. My data collection in the autumn allowed me to estimate biomass while maximizing growing season length and minimizing disturbance to future growth. I partitioned each plant and its associated independent cormlets into aboveground and belowground parts; I cut each stem 1 cm above the corm and recorded the mass of all parts. If the corm of a focal plant had attached cormlets, I recorded their quantity. I then returned all 120 plants to their original location in the garden to overwinter. To control for resource competition with their parent plant, I discarded the independent cormlets. [Note: Cormlets production was not a significant covariate in the analyses of any life history traits I examined-detailed below]. The experiment ended in June 2011, when I excavated all plants and partitioned individuals and took final size and weight measurements, as described above.

During the course of the experiment, I was unable to collect biomass measurements in 2007 and on some plants in other years because their aboveground parts senesced significantly earlier relative to the majority of plants within the garden (104 of 480 measurements across all 5

years). To provide estimates for these missing data, I determined that stem diameter is a significant predictor of biomass ($P<0.01$, $r^2=0.86$) using the model: Biomass = Stem diameter (mm) + Population + Stem diameter * Population + exp(Stem diameter). I confirmed that a high and significant correlation exists between the predicted biomass from this model and the actual biomass for plants that were not missing data ($\rho= 0.86$, $P<0.001$). Therefore, I estimated all missing biomass values using individuals' stem diameter data collected earlier in the season with the above model.

3.2.4 Analysis of life history traits

I fit generalized linear mixed-effects models to evaluate adaptive divergence among populations in a set of life history traits: threshold size of switch from vegetative to flowering stage and switch from male to female, relative growth rate, biomass allocation, and asexual reproduction. To evaluate the size-based probability to switch from vegetative to flowering stage among populations, I treated the reproductive status (vegetative or flowering) as a binomial response variable and analyzed it using a binomially-distributed repeated measures generalized mixed model (RM GLMM, Table 3.1A). I used the output of the binomial RM GLMM to compare flowering size thresholds among populations. I defined the flowering size threshold and male → female or female → male size switch threshold (detailed below) as the inflection point of the fitted logistic regression curve; this is the size at which 50% of plants are expected to be flowering or switching from male to female and corresponds to the curve's maximum slope that informs about the steepness of the threshold (Agresti, 2007). High slope values indicate abrupt or narrow threshold ranges. I examined the Type II sums of squares to determine whether fixed effect variables have significant effects on response variables and used Tukey HSD test to

examine pairwise differences between levels of fixed effects. To evaluate differences among populations in size-based probabilities to switch from male to female flowering across sites, I treated sex (male or female flowers) as a binomial response variable and fit a RM GLMM (Table 3.1B).

Since the cost to produce reproductive structures for female flowering plants > male flowering plants > non-flowering plants (Bierzychudek, 1982), I expect that plants that flowered will show reduced growth in the year after flowering events relative to non-flowering plants, with females exhibiting lowest relative growth rate (RGR). To estimate yearly RGR of each individual I use the equation: $RGR = (biomass_{(year\ t+1)} - biomass_{(year\ t)})/\ biomass_{(year\ t)}$. To test for among-population differences in RGR I analyze each plant's RGR using a RM GLMM (Table 3.1C). To assess the effects of flowering transitions between these stages on yearly RGR, for all individuals I coded yearly transitions between flowering statuses [stasis; advance to next status (e.g. male → female); revert to previous status (e.g. female → male)] and fit RM GLMM to evaluate flowering effects on RGR (Table 3.1D).

I quantified biomass allocation at the end of the experiment using each plant's final biomass partitioned into aboveground vegetative, belowground vegetative, sexual, and asexual reproductive biomass. Response variables are log-transformed to improve data fit to model assumptions. I test if populations allocate to above- and belowground vegetative and reproductive structure differently after five years in the common garden using the MANOVA model: Biomass = Population + Flowering status.

I define annual per capita asexual reproduction as the number of cormlets produced per plant each year. To investigate among population differences in asexual reproduction, I analyze annual per capita cormlet production with a zero-inflated negative binomial (ZINB) model with

nested random effects (Table 3.1E). Many *Arisaema* plants in my experiment did not produce cormlets resulting in an over-dispersion of zeros in the data that required use of ZINB (Zuur *et al.*, 2009). If *Arisaema* plants trade-off sexual and asexual reproduction, then I would expect a negative correlation between these traits. I test for this trade-off by examining the correlation between biomass allocation to sexual and asexual reproduction using biomass partitions collected in 2011.

All statistical analyses were performed using R version 2.11.0 (R Core Team, 2013). Gaussian and binomially-distributed RM GLMMs were performed using the lme4 package. The GlmmADMB package was used to perform zero-inflated Poisson with nested effects. Goodness of fit for the mixed-effects models was estimated using $R^2_{GLMM(c)}$ (whole model) values following the methods of Nakagawa and Schielzeth (2013).

3.3 RESULTS

The probability of becoming female at a given size differed significantly among populations (Figure 3.1, $\chi^2_{df=5}$=13.2, N=186, P=0.02) and increased with biomass ($\chi^2_{df=1}$=47.6, N=186, P<0.001). Because nearly all plants flowered at some point during the experiment, populations do not differ in their five-year probability of flowering (Figure 3.1; $\chi^2_{df=5}$=5.0, N=623, P=0.41). Likelihood of flowering increases with biomass ($\chi^2_{df=1}$=117.2, N=623, P<0.001) and with time in the common garden ($\chi^2_{df=1}$=34.0, N=623, P<0.001).

Mean RGR differs significantly among populations ($F_{5,130}$=20.6, P<0.001) and among years ($F_{4,130}$=102.1, P<0.0001). Population mean RGR in the common garden ranges from a low

of 0.81±0.16 (SE) g yr^{-1} (WL site) to a high of 1.67±0.24 (SE) g yr^{-1} (TW site). The mean RGR in the TW population, the highest browse site, is significantly greater than all other populations except in WW (RGR_{TW} - RGR_{WW} = 0.76 (P=0.07); Tukey HSD P<0.01 for all other comparisons). Flowering status significantly affects RGR ($F_{2,130}$=15.9, P<0.001). As expected, flowering transitions to the production of more costly female reproductive structures significantly negatively affect RGR ($F_{4,130}$=22.5, P<0.001). Plants that advanced or remained in their prior year's status increased in biomass by 99.7% (±12.4). Irrespective of population, plants that reverted in flowering status after producing an inflorescence grew significantly less than plants that remained in the same status or advanced in status (Tukey HSD, P<0.04 for all comparisons) and in many cases exhibited shrinkage.

At the end of the experiment, populations did not differ significantly in their biomass allocation (Figure 3.2; $F_{(20,420)}$=0.78, P=0.37). Thus, pooling all populations, I found that in general, biomass allocation differs with flowering status ($F_{(8,206)}$=0.78, P<0.001). On average, non-flowering plants allocate ~10% more biomass (38 ± 2%) to belowground structures compared to female flowering plants (29 ± 3%, Tukey HSD: P=0.04). Belowground allocations of male-flowering plants (35 ± 3%) vs. non-flowering plants and of male vs. female flowering plants are not significantly different (Tukey HSD: P=0.85, P=0.26 respectively). Females allocate significantly more biomass to reproductive structures than male plants (10 ± 1% vs. 4 ± 2%, Tukey HSD: P=0.001).

Mean annual per capita cormlet production in the common garden is low and never exceeds one cormlet per plant per year. Annual per capita cormlet production does not differ by population (χ^2=5.9, df=5, P=0.31), plant size (χ^2=0.8, df=1, P=0.36), or plant flowering status (χ^2=2.9, df=2, P=0.24). In addition, I find no correlation between biomass allocated to sexual

structures versus cormlets (ρ= -0.03, df=32, P=0.62) suggesting either a lack of trade-off between sexual and asexual reproduction, or insufficient variation in asexual reproduction among the populations I investigated.

3.4 DISCUSSION

When environments differ among sites in a consistent manner and those differences are of large magnitude, population divergence can result (Clausen *et al.,* 1947). My study demonstrates that populations of *Arisaema* have diverged in life history traits in a manner that matches predictions. Life history theory suggests that under stressful conditions, plants may reproduce at a smaller size, which maximizes lifetime fitness (Stearns & Crandall, 1981). Further, if the stressful conditions increase mortality risk, then faster growth rates may increase the likelihood of reaching reproductive size before dying (Sibly & Calow, 1989). I found both local adaptation and population-level plasticity in life history traits of *Arisaema*. Populations grown in the common garden differed significantly in two traits predicted to respond to environmental stress: RGR and female size threshold. The magnitude of *Arisaema's* across population responses match the predictions of life history theory and consistently rank with our deer IE metrics. Thus, random processes such as genetic drift are unlikely explanations for our results. Rather, they indicate genetic divergence among *Arisaema* populations in RGR and the sex-switch size threshold in response to stressful conditions created by the indirect effects of deer.

3.4.1 Indirect effects of deer on sex-switch size threshold

Under chronic stressful conditions, iteroparous perennial plant species, like *Arisaema*, are predicted to flower, or switch to female, at smaller sizes due to either phenotypic plasticity (Wesselingh *et al.*, 1997) or evolved adaptive responses (Kozlowski & Uchmanski, 1987; Bonser & Aarssen, 2009). *Arisaema* from sites with the highest deer impact scores are more likely to flower as females at smaller sizes in our common garden experiment (Figure 3.1, right panel). The maximum slope for the probability of switching to female was steepest in sites with the highest deer impact scores (Figure 3.1). Increasing steepness of slopes across sites to near vertical lines in the most deer impacted sites indicates that the threshold size for switching to female occurs more abruptly, (i.e. in a narrower size range) in the highest browse sites (Figure 3.1). The lower sex-switch size threshold from high-browse sites conforms to my earlier field results (Heckel *et al.,* 2010; Figure 1B therein). In addition, the steep slopes for the probability of switching to female may indicate lower variance among individuals in sex-switch size threshold within populations experiencing the highest browse levels (Figure 3.1, right panel). The loss of genetic variation for sex-switch size threshold in populations that have high deer IE relative to populations experiencing low deer IE could explain this finding. The results of my common garden experiment suggest the potential for local adaptation and population differentiation in the sex switch threshold of our focal *Arisaema,* in support of the hypothesis that deer IE can cause life history divergence in non-target species (Heckel *et al.* 2010).

The activities of herbivores are known to drive belowground biotic and abiotic stressors that can negatively influence plant population performance (Kardol *et al.,* 2014). Chronic overabundance of ungulates is known to increase soil compaction which reduces nutrient flow

(Gass & Binkley, 2011) and reduces abundance of beneficial mycorhizzal fungi (Kardol *et al.,* 2014). In my study sites, Heckel *et al.* (2010) previously showed that indirect effects associated with increasing deer browsing produces a progressively more stressful environment through chronic conditions of drier, more compacted soils. Further, *Arisaema* vital rates in at these sites (Heckel *et al.*, 2010) are negatively correlated with this sustained environmental stress. Over time, a chronic stressor can lead to genetic divergence in life history traits, which can in turn significantly influence the long-term growth rate, λ and stability of impacted populations. In a companion study examining *Arisaema* population dynamics for this same set of populations, we find that the two populations with the greatest deer impact scores (WW and TW) have significantly lower population growth rates (λs) than the other, relatively less impacted sites (Z-tests, all P <<0.001, Chapter 4). Taken together our results implicate non-trophic indirect effects of deer as drivers for local adaptation of *Arisaema* sex switch thresholds.

Throughout eastern North American forests where deer are overabundant, declines in both stature and flowering numbers are commonly trends of herbaceous herbs or woody trees (reviewed in Augustine & deCalesta, 2003; Kirschbaum & Anacker, 2005). This response is eminently clear among favored forage plants of deer like *Trillium spp., Maianthemum and Acer spp.*, which consistently show reductions in plant size and flowering rates (Anderson, 1994; Augustine & deCalesta, 2003; Kirschbaum & Anacker, 2005). Other authors suggest that deer-browsed species are now flowering at smaller sizes in sites where deer browse levels have increased relative to unbrowsed sites (Webster *et al.,* 2005). Yet non-prey unpalatable species show similar reductions in size and flowering as deer activity increases (Webster & Parker, 2000; Webster *et al.,* 2001; Heckel *et al.,* 2010). Early maturity as a result of the indirect effects of predators also occurs in aquatic systems; killifish mature at smaller size as a result of the

indirect effects of guppies on resources (Walsh & Reznick, 2010). These observations paired with my new experimental results presented here suggest the direct and indirect effects of deer may exert strong selection on native understory plants to flower at smaller sizes throughout eastern North American forests.

3.4.2 Indirect effects of deer on relative growth rate

In the common garden, the relative growth rate (RGR) of plants from the highest deer impact site (TW) grew significantly faster than all other populations (Table 3.1C, Table G1). The increasingly poor soil conditions (Heckel *et al.*, 2010) and trends toward switching sex at smaller size with increasing deer impact scores indicate that deer IE generate stressful conditions for *Arisaema*. Stress in the TW site may be great enough to increase mortality risks as well. The TW showed declining λ relative to other *Arisaema* populations studied (Chapter 4). High, stress-driven mortality rate can favor faster growth rates (Sibly & Calow, 1989). Higher mortality rates in TW may explain why this population evolved faster growth rates

In addition, my data revealed a significant reduction in RGR for plants reverting to non-flowering status after a flowering episode, with most exhibiting biomass loss ($P<0.04$, Table G1). Such losses can indicate an indirect cost to flowering in *Arisaema* and have further demographic consequences since size in iteroparous plants is closely linked to survival and reproduction probabilities (Bierzychudek, 1982; Salguero-Gómez & Casper, 2010). The observed biomass loss highlights a further selective force of IE; *Arisaema* in sites with higher deer impact scores may be at risk of lower future survival and reproduction because they flower at smaller sizes.

In general, I found that the relationship between *Arisaema* plant size and reproductive status fit expectations for long-lived iteroparous plant species (Bierzychudek, 1982). Across all populations, female plants invested significantly less to belowground storage structures compared to non-flowering plants and more than twice as much biomass to flowering tissues compared to males. Allocation differences are expected given the biology of species with separate sexes like *Arisaema*; higher biomass investment in female inflorescences is required because they support multiple, heavy seeds and must last longer to complete seed maturation (Bierzychudek, 1982). In contrast, asexual reproduction is uncorrelated to any status or size metric I considered. My results match previous work in *Arisaema* (Bierzychudek, 1982), and suggest that asexual reproduction is unlikely to be a response to increased stress associated with IE of deer.

Interestingly, size-dependent sex expression in *Arisaema* presents an additional hypothesis for why plants from sites with high deer impact scores are expected to flower at smaller sizes. If a population's sex ratio is highly skewed, then individuals of the rare sex gain a fitness advantage over the more common sex (Charnov, 1982). I observed a significant positive correlation between our wild *Arisaema* populations' sex ratio and deer browse level, with the highest browsed sites sex ratios skewed to all males (Heckel *et al.*, 2010). Therefore, my results support the idea that the switch to female at smaller sizes may be driven by the rare sex advantage in sites with the highest deer IE. A rare sex advantage could synergistically enhance the response to IE of deer to speed local adaptation of threshold flowering size and sex where conditions are most stressful.

3.4.3 Evolutionary implications of indirect effects

Palatable plant species are known to adapt to the direct effects of browsing through phenotypic evolution including evolution of life history traits (e.g. Ohgushi, 2005; Agrawal *et al.*, 2006). Other studies in terrestrial systems have shown that plant-herbivore interactions indirectly affect the interaction between plants and a third interacting species such as a mutualist or a second antagonist (reviewed in Walsh, 2013). However, my study is among the first to suggest that non-trophic IE of herbivores has evolutionary consequences for unpalatable, non-target plant species. Unpalatable or non-browsed species are generally expected to gain an advantage in environments where competitors experience high browse levels (Jacquemyn *et al.*, 2003; Wiegmann & Waller, 2006), but my prior findings indicate that this is not the case. Using a combination of observational field data and paired deer exclusion/deer access plot studies, Heckel *et al*. (2010) demonstrated that *Arisaema* populations in sites experiencing chronically high deer levels browse are of significantly smaller size, have significantly fewer reproductive plants, and have significantly degraded soil conditions relative to low browse sites. Together, the results from the field (Heckel *et al.*, 2010) and this common garden study suggest that *Arisaema's* life history responses are similar to that seen in palatable browsed species due to powerful indirect effects. Thus, population differentiation in sex-switch size threshold and growth rate seen in the common garden experiment indicate genetic divergence to non-trophic IE of deer. The greatest effects on *Arisaema* life history in this study were observed for populations from sites that experienced >15% of deer browse. Interestingly, studies of two palatable species found that deer browse levels >12% drove significant declines in their population growth rates: *Trillium grandiflorum* (Knight *et al.*, 2009) and *Panax quinquefolius* (ginseng, McGraw & Furedi, 2005). Similar

results are anticipated for *Arisaema* and other unpalatable species where deer are overabundant and exert strong direct and indirect effects. Unfortunately, the evolution of life history traits in populations of *Arisaema* experiencing negative IE, like the populations used in my study, does not imply that these populations will maintain high fitness and persist if the environment continues to decline further (*sensu* Gomulkiewicz & Holt, 1995). I am use demographic analyses to explore the extent to which the life history changes exhibited by *Arisaema* across our study sites affect long-term population stability (Chapter 4).

Evolutionary responses to community interactions can be far reaching with significant implications for species conservation and population growth (Johnson & Stinchcombe, 2007). The stressful environments within native plant communities created by deer overabundance are recent phenomena (Côté *et al.*, 2004; Vavra *et al.*, 2007; Bressette *et al.*, 2012). If other unpalatable species respond to indirect effects of overabundant herbivores similarly to *Arisaema* (see Heckel *et al.*, 2010), then many additional prey and non-prey native species may be cryptically evolving new life histories.

Table 3.1. Mixed-effects models used to test for adaptive divergence and plasticity of *Arisaema* life history traits. Analyses were performed on data from a 5-year common garden experiment. Final models used to evaluate adaptive divergence and plasticity are presented. While model fitting, any non-significant explanatory variables and interactions, except Population, were dropped from the model. Underlined explanatory variables are covariates and italicized explanatory variables were modeled as random effects (required for a repeated-measures structure). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Model	Response Variable	Explanatory Variables	R^2	Outcome
A	logit Reproductive Status	Population + *Plant ID* + Year*** + <u>Size</u>***	0.44	Plastic
B	logit Sex	Population* + *Plant ID* + Year + <u>Size</u>***	0.72	Adaptive
C	Relative Growth Rate (RGR)	Population** + *Plant ID* + *Year**** + Flowering Status**	0.26	Adaptive
D	RGR	Population** + *Plant ID* + *Year**** + Transition**	0.32	Adaptive
E	Annual Per Capita Cormlet Production	Population + *Plant ID* + *Year* + Flowering Status + <u>Size</u>	0.47	Plastic

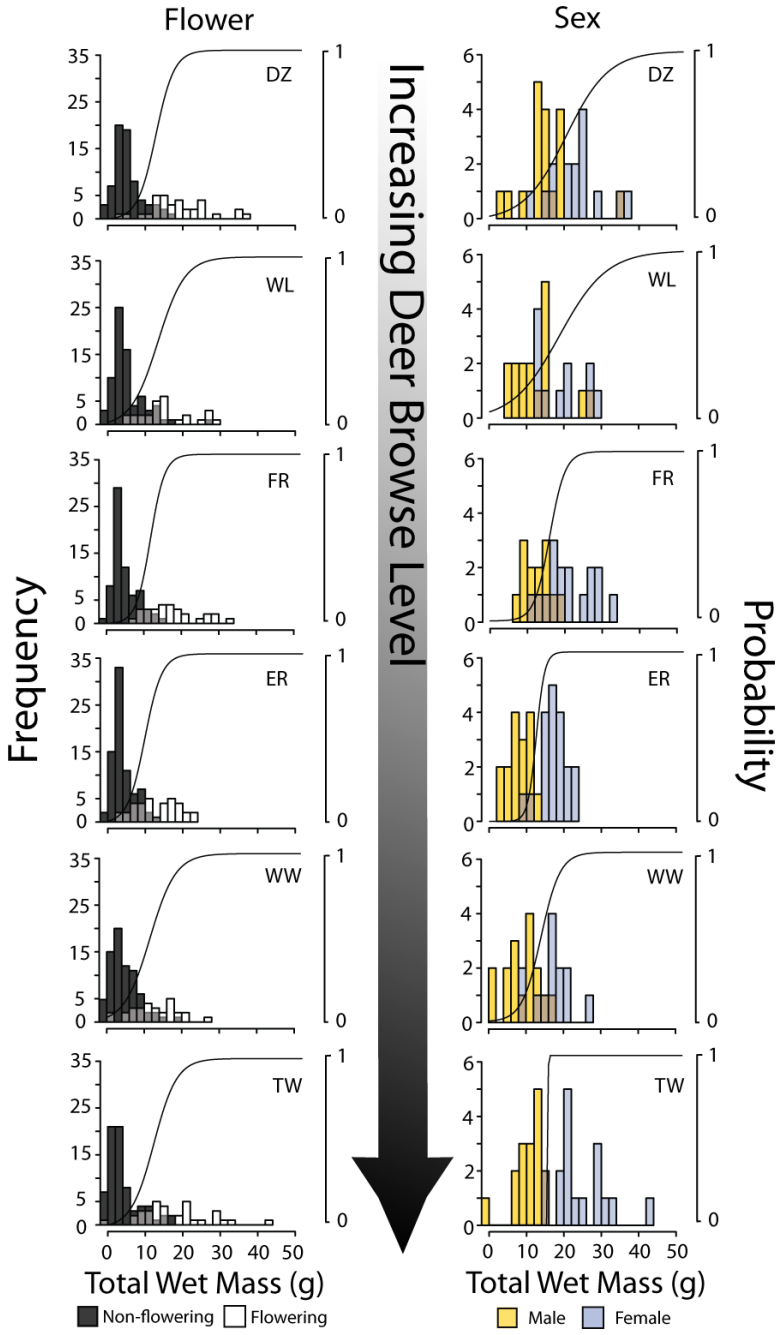

Figure 3.1. Logistic regression derived probabilities of Size of switch from vegetative to flowering and Size of switch from male to female flowering of *Arisaema* from six populations experiencing a range of deer browse levels. Populations are arranged so that deer browse level

increases from lowest at the top to highest at the bottom of each panel. Left panel: Fitted logistic regression curve for size-dependent probability of switch from vegetative to flowering (solid line); units on right y-axis. Histograms for vegetative (black) and flowering (white); units on left y-axis. Right panel: Fitted logistic regression curve for size-dependent probability of transitioning to female (solid line); units on right y-axis. Histograms for male (yellow) and female (blue); units on left y-axis. Both panels: An intermediate color indicates histograms overlap. Dashed lines on all graphs reference the size at which there is a 50% chance of flowering (left panel) or being female (right panel) for plants from TW, the population with the highest expected indirect effects from deer (Heckel *et al.*, 2010).

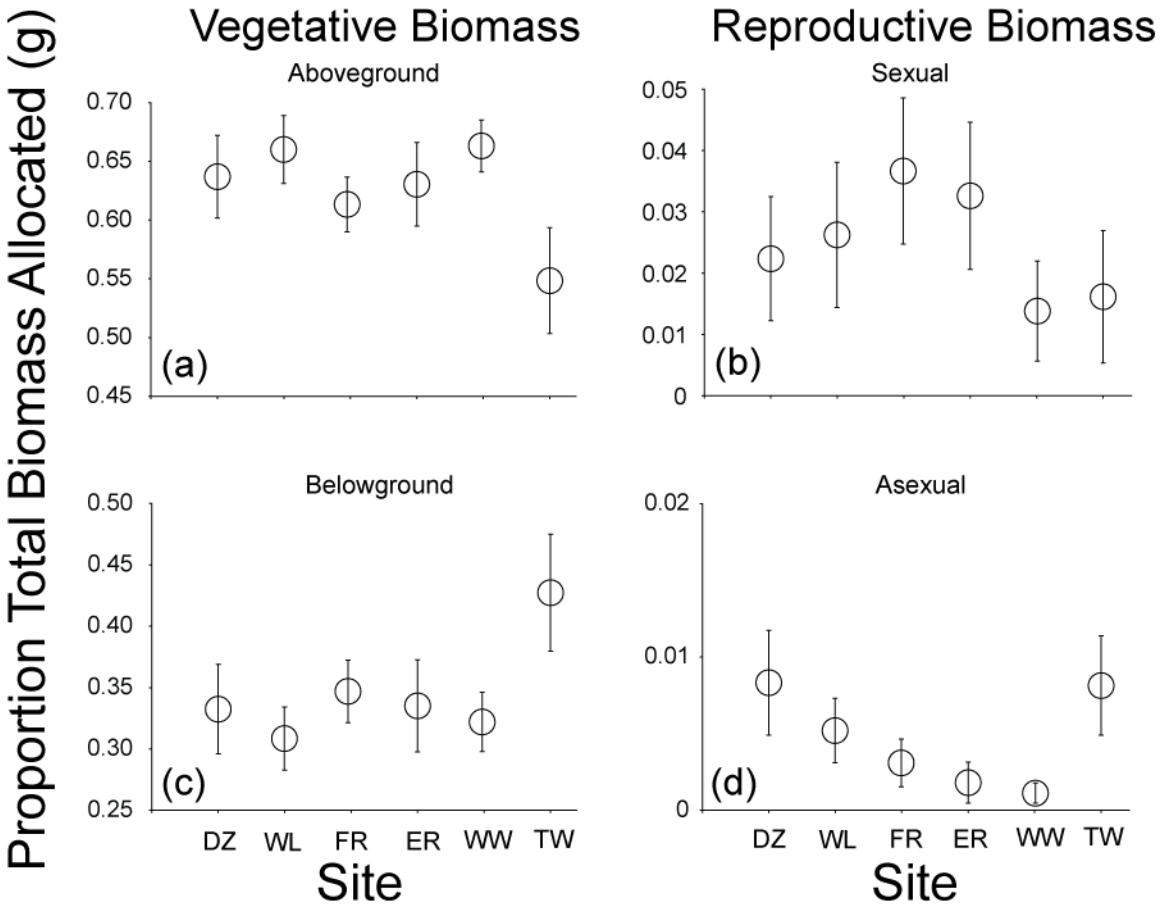

Figure 3.2. Mean allocation to vegetative and reproductive total biomass across *Arisaema* from six populations that spanned a gradient of deer browse grown in a common garden for five years. Mean (± 1 SE) proportion of total plant wet-biomass plants allocated to (a) aboveground and (c) belowground vegetative and (b) aboveground and (d) belowground reproductive structures.

4.0 INVESTIGATING THE INDIRECT EFFECTS OF UNGULATE HERBIVORES ON THE POPULATION DYNAMICS OF AN UNPALATABLE FOREST HERB

4.1 INTRODUCTION

A central goal of ecology is to understand which factors influence the size and growth of populations. For plant populations, abiotic factors like climate and nutrient availability can impact population dynamics (Salguero-Gomez *et al*. 2012, von Euler *et al*. 2014). Likewise, biotic factors like the presence of herbivores (Kuss *et al*. 2008, Brys *et al*. 2010) and mutualists (Rudgers *et al*. 2012), can also affect population dynamics. However, biotic and abiotic factors can interact and create environmental differences among sites that further affect local population dynamics (Dahlgren & Erlen 2009).

Herbivory can be one of the most influential factors affecting plant population dynamics (Maron & Crone 2006). Large herbivores can directly alter target prey plant's population dynamics because browsing is detrimental to growth and survival. High rates of ungulate herbivory can halt or reverse biomass accumulation and growth that in turn interrupts the natural stage progression in forest perennial herbs (Knight et al. 2009, Ehrlen 1995, Augustine and DeCalesta 2003). For example, in *Trillium* spp., deer browse results in smaller average plant size, a reduced proportion of flowering plants, and significant population declines [i.e. population growth rate <1] (Augustine and Frelich 1998, Knight *et al*. 2009, Rooney and Gross

2003, Kalisz *et al.* 2014). Similarly, population viability analysis of *Panax quinquefolius* L. (American ginseng) revealed that 80% of the 36 deer-browsed populations studied had a greater than 99% chance of extinction within 100 years. Loss of *Panax* population viability was driven by declines in individual plant's stage and size (McGraw and Furedi 2005). Herbivory can lead to changes in size dependent flowering probabilities (Jacquemyn *et al.* 2011). Herbivores can alter fecundity components as well when browsing by large herbivores results in the complete loss of flowering parts in herbaceous perennials (Ehrlen 1995, Knight *et al*. 2009). In addition, large ungulates can have indirect effects within plant communities (Wootton 2002, D'avalos *et al.* 2014) which, if large enough, can further influence plant vital rates and plant population dynamics.

The aboveground activities of large herbivores are tied to a number of belowground biotic and abiotic consequences than can influence plant populations (Kardol *et al.* 2014). Soil nutrient quality can be improved by herbivores via their inputs from excrement and decomposing carcasses (Bardgett & Wardle 2003). Conversely, large ungulate herbivores may negatively impact soil quality by both reducing leaf litter inputs necessary for the development of new soil humus (Sharrow 2007, Wardle et al. 2002), and increasing soil compaction (Vavra *et al.* 2007, Cumming and Cumming 2003) that can further lead to limited nutrient flow (Gass & Binkley 2011). Altered physical and chemical soil properties can further interfere with soil microbiological properties (Pengthamkeerati *et al*. 2011) and inhibit the growth of beneficial arbuscular-mycorrhizal fungi (Nadian *et al*. 1997). These herbivore-mediated changes to soil quality can modify plant population growth rates (Dahlgren & Erlen 2009, Heglend *et al.* 2010). My previous work has shown that life history traits of the unpalatable, unbrowsed forest herb, *Arisaema triphyllum* (hereafter, *Arisaema*), respond to the indirect effects of the ungulate

herbivores, white-tailed deer (*Odocoileus virginianus*), in a manner parallel to that of their browsed neighbors (Heckel *et al.* 2010). These indirect effects are non-trophic, likely mediated through changes in soil quality (Kardol *et al.* 2014, Heckel *et al.* 2010). In addition, using a common garden experiment I found that chronic stresses associated with non-trophic indirect effects of deer can lead to population level differentiation in *Arisaema* vital rates including relative growth rate and timing of maturity (i.e. size of flowering as females; Chapter 3). Since growth rate and flowering probabilities underlie the population dynamics of long-lived iteroparous plants, the question now becomes: do non-trophic indirect effects of deer drive declines in population growth rates for this unpalatable species similarly to the way deer browsing drives palatable species declines? I predict that population growth rates (λ) will be lowest for populations with the highest indirect effects of deer. I test this prediction using Integral Projection Modeling (Easterling *et al.* 2000) to calculate λ and Life Table Regression Analysis approach (Caswell 2001).

4.2 MATERIALS AND METHODS

4.2.1 Study system

Arisaema triphyllum (L.) Schott (Araceae) is a common perennial herb of eastern North American forests (Bierzychudek 1982). This species produces calcium oxalate crystals, is highly unpalatable to deer (Bierzychudek 1982), and is rarely browsed by deer in my study sites (only 0.6% of 9746 *Arisaema* stems; Heckel *et al.* 2010). Plants have an underground bulb-like

storage organ, the corm, and a single aboveground stem that bears both leaves and reproductive structures. Reproductive individuals produce a leaf-like spathe surrounding a columnar spadix that bears either male or female flowers. *Arisaema* can reproduce asexually by vegetative side shoots from the corm, termed cormlets (Bierzychudek 1982).

Arisaema individuals are sequential hermaphrodites. In their first reproductive season an individual typically bears male flowers (Bierzychudek 1982). In later years, when an individual has grown larger, it switches sex and produces only female flowers. A reproductive plant can switch between male and female flower production throughout its lifetime as it gains (male → female) or loses (female → male) biomass (Vitt *et al*. 2003). Prior studies with *Arisaema* provide strong support of the size-advantage hypothesis (Vitt *et al.* 2003), which predicts that individuals will switch sex as they increase in size if one sex experiences higher reproductive success when small and lower reproductive success when large, but the opposite is true for the other sex (Ghiselin 1969).

4.2.2 Estimating deer impacts

All six *Arisaema* populations studied occur within a 42 km radius in northwestern Pennsylvania in mature beech-maple forests that were matched for understory community composition and general physical characteristics (Heckel *et al.* 2010). In 2005, after a visual search of study sites for areas that contained co-occurring *Arisaema* and *Trillium* spp. populations, I established a 50x50m study plot in each of the six sites to be monitored annually until 2009.

Since *Arisaema* is not browsed, I used *Trillium* as a phyto-indicator for the impacts of deer in a site because deer commonly browse this species (*e.g.* Knight 2004). The proportion of stems browsed (Augustine & Frelich 1998, Knight 2003), the proportion of plants producing

flowers (Augustine & deCalesta 2003), or the size distribution of browsed plant species (Anderson 1994, Augustine & deCalesta 2003) have all been used as reliable estimates of deer abundance or impacts on palatable plant populations. I developed a deer impact index using three commonly used metrics of deer abundance (*sensu* Augustine & deCalesta 2003). In each year of the study I quantified the percent herbivory on all *Trillium* plants within three parallel 1x50m transects in my study sites. Each transect originated at a random location along one side of the 50x50m plots and extended the entire 50 m through the plot. In each transect I counted all stems of *Trillium* and recorded their life stage (seedling, juvenile, vegetative, or flowering) and browse status. Browsing by deer on any herbaceous species is discernable as a clean cut of the stem parallel to the ground and the removal of all leaf tissue (Augustine *et al.* 1998). During the years 2005 and 2007 I also measured length of the largest leaf of each *Trillium* individual encountered in each census. To create my deer impact index I calculated the mean percent *Trillium* stems browsed, the mean proportion of flowering *Trillium*, and median *Trillium* leaf length in each site (Table 4.1). I then ranked each site from least to most deer impacted (i.e. lowest browse %, greatest % flowering, and greatest median leaf length all rank = 1; highest browse %, fewest % flowering, and smallest median size have rank = 6). I then calculated Kendall's coefficient of concordance (Wt) to assess agreement of rankings among variables. I found that among my study sites the rankings of my deer impact index variables were relatively consistent (Wt=0.937, P=0.02). I used the sum of the ranks to order sites based on deer impacts in later analyses. I expect that populations in sites with relatively higher deer index rank sums will experience greater amounts of indirect effects of deer because Heckel *et al.* (2010; Chapter 2) showed that soil quality was negatively related to deer browse on palatable species in both Pennsylvania and Virginia sites. Highly browsed sites exhibited extremely low soil quality metrics (i.e. drier, more

compacted soil with a smaller humus layer) indicating that through their browsing activity deer could indirectly generate a more stressful environment for all forest plant species (Heckel *et al*. 2010). Therefore, my deer impact index rank sums act as a proxy for the magnitude of indirect effects of deer (Chapter 3).

4.2.3 Demographic sampling procedures

To determine the rates of growth, survival, and fecundities of *Arisaema* I permanently tagged all flowering individuals in each 50m x 50m study plot at each of the six sites beginning in May 2005. In May 2006, I established three permanent1m x 50m belt transects that were parallel to each other in the DZ, WW, and TW study plots to increase sampling in those sites. In each belt transect I tagged all *Arisaema* individuals, flowering and non-flowering, within the belt transect to better estimate vital rates with the full size distribution of plants. I tagged new recruits or previously untagged plants during each census. Each subsequent May I censused study plots and belt transects for four of the sites (DZ, WW, WL, and TW) in all five census periods (2005-2009); however I was only able to census individuals at the ER and FR sites for three and two years, respectively, due to logging and heavy ATV use in forests at those sites. By 2009, I tagged 3950 individual *Arisaema* over the six populations (DZ: n=634, WW: n=1325, WL: n=431, ER: n=329, FR: n=185, TW: n=1046).

For each tagged *Arisaema* individual in my plots, I recorded size, flowering status, and sex status during each census. I determined the sex of each flowering plant in my plots by visual inspection of the inflorescences. In 2005 and 2007, I collected infructescences from female plants and counted the total number of seeds produced per female and returned seeds to the study plot. To develop a non-destructive metric of total plant size, in 2006, I excavated, washed, dried

Arisaema from outside the study plots and found that the stem diameter at the soil surface was the best predictor of total plant mass (Pearson's $r=0.70$, $P<0.0001$, $n=137$). I used stem diameter (mm) at ground level as my measure of plant size on all tagged plants in my study as an estimate of individual plant mass. Some individuals were not seen above ground in one year but could reappear the following year; these individuals were re-scored as having survived the previous year in dormancy. Finally, I scored any plant whose tag was found but there was no aboveground tissue as dead. I did not excavate plants to confirm mortality so my estimates of survival are likely to be conservative.

4.2.4 Parameter estimation

To evaluate the vital rates and generate parameters for the size based IPM of each *Arisaema* population I used generalized linear mixed models (GLMMs) from the lme4 package (Bates *et al*. 2012) in the statistical software R version 3.1.0 (R Core Team 2013). First, I modeled vital rates using all data collected from 2005-2009 with hierarchical models to generate slopes and intercepts of the functions that describe vital rates in the IPM. The use of the complete data set and hierarchical modeling of parameters allowed me to get more sensible, biologically realistic parameter estimates for some of my sites that had sparse data for some stages while still accounting for individual and population-level variation (Gelman & Hill 2006, Merow *et al.* 2014). All size data were log-transformed before estimating model parameters; log-transformation improved the fit of all models compared to non-transformed data.

The probabilities of survival, flowering as female, and producing asexual cormlets for each population were analyzed with binomial logistic regressions using GLMMs. Individual plant size, size^2, population, year, and the size*population interaction were treated as fixed

effects in binomial repeated measures GLMMs to assess their effect on survival, female flowering, and cormlet production probabilities. I then set population and year as nested random variables in a hierarchical model to generate year and population specific intercepts and slopes, which were loaded into IPM kernels. I did not have cormlet data for two sites, ER and FR, and applied the main model intercept and slopes to the cormlet production functions in their IPMs.

I analyzed growth using repeated measures mixed effects linear model with Gaussian distribution that had size at time t+1 as the response variable and size at time t, size^2 at time t, population, year, and the size*population interaction as fixed effect explanatory variables. To generate intercepts and slopes to load the IPM growth functions, population and year were then set as nested random variables in a hierarchical model. The quadratic size term was only significant in the models for survival and growth and was dropped from all other models. When independent variables were not significant population and year specific intercepts and slopes were still produced using the hierarchical models because the goal of the study was to see if λ differed among sites.

I estimated the seeds per female flowering plant using Poisson distributed glm with the seed data collected in 2005 and 2007. Poisson distributed glm was also used to estimate the number of cormlets produced by plants. Due to the rarity of seedling recruits in my study plots and the inability to assess parentage of seedlings I parameterized the size distribution of recruits independent of adult size. The sizes of new of recruits, both sexual and asexual, were drawn from a probability density function based on the distribution of recruits observed in the field. The establishment probability of sexual recruits was calculated for each population by taking the number of seeds produced in year t and dividing by the number of seedlings in year t+1. Sample size for estimating asexual establishment rates was low and since production of cormlets was

rare, I applied the establishment probability used by Bierzychudek (1982) for cormlet establishment rates.

4.2.5 Size based integral projection model for *Arisaema triphyllum*

The integral projection model (IPM) approach can eliminate the use of arbitrarily defined size-classes sometimes used in matrix models and can describe how continuously size structured populations change through time (Easterling *et al*. 2000, Ellner and Rees 2006). The IPM components are continuous functions that describe how a continuous state variable, like size, influences its state in the next time step and determines the population's properties (i.e. vital rates). These functions are determined using standard statistical techniques, usually generalized linear mixed models (Merow *et al.* 2014). The projection kernel, *K*, represents all potential survival, growth and fecundity transitions similar to a projection matrix **A** (see Caswell 2001). The n(*x*,*t*)d*x* is the number of individuals with size in the range (*x*, *x*+d*x*) at time t whose dynamics are described by

$$n(y,t+1) = \int_L^U [P(y,x) + F(y,x)] n(x,t)\,dx = \int_L^U Kn(x,t)\,dx \qquad \text{eqn. 1}$$

where size = *x* is and *U* and *L* represent the size range of all *Arisaema* individuals in the population. The growth/survival and fecundity components, P(*y*,*x*) and F(*y*,*x*), represent the movement of size *x* individuals to size *y* and the production size *y* offspring by size *x* parents, respectively. The growth/survival and fecundity components together make up the kernel, *K*.

I used a size-based IPM to describe the population dynamics of *Arisaema* at each site. The growth/survival component of the kernel is given by

$P(y,x) = \int s(x)\, g(y,x)$ eqn. 2

where s(x) is the probability of a size x plant surviving and g(y,x) gives the probability of a size x individual becoming size y. The fecundity function of the kernel is given by

$$F(y,x) = \int p_{female}(x)\, fn_{seed}(x)\, fd_{sex}(y,x)\, p_{est} + \int p_{cormlet}(x)\, fn_{cormlet}(x)\, fd_{asex}(x,y)\, p_{est} \quad \text{eqn. 3}$$

where the first term of the equation gives the number new recruits produced from seed: where $p_{female}(x)$ gives the probability of a size x plant flowering as a female, $fn_{seed}(x)$ is the number of seeds produced by a size x female, $fd_{sex}(y,x)$ gives the size distribution of recruits from seed produced by size x females, and p_{est} is the establishment probability of new recruits. The second term of equation three represents the production of new recruits by asexual reproduction where: $p_{cormlet}(x)$ gives the probability a size x plant produces a cormlet, $fn_{cormlet}(x)$ gives the number of cormlets produced by a size x plant, $fd_{asex}(x,y)$ gives the size distribution of cormlets produced by size x plants, and p_{est} is the establishment probability of new recruits. Integral projection models have an identical set of analyses for evaluating population dynamics as matrix models (Easterling *et al*. 2000, Hegland *et al*. 2010, Merow *et al*. 2014).

4.2.6 Size x flowering stage IPM for *Arisaema triphyllum*

Arisaema can transition back and forth between their flowering stages throughout their life history. To incorporate this behavior into the IPM, I created mega-matrices that allowed the vital rates of individuals of different flowering stages to vary and allow individuals to transition between flowering stages (Caswell 2001, Yule *et al.* 2013). I used the R package IPMpack to build and analyze mega-matrices for each population (Merow *et al.* 2014). To build the models functions that described flowering stage specific vital rates were first fitted. Vital rate fitting for the size x flowering stage IPM was constrained by the capabilities of IPMpack and hierarchical

modeling could not be done as in the size based IPM; this led to fixed survival probabilities in some populations (WL, FR, and ER). Growth and survival were regressed against size, flowering stage, size*flowering stage, and size^2 with Gaussian and binomial GLMs, respectively. Survival for these three populations was modeled with a survival function created using all *Arisaema* data. Fecundity was modeled as a Poisson regression with size as the fixed effect. I then used vital rate functions to build survival-growth (*P*) and fecundity (*F*) kernels for each population. To build the mega-matrices, I first created population specific 3x3 transition matrices that showed how surviving individuals moved through non-flowering, male flowering and female flowering stages. Some populations had specific transition values that were not realistic for *Arisaema*, e.g. no stasis of non-flowering or female stages or females never retrogressing to males. These transition probabilities were adjusted to assure that transitions that happen in nature could happen in the model (Table 4.4). Transition matrices were then multiplied by *P* to establish size based growth and survival rates within the mega-matrix. The *F* kernel was added to the top right sub-matrix of the mega-matrix to represent sexual reproduction of females. I created an overall *Arisaema* mega-matrix using data from all populations and separate mega-matrices for each population for use in demographic analysis.

4.2.7 Demographic analyses

I integrated over the kernel (*K*) of each population in my study to find the dominant eigenvalue, which is equal to the population growth rate, λ. I then used parametric bootstrapping procedures to find the mean λ and 95% confidence intervals for each population. I used the bootMer function in the lme4 package of R (Bates *et al*. 2012) to generate bootstrapped vital rate

regressions and used the intercepts and slopes of the bootstrapped regressions to build 50 new IPM kernels for evaluation of λ. I calculated mean λ based on 50 bootstrapped IPM kernels. I determined the mean λ for each population and also calculated a grand mean λ for *Arisaema* across all populations by pooling the data from all populations and recalculating overall vital rates.

To better understand how indirect effects of deer influence *Arisaema* population growth rates, I conducted Life Table Response Experiment analyses (LTRE, Caswell 2001). In LTREs population vital rates, (e.g. λ), are used as response variables (Caswell 2001). To quantify the relationship between deer impact index scores and population growth rates I used a regression design LTRE termed a Life Table Regression Analysis (LTRA, Caswell 2001, Knight *et al.* 2009). In this analysis, I regressed the mean λs from the size based IPM for each site in each annual transition against the deer impact index score for that site. This analysis provides a clue to how *Arisaema* λ generally responds to indirect effects of deer. In addition, I made between site and between annual transitions comparisons of mean λ with Tukey's HSD test.

To understand how flowering stage transitions contribute to any differences in λ between populations, I used a one-way fixed LTRE. This type of design allows for a comparison of vital rates among levels of a single treatment factor (Caswell 2001, Heglend *et al.* 2010, Jacquemyn *et al.* 2010), in this case the observed differences in deer impact index scores among populations. Here I used the overall *Arisaema* λ from the size x flowering stage IPM as a baseline to ask how the vital rates of the three flowering stages contributed to differences in λ across populations when weighted by their sensitivities. I chose to use this 'overall' *Arisaema* model as the baseline, rather than the use of a grand mean kernel, *K*, because the overall *K* could be built from a larger dataset, which should provide the best estimates of the vital rates underlying the model. To

perform the analysis I found the mid-way *K* for the baseline *K* and the population under comparison by finding the mean *K*. I then calculated the differences between the baseline *K* and comparison population's *K*. These differences are then weighted by the sensitivities of the mid-way *K* and plotted for visual comparison. Mega-matrices of the sensitivity-weighted contributions to λ of the comparison kernel were plotted with 3-d wireframe plots to better depict how the differences in kernels contributed to λ.

4.3 RESULTS

4.3.1 Demographic parameters

Arisaema plants from all populations exhibited similar size distributions although populations with higher deer impact index values were skewed more toward smaller plant sizes (Figure 4.1). Across all populations, survival was not dependent on size (P=0.10) but tended to increase with size (Figure 4.2). The probability of survival also did not differ among populations and the interaction between interaction between size and population was also not significant (Table 2). Growth rate of *Arisaema* tended to slow with increasing size and sometimes appear as shrinkage of larger plants (Figure 4.3). Growth rate was significantly dependent on size and differed significantly among populations and years (Table 4.2). The size*population interaction on growth was not significant. Growth models revealed relatively slow growth rates since slopes for most of the growth regression had values less than 1 (Table 4.3, Figure 4.3).

The probability of producing an inflorescence with female flowers was significantly dependent on size (Table 4.2, Figure 4.4). Larger plants were most likely to flower as females

(Figure 4.4) and there was no significant difference in size for female flowering probability among populations. The size*population interaction term for the probability of flowering as female was only marginally significant (P=0.16) but population specific slope parameters were estimated for the IPM (Table 4.3).

The probability of an individual producing a cormlet was significantly related to size (Table 4.2). Because population and the size*population interactions were not significant predictors of cormlet production probability, I used a single size dependent slope and intercept estimate for all populations to parameterize my IPM (Table 4.3). The per capita number of cormlets produced was much less one cormlet per individual and was significantly related to size, population, and their interaction (Table 4.2). The number of seeds produced per female was significantly dependent on size (Table 4.2). Seeds per female showed a slight increase in seed number with size, but the largest female did not always produce the most seeds (Figure 4.5). The effect of population on seed production is significant, so I estimated individual population's specific seed production parameters for use in their IPM (Table 4.3).

4.3.2 Demographic analyses

I combined growth/survival (P) and fecundity (F) kernels into the IPM kernels (K) for each site (Figure 4.6). IPM kernels for all sites were similar in form. Visual comparison showed the sites DZ, WL, and FR had growth/survival components with higher probabilities, while DZ and ER had larger fecundity components, (see Figure 4.6). Regression design LTRE indicated that population mean λ declined significantly as deer impact index ranks of sites increased (Figure 4.7; Chisq = 112, df=1, n=1336, $P < 0.001$). Confidence bands around the regression line describing the relationship between mean λ and deer impact index suggests that populations in

sites with deer impact index value greater than 10 are expected to have $\lambda < 1$ and therefore be in decline. Bootstrap iterations of the kernels showed that mean bootstrapped λs ranged from 0.94 – 1.06 with the two sites with the highest deer impact index ratings, WW and TW, having the smallest λs (Table 4.5). The population with the lowest average indirect effects of deer, DZ, had mean λ significantly greater than the mean λ for all other sites in all years (Tukey HSD: $P < 0.003$ for all comparisons) except one (DZ-ER in 2005-06: $P = 0.37$). Mean λ values for three DZ annual transitions and the mean λ for ER in 2005-06 were the only instances of a populations with mean $\lambda > 1$ and confidence intervals that did not overlap with one (Figure 4.7). Conversely, the two sites expected to experience the greatest indirect effects of deer, WW and TW, had mean λ values that were always less than one with confidence intervals that did not overlap one (Figure 4.7). Elasticity analyses of each IPM showed that λ was most dependent on individuals in the mid- to upper range size classes surviving and advancing to larger states (Figure 4.8). Sensitivity analyses showed that growth rate was most responsive to changes in fecundity.

The size x flowering stage IPMs estimated λs of greater magnitude than the size based IPM produced, ranging from 0.89 to 1. 17 (Table 4.6). The λs produced by the model generally declined with increasing deer impact index values for populations. The fixed LTRE indicated why the λs varied. In the fixed LTRE, all populations were compared to a baseline *Arisaema* model that was built using data from all populations (Figure 4.9), which produced a λ of 1.02. Plots of the sensitivity-weighted differences in IPM elements showed that the LTRE comparisons from the overall model were spread across all life history transitions with smaller magnitude peaks exhibited by populations with lower deer impact index scores, while in the more highly impacted populations effects were more extreme (higher peaks) and localized to fewer life history transitions (Figure 4.10). Specifically, in the population with the highest deer

impact score, TW ($\lambda = 0.97$), the rates of non-flowering individuals remaining as non-flowering, and non-flowering individuals transitioning to males, had large negative effects on λ (Figure 4.10 lower right). For the second most impacted population, WW ($\lambda = 0.89$), the non-flowering to male transition, male to female transition, and likelihood of females remaining females all had a negative effects on λ (Figure 4.10 lower middle). These results from TW and WW contrast sharply with the fixed LTRE results for the least impacted population, DZ ($\lambda = 1.11$), which showed that differences in IPM kernel elements resulted in an increase in λ for all flowering stage transitions.

4.4 DISCUSSION

Population dynamics of *Arisaema* declined with increases in the deer impact index ranks of study sites. This result supports my hypothesis that increasing non-trophic indirect effects of deer will lead to declines in population growth rates of unpalatable plants since my deer impact index is expected to correlate with indirect effects of deer. My size based IPMs suggest that most of the populations along the quantified deer impact index gradient had λ values just less that unity indicating that they could be in slow decline (Figure 4.7). However it is interesting to examine the mean λ values of populations at the ends of the deer impact index gradient. For the population with lowest deer impact index rank, DZ, most estimates of the mean λ values are above one, indicating population growth (Figure 4.7). The two *Arisaema* populations located in sites with the highest deer impact index, WW and TW, have mean λs significantly lower than unity. While λs produced by the size by flowering stage IPM were higher than those of the size-based IPM, my results indicate a negative trend in λ with increasing deer impact index scores of

populations. These results from the regression and fixed design LTREs confirm that indirect effects of deer can have negative impacts on population growth rates (Heckel *et al.* 2010). Elasticity analyses of size based IPMs revealed that the survival and growth of moderate to large sized plants made the greatest contributions to λ (Figure 4.8) while the sensitivity of λ to the reproductive components of the IPM kernel was high. My results describing population dynamics of *Arisaema* are in line with previous studies of this species, where λ ranged from 0.85 – 1.32 (Bierzychudek 1982). However, Bierzychudek (1982) did not quantify deer impacts.

I predicted that *Arisaema* populations in sites with the highest deer impacts would exhibit the lowest lambdas for several reasons. First, my previous study documented the smallest mean flowering sizes of *Arisaema*, male skewed population sex ratios, and low seed rain in sites with high deer browse on *Trillium* (Heckel *et al.* 2010). In many plant species vital rates are size dependent (Jacquemyn *et al.* 2010), thus I would expect that the decrements in size associated with indirect deer impacts documented by Heckel *et al.* (2010) would lead to declines in population growth rates. Second, intense deer browsing can indirectly create soils that are drier and more compacted (Heckel *et al*. 2010, Frerker *et al.* 2013). The ungulate-mediated changes to soils can lead to reduced plant size (Kardol *et al.* 2014), which may in turn affect population vital rates. Finally, a common garden experiment with *Arisaema* individuals from the populations used in this study found significant population differentiation in female flowering size threshold and growth rate (Chapter 3). Local habitat conditions can have a strong influence on flowering strategies (Hesse *et al.* 2008), which underlie vital rates used to estimate population growth rate. The populations I studied were located in sites that differed mainly in the amount of deer browse: forest type and vegetative cover were similar for all sites. Since I found significant population-level effects on growth and flowering probability (Table 4.2), I assert that indirect effects of deer

are responsible for lower λs estimated for the *Arisaema* populations in the sites with the highest deer impact ranks, WW and TW.

Population growth rates of long-lived perennial plants are generally not expected to deviate greatly from λ=1 (Silvertown *et al.* 1993). Previous demographic studies of two eastern North American *Arisaema* populations using stage-structured projection matrix models estimated λ to range from 0.85 – 1.32 (Bierzychudek 1982). However, λs for the two populations based on the ratio of the number of individuals across years (i.e. 1974-1994) were 0.89 and 0.94 (Bierzychudek 1999). The size based IPM I used produced mean λs that ranged from 0.94 to 1.06 while the size x flowering stage IPM λs ranged from 0.89 to 1.17. The similarity of my IPM-projected λs to those of Bierzychudek (1982, 1999) and the general expectations for long-lived perennials of λ =1, suggest that my models are an accurate representation of *Arisaema* life history. My size based IPM shows that elasticity of λ to the growth/survival components of the IPM kernel was high, especially for moderate to large sized plants (Figure 4.8). The large effects on λ of individuals moving in an out of male and female flowering stages shown by the LTRE of the size x flowering stage IPM (Figure 4.10) further underscores the importance of these flowering stages to *Arisaema* life history. Large contributions of growth and survival of moderate to large sized and reproductive plants also fits with conclusions about perennial plant demography borne out of matrix projection models (Silvertown *et al.* 1993, Franco & Silvertown 2004).

4.4.1 Advantages of IPMs for this data set

Integral projection models combined with hierarchical linear models provide advantages in estimating population growth rates of *Arisaema.* During the lifetime of *Arisaema*, an individual

typically progresses from non-flowering, to male flowering, to a female flowering plant, and these transitions largely depend on plant size (Bierzychudek 1982). Due to continuous growth and flowering stage transitions, the size of *Arisaema* individuals within populations do not fall into clear size classes that could be used in a projection matrix model, but rather vary continuously. While *Arisaema* may be classified into a matrix models based on three flowering stages categories, this approach would yield low matrix dimension (i.e. 3x3) and suffer from errors of distribution since transition probabilities are skewed by the size distribution of individuals within a category (Vandermeer 1978) and high impact populations have few flowering individuals. In addition, a common garden experiment with *Arisaema* revealed that populations differ in their size thresholds for flowering as females (Chapter 3), which would make it difficult to assign size classes that would have the same biological meaning and encompass similar life history stages across populations. Since IPMs are based on continuous state variables (Easterling *et al.* 2000) and can be coupled with discrete flowering stages they are excellently suited to analyses of *Arisaema* populations.

Further, I had unequal sample sizes for flowering stages across populations. Integral projections models are well equipped to handle low sample sizes for some stages and provide reliable λ estimates even when sample sizes are small (Zuidema *et al.* 2010). In addition, I used hierarchical models to estimate vital rates for the IPM. Hierarchical modeling techniques borrow information from the population- and individual-level variation among all observations to improve estimated vital rates for any population's transition year for which too few observations exist (Gelman & Hill 2006, Merow *et al.* 2013). Coupled with the use of hierarchical modeling techniques, my IPMs allowed me to produce mean λ estimates for six populations and up to four yearly transitions/population, which would have been impossible if modeled with projection

matrix models. In addition, IPMs are capable of performing all analyses that are often applied to matrix models. Finally, I could apply LTREs of two different design to my IPMs to more deeply explore how indirect effects of deer can drive *Arisaema* population growth rate declines and what transitions in *Arisaema's* life history are responsible for the changes.

4.4.2 Indirect effects of deer on population dynamics

Increasing levels of browse is known to lead to declines in plant population growth rates of palatable plant species (*e.g.* McGraw & Furedi 2005, Knight *et al.* 2009, Heglend *et al.* 2010, Jacquemyn *et al.* 2010). My IPMs showed that the two populations of unpalatable *Arisaema* from sites with the highest deer impact index ranks, WW and TW, had significantly lower λs, suggesting that soil-mediated indirect effects of deer may be slowing population growth. The mean annual percent browse on *Trillium* stems in the WW and TW sites were 12% and 13% respectively (Table 1). The browse levels of WW and TW are close to the threshold percent browse on *Trillium* where annual population growth rates of *Trillium* switch from growth to decline (14.5% of *Trillium* stems browsed, Knight *et al.* 2009). The low λs I found for *Arisaema* populations in sites that receive intermediate levels of deer browse (Knight *et al.* 2009) suggest that overabundant deer are indirectly exerting soil-mediated ecosystem level effects (Kardol *et al.* 2014).

Abiotic and biotic interactions can have significant impacts on plants species' population growth rates (Dahlgren & Erlen 2009, Heglend *et al.* 2010). My study presents a novel perspective on abiotic and biotic interaction on plant population dynamics because my study species does not directly interact with the herbivore that is the driver of environmental variation among sites. It is likely that the negative indirect effects of deer on unpalatable plants species'

population dynamics are not specific to the Pennsylvania populations of *Arisaema* I studied. A pattern of smaller unpalatable plants associated with high deer impacts has been observed in long-term experimental deer exclusion studies in Virginia (Heckel *et al.* 2010) and in Indiana (Frerker *et al*. 2013), regions where deer are overabundant (McShea *et al.* 1997). Since the vital rates that inform demographic models are generally found to be size-dependent (Jacquemyn *et al.* 2010), I expect other unpalatable plant species will also exhibit λs that indicate population decline in areas where deer have become overabundant. This work further suggests that the relatively recent global phenomena of ungulate overabundance (Côté *et al.* 2004; Vavra *et al.* 2007; Bressette *et al.* 2012) may exert more far reaching negative effects on plant communities than was previously considered.

Table 4.1. *Trillium* metrics used to created deer impact index. Sites have been placed in order of least to most deer impacted from top to bottom.

Site	Mean % Stems Browsed	Mean % Flowering Stems	Median Leaf Length (cm)
DZ	0.03	0.50	7.2
WL	0.08	0.35	6.7
FR	0.01	0.16	6.2
ER	0.06	0.17	5.9
WW	0.12	0.05	5.3
TW	0.13	0.01	3.7

Table 4.2. Chi-square values from tests of significance on fixed effects from GLMMs fitted to vital rates that inform the IPM. Probabilities of survival, flowering, flowering as female, and producing a cormlet were analyzed with logistic regression. Growth was fitted with a Gaussian distribution and per capita cormlet and seed production were fitted with a Poisson regression. Chi-square P -values are based on type III sums of squares.

Fixed Effects	**Chi-square**	**df**	**P-value**
Survival Probability			
Size	2.71	1	0.10
$Size^2$	1.9	1	0.17
Population	3.01	5	0.69
Size*Population	0.23	5	0.99
Year	5.5	3	0.14
Growth			
Size	184.9	1	< 0.001
$Size^2$	20.8	1	< 0.001
Population	27.6	5	< 0.001
Size*Population	20.4	5	0.11
Year	41.8	3	< 0.001
Female Flowering Probability			
Size	13.8	1	< 0.001
Population	3.8	5	0.57
Size*Population	7.8	5	0.16
Year	4	3	0.26
Cormlet Probability			
Size	4.5	1	0.03
Population	46.6	3	< 0.001
Size*Population	12.4	3	0.006
Year	4.5	1	0.03
Cormlet Production			
Size	5.2	1	0.02
Population	78.9	3	< 0.001
Size*Population	10.2	3	0.02
Year	15.6	1	< 0.001

Table 4.2 (continued)

Seed Production Per Female			
Size	144.6	1	< 0.001
Population	363.5	5	< 0.001
Size*Population	169.47	5	< 0.001
Year	180.5	1	< 0.001

Table 4.3. Statistical models and parameter estimates used to inform *Arisaema* IPM. I used generalized linear models generate parameters. Populations are ordered in increasing mean deer browse levels from top to bottom.

Demographic Parameter/ Model	Population	Intercept	Slope	Slope^2
Growth				
$\mu_g = a_g + b_g x + c_g x$	DZ	0.37	0.55	0.08
	WL	0.60	0.48	0.05
	FR	0.85	0.53	0.07
	ER	0.38	0.55	0.08
	WW	0.18	0.62	0.11
	TW	0.27	0.59	0.09
Variance about growth curve				
$\sigma^2_g = 0.41\exp(-2\beta_g \mu_g(x))$	all	0.39		
Survival probability				
logit $(p_s) = a_s + b_s x + c_s x$	DZ	2.26	1.90	-0.26
	WL	2.13	2.30	-0.004
	FR	2.23	1.63	-0.37
	ER	2.24	1.73	-0.36
	WW	2.20	1.27	-0.52
	TW	2.27	1.16	-0.62
Female flowering probability				
$\text{logit}(p_f) = a_f + b_f x$	DZ	-18.90	9.70	
	WL	-18.40	8.48	
	FR	-26.10	13.90	
	ER	-25.20	12.30	
	WW	-18.70	9.72	
	TW	-21.30	10.40	
Cormlet producing probability				
$\text{logit}(p_f) = a_f + b_f x$	all	-4.34	1.35	
Seeds per female flower				
$\theta_{seed} = a_{seed} + b_{seed} x$	DZ	-7.30	3.93	
	WL	-5.51	3.25	
	FR	-5.63	3.29	
	ER	-4.03	2.67	
	WW	-11.80	5.72	
	TW	-7.20	3.91	

Table 4.3 (continued)

Cormlets per individual			
$\theta_{seed} = a_{seed} + b_{seed}x$	all	-4.07	1.14
Probability of establishment		sex	asex
	DZ	0.0321	0.20
	WL	0.0011	0.20
	FR	0.0011	0.20
	ER	0.0218	0.20
	WW	0.0011	0.20
	TW	0.0011	0.20
Sexual recruits			
Mean size	all	0.05	
Variance	all	0.21	
Asexual recruits			
Mean size	all	0.58	
Variance	all	0.31	

Table 4.4. Transition matrices used to construct size by flowering stage IPMs. Bolded values indicate transitions that were originally 0 or 1 due to low sample sizes that were adjusted to allow all biologically relevant *Arisaema* transitions to occur in the model. Populations are ordered from lowest deer impact index score to highest from top to bottom then left to right.

DZ	**non-flowering**	**male**	**female**
non-flowering	0.777	0.179	0.069
male	0.214	0.643	0.310
female	0.009	0.179	0.621

ER	**non-flowering**	**male**	**female**
	0.095	0.125	0.000
	0.857	0.750	**0.900**
	0.048	0.125	**0.100**

WL			
non-flowering	0.154	0.169	0.040
male	0.846	0.800	0.600
female	0.000	0.031	0.360

WW			
	0.701	0.263	0.045
	0.284	0.675	0.364
	0.015	0.063	0.591

FR			
non-flowering	**0.250**	0.091	0.000
male	0.667	0.727	**0.100**
female	**0.083**	0.182	**0.900**

TW			
	0.801	0.433	0.000
	0.193	0.500	**0.900**
	0.006	0.067	**0.100**

Table 4.5. Bootstrapped mean λ values (± 95% CI) for each populations of study. Data sets were sampled 50 times to generate bootstrap IPM matrices that produced λ values. Populations are ordered in increasing mean deer browse levels from top to bottom.

Population	**λ**	**95% C.I.**
Transition: 2005-06		
DZ	1.004	0.013
WL	0.975	0.001
FR	0.965	0.003
ER	1.018	0.017
WW	0.963	0.031
Transition: 2006-07		
DZ	0.989	0.002
WL	0.985	0.000
FR	0.973	0.000
ER	0.987	0.002
WW	0.980	0.001
TW	0.985	0.001
Transition: 2007-08		
DZ	1.026	0.015
WL	0.972	0.001
ER	0.998	0.013
WW	0.975	0.003
TW	0.938	0.003
Transition: 2008-09		
DZ	1.058	0.023
WL	0.979	0.000
ER	0.987	0.006
WW	0.981	0.001
TW	0.969	0.001
Pooled year data		
DZ	1.012	0.011
WL	0.965	0.005
FR	0.967	0.001
ER	0.968	0.012
WW	0.963	0.009
TW	0.943	0.015

Table 4.6. *Arisaema* λ values from size x flowering stage IPM for each population of study. Data from all *Arisaema* populations was used in the size x flowering stage IPM to produce the overall λ. The kernel, *K*, used to determine overall λ was used as a baseline value in a one-way fixed design LTRE. Populations are ordered in increasing mean deer browse levels from top to bottom (excluding overall). Note: WW and TW are significantly lower than DZ, WL, FR and ER, based on regression LTRE, see Figure 4.8.

Population	**λ**
DZ	1.12
WL	1.09
FR	0.97
ER	1.17
WW	0.89
TW	0.97
overall	1.02

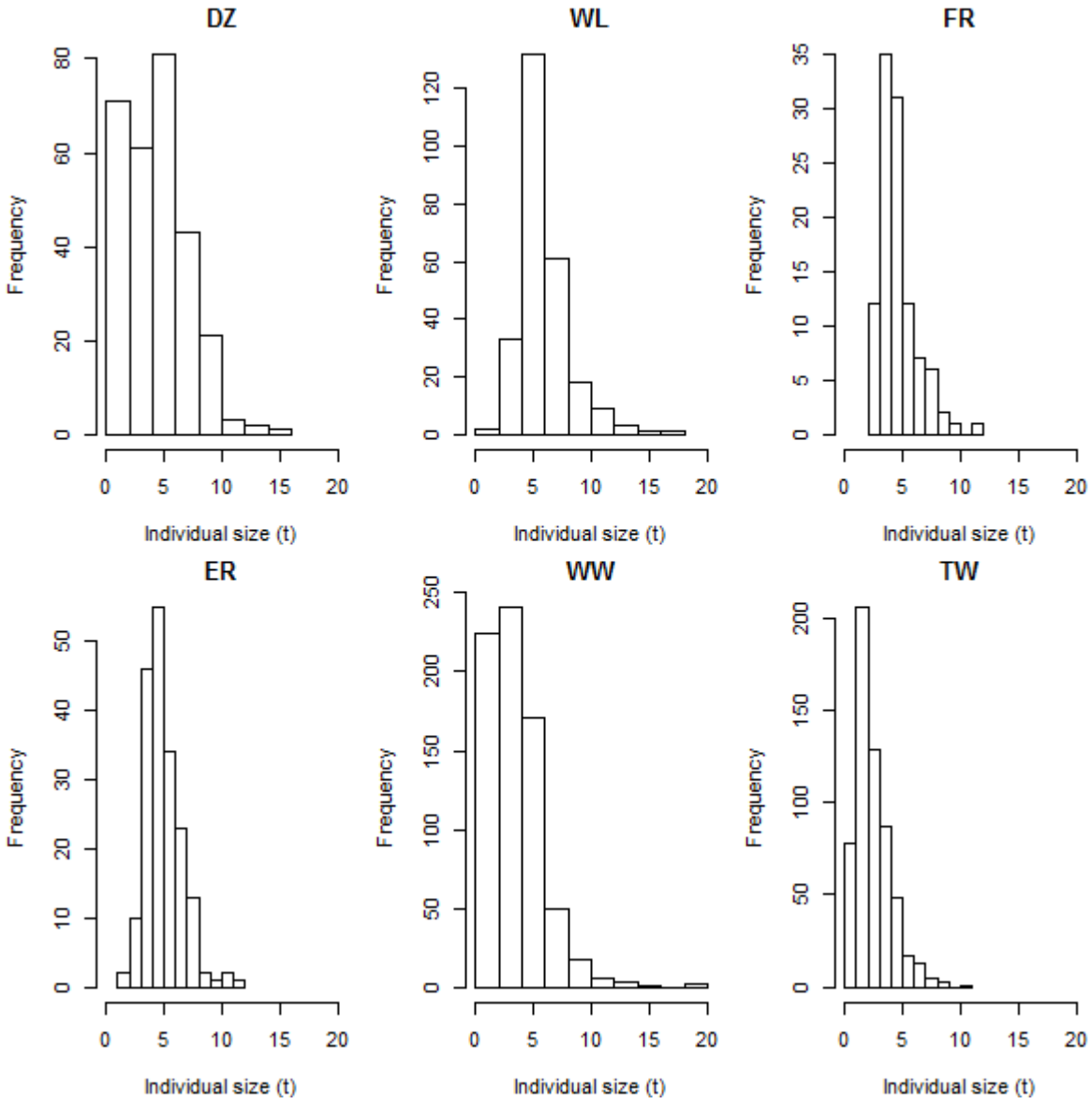

Figure 4.1. Size distributions of *Arisaema triphyllum* in six populations that span a gradient of deer browse intensity in western PA, USA. Populations are ordered in increasing mean deer browse levels from left to right and top to bottom. Data are combined for years 2005-2009. Stem diameter (mm) at soil level was my measure of size.

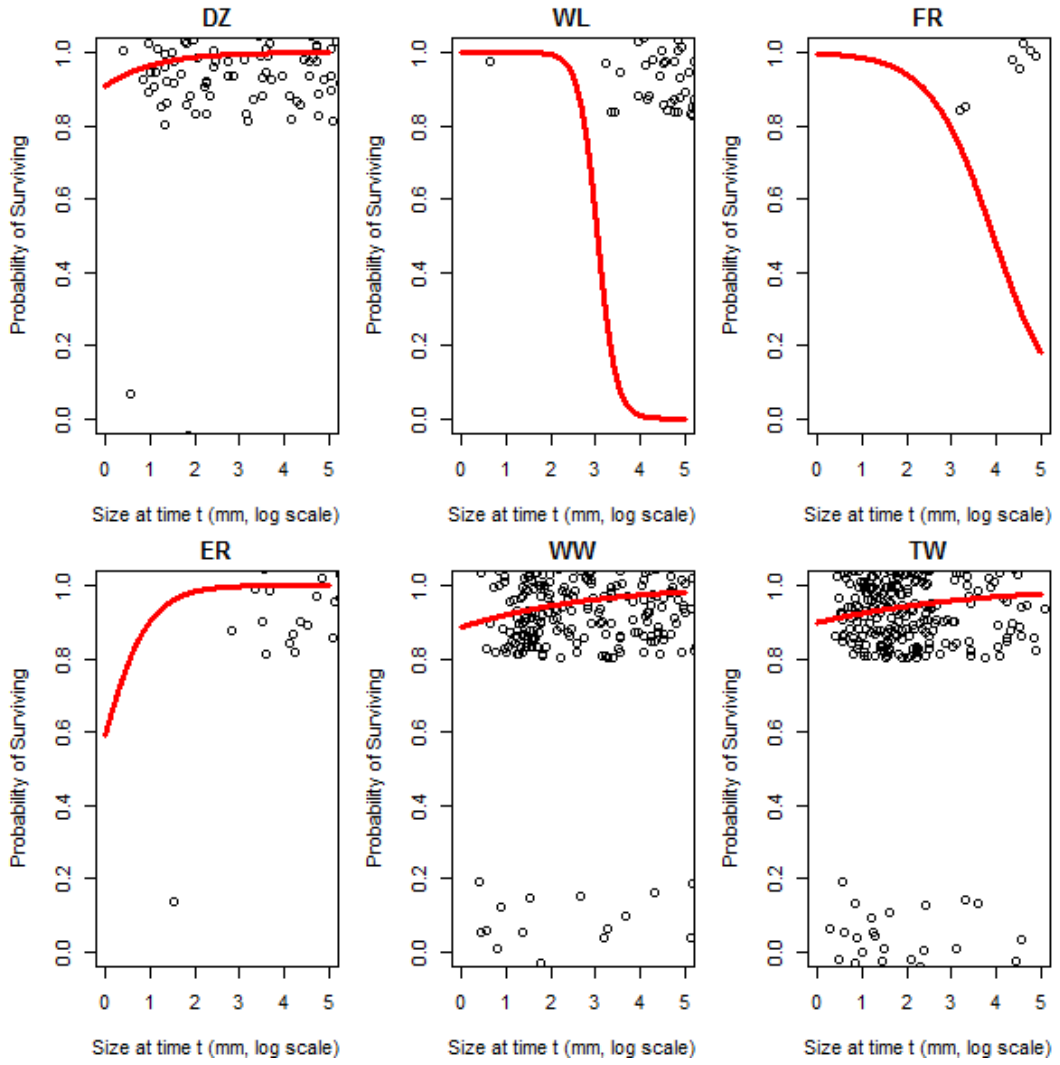

Figure 4.2. Survival of *Arisaema triphyllum* in six populations that span a gradient of deer browse intensity in western PA, USA. Data are pooled over four transitions: 2005-2006, 2006-2007, 2007-2008, and 2008-2009. Populations are ordered in increasing mean deer browse levels from left to right and top to bottom. Log transformed stem diameter (mm) at soil level was my measure of size. Data points are jittered around survival (y=1.0) and not surviving (y=0.0) to better show sample size. The logistic regression lines shown were fitted to the plotted data and therefore not the same as those from the hierarchical analyses used in population models.

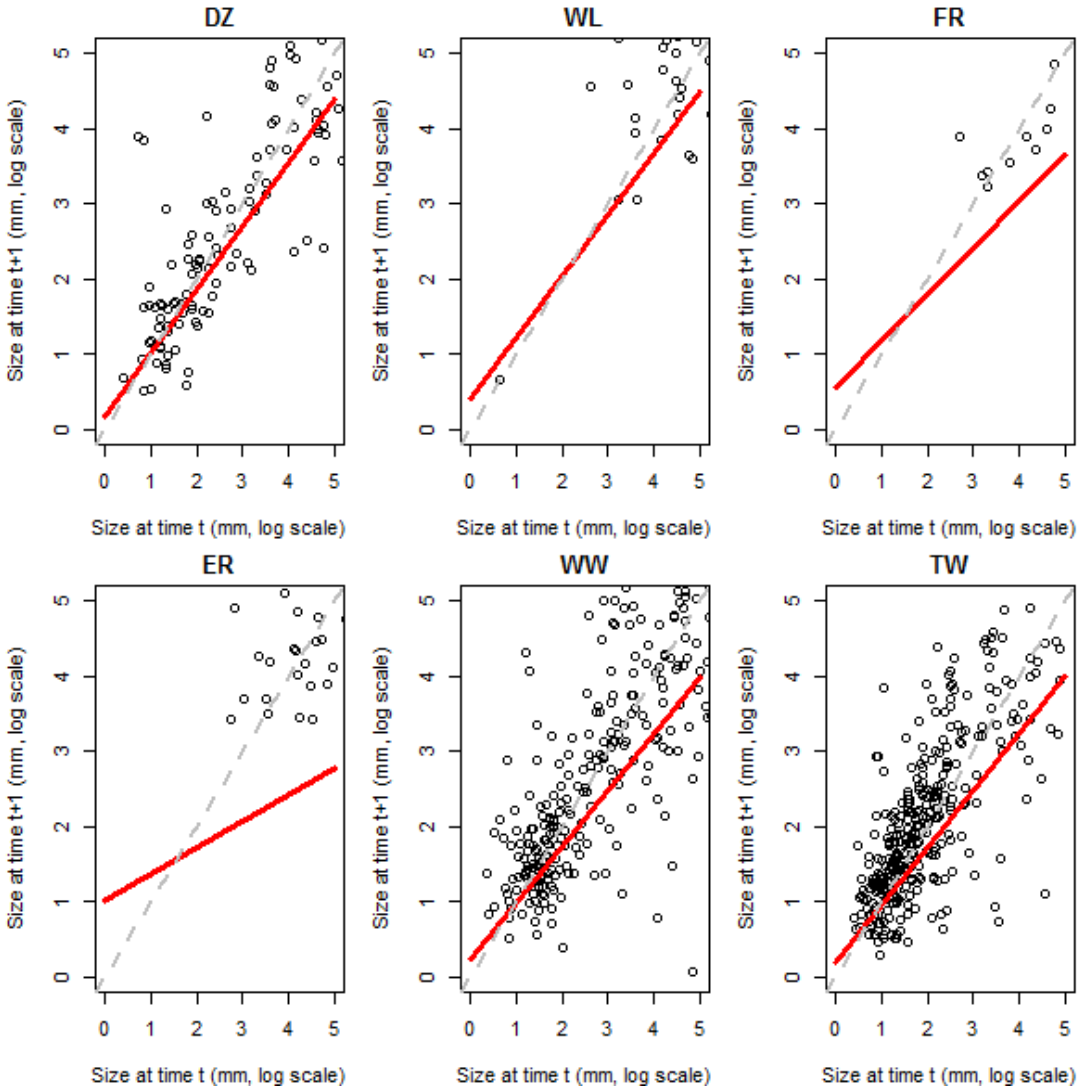

Figure 4.3. Growth of *Arisaema triphyllum* in six populations that span a gradient of deer browse intensity in western PA, USA. Data are pooled over four transitions: 2005-2006, 2006-2007, 2007-2008, and 2008-2009. Populations are ordered in increasing mean deer browse levels from left to right and top to bottom. Log transformed stem diameter (mm) at soil level was my measure of size. The regression lines shown were fitted to the plotted data and therefore not the same as those from the hierarchical analyses used in population models. The dashed gray line is presented for comparison and represents no change in size (slope = 1).

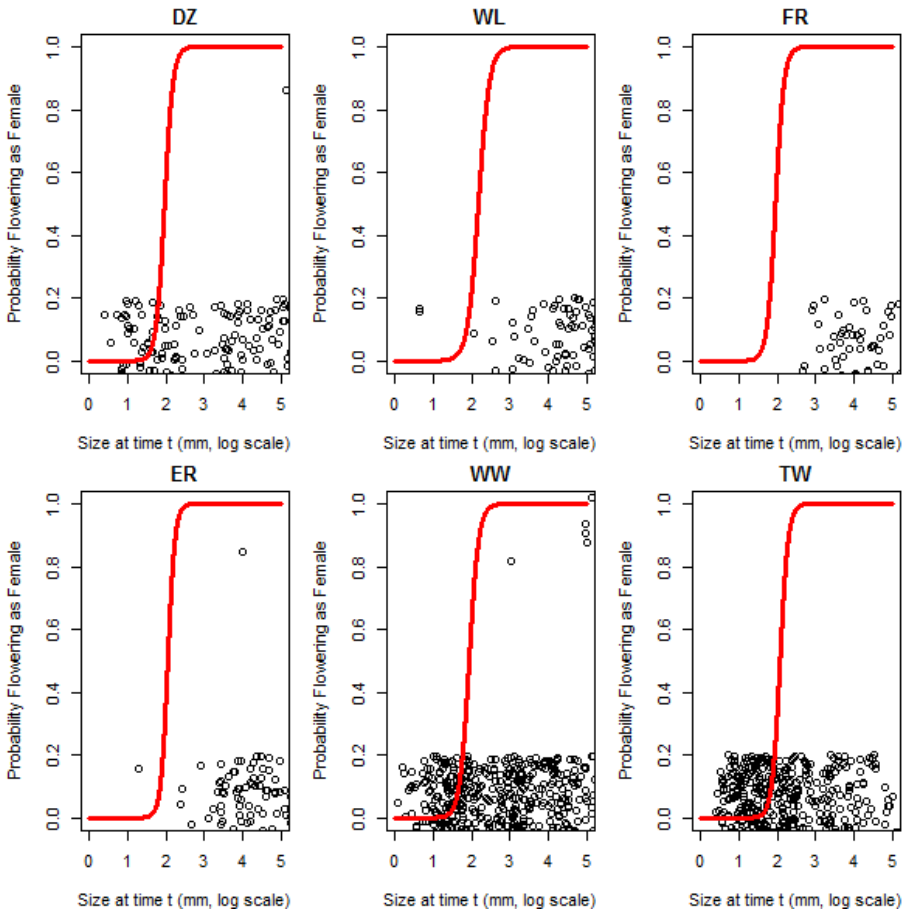

Figure 4.4. Size of female flowering at time of census for *Arisaema triphyllum* in six populations that span a gradient of deer browse intensity in western PA, USA. Populations are ordered in increasing mean deer browse levels from left to right and top to bottom. Data are combined for years 2005-2009. Log transformed stem diameter (mm) at soil level was my measure of size. Data points are jittered around female flowering (y=1.0) and not flowering as female (y=0.0) to better show sample size. The logistic regression lines shown were fitted to the plotted data and therefore not the same as those from the hierarchical analyses used in population models.

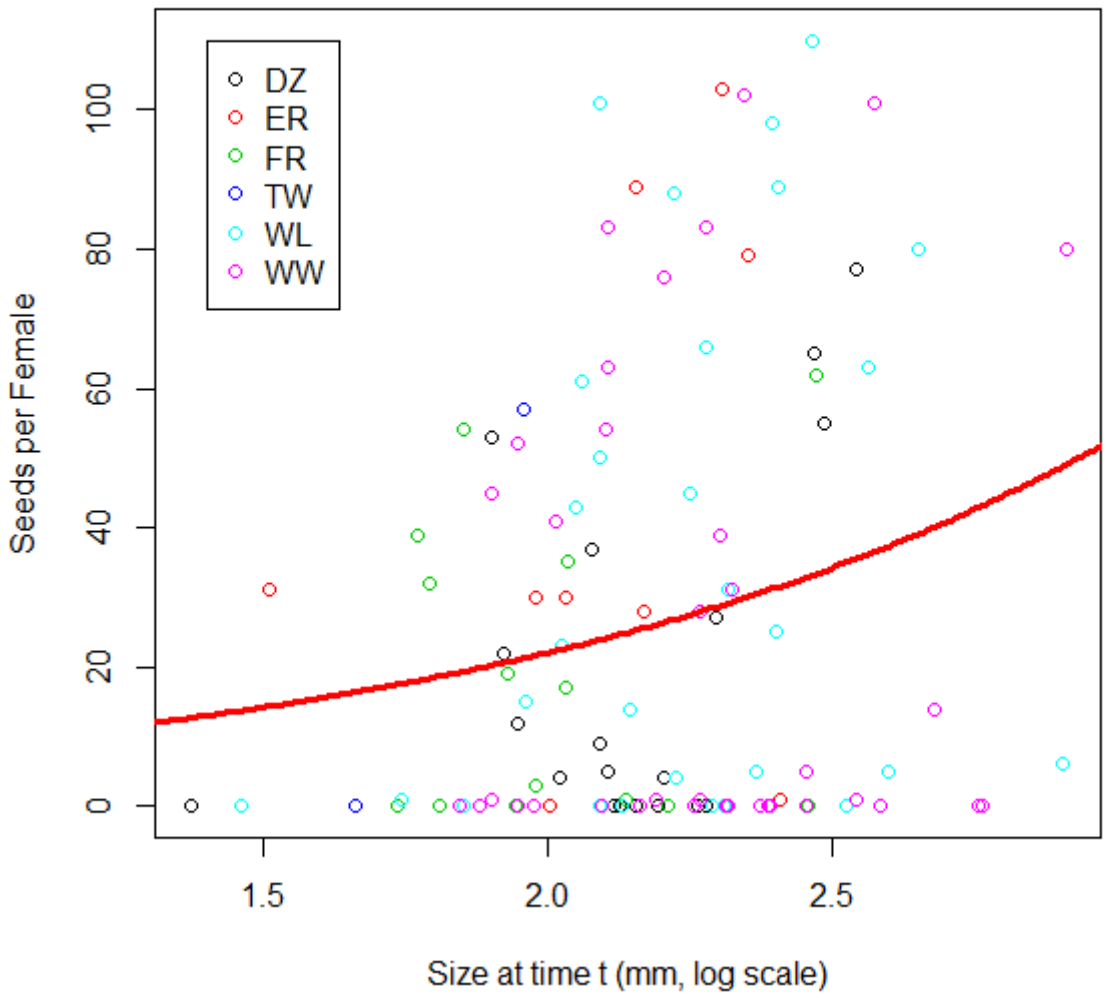

Figure 4.5. Number of seeds produced by female flowering *Arisaema triphyllum*. Regression line (red) shows the predicted fit of a Poisson regression. Stem diameter (mm) at soil level was my measure of size.

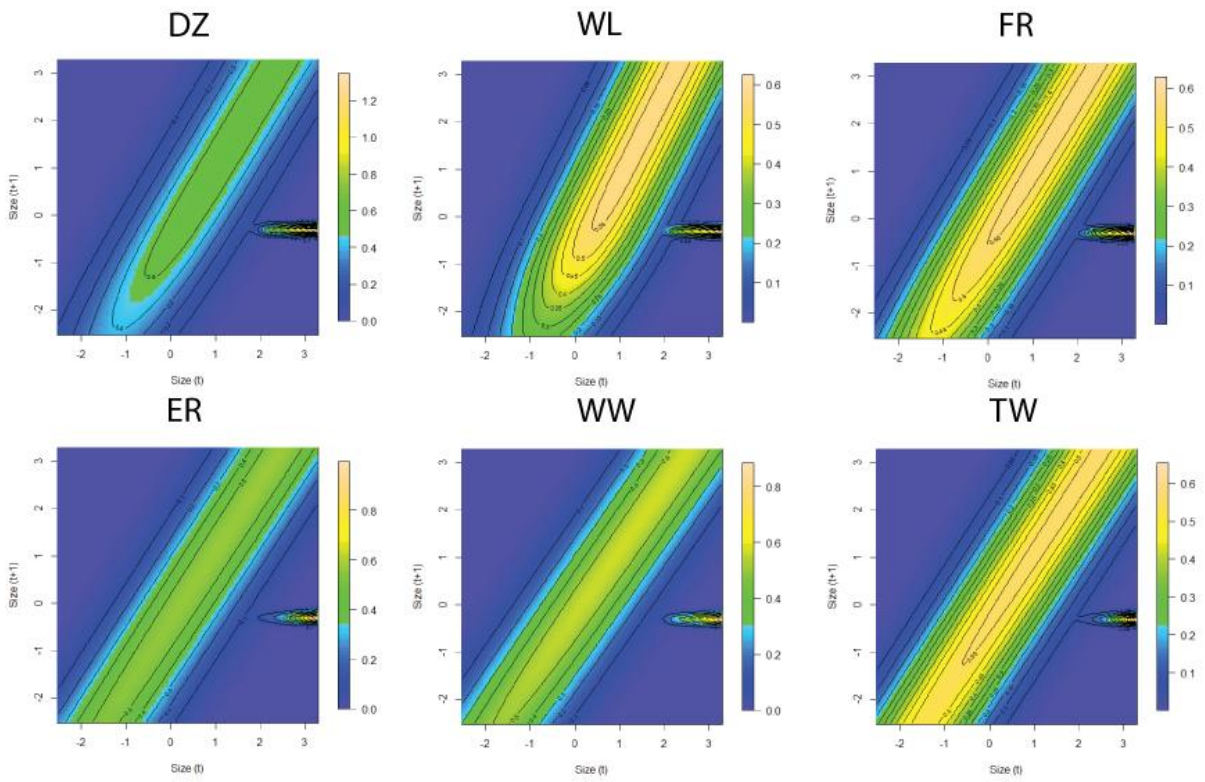

Figure 4.6. K matrices for each *Arisaema* population based on vital rates calculated with data pooled across all transition years. Warmer colors indicate greater probability of that transition occurring. Populations are ordered in increasing mean deer browse levels from left to right and top to bottom. Stem diameter (mm) at soil level was my measure of size. Data are combined for years 2005-2009.

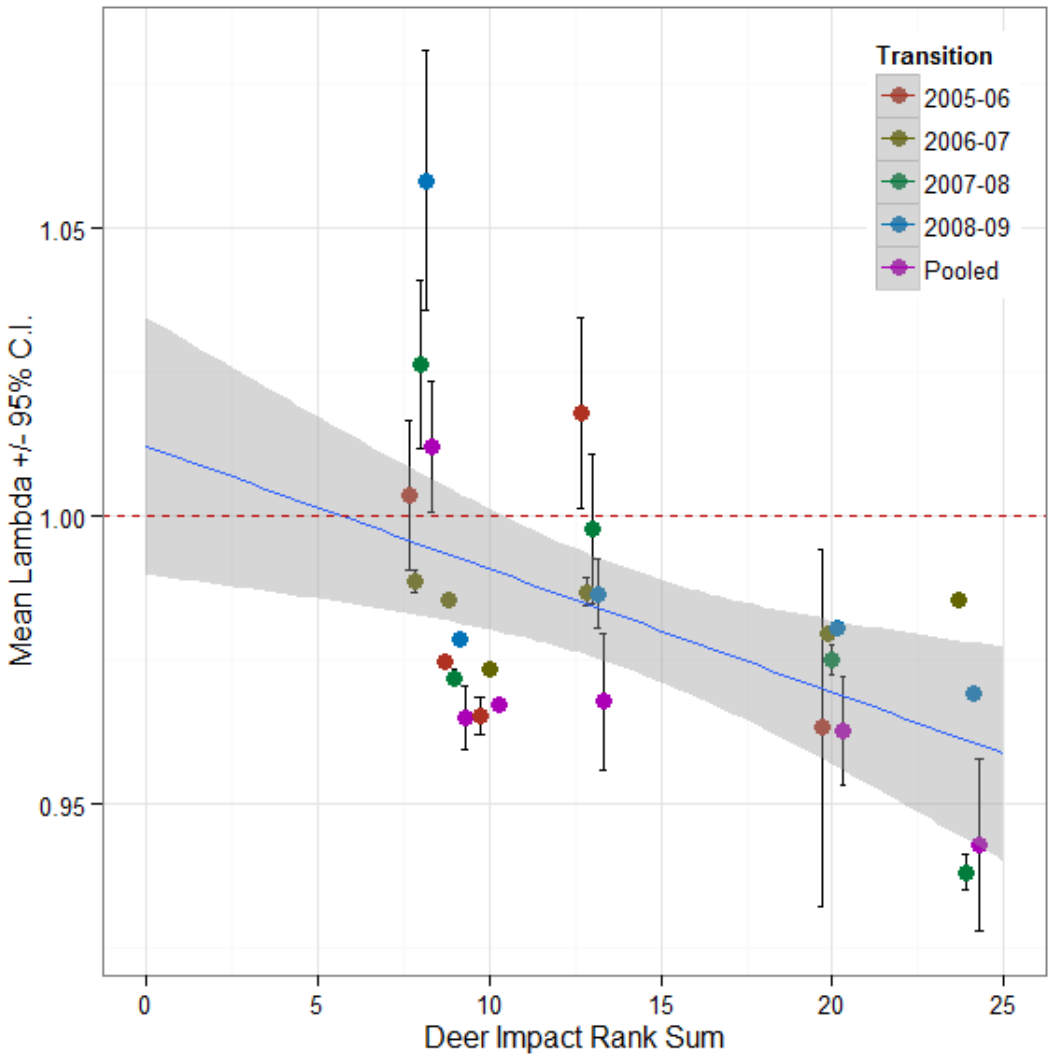

Figure 4.7. Bootstrapped mean λ (± 95 % C.I.) of each annual transition for each of the six study populations. The regression line (blue) suggests that as the indirect effects of deer associated with increased deer impact rank scores increases the likelihood of population decline, or $\lambda < 1$, for unpalatable *Arisaema* populations. Points are jittered to make error bars discernable. Gray bands around the regression line are 95% confidence intervals. The red dashed line is a reference point for $\lambda = 1$.

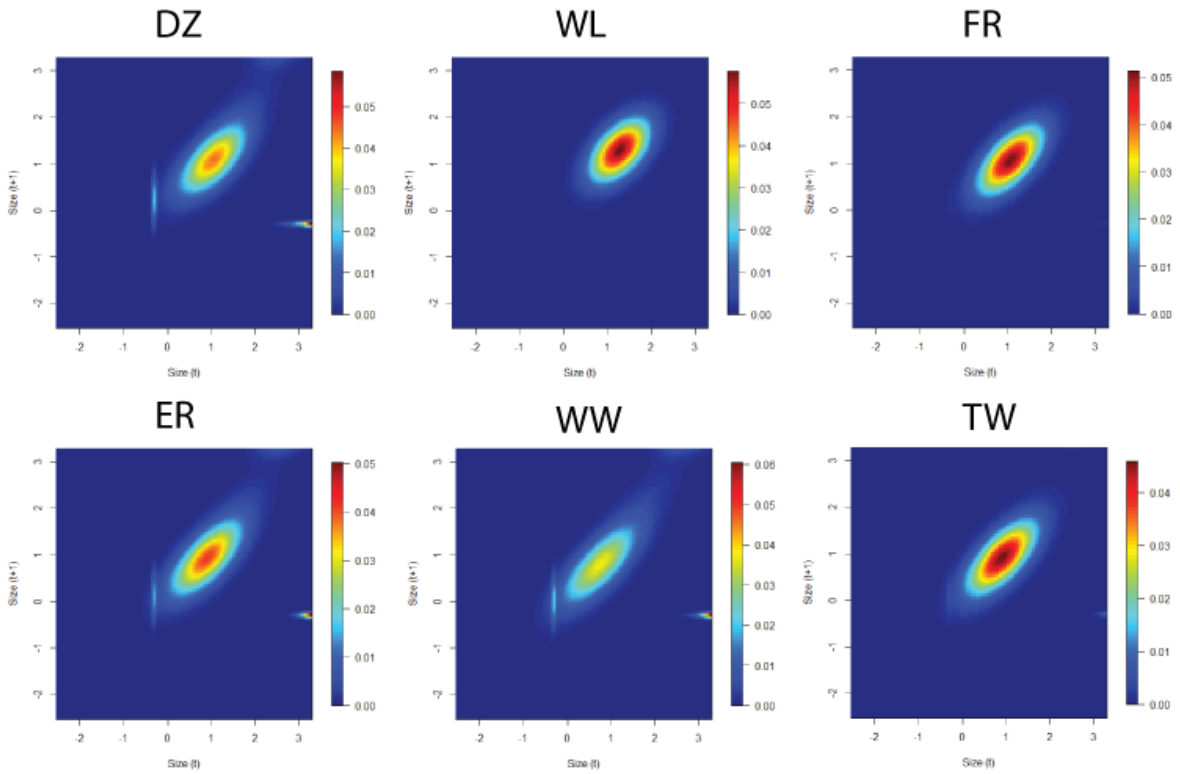

Figure 4.8. Heat map of elasticity matrix values for each *Arisaema* population based on vital rates calculated with data pooled across all transition years. Warmer colors indicate with the greatest elasticity of lambda.

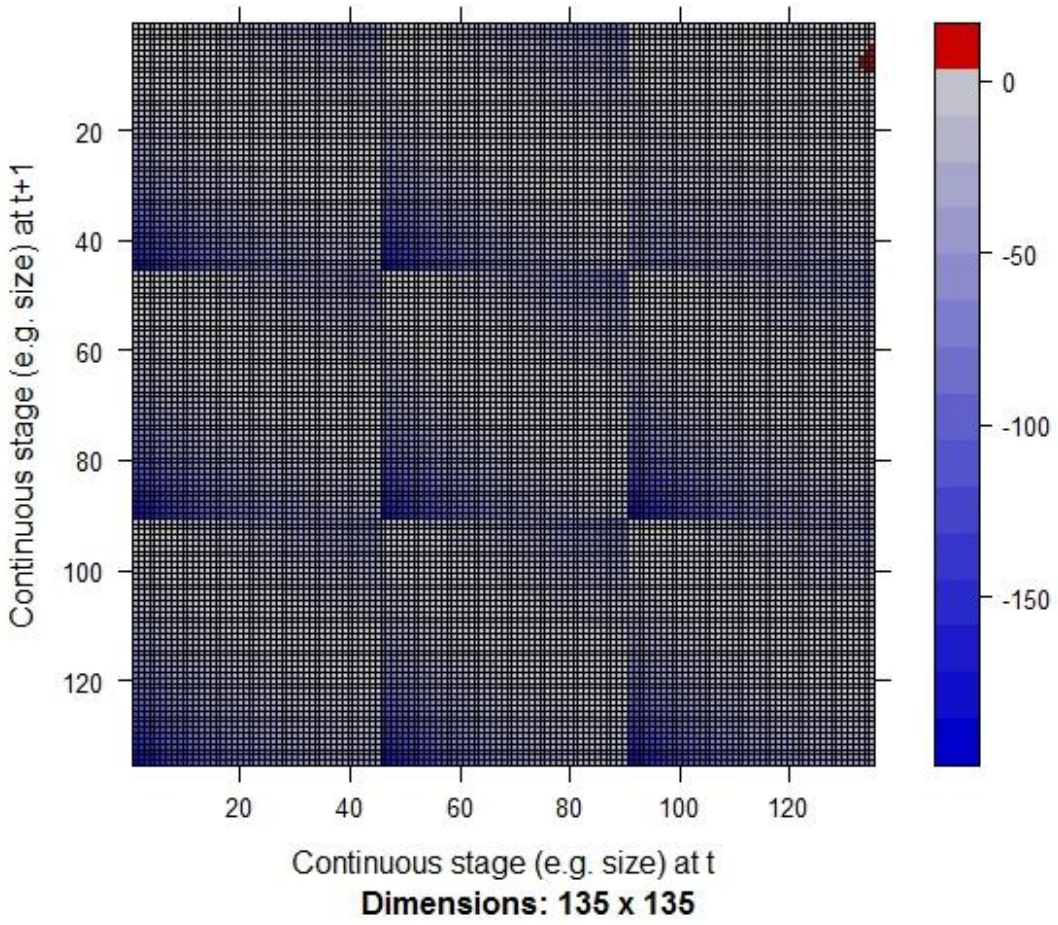

Figure 4.9. Mega-matrix for *Arisaema* size x flowering stage IPM. Matrix shown was built using data from all *Arisaema* populations. Gray colors indicate the greatest probability of moving through the state space and blue represents low probability. The red dot in the upper right submatrix indicates the addition of sexual recruits into the population.

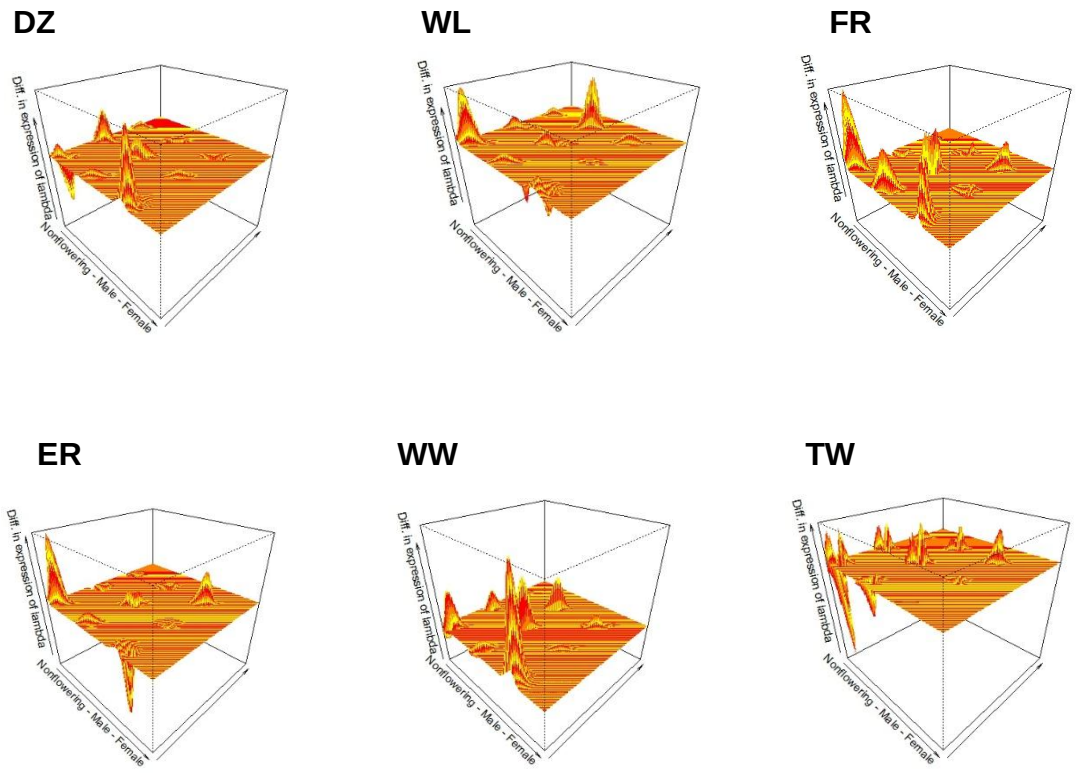

Figure 4.10. Sensitivity weighted differences of λ on the effects of life history transitions for each *Arisaema* population compared to the model built using data from all populations. Peaks in the surface plots show where a populations' mega-matrices differed from the overall *Arisaema.* Larger peaks indicate a larger effect on λ for a specific life history transition.

5.0 CONCLUSIONS

In total, the results presented in this dissertation expose novel factors that influence plant population dynamics and life history trait evolution. Specifically, my research demonstrates that chronic effects of overabundant herbivores can indirectly drive population decline and local adaptation of life history traits in an unpalatable forest herb. While the advances in the field of ecology have been substantial in recent decades, we still lack knowledge of how biotic and abiotic contexts can shape species interactions (Agrawal *et al.* 2007). Although the concept of indirect effects is well accepted (Wooton 1994), understanding the relative importance of indirect vs. direct and trophic vs. non-trophic interactions are questions of top concern in ecology (Sutherland *et al.* 2013). Likewise, the ability of indirect effects to drive evolutionary change are only recently being considered (Walsh 2013). Below I highlight the outcomes of my dissertation and discuss how they begin to fill some of these knowledge gaps.

The impacts of overabundant ungulate herbivore for palatable forest herb species can be severe and lead local extinction in the worst cases (Côté et al. 2004). Unpalatable forest herb species are thought to benefit from the release from competition and increases in relative abundance have been measured after large herbivore outbreaks in some cases (Anderson and Loucks 1979, Horsley et al. 2003, Wiegmann and Waller 2006). However, indirect metrics of population fitness such as relative abundance may not provide a complete picture of the health and stability of a population (*e.g.* Kalisz *et al.* 2014). In Chapter 2 I showed how increased levels of deer browse on a co-occurring forest herb can have cryptic indirect effects on unpalatable

plant life history traits. I found that *Arisaema* attained smaller sizes and male biased population sex-ratios in areas where deer browse was highest and that five unpalatable species, including *Arisaema*, were smaller on average in deer access plots compared to plants inside large, long-term, deer exclusion plots. Principal component analysis of several abiotic site variables further revealed a significant correlation between high deer-browse levels and poorer soil quality: drier more compacted soils. These results suggested that the activities of deer were cascading through soil pathways to indirectly affect unpalatable plant species (Heckel *et al.* 2010). This idea is gaining support as others have recently shown that unpalatable plants are smaller where the impacts of deer are high (Shelton *et al.* 2014) and as a result of changing soil quality, both abiotic and biotic (Frerker *et al.* 2013, Kardol *et al.* 2014). Results like these highlight the idea that non-trophic indirect effects can have large and far-reaching effects within communities.

Building off these observed differences in *Arisaema* life history traits quantified across a gradient of deer impacts in Chapter 2 (Heckel *et al.* 2010), in Chapter 3 I sought to determine whether the non-trophic indirect effects of deer were due to local adaptation or phenotypic plasticity in plant traits. If indirect effects of deer are causing *Arisaema* plants to reach smaller sizes then there may be fitness advantages to either growing at different rates, flowering at smaller sizes, or allocating resources differently (Stearns & Koella 1986). Using a common garden experiment I found evidence for local adaptation in two key life history traits; plants from sites that had the greatest amounts of deer browse, and therefore indirect effects, flowered as females at smaller sizes and had higher growth rates. Indirect effects are known to produce evolution of life history traits (*e.g.* Walsh & Reznick 2010, Lau 2012) yet the evolutionary changes seen are often the result of increased resources or change in trait mean mediated by a trophic interaction with a third species (reviewed in Walsh 2013). The local adaptation I show

for *Arisaema*'s threshold size for female flowering is unique as my results point to the creation of a more stressful, resource poor environment through non-trophic indirect effects as the driver of this change. The extent to which non-trophic indirect effects can generate selection on life history traits in general invites further research.

The results presented in Chapters 2 and 3 describe how unpalatable *Arisaema* plants are smaller in the field and likely adapted to flower as females at smaller sizes where the indirect effects of deer are greatest. Both plant size, through growth, and the timing of flowering underlie the vital rates that control plant population dynamics. This begs the question: do *Arisaema* populations have lower population growth rates where indirect effects of deer are highest? Chapter 4 answers this question in the affirmative with the use of integral projection models (IPMs). Understanding how population dynamics may be affected as a result of non-trophic indirect effects that drive evolutionary change in life history traits is a novel emerging subfield at the nexus of ecology and evolution (Sutherland *et al.* 2013). Using a size based IPM I found that population growth rates of my *Arisaema* study populations do decrease with increases in the indirect effects of deer. However, the unique life history of this sex-switching plant begs for more complex analyses, which could allow more detailed dissection and greater insight into the population dynamic responses of *Arisaema*. In the future, I would like to expand my size based IPM analyses to better capture the life cycle of *Arisaema* and incorporate sex-changing into the model. This expansion would help to fill in gaps about the influence of selection on sex differences in life history on population dynamics (Sutherland *et al.* 2013).

An important current focus in ecology is to better understand how species interactions can change in response to biotic and abiotic contexts (Agrawal *et al.* 2007). In this dissertation I have shown how ungulate herbivores may change the interactions between unpalatable herbs and

their abiotic surroundings. This research sheds new light on the impacts of large ungulate herbivores on forest herb communities. My results can be important to conservationists because they show how the full impacts of overabundant or irrupting herbivores may be cryptic in nature and act on members of the community that were thought to be safe from impacts.

APPENDIX A

LOCATIONS OF *ARISAEMA TRIPHYLLUM* STUDY POPULATIONS

Table A1. Locations of *Arisaema triphyllum* study populations.

Site	Symbol	Location (longitude, latitude)
Deezik Creek	■	Crawford County, Pennsylvania (80°26'W, 41°31'N)
Dibble Hill	●	Crawford County, Pennsylvania (80°02'W, 41°43'N)
Ellis Road	▲	Crawford County, Pennsylvania (80°05'W, 41°47'N)
Fox Road	◊	Crawford County, Pennsylvania (80°12'W, 41°48'N)
Tryon Weber Woods	★	Crawford County, Pennsylvania (80°21'W, 41°36'N)
Wallace Woods	○	Crawford County, Pennsylvania (80°42'W, 41°67'N)
Woodcock Lake	♦	Crawford County, Pennsylvania (80°04'W, 41°41'N)

APPENDIX B

METHODS AND RESULTS FOR DEVELOPING NON-DESTRUCTIVE BIOMASS ESTIMATION FROM ABOVE GROUND PLANT SIZE DATA FOR *ARISAEMA*

To estimate the relationship between total fresh mass and above ground size, I excavated 20-25 vegetative plants outside our permanent study plots at each natural site in 2006. For each excavated plant, I measured the center leaflet length, stem height, and stem diameter at the soil surface. I then washed the soil from the corm and roots, blotted and individually weighed each plant to obtain total fresh biomass. Using bivariate regression, I found that the stem diameter at the soil surface was the best predictor of total plant mass (Pearson's $r=0.70$, $P<0.0001$, $n=137$) and that sites did not differ in this relationship (ANCOVA stem*home site $P=0.19$).

APPENDIX C

EFFECT SIZE ANALYSIS OF DEER EXCLUSION ON UNPALATABLE PLANT SIZE FOR FIVE FOCAL SPECIES MEASURED IN PAIRED DEER ACCESS/DEER EXCLUSION PLOTS

$L = \ln(R) = \ln(\bar{X}_E) - \ln(\bar{X}_A)$ where $\bar{X}_E$ is the mean species size in deer exclusion plots and $\bar{X}_A$ is the mean species size of in deer access plots. The variance, *v*, in *L* was calculated as: $\frac{(\mathrm{SD}_E)^2}{n_E \bar{X}_E^2} + \frac{(\mathrm{SD}_A)^2}{n_A \bar{X}_A^2}$ where SD_x is the standard deviation of plant size in a treatment and n_x is the number of individual plants measured per treatment. We calculated the 95% confidence limits as $L \pm 1.96 * \sqrt{v}$ (Gurevitch and Hedges 2001). Values of *L* with confidence limits that do not overlap zero indicate a significant effect of deer exclusion on a species' mean plant size. Thus, *L* provides a measure of the effect size of deer exclusion on plant size.

We calculated an across site mean effect size for each species as $\bar{L}^* = \frac{\sum_{i=1}^{k} w_i^* L_i}{\sum_{i=1}^{k} w_i^*}$ where w_i^* is the total variance of L_i, and L_i is the mean effect size in site *i*. To determine if deer exclusion had a *general* effect on plant size across all unpalatable species measured, we calculated the grand mean effect size across all species as , $\bar{\bar{L}}^* = \frac{\sum_{i=1}^{m} \sum_{j=1}^{k_i} w_{ij}^* L_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{k_i} w_{ij}^*}$ where w_{ij}^* is the total variance in L_{ij} effect size across all *i* species in all *j* sites.

APPENDIX D

TABLE OF EFFECT SIZES FOR DEER EXCLUSION OF FIVE UNPALATABLE PLANT SPECIES IN VIRGINIA

Table D1. Deer access has significant negative effects on unpalatable plant size in paired deer exclusion vs. deer access plots near Front Royal, VA, U.S.A. The grand mean effect size, $\bar{\bar{L}}^*$, shows that individual plant size is significantly smaller for all five herbaceous unpalatable species in deer access plots compared to deer exclusion plots across all sites. Size: Diameter = stem diameter (mm) and Height = height of main stem (cm). Positive values of *L* indicate that plants in deer exclusion plots were larger than those in deer access plots. $\bar{L}^*$ represents the mean effect size for a species. Sample size (E:A) indicates the number of plants measured in the deer exclusion (E) and deer access plot (A) at each site. Bold values are significantly greater than zero. Means ± 1 standard error of the mean (s.e.m) are shown.

				Mean Size (± s.e.m.)		Effect Size	
Species	**Site**	**Sample size (E:A)**	**Size**	**Exclusion Plot**	**Access Plot**	***L***	**(95% C.L.)**
Arisaema triphyllum	CRC	32/30	Diameter	3.55±0.32	2.17±0.22	**0.49**	**0.26**
	KR	47/46	Diameter	2.32±0.14	1.67±0.11	**0.33**	**0.18**
	MA	30/30	Diameter	2.59±0.31	2.03±0.16	0.24	0.28
Mean effect *Arisaema triphyllum*						$\bar{L}^*$**=0.35**	**0.21**
Actea racemosa	CRC	30/30	Height	46.5±4.15	25.1±1.20	**0.62**	**0.20**
	KR	30/30	Height	45.3±2.72	38.9±2.58	0.15	0.18

	MA	30/30	Height	49.0±2.48	39.3±2.49	**0.22**	**0.16**

Table D1 (continued)

Mean effect *Actea racemosa*						**$\bar{L}^{\bullet}$=0.32**	**0.19**
Osmorhiza claytonii	KR	30/29	Height	35.8±2.09	29.1±2.30	**0.21**	**0.20**
	MA	24/22	Height	37.4±3.09	27.5±2.14	**0.31**	**0.22**
Mean effect *Osmorhiza claytonii*						$\bar{L}^{\bullet}$=0.25	0.25
Podophyllum peltatum	CRC	31/23	Diameter	4.58±0.26	1.37±0.14	**1.12**	**0.19**
Botrychium virginianum	CRC	30/30	Diameter	2.67±0.16	1.80±0.10	**0.39**	**0.17**
Grand mean effect size of deer exclusion on plant size across 5 species						**$\bar{\bar{L}}^{\bullet}$=0.41**	**0.11**

APPENDIX E

STATISTICAL METHODS AND RESULTS OF ANALYSIS OF INDEPENDENT ABIOTIC VARIABLES

To compare the soil moisture and leaf litter depth variables among natural sites, we used one-way ANOVA. Because the normality assumption could not be met for the light data, we used a Kruskal-Wallis test to compare site means. We used MANOVA (PROC GLM SAS Institute 2008) to test for a site effect on soil penetration resistance profiles. Among the natural sites, soil moisture levels (ANOVA $F_{5,59}$=5.1, P<0.001), leaf litter depth (ANOVA $F_{5,59}$=5.1, P<0.001), soil compaction (MANOVA: Pillai's Trace=0.19, $F_{35,2210}$=2.54, P<0.0001), and light levels reaching the forest floor (Kruskal-Wallis: df=5, P<0.001) all differed significantly.

APPENDIX F

TABLE OF MEAN ABIOTIC VARIABLES USED IN PCA

Table F1. Deer browse level on *Trillium* (% *Trillium* browsed) is the strongest predictor of the demographic metrics of unpalatable, unbrowsed *Arisaema triphyllum* across seven PA natural sites where the two species co-occur. Stepwise backward regression model was performed using % *Trillium* browsed, density of flowering *Trillium*, total *Arisaema* population density, and soil quality scores (PC1 from PCA – see methods) as predictors. Variables not listed in the table were not significant for that analysis.

Dependent Variable	**Predictors**	**Model Significance**	**Model R^2**	**Coefficient (β)**	**t-stat**	**P-value**
Reproductive plant size		**0.001**	0.98			
	% Trillium browsed			-0.12	-12.8	**0.001**
	Soil quality score (PC1)			0.12	2.4	0.16
	Flowering Trillium density			0.75	6.2	**0.009**
Population sex ratio		**0.005**	0.85			
	% Trillium browsed			1.55	5.6	**0.005**
	Soil quality score (PC1)			-1.1	-0.47	0.67
	Flowering Trillium density			3	0.73	0.51
Seed rain m^{-2}		**0.009**	0.81			
	% Trillium browsed			-0.01	-4.7	**0.009**
	Soil quality score (PC1)			-0.02	-1.4	0.24
	Flowering Trillium density			-0.01	-0.46	0.68

APPENDIX G

TABLE OF SITE SPECIFIC EFFECT SIZES USED TO EVALUATE ADAPTIVE DIVERGENCE IN COMMON GARDEN PLANTS

Table G1. Effect sizes and test statistics for fixed effects from Gaussian and binomial RM GLMMs. P-values for GLMMs with RGR as the response variable are based on t-values.

Response Variable	Fixed Effects	Estimate	Std. Err.	z value	P value
logit Reproductive Status	Intercept	-3.52	0.679	-5.184	<0.0001
	SiteWW	0.516	0.546	0.946	0.3443
	SiteWL	-0.034	0.563	-0.060	0.9518
	SiteER	0.940	0.539	1.745	0.0809
	SiteFR	0.120	0.561	0.213	0.8311
	SiteTW	0.361	0.558	0.647	0.5174
	Cmass	0.355	0.033	10.825	<0.0001
	Year	0.631	0.108	5.832	<0.0001
logit Sex	Intercept	-532.125	471.680	-1.128	0.2600
	SiteWW	1.975	0.748	2.639	0.0083
	SiteWL	0.837	0.749	1.117	0.2639
	SiteER	2.475	0.740	3.343	0.0008
	SiteFR	1.308	0.711	1.838	0.0660
	SiteTW	1.000	0.725	1.379	0.1680
	Cmass	0.361	0.053	6.834	<0.0001

Table G1 (continued)

Relative Growth Rate (RGR)	Intercept	0.652	0.166	3.933	<0.0001
	SiteWW	0.280	0.243	1.150	0.2510
	SiteWL	-0.017	0.245	-0.069	0.9453
	SiteER	0.119	0.235	0.508	0.6120
	SiteFR	0.033	0.245	0.136	0.8917
	SiteTW	0.903	0.242	3.729	0.0002
	Stagemale	0.531	0.219	2.424	0.0158
	Stagefemale	1.044	0.264	3.955	<0.0001
	Year2008	0.992	0.183	5.408	<0.0001
	Year2009	-0.923	0.248	-3.714	0.0002
	Year2010	-1.750	0.417	-4.192	<0.0001
	Year2011	-1.161	0.378	-3.068	0.0023
RGR	Intercept	1.710	0.324	5.269	0.0001
	SiteWW	0.063	0.205	0.306	0.8900
	SiteWL	-0.083	0.205	-0.406	0.8300
	SiteER	0.064	0.197	0.325	0.0020
	SiteFR	0.028	0.204	0.139	0.6900
	SiteTW	0.667	0.203	3.290	0.9400
	Transitionadvance	0.384	0.182	2.114	0.9500
	Transitionadvance.plus	0.905	0.255	3.548	0.0040
	Transitionrevert	-0.329	0.377	-0.874	0.0080
	Transitionrevert.plus	-0.910	0.665	-1.369	0.9200
	Year2008	1.079	0.154	7.028	0.0001
	Year2009	-0.617	0.210	-2.944	0.0035
	Year2010	-0.922	0.335	-2.751	0.0063
	Year2011	-0.532	0.369	-1.441	0.1504

Table G1 (continued)

Annual per Capita Cormlet Production	Intercept	-1.615	0.623	-2.592	0.0095
	SiteWW	0.577	0.307	1.880	0.0602
	SiteWL	0.824	0.299	2.750	0.0059
	SiteER	0.459	0.309	1.480	0.1382
	SiteFR	0.295	0.329	0.900	0.3689
	SiteTW	0.444	0.317	1.400	0.1614
	Cmass	-0.007	0.010	-0.710	0.4747
	Stagemale	-0.116	0.207	-0.560	0.5745
	Stagefemale	0.275	0.256	1.070	0.2828

APPENDIX H

R CODE FOR SIZE BASED INTEGRAL PROJECTION MODEL

```
### IPM Analysis for Arisaema
## December 16 2014
#clear everything just in case#
rm(list = ls(all=TRUE))

#set the working directory#
setwd("C:/Users/Christopher/Desktop/Heckel Research Projects/Demography Chapter/2014 analyses")

#load the packages needed for model fitting -- usually more than I need#
require(MASS);  require(car);
require(lme4); require(IPMpack);
require(boot);

#########################################################################
### Set up all the model parameters -- following Merow Appenix A
#########################################################################
### full parameter set that accounts for asex and sex repro
### as well as transitioning between sexes
### dormancy parameters not included at this time
#########################################################################

params=data.frame(

surv.int = NA,  ## intercept from logistic regression of survival

surv.slope= NA,  ## slope from log. regression ofsurvival

surv.slope2= NA,  ## polynomial termslope from log. regression of survival

growth.int = NA,  ##  intercept from linear regression of growth

growth.slope = NA,   ## slope from linear regression of growth

growth.slope2 = NA,   ## squared slope term from linear regression of growth

growth.sd =  NA,  ## residual sd from linear regression of growth
```

```
sex.est = NA,    ## probability a seed produced establishes and survives
## to be a three-leaved recruit (DZ=0.0321, ER=0.0218, WW = 0.00111, all other were 0 so set to WW)

seed.recruit.mean.size = NA,  ## mean sexual recruit size

seed.recruit.var.size = NA, ## standard deviation of sexual recruit size

recruit.mean.size = NA,  ## mean asexual recruit size

recruit.var.size = NA, ## standard deviation of asexual recruit size

asex.est = NA,   ## probability that an asexual recruit survives to the next time step

seed.int = NA,   ##  intercept from Poisson regression on seed number

seed.slope = NA,  ##  slope from Poisson regression on seed number

p.germ = NA,   ## probability that a seed will germinate in the spring - a constant from seed basket data

cormlet.prob.slope = NA,   ##  probability an individual produces an asex recruit

cormlet.prob.int = NA,   ##  probability an individual produces an asex recruit

cormlet.number.slope = NA,  ##  average number of asex recruits produced

cormlet.number.int = NA,  ##  average number of asex recruits produced

female.int= NA,  ## intercept of probability of female flowering

female.slope = NA   ### slope of prob. of female flowering
)

#################################################################
######## Find regressions that best describe vital rates
#################################################################
##=======================================#
##  Fit survival probability (binomial)  #
##=======================================#

# load in data to work with##
d <- read.csv(file("IPM.noNA.data.csv"), header = TRUE)  ## already log transformed
summary(d)

## creating log-transformed data frame
dff <- d
## make Year1 and surv factors
dff$Year1 <- factor(dff$Year1, levels = c("2005", "2006", "2007", "2008"))
```

```
dff$Year2 <- factor(dff$Year2, levels = c("2006", "2007", "2008", "2009"))
dff$status <- factor(dff$status, levels = c("n", "m", "f"))

#drop records with a status of dead ('ne') and dormant ('d') also 's' (only one)
dff.2 <- dff[dff$status != "ne" & dff$status!= "d" & dff$status != "s",]
summary(dff.2)

#find best fit hierarchical model
### but first up the iterations to help assure convergence
# use control = control_setting within call to glmer/lmer

control_setting <- glmerControl(optCtrl=list(maxfun=90000),
                        optimizer="bobyqa",
                        boundary.tol=1e-2,
                        check.conv.singular =.makeCC(action="ignore",tol=1e-2),
                        tolPwrss=1e-2)

surv.fit <- glmer(surv ~ size + I(size^2)+ (1+size|Site/Year1) +(1|ID), family=binomial, data=dff.2)
Anova(surv.fit)
coef(surv.fit)

surv.fit2 <- glmer(surv ~ size + I(size^2)+ (1+I(size^2)|Site/Year1) +(1|ID), family=binomial, data=dff.2)
Anova(surv.fit2)
coef(surv.fit2)

surv.mod <- glmer(surv ~ size*Site + I(size^2)+ Site + Year1 +(1|ID), family=binomial, data=dff.2)
Anova(surv.mod)
##=======================================#
##  Fit growth (Guassian distributed)  #
##=======================================#

growth.reg <- lmer(sizeNext ~ size +I(size^2) + (1 + size|Site/Year1)+ (1|ID), data=dff.2)
Anova(growth.reg)
coef(growth.reg)

growth.reg2 <- lmer(sizeNext ~ size +I(size^2) + (1 + I(size^2)|Site/Year1)+ (1|ID), data=dff.2)
Anova(growth.reg2)
coef(growth.reg2)

growth.mod <- glmer(sizeNext ~ size*Site + I(size^2)+ Year1 +(1|ID), data=dff.2)
Anova(growth.mod)


##============================================#
##  Fit female flowering (logistic regression)  #
##============================================#

female.reg <- glmer(femNext ~ size + (1|ID)+ (1+size|Year1/Site), family=binomial, data=dff.2)
```

```
summary(female.reg)
Anova(female.reg)
coef(female.reg)

female.reg2 <- glmer(femNext ~ size + (1|ID)+ (1+size|Site/Year1), family=binomial, data=dff.2)
summary(female.reg2)
Anova(female.reg2)
coef(female.reg2)

fem.mod <- glmer(femNext ~ size * Site + Year1 + (1|ID), family=binomial, data=dff.2)
Anova(fem.mod)

##============================================#
##  Fit seed production (poisson regression)  #
##============================================#

# load in data to work with##
seeds <- read.csv(file("Jack_seeds.csv"), header = TRUE)
## log transform the data
seeds$Stem <- log(seeds$Stem)
summary(seeds)

seed.reg5 <- glmer(Seeds ~ Stem + (1 + Stem|Site) + (1|Tag), family="poisson", na.action=na.omit,
data=seeds)
Anova(seed.reg5)
summary(seed.reg5)
coef(seed.reg5)

seed.mod <- glm(Seeds ~ Stem * Site + Year , family="poisson", na.action=na.omit, data=seeds)
Anova(seed.mod)
##=========================================================#
##  Cormlet production (logistic and poisson regressions)  #
##=========================================================#
# load in data to work with##
corms <- read.csv(file("field_cormlet.csv"), header = TRUE)
## log transform the data
corms$Stem <- log(corms$Stem)
summary(corms)
corms$Year <- factor(corms$Year, c("2008", "2009"))
## probability of producing cormlets (logistic regression)

cprob.reg <- glmer(Pcorm ~ Stem + (1+Stem|Site/Year) + (1|ID), family=binomial, data=corms)
Anova(cprob.reg)
coef(cprob.reg)

cprob.reg2 <- glmer(Pcorm ~ Stem + (1+Stem|Year/Site) + (1|ID), family=binomial, data=corms)
Anova(cprob.reg2)
coef(cprob.reg2)$`Year:Site`
```

```
corm.prob.mod <- glm(Pcorm ~ Stem * Site + Year + (1|ID), family=binomial, data=corms)
Anova(corm.prob.mod)
## poisson regression of number of cormlets produced

cnum.reg <- glmer(Cormlets ~ Stem + (1+Stem|Site/Year), family=poisson, data=corms)
Anova(cnum.reg)
coef(cnum.reg)$`Year:Site`
coef(cnum.reg)$`Site`

corm.num.mod <- glm(Cormlets ~ Stem * Site + Year, family=poisson, data=corms)
Anova(corm.num.mod)
##=====================================================##
#  Fit recruit distribution - normal truncated at zero
##=====================================================##
# load in data to work with##
# distribution will be same for all sites#
# seedling and cormlets distributions treated as same - may not be
cormlets <- read.csv(file("Jack_cormsize.csv"), header = TRUE)
summary(cormlets)
asex.recruits <- cormlets
asex.recruits <- subset(cormlets, Stem<=1.5) # not putting an upper limit on cormlet size
#seedlings in field are less than 1mm so upper bound of 2 is generous
## log transform the data
asex.recruits$Stem <- log(asex.recruits$Stem)

lik<-function(p){
        lik<-sum(log(dnorm(asex.recruits$Stem,p[1],p[2])/(1-pnorm(0,p[1],p[2]))))
return(-lik)
}
tmp<-optim(c(1,1),lik)
recruit.mean.size<-tmp$par[1]
recruit.var.size<-tmp$par[2]^2

### graph the size distribution of asex recruits
win.graph(); par(bty="l")
hist(asex.recruits$Stem,col="grey",ylim=c(0,50), xlim=c(-2,3), xlab="Asex.Recruits size (log Stem
(mm))",main="pooled sites")

s<-seq(-3,3,length=100)
d<-dnorm(s,tmp$par[1],tmp$par[2])/(1-pnorm(0,tmp$par[1],tmp$par[2]))
diff<-s[2]-s[1]
lines(s,d*length(asex.recruits$Stem)/(2*sum(d*diff)))

# overplot normal distribution with same mean and variance
d<-dnorm(s,mean(asex.recruits$Stem),sd(asex.recruits$Stem))
lines(s,d*length(asex.recruits$Stem)/(2*sum(d*diff)),col="blue")
```

```
## make seed recruits size dist
seed.recruits <- subset(cormlets, Stem<=1.1) # not putting an upper limit on cormlet size
#seedlings in field are less than 1mm so upper bound of 2 is generous
## log transform the data
seed.recruits$Stem <- log(seed.recruits$Stem)

lik2<-function(p){
        lik2<-sum(log(dnorm(seed.recruits$Stem,p[1],p[2])/(1-pnorm(0,p[1],p[2]))))
return(-lik2)
}
tmp2<-optim(c(1,1),lik2)
seed.recruit.mean.size<-tmp2$par[1]
seed.recruit.var.size<-tmp2$par[2]^2

## graph size dist. of sex recruits
win.graph(); par(bty="l")
hist(seed.recruits$Stem,col="grey",ylim=c(0,40),xlim=c(-1,1), xlab="Recruits size (log Stem
(mm))",main="pooled sites")

s<-seq(-1,1,length=100)
d<-dnorm(s,tmp2$par[1],tmp2$par[2])/(1-pnorm(0,tmp2$par[1],tmp2$par[2]))
diff<-s[2]-s[1]
lines(s,d*length(seed.recruits$Stem)/(2*sum(d*diff)))

# overplot normal distribution with same mean and variance
d<-dnorm(s,mean(seed.recruits$Stem),sd(seed.recruits$Stem))
lines(s,d*length(seed.recruits$Stem)/(2*sum(d*diff)),col="blue")

##=================================================##
#    Probability of seedling establishment
##=================================================##
# load in data to work with##
seedling <- read.csv(file("Jack_seedlings.csv"), header = TRUE)
summary(seedling)

# sort data for first germinatation time June 2008
seedling2 <- subset(seedling, Year==2008 & Month=="June", select=c(Seeds,Seedlings))
summary(seedling2)
p.est.June <- (sum(seedling2$Seedlings))/(sum(seedling2$Seeds))
p.est <- p.est.June
p.est
# sort data for first germinatation time July 2008
seedling3 <- subset(seedling, Year==2008 & Month=="July", select=c(Seeds,Seedlings))
summary(seedling3)
p.est.July <- (sum(seedling3$Seedlings))/(sum(seedling3$Seeds))
p.est.July
sex.germ <- p.est.July
```

```
## sort data for two year survival
#germination occured (first) in 2008, survival not assessed in 2009
# but survival was assessed again in 2010
# sort data for probability of emerged seedlings (June 2008) surviving two years
p.sdlg.survive <- (sum(seedling$Seedlings[seedling$Year==2010]))/(sum(seedling3$Seeds))
sex.est <-p.sdlg.survive
sex.est


#####################################################
### Build functions that describe life history
#####################################################

# 1.0 survival probability function
s.x=function(x,params) {
u=exp(params$surv.int+params$surv.slope*x+params$surv.slope2*x)
return(u/(1+u))
}

# 2.0 growth function
g.yx=function(y,x,params) {
dnorm(y,mean=params$growth.int + params$growth.slope*x + params$growth.slope2*x,
sd=params$growth.sd)
}

## 3.0 Flowering probability function
p.flower.x=function(x,params) {
u=exp(params$flower.int+params$flower.slope*x)
return(u/(1+u))
}

## 3.1 Female Flowering probability function
p.female.x=function(x,params) {
u=exp(params$female.int+params$female.slope*x)
return(u/(1+u))
}

#3.2  sexual reproduction function
fxy<-function(y,x,params) {
        nkids<-params$sex.est*exp(params$seed.int+params$seed.slope*x);
        kidsize.mean<- params$seed.recruit.mean.size;
        kidsize.var<- params$seed.recruit.var.size;
        fac1<-sqrt(2*pi)*sqrt(kidsize.var);
        fac2<-((y-kidsize.mean)^2)/(2*kidsize.var);
        f<-p.female.x(x,params)*nkids*exp(-fac2)/fac1;
        return(f);
}
```

```
## DON'T USE THIS ONE
# 3.2 sexual reproduction function
#fs.yx=function(x,y,params) {
#expected number of recruits after seedling establishment
#nkids<-params$sex.est*exp(params$seed.int+params$seed.slope*x);
#kidsize.mean<- params$recruit.mean.size;
#kidsize.var<- params$recruit.var.size;
#temp<-dnorm(y,kidsize.mean,sqrt(kidsize.var))/(1-pnorm(0,kidsize.mean,sqrt(kidsize.var)));
# surviving to reproduce, flower, and be female times offspring # and size
#f<-s.x(x,params) * p.flower.x(x,params)* p.female.x(x,params)*nkids*temp;
#return(f);
#}

## 4.0 Cormlet Production Probability function
p.asex.x=function(x,params) {
u=exp(params$cormlet.prob.int+params$cormlet.prob.slope*x)
return(u/(1+u))
}

# 4.1 asexual reproduction function
fa.yx=function(y,x,params) {
p.asex.x(x,params)*
params$asex.est*
dnorm(y,mean=params$recruit.mean.size,sd=params$recruit.var.size)*
exp(params$cormlet.number.int+params$cormlet.number.slope*x)
}

#### BUILD THE KERNELS
## establish mesh points and boundary sizes
min.size=.9*min(c(dff$size,dff$sizeNext),na.rm=T)
max.size=1.1*max(c(dff$size,dff$sizeNext),na.rm=T)
n=100 # number of cells in the matrix
b=min.size+c(0:n)*(max.size-min.size)/n # boundary points
y=0.5*(b[1:n]+b[2:(n+1)]) # mesh points
h=y[2]-y[1] # step size

##============================##
### Collect Parameters
##============================##
### Deezik Creek Parameters
## DZ params 2005
## Survival
params$surv.int=coef(surv.fit)$'Year1:Site'[1,1]
params$surv.slope=coef(surv.fit)$'Year1:Site'[1,2]
params$surv.slope2=coef(surv.fit2)$'Year1:Site'[1,3]

#Growth
params$growth.int=coef(growth.reg)$'Year1:Site'[1,1]
```

```
params$growth.slope=coef(growth.reg)$'Year1:Site'[1,2]
params$growth.slope2=coef(growth.reg2)$'Year1:Site'[1,3]
params$growth.sd=sd(resid(growth.reg))


## Female Flowering
params$female.int=coef(female.reg)$'Site:Year1'[1,1]
params$female.slope=coef(female.reg)$'Site:Year1'[1,2]


## Seed Production
params$seed.int=coef(seed.reg5)$'Site'[1,1]
params$seed.slope=coef(seed.reg5)$'Site'[1,2]

## Cormlet Probability (of a plant making one)
params$cormlet.prob.int=coef(cprob.reg)$'Site'[1,1]
params$cormlet.prob.slope=coef(cprob.reg)$'Site'[1,2]

## Cormlet Production
params$cormlet.number.int=coef(cnum.reg)$'Site'[1,1]
params$cormlet.number.slope=coef(cnum.reg)$'Site'[1,2]

## offspring sizes - sex and asex rectruits the same right now
params$recruit.mean.size <- recruit.mean.size
params$recruit.var.size <- recruit.var.size
params$seed.recruit.mean.size <- seed.recruit.mean.size
params$seed.recruit.var.size <- seed.recruit.var.size

## constants
params$asex.est = 0.20
params$sex.est <- 0.0321


## create IPM matrices

G=h*outer(y,y,g.yx,params=params) # growth matrix

S=s.x(y,params=params) # survival matrix

Fs=h*outer(y,y,fxy,params=params) # sexual reproduction matrix
Fa=h*outer(y,y,fa.yx,params=params) # asexual reproduction matrix
F1=Fs + Fa  # total recruit/fecundity matrix

P1=G # placeholder; redefine P on the next line
for(i in 1:n) P1[,i]=G[,i]*S[i] # growth/survival matrix

DZ05=P1+t(F1) # full matrix
```

```
## BASIC ANALYSIS
## find lambda
(lam <- Re(eigen(DZ05)$values[1]))

## find Net reproductive rate (R0)
(R0 <- R0Calc(P1, F1))

## calculate mean generation time (T)
(T <- log(R0)/log(lam))

DZ05.IPM.results <- cbind(lam,R0,T)
print(DZ05.IPM.results)

## DZ params 2006
## Survival
params$surv.int=coef(surv.fit)$'Year1:Site'[6,1]
params$surv.slope=coef(surv.fit)$'Year1:Site'[6,2]
params$surv.slope2=coef(surv.fit2)$'Year1:Site'[6,3]

#Growth
params$growth.int=coef(growth.reg)$'Year1:Site'[6,1]
params$growth.slope=coef(growth.reg)$'Year1:Site'[6,2]
params$growth.slope2=coef(growth.reg2)$'Year1:Site'[6,3]
params$growth.sd=sd(resid(growth.reg))


## Female Flowering
params$female.int=coef(female.reg)$'Site:Year1'[2,1]
params$female.slope=coef(female.reg)$'Site:Year1'[2,2]


## Seed Production
params$seed.int=coef(seed.reg5)$'Site'[1,1]
params$seed.slope=coef(seed.reg5)$'Site'[1,2]

## Cormlet Probability (of a plant making one)
params$cormlet.prob.int=coef(cprob.reg)$'Site'[1,1]
params$cormlet.prob.slope=coef(cprob.reg)$'Site'[1,2]

## Cormlet Production
params$cormlet.number.int=coef(cnum.reg)$'Site'[1,1]
params$cormlet.number.slope=coef(cnum.reg)$'Site'[1,2]

## offspring sizes - sex and asex rectruits the same right now
params$recruit.mean.size <- recruit.mean.size
params$recruit.var.size <- recruit.var.size
params$seed.recruit.mean.size <- seed.recruit.mean.size
params$seed.recruit.var.size <- seed.recruit.var.size
```

```
## constants
params$asex.est = 0.20
params$sex.est <- 0.0321


## create IPM matrices

G=h*outer(y,y,g.yx,params=params) # growth matrix

S=s.x(y,params=params) # survival matrix

Fs=h*outer(y,y,fxy,params=params) # sexual reproduction matrix
Fa=h*outer(y,y,fa.yx,params=params) # asexual reproduction matrix
F1=Fs + Fa  # total recruit/fecundity matrix

P1=G # placeholder; redefine P on the next line
for(i in 1:n) P1[,i]=G[,i]*S[i] # growth/survival matrix

DZ06=P1+t(F1) # full matrix

## BASIC ANALYSIS
## find lambda
(lam <- Re(eigen(DZ06)$values[1]))

## find Net reproductive rate (R0)
(R0 <- R0Calc(P1, F1))

## calculate mean generation time (T)
(T <- log(R0)/log(lam))

DZ06.IPM.results <- cbind(lam,R0,T)
print(DZ06.IPM.results)

###  REPEAT FOR ALL POPULATIONS IN ALL POSSIBLE TRANSISTIONS

### PUT ALL RESULTS IN ONE FILE
IPM.output <- cbind(DZ05.IPM.results, DZ06.IPM.results,DZ07.IPM.results,DZ08.IPM.results,
WL05.IPM.results, WL06.IPM.results,WL07.IPM.results,WL08.IPM.results,
FR05.IPM.results,FR06.IPM.results,
ER05.IPM.results,ER06.IPM.results,ER07.IPM.results,ER08.IPM.results,
WW05.IPM.results,WW06.IPM.results,WW07.IPM.results,WW08.IPM.results,
TW06.IPM.results,TW07.IPM.results,TW08.IPM.results,
DZ.IPM.results,WL.IPM.results,FR.IPM.results,ER.IPM.results,WW.IPM.results,TW.IPM.results)
print(IPM.output)
write.csv(IPM.output, file="Dec15.sizeIPM.csv")

##FIND ELASTICITIES AND STABLE STAGE DISTRIBUTIONS AND GRAPH
```

```
w.eigen <- Re(eigen(FR)$vectors[,1])
stable.dist <- w.eigen/sum(w.eigen)
v.eigen <- Re(eigen(t(FR))$vectors[,1])
repro.val <- v.eigen/v.eigen[1]

v.dot.w=sum(stable.dist*repro.val)*h
sens=outer(repro.val,stable.dist)/v.dot.w
elas=matrix(as.vector(sens)*as.vector(FR)/lam,nrow=n)

library(fields)
par(mfrow=c(2,3),mar=c(4,5,2,2))
image.plot(y,y,(FR^(1/5)), xlab="Size (t)",ylab="Size (t+1)",
col=topo.colors(100), main="IPM matrix")
contour(y,y,(FR^(1/5)), add = TRUE, drawlabels = TRUE)
plot(y,stable.dist,xlab="Size",type="l",main="Stable size distribution")
plot(y,repro.val,xlab="Size",type="l",main="Reproductive values")
image.plot(y,y,(elas),xlab="Size (t)",ylab="Size (t+1)",main="Elasticity")
image.plot(y,y,(sens),xlab="Size (t)",ylab="Size (t+1)", main="Sensitivity")

## Plot the survival-growth matrix
image.plot(y,y,t(DZ), xlab="Size (t)",ylab="Size (t+1)",
col=topo.colors(100), main="Survival-Growth matrix")
contour(y,y,t(DZ), add = TRUE, drawlabels = TRUE)

## Plot the fecundity matrix
image.plot(y,y,t(F1), xlab="Size (t)",ylab="Size (t+1)",
col=topo.colors(100), main="Fecundity matrix")
contour(y,y,t(F1), add = TRUE, drawlabels = TRUE)

#=========================================================================#
#  Bootstrap lambda, R0 and generation time (see Appendix S4 of Kuss et al.)
#=========================================================================#
### function to extract parameters from bootMER
mySumm <- function(.) {
c(beta=fixef(.),sigma=sigma(.))
}

n.boot=10

dem.stats=array(NA, dim=c(n.boot,27))
#demog.stats <- matrix(NA, ncol=4, nrow=n.boot)

for(b.samp in 1:n.boot){

## set up bootstrap parameters
params=data.frame(
```

```
surv.int = NA,  ## intercept from logistic regression of survival

surv.slope= NA,  ## slope from log. regression ofsurvival

growth.int = NA,  ##  intercept from linear regression of growth

growth.slope = NA,   ## slope from linear regression of growth

growth.slope2 = NA,   ## squared slope term from linear regression of growth

growth.sd =  NA,  ## residual sd from linear regression of growth

sex.est = NA,    ## probability a seed produced establishes and survives
## to be a three-leaved recruit (DZ=0.0321, ER=0.0218, WW = 0.00111, all other were 0 so set to WW)

recruit.mean.size = NA,  ## mean asexual recruit size

recruit.var.size = NA, ## standard deviation of asexual recruit size

seed.recruit.mean.size = NA,  ## mean asexual recruit size

seed.recruit.var.size = NA, ## standard deviation of asexual recruit size

asex.est = NA,   ## probability that an asexual recruit survives to the next time step

seed.int = NA,   ##  intercept from Poisson regression on seed number

seed.slope = NA,  ##  slope from Poisson regression on seed number

cormlet.prob.slope = NA,   ##  probability an individual produces an asex recruit

cormlet.prob.int = NA,   ##  probability an individual produces an asex recruit

cormlet.number.slope = NA,  ##  average number of asex recruits produced

cormlet.number.int = NA,  ##  average number of asex recruits produced

female.int= NA,  ## intercept of probability of female flowering

female.slope = NA   ### slope of prob. of female flowering
)

### sample data to generate regressions
#growth
## set up resample data frame
#sample.boot <- dff.2[sample(1:nrow(dff.2)-1,replace=TRUE),]

## fit model and generate parameter values
```

```
growth.reg <- lmer(sizeNext ~ size +I(size^2) + (1 + size|Site/Year1)+ (1|ID), data=dff.2)

growth <- bootMer(growth.reg, mySumm, nsim=1, type="parametric")
#growth$t0

growth.reg2 <- lmer(sizeNext ~ size +I(size^2) + (1 + I(size^2)|Site/Year1)+ (1|ID), data=dff.2)
growth2 <- bootMer(growth.reg2, mySumm, nsim=1, type="parametric")
#growth2$t0

## survival
## set up resample data frame
#sample.boot2 <- dff.2[sample(1:nrow(dff.2)-1,replace=TRUE),]

## fit survival model and generate parameter values
surv.fit <- glmer(surv ~ size + I(size^2)+ (1+size|Site/Year1) +(1|ID), family=binomial, data=dff.2)
survival <- bootMer(surv.fit, mySumm, nsim =1, type="parametric")

surv.fit2 <- glmer(surv ~ size + I(size^2)+ (1+I(size^2)|Site/Year1) +(1|ID), family=binomial, data=dff.2)
survival2 <- bootMer(surv.fit2, mySumm, nsim =1, type="parametric")


## female flowering
## set up resample data frame
#sample.boot3 <- dff.4[sample(1:nrow(dff.4)-1,replace=T),]

## fit female flowering model and generate parameter values
female.reg <- glmer(femNext ~ size + (1|ID)+ (1+size|Year1/Site), family=binomial, data=dff.2)
female <- bootMer(female.reg, mySumm, nsim=1, type="parametric")

female.reg2 <- glmer(femNext ~ size + (1|ID)+ (1+size|Site/Year1), family=binomial, data=dff.2)
female2 <- bootMer(female.reg2, mySumm, nsim=1, type="parametric")


## seed production
## set up resample data frame
sample.boot4 <- seeds[sample(1:nrow(seeds)-1,replace=TRUE),]

## fit seed production and generate parameter values
seed.reg5 <- glmer(Seeds ~ Stem + (1 + Stem|Site) + (1|Tag),family="poisson", na.action=na.omit,
data=sample.boot4)
#seeds <- bootMer(seed.reg5, mySumm, nsim=1, type="parametric")
## cormlet production and probability distribution
## set up resample data frame
#sample.boot5 <- corms[sample(1:nrow(corms)-1,replace=TRUE),]

## fit survival and production models and generate parameter values
cprob.reg <- glmer(Pcorm ~ Stem + (1+Stem|Site/Year) + (1|ID), family=binomial, data=corms)
corm.prob <- bootMer(cprob.reg, mySumm, nsim=1,type="parametric")
```

```
## poisson regression of number of cormlets produced
cnum.reg <- glmer(Cormlets ~ Stem + (1+Stem|Site/Year), family=poisson, data=corms)
corm.number <- bootMer(cnum.reg, mySumm, nsim=1,type="parametric")

### asex recruit sizes
## set up resample data frame
asex.recruit.boot <- asex.recruits[sample(1:nrow(asex.recruits),replace=TRUE),]

lik<-function(p){
        lik<-sum(log(dnorm(asex.recruit.boot$Stem,p[1],p[2])/(1-pnorm(0,p[1],p[2]))))
return(-lik)
}
tmp<-optim(c(1,1),lik)
recruit.mean.size<-tmp$par[1]
recruit.var.size<-tmp$par[2]^2

### seed recruit sizes
## set up resample data frame
seed.recruit.boot <- seed.recruits[sample(1:nrow(seed.recruits),replace=TRUE),]

lik2<-function(p){
        lik2<-sum(log(dnorm(seed.recruit.boot$Stem,p[1],p[2])/(1-pnorm(0,p[1],p[2]))))
return(-lik2)
}
tmp2<-optim(c(1,1),lik2)
seed.recruit.mean.size<-tmp2$par[1]
seed.recruit.var.size<-tmp2$par[2]^2

#####################################################
### Build functions that describe life history
#####################################################
# 1.0 survival probability function
s.x=function(x,params) {
u=exp(params$surv.int+params$surv.slope*x+params$surv.slope2*x)
return(u/(1+u))
}

# 2.0 growth function
g.yx=function(y,x,params) {
dnorm(y,mean=params$growth.int + params$growth.slope*x + params$growth.slope2*x,
sd=params$growth.sd)
}

## 3.0 Flowering probability function
p.flower.x=function(x,params) {
u=exp(params$flower.int+params$flower.slope*x)
return(u/(1+u))
```

```
}

## 3.1 Female Flowering probability function
p.female.x=function(x,params) {
u=exp(params$female.int+params$female.slope*x)
return(u/(1+u))
}

#3.2  sexual reproduction function
fxy<-function(y,x,params) {
        nkids<-params$sex.est*exp(params$seed.int+params$seed.slope*x);
        kidsize.mean<- params$seed.recruit.mean.size;
        kidsize.var<- params$seed.recruit.var.size;
        fac1<-sqrt(2*pi)*sqrt(kidsize.var);
        fac2<-((y-kidsize.mean)^2)/(2*kidsize.var);
        f<-p.female.x(x,params)*nkids*exp(-fac2)/fac1;
        return(f);
}

## 4.0 Cormlet Production Probability function
p.asex.x=function(x,params) {
u=exp(params$cormlet.prob.int+params$cormlet.prob.slope*x)
return(u/(1+u))
}

# 4.1 asexual reproduction function
fa.yx=function(y,x,params) {
p.asex.x(x,params)*
params$asex.est*
dnorm(y,mean=params$recruit.mean.size,sd=params$recruit.var.size)*
exp(params$cormlet.number.int+params$cormlet.number.slope*x)
}

#### BUILD THE KERNELS
## establish mesh points and boundary sizes
min.size=.9*min(c(dff$size,dff$sizeNext),na.rm=T)
max.size=1.1*max(c(dff$size,dff$sizeNext),na.rm=T)
n=100 # number of cells in the matrix
b=min.size+c(0:n)*(max.size-min.size)/n # boundary points
y=0.5*(b[1:n]+b[2:(n+1)]) # mesh points
h=y[2]-y[1] # step size

##============================##
### Collect Parameters
##============================##
### Deezik Creek Parameters
## DZ params 2005
## Survival
```

```
params$surv.int=coef(surv.fit)$'Year1:Site'[1,1]
params$surv.slope=coef(surv.fit)$'Year1:Site'[1,2]
params$surv.slope2=coef(surv.fit2)$'Year1:Site'[1,3]

#Growth
params$growth.int=coef(growth.reg)$'Year1:Site'[1,1]
params$growth.slope=coef(growth.reg)$'Year1:Site'[1,2]
params$growth.slope2=coef(growth.reg2)$'Year1:Site'[1,3]
params$growth.sd=sd(resid(growth.reg))


## Female Flowering
params$female.int=coef(female.reg)$'Site:Year1'[1,1]
params$female.slope=coef(female.reg)$'Site:Year1'[1,2]


## Seed Production
params$seed.int=coef(seed.reg5)$'Site'[1,1]
params$seed.slope=coef(seed.reg5)$'Site'[1,2]

## Cormlet Probability (of a plant making one)
params$cormlet.prob.int=coef(cprob.reg)$'Site'[1,1]
params$cormlet.prob.slope=coef(cprob.reg)$'Site'[1,2]

## Cormlet Production
params$cormlet.number.int=coef(cnum.reg)$'Site'[1,1]
params$cormlet.number.slope=coef(cnum.reg)$'Site'[1,2]

## offspring sizes - sex and asex rectruits the same right now
params$recruit.mean.size <- recruit.mean.size
params$recruit.var.size <- recruit.var.size
params$seed.recruit.mean.size <- seed.recruit.mean.size
params$seed.recruit.var.size <- seed.recruit.var.size

## constants
params$asex.est = 0.20
params$sex.est <- 0.0321


## create IPM matrices

G=h*outer(y,y,g.yx,params=params) # growth matrix

S=s.x(y,params=params) # survival matrix

Fs=h*outer(y,y,fxy,params=params) # sexual reproduction matrix
Fa=h*outer(y,y,fa.yx,params=params) # asexual reproduction matrix
F1=Fs + Fa  # total recruit/fecundity matrix
```

```
P1=G # placeholder; redefine P on the next line
for(i in 1:n) P1[,i]=G[,i]*S[i] # growth/survival matrix

DZ05=P1+t(F1) # full matrix

## BASIC ANALYSIS
## find lambda
(lam <- Re(eigen(DZ05)$values[1]))

DZ05.IPM.results <- lam
print(DZ05.IPM.results)

#### REPEAT FOR ALL POPULATIONS IN ALL POSSIBLE TRANSITIONS

boot.results <- cbind(DZ05.IPM.results, DZ06.IPM.results,DZ07.IPM.results,DZ08.IPM.results,
WL05.IPM.results, WL06.IPM.results,WL07.IPM.results,WL08.IPM.results,
FR05.IPM.results,FR06.IPM.results,
ER05.IPM.results,ER06.IPM.results,ER07.IPM.results,ER08.IPM.results,
WW05.IPM.results,WW06.IPM.results,WW07.IPM.results,WW08.IPM.results,
TW06.IPM.results,TW07.IPM.results,TW08.IPM.results,
DZ.IPM.results,WL.IPM.results,FR.IPM.results,ER.IPM.results,WW.IPM.results,TW.IPM.results)
dem.stats[b.samp,] <- boot.results
}
## PUT ALL BOOTSTRAP RESULTS IN ONE CSV FILE
write.csv(dem.stats, file="Bootstrap.Dec15B.csv")

###=====================================================###
###  BUILDING SIZE X FLOWERING STAGE IPM
###=====================================================###
# load in data to work with##
d <- read.csv(file("IPM.noNA.5IPMpack.data.csv"), header = TRUE)
summary(d)
dff<- d

d2 <- read.csv(file("IPM.noNA.4IPMpack.data.csv"), header = TRUE)
summary(d2)
dff2<- d2


g <- growthModelComp(dff, makePlot = TRUE, legendPos = "bottomright",
          mainTitle = "Growth")

gr1 <- makeGrowthObj(dataf = dff,
               Formula=sizeNext~size:covariate+size2,
               regType="constantVar",
               Family="gaussian")
picGrow(dff,gr1)
```

```
gr1List=sampleVitalRateObj(gr1,nSamp=15)


survModelComp(dataf = dff, makePlot = TRUE, legendPos = "bottomright",
          mainTitle = "Survival")

sv1 <- makeSurvObj(dff, Formula = surv~size2 + size:covariate)
picSurv(dff,sv1)
sv1List=sampleVitalRateObj(sv1,nSamp=15)

env1 <- makeEnvObj(dff2)
env1


Pmatrix <- makeCompoundPmatrix(nBigMatrix = 45, minSize = 0.1,
                        maxSize = 25,
                        envMatrix = env1,
                        growObj = gr1,
                        survObj = sv1,
                        correction = "constant")

image(as(Pmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)
library(fields)

image.plot(t(Pmatrix[nrow(Pmatrix):1,]),
          col=topo.colors(36),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(t(Pmatrix[nrow(Pmatrix):1,]),add=TRUE)


fv1 <- makeFecObj(dff, Formula = fec3~size, offspringSplitter=data.frame(continuous=1.0),
             Family = "poisson")

fv1List=sampleVitalRateObj(fv1,nSamp=15, nDiscreteOffspringTransitions =100,
nOffspring=100)

n.age.classes <- max(dff2$covariate,na.rm=TRUE)
ageMat1 <- new("envMatrix", nEnvClass = n.age.classes)
ageMat1@.Data <- matrix(0,n.age.classes,n.age.classes)
ageMat1@.Data[1,3:n.age.classes] <- 1
ageMat1


Fmatrix <- makeCompFmatrix(nBigMatrix = 45, minSize = 0.1,
                        maxSize = 25,
```

```
                envMatrix = ageMat1,
                                    fecObj = fv1,
                correction = "constant")


image(as(Fmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)

image.plot(t(Fmatrix[nrow(Fmatrix):1,]),
          col=topo.colors(36),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(t(Fmatrix[nrow(Fmatrix):1,]),add=TRUE)


IPM.base <- Pmatrix+Fmatrix
image.plot(as(log(IPM.base),'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(IPM.base@meshpoints, IPM.base@meshpoints, t(log(IPM.base)), add=TRUE)


### ANALYZE the MEGAMATRIX  (OVERALL MATRIX for ALL ARISEAMA POPS)
lambda.base <- Re(eigen(IPM.base)$value[1])
lambda.base

sensitivity <- sens(IPM.base)
elasticity <- elas(IPM.base)

##=============================================================================
##subset for DZ
DZ <- subset(dff, dff$Site=="DZ")
DZ2 <- subset(dff2, dff2$Site=="DZ")


growthModelComp(dataf = DZ, makePlot = TRUE, legendPos = "bottomright",
           mainTitle = "Growth")

gr1 <- makeGrowthObj(dataf = DZ,
               Formula=sizeNext~size:covariate+size2,
               regType="constantVar",
               Family="gaussian")
DZgrowth <- picGrow(DZ,gr1)

survModelComp(dataf = DZ, makePlot = TRUE, legendPos = "bottomright",
          mainTitle = "Survival")
```

```
sv1 <- makeSurvObj(DZ, Formula = surv~size:covariate+size2)
DZsurv <- picSurv(DZ,sv1)

env1 <- makeEnvObj(DZ2)
env1


Pmatrix <- makeCompoundPmatrix(nBigMatrix = 45, minSize = 0.1,
                        maxSize = 25,
                        envMatrix = env1,
                        growObj = gr1,
                        survObj = sv1,
                        correction = "constant")

image(as(Pmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


fv1 <- makeFecObj(DZ, Formula = fec3~size,
             Family = "poisson")

n.age.classes <- max(DZ2$covariate,na.rm=TRUE)
ageMat1 <- new("envMatrix", nEnvClass = n.age.classes)
ageMat1@.Data <- matrix(0,n.age.classes,n.age.classes)
ageMat1@.Data[1,3:n.age.classes] <- 1
ageMat1
Fmatrix <- makeCompFmatrix(nBigMatrix = 45, minSize = 0.1,
                        maxSize = 25,
                        envMatrix = ageMat1,
                        fecObj = fv1,
                        correction = "constant")

image(as(Fmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


IPM.dz <- Pmatrix+Fmatrix
image(as(log(IPM.dz),'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(IPM.dz@meshpoints, IPM.dz@meshpoints, t(log(IPM.dz)), add=TRUE)

### ANALYZE the MEGAMATRIX
lambda.dz <- Re(eigen(IPM.dz)$value[1])
lambda.dz
```

```
sensitivity <- sens(IPM.dz)
elasticity <- elas(IPM.dz)

##=============================================================================
##subset for TW
TW <- subset(dff, dff$Site=="TW")
TW2 <- subset(dff2, dff2$Site=="TW")


growthModelComp(dataf = TW, makePlot = TRUE, legendPos = "bottomright",
            mainTitle = "Growth")

gr1 <- makeGrowthObj(dataf = TW,
                 Formula=sizeNext~size:covariate+size2,
                 regType="constantVar",
                 Family="gaussian")
TWgrowth <- picGrow(TW,gr1)

survModelComp(dataf = TW, makePlot = TRUE, legendPos = "bottomright",
           mainTitle = "Survival")

sv1 <- makeSurvObj(TW, Formula = surv ~ size:covariate+size2)
TWsurv <- picSurv(TW,sv1)

env1 <- makeEnvObj(TW2)
env1

### make adjustment to env matrix
# build adjustment matrix
adj <- matrix(c(0,0,0, 0, 0, 0, 0, -0.1, 0.1), nrow=3, ncol=3)
adj
## create new env mat
env2 <- env1 + adj
env2

Pmatrix <- makeCompoundPmatrix(nBigMatrix = 45, minSize = 0.1,
                       maxSize = 25,
                       envMatrix = env2,
                       growObj = gr1,
                       survObj = sv1,
                       correction = "constant")

image(as(Pmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


fv1 <- makeFecObj(dff, Formula = fec3~size,
```

```
            Family = "poisson")

n.age.classes <- max(TW2$covariate,na.rm=TRUE)
ageMat1 <- new("envMatrix", nEnvClass = n.age.classes)
ageMat1@.Data <- matrix(0,n.age.classes,n.age.classes)
ageMat1@.Data[1,3:n.age.classes] <- 1
ageMat1
Fmatrix <- makeCompFmatrix(nBigMatrix = 45, minSize = 0.1,
                        maxSize = 25,
                        envMatrix = ageMat1,
                        fecObj = fv1,
                        correction = "constant")

image(as(Fmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


IPM.tw <- Pmatrix+Fmatrix
image(as(log(IPM.tw),'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(IPM.tw@meshpoints, IPM.tw@meshpoints, t(log(IPM.tw)), add=TRUE)

image.plot(t(IPM.tw[nrow(IPM.tw):1,])^(1/5),
           col=topo.colors(36),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(t(IPM.tw[nrow(IPM.tw):1,])^(1/5),add=TRUE)
abline(a = 0, b = 1, lty= 2, col = "white", lwd=2)

### ANALYZE the MEGAMATRIX
lambda.tw <- Re(eigen(IPM.tw)$value[1])
lambda.tw


##=====================================================================
##subset for WW
WW <- subset(dff, dff$Site=="WW")
WW2 <- subset(dff2, dff2$Site=="WW")


growthModelComp(dataf = WW, makePlot = TRUE, legendPos = "bottomright",
           mainTitle = "Growth")

gr1 <- makeGrowthObj(dataf = WW,
                Formula=sizeNext~size:covariate+size2,
                regType="constantVar",
```

```
            Family="gaussian")
WWgrowth <- picGrow(WW,gr1)

survModelComp(dataf = WW, makePlot = TRUE, legendPos = "bottomright",
        mainTitle = "Survival")

sv1 <- makeSurvObj(WW, Formula = surv~ size:covariate+size2)
WWsurv <- picSurv(WW,sv1)

env1 <- makeEnvObj(WW2)
env1


Pmatrix <- makeCompoundPmatrix(nBigMatrix = 45, minSize = 0.1,
                    maxSize = 25,
                    envMatrix = env1,
                    growObj = gr1,
                    survObj = sv1,
                    correction = "constant")

image(as(Pmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


fv1 <- makeFecObj(WW, Formula = fec3~size,
            Family = "poisson")

n.age.classes <- max(WW2$covariate,na.rm=TRUE)
ageMat1 <- new("envMatrix", nEnvClass = n.age.classes)
ageMat1@.Data <- matrix(0,n.age.classes,n.age.classes)
ageMat1@.Data[1,3:n.age.classes] <- 1
ageMat1
Fmatrix <- makeCompFmatrix(nBigMatrix = 45, minSize = 0.1,
                    maxSize = 25,
                    envMatrix = ageMat1,
                    fecObj = fv1,
                    correction = "constant")

image(as(Fmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


IPM.ww <- Pmatrix+Fmatrix
image(as(log(IPM.ww),'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
```

```
contour(IPM.ww@meshpoints, IPM.ww@meshpoints, t(log(IPM.ww)), add=TRUE)


### ANALYZE the MEGAMATRIX
lambda.ww <- Re(eigen(IPM.ww)$value[1])
lambda.ww

##=============================================================================
##subset for WL
WL <- subset(dff, dff$Site=="WL")
WL2 <- subset(dff2, dff2$Site=="WL")


growthModelComp(dataf = WL, makePlot = TRUE, legendPos = "bottomright",
            mainTitle = "Growth")

gr1 <- makeGrowthObj(dataf = WL,
                 Formula=sizeNext~size:covariate+size2,
                 regType="constantVar",
                 Family="gaussian")
WLgrowth <- picGrow(WL,gr1)

survModelComp(dataf = WL, makePlot = TRUE, legendPos = "bottomright",
           mainTitle = "Survival")

sv1 <- makeSurvObj(dff, Formula = surv ~ size:covariate+size2)
WLsurv <- picSurv(dff,sv1)

env1 <- makeEnvObj(WL2)
env1


Pmatrix <- makeCompoundPmatrix(nBigMatrix = 45, minSize = 0.1,
                       maxSize = 25,
                       envMatrix = env1,
                       growObj = gr1,
                       survObj = sv1,
                       correction = "constant")

image(as(Pmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


fv1 <- makeFecObj(WL, Formula = fec3~size,
              Family = "poisson")

n.age.classes <- max(WL2$covariate,na.rm=TRUE)
```

```
ageMat1 <- new("envMatrix", nEnvClass = n.age.classes)
ageMat1@.Data <- matrix(0,n.age.classes,n.age.classes)
ageMat1@.Data[1,3:n.age.classes] <- 1
ageMat1
Fmatrix <- makeCompFmatrix(nBigMatrix = 45, minSize = 0.1,
                        maxSize = 25,
                        envMatrix = ageMat1,
                        fecObj = fv1,
                        correction = "constant")

image(as(Fmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


IPM.wl <- Pmatrix+Fmatrix
image(as(log(IPM.wl),'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(IPM.wl@meshpoints, IPM.wl@meshpoints, t(log(IPM.wl)), add=TRUE)


### ANALYZE the MEGAMATRIX
lambda.wl <- Re(eigen(IPM.wl)$value[1])
lambda.wl

##=============================================================================
##subset for ER
ER <- subset(dff, dff$Site=="ER")
ER2 <- subset(dff2, dff2$Site=="ER")


growthModelComp(dataf = ER, makePlot = TRUE, legendPos = "bottomright",
            mainTitle = "Growth")

gr1 <- makeGrowthObj(dataf = ER,
                Formula=sizeNext~size:covariate+size2,
                regType="constantVar",
                Family="gaussian")
ERgrowth <- picGrow(ER,gr1)

survModelComp(dataf = dff, makePlot = TRUE, legendPos = "bottomright",
          mainTitle = "Survival")

sv1 <- makeSurvObj(dff, Formula =surv ~ size:covariate+size2)
ERsurv <- picSurv(dff,sv1)

env1 <- makeEnvObj(ER2)
```

```
env1

### make adjustment to env matrix
# build adjustment matrix
adj <- matrix(c(0,0,0, 0, 0, 0, 0, -0.1, 0.1), nrow=3, ncol=3)
adj
## create new env mat
env2 <- env1 + adj
env2


Pmatrix <- makeCompoundPmatrix(nBigMatrix = 45, minSize = 0.1,
                        maxSize = 25,
                        envMatrix = env2,
                        growObj = gr1,
                        survObj = sv1,
                        correction = "constant")

image(as(Pmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


fv1 <- makeFecObj(ER, Formula = fec3~size,
              Family = "poisson")

n.age.classes <- max(ER2$covariate,na.rm=TRUE)
ageMat1 <- new("envMatrix", nEnvClass = n.age.classes)
ageMat1@.Data <- matrix(0,n.age.classes,n.age.classes)
ageMat1@.Data[1,3:n.age.classes] <- 1
ageMat1
Fmatrix <- makeCompFmatrix(nBigMatrix = 45, minSize = 0.1,
                        maxSize = 25,
                        envMatrix = ageMat1,
                        fecObj = fv1,
                        correction = "constant")

image(as(Fmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


IPM.er <- Pmatrix+Fmatrix
image(as(log(IPM.er),'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(IPM.er@meshpoints, IPM.er@meshpoints, t(log(IPM.er)), add=TRUE)
```

```
### ANALYZE the MEGAMATRIX
lambda.er <- Re(eigen(IPM.er)$value[1])
lambda.er


##=============================================================================
##subset for FR
FR <- subset(dff, dff$Site=="FR")
FR2 <- subset(dff2, dff2$Site=="FR")


growthModelComp(dataf = FR, makePlot = TRUE, legendPos = "bottomright",
            mainTitle = "Growth")

gr1 <- makeGrowthObj(dataf = FR,
                 Formula=sizeNext~size:covariate+size2,
                 regType="constantVar",
                 Family="gaussian")
FRgrowth <- picGrow(FR,gr1)

survModelComp(dataf = FR, makePlot = TRUE, legendPos = "bottomright",
           mainTitle = "Survival")

sv1 <- makeSurvObj(dff, Formula = surv ~ size:covariate+size2)
FRsurv <- picSurv(dff,sv1)

env1 <- makeEnvObj(FR2)
env1

### make adjustment to env matrix
# build adjustment matrix
adj <- matrix(c(0.249999997,0,-0.25, 0, 0, 0, 0, 0.1, -0.1), nrow=3, ncol=3)
adj
## create new env mat
env2 <- env1 + adj
env2

Pmatrix <- makeCompoundPmatrix(nBigMatrix = 45, minSize = 0.1,
                       maxSize = 25,
                       envMatrix = env2,
                       growObj = gr1,
                       survObj = sv1,
                       correction = "constant")

image(as(Pmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)
```

```
fv1 <- makeFecObj(FR, Formula = fec3~size,
            Family = "poisson")

n.age.classes <- max(FR2$covariate,na.rm=TRUE)
ageMat1 <- new("envMatrix", nEnvClass = n.age.classes)
ageMat1@.Data <- matrix(0,n.age.classes,n.age.classes)
ageMat1@.Data[1,3:n.age.classes] <- 1
ageMat1
Fmatrix <- makeCompFmatrix(nBigMatrix = 45, minSize = 0.1,
                       maxSize = 25,
                       envMatrix = ageMat1,
                       fecObj = fv1,
                       correction = "constant")

image(as(Fmatrix[,],'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = FALSE)


IPM.fr <- Pmatrix+Fmatrix
image(as(log(IPM.fr),'sparseMatrix'),
    xlab = "Continuous stage (e.g. size) at t",
    ylab = "Continuous stage (e.g. size) at t+1", axes = TRUE)
contour(IPM.fr@meshpoints, IPM.fr@meshpoints, t(log(IPM.fr)), add=TRUE)


### ANALYZE the MEGAMATRIX
lambda.fr <- Re(eigen(IPM.fr)$value[1])
lambda.fr

################=====================================###################
#######  SENSITIVITIES AND ELASTICIES OF COMPOUND MATRICES  ##########
#############=============================================############

base.sens <- sens(IPM.base)
base.elas <- elas(IPM.base)
dz.sens <- sens(IPM.dz)
dz.elas <- elas(IPM.dz)
tw.sens <- sens(IPM.tw)
tw.elas <- elas(IPM.tw)
wl.sens<- sens(IPM.wl)
wl.elas <- elas(IPM.wl)
fr.sens <- sens(IPM.fr)
fr.elas <- elas(IPM.fr)
er.sens <- sens(IPM.er)
er.elas <- elas(IPM.er)
```

```
ww.sens <- sens(IPM.ww)
ww.elas <- elas(IPM.ww)

## rotate matrices for plotting
rotate <- function(x) t(apply(x, 2, rev))
tw.IPM <- rotate(IPM.tw)
image.plot(dz.k^(1/3))

dz.k <- rotate(IPM.dz)


### PLot Elasticities
base.K <- rotate(IPM.base)
base.elas <- elas(base.K)
image.plot(base.elas,xlab = "Size at t, mm", main = "Arisaema",
ylab = "Size at t+1, mm",col = topo.colors (48))
contour(base.elas,add=TRUE)

image.plot(dz.elas[nrow(dz.elas):1,]^(1/2), main="DZ",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(dz.elas[nrow(dz.elas):1,]^(1/2),add=TRUE)

image.plot(wl.elas[nrow(wl.elas):1,]^(1/2), main="WL",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(wl.elas[nrow(wl.elas):1,]^(1/2),add=TRUE)

image.plot(fr.elas[nrow(fr.elas):1,]^(1/2), main="FR",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(fr.elas[nrow(fr.elas):1,]^(1/2),add=TRUE)

image.plot(er.elas[nrow(er.elas):1,]^(1/2), main="ER",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(er.elas[nrow(er.elas):1,]^(1/2),add=TRUE)

image.plot(ww.elas[nrow(ww.elas):1,]^(1/2), main="WW",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(ww.elas[nrow(ww.elas):1,]^(1/2),add=TRUE)

image.plot(tw.elas[nrow(tw.elas):3,]^(1/2), main="TW",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(tw.elas[nrow(tw.elas):3,]^(1/2),add=TRUE)


### plot sensitivities

image.plot(base.sens[nrow(base.sens):1,]^(1/2),xlab = "Size at t, mm", main = "Arisaema",
ylab = "Size at t+1, mm",col = topo.colors (48))
contour(base.sens[nrow(base.sens):1,]^(1/2),add=TRUE)
```

```
image.plot(dz.sens[nrow(base.sens):1,]^(1/2), main="DZ",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(dz.sens[nrow(base.sens):1,]^(1/2),add=TRUE)

image.plot(wl.sens[nrow(base.sens):1,]^(1/2), main="WL",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(wl.sens[nrow(base.sens):1,]^(1/2),add=TRUE)

image.plot(fr.sens[nrow(base.sens):1,]^(1/2), main="FR",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(fr.sens[nrow(base.sens):1,]^(1/2),add=TRUE)

image.plot(er.sens[nrow(base.sens):1,]^(1/2), main="ER",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(er.sens[nrow(base.sens):1,]^(1/2),add=TRUE)

image.plot(ww.elas[nrow(base.sens):1,]^(1/2), main="WW",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(ww.sens[nrow(base.sens):1,]^(1/2),add=TRUE)

image.plot(tw.sens[nrow(base.sens):1,]^(1/2), main="TW",
xlab = "Size at t, mm", ylab = "Size at t+1, mm",col = topo.colors (48))
contour(tw.sens[nrow(base.sens):1,]^(1/2),add=TRUE)


#######  LTRE ANALYSIS - understand how transition differences might be influencing lambda
## I'll use the overall IPM kernel with probabilities based on all data for the baseline matrix

### comparison to TW
##get arithemetic mean if the IPMs
IPM_mid1 <- (IPM.tw + IPM.base)/2

## calculate the differences in the IPM kernels
IPM_diff1 <- IPM.base - IPM.tw

## weight the IPM differences by the sensitivity of the arithmetic mean
Sensi_IPM_mid1 <- sens(IPM_mid1)
IPM_contrib1 <- IPM_diff1 * Sensi_IPM_mid1

persp(t(IPM_contrib1), phi = 30, theta = 45, border=NA,
xlab = "Nonflowering - Male - Female", ylab = " ", zlab= "Diff. in expression of lambda              ",
col = heat.colors(3))


### comparison to DZ
##get arithemetic mean if the IPMs
IPM_mid2 <- (IPM.dz + IPM.base)/2
```

```
## calculate the differences in the IPM kernels
IPM_diff2 <- IPM.base - IPM.dz

## weight the IPM differences by the sensitivity of the arithmetic mean
Sensi_IPM_mid2 <- sens(IPM_mid2)
IPM_contrib2 <- IPM_diff2 * Sensi_IPM_mid2

persp(IPM_contrib2, phi = 45, theta = 60,
xlab = "Size at t, mm", ylab = "Size at t+1, mm", zlab= "Differences in expression of lambda",
col = heat.colors (3))

persp(t(IPM_contrib2), phi = 30, theta = 45, border=NA,
xlab = "Nonflowering - Male - Female", ylab = " ", zlab= "Diff. in expression of lambda              ",
col = heat.colors(3))


### comparison to WL
##get arithemetic mean if the IPMs
IPM_mid3 <- (IPM.wl + IPM.base)/2

## calculate the differences in the IPM kernels
IPM_diff3 <- IPM.base - IPM.wl

## weight the IPM differences by the sensitivity of the arithmetic mean
Sensi_IPM_mid3 <- sens(IPM_mid3)
IPM_contrib3 <- IPM_diff3 * Sensi_IPM_mid3

persp(t(IPM_contrib3), phi = 30, theta = 45, border=NA,
xlab = "Nonflowering - Male - Female", ylab = " ", zlab= "Diff. in expression of lambda              ",
col = heat.colors(3))

### comparison to WW
##get arithemetic mean if the IPMs
IPM_mid4 <- (IPM.ww + IPM.base)/2

## calculate the differences in the IPM kernels
IPM_diff4 <- IPM.base - IPM.ww

## weight the IPM differences by the sensitivity of the arithmetic mean
Sensi_IPM_mid4 <- sens(IPM_mid4)
IPM_contrib4 <- IPM_diff4 * Sensi_IPM_mid4

persp(t(IPM_contrib4), phi = 30, theta = 45, border=NA,
xlab = "Nonflowering - Male - Female", ylab = " ", zlab= "Diff. in expression of lambda              ",
col = heat.colors(3))
```

```
### comparison to FR
##get arithemetic mean if the IPMs
IPM_mid5 <- (IPM.fr + IPM.base)/2

## calculate the differences in the IPM kernels
IPM_diff5 <- IPM.base - IPM.fr

## weight the IPM differences by the sensitivity of the arithmetic mean
Sensi_IPM_mid5 <- sens(IPM_mid5)
IPM_contrib5 <- IPM_diff5 * Sensi_IPM_mid5

persp(t(IPM_contrib5), phi = 30, theta = 45, border=NA,
xlab = "Nonflowering - Male - Female", ylab = " ", zlab= "Diff. in expression of lambda ",
col = heat.colors(3))

### comparison to ER
##get arithemetic mean if the IPMs
IPM_mid6 <- (IPM.er + IPM.base)/2

## calculate the differences in the IPM kernels
IPM_diff6 <- IPM.base - IPM.er

## weight the IPM differences by the sensitivity of the arithmetic mean
Sensi_IPM_mid6 <- sens(IPM_mid6)
IPM_contrib6 <- IPM_diff6 * Sensi_IPM_mid6

persp(t(IPM_contrib6), phi = 30, theta = 45, border=NA,
xlab = "Nonflowering - Male - Female", ylab = " ", zlab= "Diff. in expression of lambda ",
col = heat.colors(3))
```

BIBLIOGRAPHY

Agrawal AA, JA Lau, PA Hamback. 2006. Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quart. Rev. Biol*. 81: 349-376.

Agrawal, AA, DD Ackerly, F Adler, AE Arnold, C Cáceres, DF Doak ... and E Werner. 2007. Filling key gaps in population and community ecology. *Front. Ecol. Env. 5*(3): 145-152.

Agresti A. 2007. An introduction to categorical data analysis. Wiley-Blackwell, Hoboken, NJ.

Alberti, J, M Escapa, O Iribarne, B Silliman, and M Bertness. 2008. Crab herbivory regulates plant facilitative and competitive processes in Argentinean marshes. *Ecology* 89:155-164.

Anderson, RC. 1994. Height of white-flowered Trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecol. Apps*. 4:104-109.

Anderson, RC and OL Loucks. 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *J. App. Ecol*. 16:855-861.

Andow, DA. 1991. Vegetational diversity and arthropod population response.*Ann. Review Ent. 36*(1):561-586.

Augustine, DJ and D DeCalesta. 2003. Defining deer overabundance and threats to forest communities: From individual plants to landscape structure. *Ecoscience* 10:472-486.

Augustine, DJ and PA Jordan. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. *J. Wild. Mgmt*. 62:1076-1085.

Augustine DJ, LE Frelich, and PA Jordan. 1998. Evidence for two alternate stable states in an ungulate grazing system. *Ecol. Apps.* 8:1260-1269.

Augustine D., and LE Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Cons. Biol.* 12:995-1004.

Bakker, E. S., H. Olff, M. Boekhoff, J. M. Gleichman, and F. Berendse. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138:91.

Bardgett RD, and DA Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258-2268.

Bates D, M Maechler, and B Bolker. 2012. lme4: Linear mixed-effects models using S4 classes. R Package Version 2.

Bassett, IE, RC Simcock, and ND Mitchell. 2005. Consequences of soil compaction for seedling establishment: Implications for natural regeneration and restoration. *Austral Ecology* 30:827-833.

Benkman CW. 2013. Biotic interaction strength and the intensity of selection. *Ecol. Lett*., 16: 1054-1060.

Bierzychudek, P. 1982. The demography of Jack-in-the-Pulpit, a forest perennial that changes sex. *Ecol. Mono*. 52:335-351.

Bierzychudek, P. 1999. Looking backwards: Assessing the projections of a transition matrix model. *Ecol. Apps.* 9:1278-1287.

Bonser SP, LW Aarssen. 2009. Interpreting reproductive allometry: Individual strategies of allocation explain size-dependent reproduction in plant populations. *Perspect. Plant Ecol. Evol. Syst*. 11: 31-40.

Bressette JW, H Beck, VB Beauchamp. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. *Oikos* 121: 1749-1760.

Brooker, R, F Maestre, R Callaway, C Lortie, L Cavieres, G Kunstler, P Liancourt, K Tielborger, J Travis, and F Anthelme. 2008. Facilitation in plant communities: the past, the present, and the future. *J Ecol* 96:18-34.

Brundrett, M. C. and B. Kendrick. 1988. The mycorrhizal status, root anatomy, and phenology of plants in sugar maple forest. *Can. J. Bot*. 66:1153-1173.

Brys R, RP Shefferson, and H Jacquemyn. 2010. Impact of herbivory on flowering behaviour and life history trade-offs in a polycarpic herb: a 10-year experiment. *Oecologia* 166:293-303.

Callaway, R. 2007. Positive Interactions and Interdependence in Plant Communities. Springer London.

Caswell H. 2001. Matrix population models: construction, analysis, and interpretation. Sunderland, MA, Sinauer.

Colling, G. and D. Matthies. 2006. Effects of habitat deterioration on population dynamics and extinction risk of an endangered, long-lived perennial herb (*Scorzonera humilis*). *J. Ecol*. 94:959-972.

Chapin III SF, K Autumn, F Pugnaire. 1993. Evolution of suites of traits in response to environmental stress. *Am. Nat*. 142: 78-92.

Charnov EL. 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ.

Clausen J, DD Keck, WM Hiesey. 1947. Heredity of geographically and ecologically isolated races. *Am. Nat*. 81: 114-133.

Côté, SD, TP Rooney, JP Tremblay, C Dussault, and DM Waller. 2004. Ecological impacts of deer overabundance. *Ann. Rev. Ecol. Evol. Syst*. 35:113-147.

Crain, CM. 2008. Interactions between marsh plant species vary in direction and strength depending on environmental and consumer context. *J. Ecol.* 96:166-173.

Cumming, DHM and GS Cumming. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia* 134:560.

Dahlgren, JP, & J Ehrlén. 2009. Linking environmental variation to population dynamics of a forest herb. *J. Ecol. 97*(4): 666-674.

Darwin, C. 1859. On the origin of species by means of natural selection, 1859.Murray, London.

D'avalos A, V Nuzzo, and B Blossey. 2014. Demographic responses of rare forest plants to multiple stressors: the role of deer, invasive species and nutrients. *Journal of Ecology*. doi 10.1111/1365-2745.12279.

DeCalesta, D. S. and S. L. Stout. 1997. Relative deer density and sustainability: A conceptual framework for integrating deer management with ecosystem management. *Wildlife Society Bulletin* 25:252-258.

Didiano, T J, NE Turley, G Everwand, H Schaefer, MJ Crawley, MT Johnson,. 2014. Experimental test of plant defence evolution in four species using long-term rabbit exclosures. *J. Ecol*. 102(3): 584-594.

Easterling MR, SP Ellner, and PM Dixon. 2000. Size-specific sensitivity: Applying a new structured population model. *Ecology* 81:694-708.

Ehrlen J. 1995. Demography of the perennial herb *Lathyrus vernus*. I. Herbivory and individual performance. *J. Ecol.* 83:297-308.

Ellner SP, and M Rees. 2006. Integral projection models for species with complex demography. *Am. Nat.* 167:410-28.

Estes, JA, J Terborgh, JS Brashares, ME Power, J Berger, WJ Bond, ... and DA Wardle. 2011 Trophic downgrading of planet Earth. *Science 333*(6040):301-306.

Facelli, JM. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75(6):1727-1735.

Franco, M, and J Silvertown. 2004. A comparative demography of plants based upon elasticities of vital rates. *Ecology 85*(2): 531-538.

Frerker K, G Sonnier, and DM Waller. 2013. Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. *For. Ecol. Mgmt.* 291:55-64.

Freschet GT, PJ Bellingham, PO Lyver, KI Bonner, DA Wardle. 2013. Plasticity in above- and belowground resource acquisition traits in response to single and multiple environmental factors in three tree species. *Ecol. Evol*. 3: 1065-1078.

Gass TM, D Binkley. 2011. Soil nutrient losses in an altered ecosystem are associated with native ungulate grazing. *J. App. Ecol*. 48:952-960.

Ghiselin MT. 1969. The evolution of hermaphroditism among animals. *Quart. Rev. Biol*. 44: 189-208.

Godefroid, S. and N. Koedam. 2004. Interspecific variation in soil compaction sensitivity among forest floor species. *Biol. Cons*. 119:207-217.

Gomulkiewicz R, RD Holt. 1995. When does evolution by natural selection prevent extinction? *Evolution* 49:201-207.

Graff, P., M. R. Aguiar, and E. J. Chaneton. 2007. Shifts in positive and negative plant interactions along a grazing intensity gradient. *Ecology* 88:188-199.

Gurevitch, J. and L. V. Hedges. 2001. Meta-analysis: Combining the results of independent experiments. Pages 347-370 *in* S. M. Scheiner and J. Gurevitch, editors. Design and Analysis of Ecological Experiments. Oxford University Press, New York.

Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: A meta-analysis of field experiments. *Am. Nat*. 155:435-453.

Hale, C. M., L. E. Frelich, P. B. Reich, and J. Pastor. 2005. Effects of European earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, USA. *Ecosystems* 8:911-927.

Heckel CD, NA Bourg, WJ McShea, S Kalisz. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive the decline of unpalatable forest herbs. *Ecology* 91:319-326.

Hedges, LV, J Gurevitch, and PS Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150-1156.

Hegland SJ, E Jongejans, and K Rydgren. 2010. Investigating the interaction between ungulate grazing and resource effects on *Vaccinium myrtillus* populations with integral projection models. *Oecologia* 163:695-706.

Horsley, SB, SL Stout, and D DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Eco. Apps*. 13:98-118.

Howe, H, and J Brown. 2001. The ghost of granivory past. *Ecol. Lett*. 4:371-378.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Ann. Rev. Ecol. Syst*. 22:477-503.

Inouye B, JR Stinchcombe. 2001. Relationships between ecological interaction modifications and diffuse coevolution: similarities, differences, and causal links. *Oikos* 95:353-360.

Jacquemyn H, R Brys, M Hermy. 2003. Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. *Biol. Cons*. 111:137-147.

Jacquemyn H, R Brys, and E Jongejans. 2010. Size-dependent flowering and costs of reproduction affect population dynamics in a tuberous perennial woodland orchid. Journal of *Ecology* 98:1204-1215.

Johnson MT, JR Stinchcombe. 2007. An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol*. 22:250-257.

Kalisz, S, RB Spigler, & CC Horvitz. 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. *PNAS*. 111(12):4501-4506.

Kardol, P, IA Dickie, MG St John, SW Husheer, KI Bonner, PJ Bellingham, DA Wardle. 2014. Soil-mediated effects of invasive ungulates on native tree seedlings. J. *Ecol*. 102(3):622-631.

Kefi S, EL Berlow, EA Wieters, SA Navarrete, OL Petchey, SA Wood, *et al.* 2012. More than a meal... integrating non-feeding interactions into food webs. *Ecol. Lett*. 15:291-300.

Kery, M, D Matthies, and H-H Spillmann. 2000. Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. *J. Ecol*. 88:17-30.

Kirschbaum, C and B Anacker. 2005. The utility of *Trillium* and *Maianthemum* as phyto-indicators of deer impact in northwestern Pennsylvania, USA. *For. Ecol. Mgmt*. 217:54-66.

Knight, TM. 2003. Effects of herbivory and its timing across populations of *Trillium grandiflorum* (Liliaceae). *Am. J. Bot*. 90:1207-1214.

Knight, TM, H Caswell, and S Kalisz. 2009a. Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory. *For. Ecol. Mgmt*. 257:1095-1103.

Knight, TM, JL Dunn, LA Smith, J Davis, and S Kalisz. 2009b. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Nat.Areas J*. 29:110-116.

Kozlowski J, J Uchmanski. 1987. Optimal individual growth and reproduction in perennial species with indeterminate growth. *Evol. Ecol*. 1:214-231.

Kuss P, M Rees, HH AEgisd'ottir, SP Ellner, and J Stocklin. 2008. Evolutionary demography of long-lived monocarpic perennials: a time-lagged integral projection model. *J. Ecol.* 96:821-832.

Kyle, G, K Beard, and A Kulmatiski. 2007. Reduced soil compaction enhances establishment of non-native plant species. *Plant Ecology* 193:223.

Lau JA. 2012. Evolutionary indirect effects of biological invasions. *Oecologia* 170:171-181.

Lawlor, L. 1979. Direct and indirect effects of n-species competition. *Oecologia* 43:355-364.

Levine, JM. 2000. Complex interactions in a streamside plant community. *Ecology* 81:3431.

Louda, S. M., M. A. Potvin, and S. K. Collinge. 1990. Predispersal seed predation, postdispersal seed predation and competition in the recruitment of seedlings of a native thistle in Sandhills prairie. *Am. Mid. Nat*. 124:105–113.

Lubbers, A. E. and M. J. Lechowicz. 1989. Effects of leaf removal on reproduction vs. belowground storage in *Trillium grandiflorum*. *Ecology* 70:85-96.

Maron JL, and E Crone. 2006. Herbivory: effects on plant abundance, distribution and population growth. *Proc. Royal Soc. B: Biological Sciences* 273:2575-2584.

McGraw, JB and MA Furedi. 2005. Deer browsing and population viability of a forest understory plant. *Science* 307:920-922.

McShea, W, H Underwood, and J Rappole. 1997. The science of overabundance: deer ecology and population management. Smithsonian Institution Press.

McShea, WJ. 2000. The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* 81:228-238.

Merow C, JP Dahlgren, CJ E. Metcalf, DZ Childs, ME Evans, E Jongejans, S Record, M Rees, R Salguero-Gomez, and SM McMahon. 2014. Advancing population ecology with integral projection models: a practical guide. *Meth. Ecol. Evol.* 5:99-110.

Michalet, R, R Brooker, L Cavieres, Z Kikvidze, C Lortie, F Pugnaire, A Valiente-Banuet, and R Callaway. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecol. Letters* 9:767-773.

Miller, TE. 1994. Direct and indirect species interactions in an early old-field plant community. *Am. Nat*. 143:1007-1025.

Miller, TE, CP terHorst, and JH Burns. 2009. The ghost of competition present. *Am. Nat.* 173:347-353.

Miller, TE, and J Travis. 1996. The evolutionary role of indirect effects in communities. *Ecology* 77(5): 1329-1335.

Morris, WF, RA Hufbauer, AA Agrawal, JD Bever, VA Borowicz, GS Gilbert, JL Maron, CE Mitchell, IM Parker, AG Power, ME Torchin, and DP Vazquez. 2007. Direct and interactive effects of enemies and mutualists on plant performance: A meta-analysis. *Ecology* 88:1021-1029.

Nadian, H, S Smith, A Alston, and R Murray. 1997. Effects of soil compaction on plant growth, phosphorus uptake and morphological characteristics of vesicular-arbuscular mycorrhizal colonization of *Trifolium subterraneum*. *New Phyt*. 135:303-311.

Nakagawa S, H Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Meth. Ecol. Evol*. 4:133-142.

Ohgushi T. 2005. Indirect interaction webs: Herbivore-induced effects through trait change in plants. *Ann. Rev. Ecol. Evol. Syst*. 36:81-105.

Olejniczak P. 2001. Evolutionarily stable allocation to vegetative and sexual reproduction in plants. *Oikos* 95:156-160.

Olofsson, J and L Oksanen. 2002. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. *Oikos* 96:507-515.

Parker JD, DE Burkepile, and ME Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459-1461.

Peckarsky BL, PA Abrams, DI Bolnick, LM Dill, JH Grabowski, B Luttbeg, …, and GC Trussell. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology* 89:2416-2425.

Pengthamkeerati P, PP Motavalli, and RJ Kremer. 2011. Soil microbial activity and functional diversity changed by compaction, poultry litter and cropping in a claypan soil. *App. Soil Ecol.* 48:71-80.

Persson, I-L, K Danell, and R Bergstrom. 2000. Disturbance by large herbivores in boreal forests with special reference to moose. *Ann. Zool. Fenn.* 37:251-263.

Pfister, CA. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *PNAS* 95:213-218.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL http://www.R-project.org.

Redding J, KW Gottschalk, and SLC Fosbroke. 1995. History of deer population trends and forest cutting on the Allegheny National Forest. In *Proceedings of 10th Central Forest Hardwoods Conference*.

Rees M, and KE Rose. 2002. Evolution of flowering strategies in *Oenothera glazioviana*: an integral projection model approach. *Proc. Royal Soc. B: Biological Sciences* 269:1509-15.

Richardson, CR and K Clay. 2001. Sex-ratio variation among *Arisaema* species with different patterns of gender diphasy. *Plant Species Biology* 16:139-149.

Rooney TP, and K Gross. 2003. A demographic study of deer browsing impacts on *Trillium grandiflorum*. *Plant Ecol*. 168:267-277.

Rooney, TP and DM Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Mgmt*. 181:165-176.

Rossow, LJ, JP Bryant, and K Kielland. 1997. Effects of above-ground browsing by mammals on mycorrhizal infection in an early successional taiga ecosystem. *Oecologia* 110:94-98.

Royo, AA and WP Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res*. 36:1345-1362.

Rudgers JA, TE Miller, SM Ziegler, and KD Craven. 2012. There are many ways to be a mutualist: endophytic fungus reduces plant survival but increases population growth. *Ecology* 93:565-574.

Ruhren, S and SN Handel. 2000. Considering herbivory, reproduction, and gender when monitoring plants: a case study of Jack-in-the-Pulpit (*Arisaema triphyllum* [L.] Schott). *Nat. Areas J.* 20:261-266.

Ryser P, L Eek. 2000. Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. *Am. J. Bot.* 87:402-411.

Salguero-Gomez R, BB Casper. 2010. Keeping plant shrinkage in the demographic loop. *J. Ecol.* 98:312-323.

Salguero-Gomez R, W Siewert, BB Casper, and K Tielborger. 2012. A demographic approach to study effects of climate change in desert plants. *Phil. Trans. Royal Soc. B:* 367:3100-3114.

Sharrow, S. 2007. Soil compaction by grazing livestock in silvopastures as evidenced by changes in soil physical properties. *Agroforestry Systems* 71:215-223.

Shelton, AL, JA Henning, P Schultz, and K Clay. 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils.*For. Ecol. .Mgmt.* 320:39-49.

Sibly R, P Calow. 1989. A life-cycle theory of responses to stress. *Biol. J. Linn. Soc*. 37:101-116.

Silvertown, J, M Franco, I Pisanty, and A Mendoza. 1993. Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. of Ecol.* 465-476.

Sokal, RR and FJ Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. Third edition. W. H. Freeman and Company, New York.

Snow AA, and D Whigham. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). *Ecology* 70:1286-1293.

Stearns SC, JC Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40:893-913.

Stearns SC, RE Crandall. 1981. Quantitative predictions of delayed maturity. *Evolution* 35:455-463.

Stinchcombe JR, MD Rausher. 2001. Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory, *Ipomoea hederacea*. *Am. Nat*. 158:376-388.

Strauss SY. 1991. Indirect effects in community ecology: their definition, study and importance. *Trends Ecol. Evol*. 6:206-210.

Strauss, SY and A.A Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol*. 14:179-185.

Strauss SY, H Sahli, JK Conner. 2005. Toward a more trait-centered approach to diffuse (co) evolution. *New Phyt*. 165:81-90.

Strauss SY, RE Irwin. 2004. Ecological and evolutionary consequences of multispecies plant-animal interactions. *Ann. Rev. Ecol. Evol. Syst*. 35:435-466.

Sultan SE. 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* 5:537.

Sutherland, WJ, RP Freckleton, HCJ Godfray, SR Beissinger, T Benton, DD Cameron, ... and T Wiegand. 2013. Identification of 100 fundamental ecological questions. *J. Ecol.* 101(1): 58-67.

Thompson JN. 2005. The geographic mosaic of coevolution. University of Chicago Press, Chicago.

Turley NE, WC Odell, H Schaefer, G Everwand, MJ Crawley, MT Johnson. 2013. Contemporary evolution of plant growth rate following experimental removal of herbivores. *Am. Nat*. 181:S21-34.

van der Heijden, MGA, RD Bardgett, and NM van Straalen. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Letters* 11:296-310.

Vandermeer, J. 1978. Choosing category size in a stage projection matrix. *Oecologia* 32(1):79-84.

Vavra, M, CG Parks, and MJ Wisdom. 2007. Biodiversity, exotic plant species, and herbivory: The good, the bad, and the ungulate. *For. Ecol. Mgmt.* 246:66.

Vitt P, KE Holsinger, CS Jones. 2003. Local differentiation and plasticity in size and sex expression in Jack-in-the-pulpit, *Arisaema triphyllum* (Araceae). *Am. J. Bot*. 90:1729-1753.

von Euler T, JA Agren, and J Ehrlen. 2014. Environmental context influences both the intensity of seed predation and plant demographic sensitivity to attack. *Ecology* 95:495-504.

Wallingford, BD and M Grund. 2003. Estimating county deer population sizes & growth rates. Page 11 *in* B. o. W. M. R. Division, editor. Pennsylvania Game Commission.

Walsh MR. 2013. The evolutionary consequences of indirect effects. *Trends Ecol. Evol*. 28:23-29.

Walsh MR, DN Reznick. 2010. Influence of the indirect effects of guppies on life-history evolution of *Rivulus hartii*. *Evolution* 64:1583-1593.

Waltert, B, V Wiemken, H-P Rusterholz, T. Boller, and B Baur. 2002. Disturbance of forest by trampling: Effects on mycorrhizal roots of seedlings and mature trees of *Fagus sylvatica*. *Plant and Soil* 243:143.

Wardle, DA, GM Barker, GW Yeates, KI Bonner, and A Ghanti. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecol. Mono.* 71:587-614.

Webster, CR and GR Parker. 2000. Evaluation of *Osmorhiza claytonii* (Michx.) C.B. Clarke, *Arisaema triphyllum* (L.) Schott, and *Actaea pachypoda* Ell. as potential indicators of white-tailed deer overabundance. *Nat. Areas J.* 20:176-186.

Weiner J, LG Campbell, J Pino, L Echarte. 2009. The allometry of reproduction within plant populations. *J. Ecol*. 97:1220-1233.

White, J and T Whitham. 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* 81:1795-1803.

Wiegman, SM and DM Waller. 2006. Fifty years of change in northern upland forest understories: Identity and traits of "winner" and "loser" plant species. *Biol. Cons.* 129:109-123.

Wise MJ, MD Rausher. 2013. Evolution of resistance to a multiple-herbivore community: genetic correlations, diffuse coevolution, and constraints on the plant's response to selection. *Evolution* 67:1767-1779.

Wootton JT. 2002. Indirect effects in complex ecosystems: recent progress and future challenges. *J. of Sea Res.* 48:157-172.

Wootton JT, M Emmerson. 2005. Measurement of interaction strength in nature. *Ann. Rev. Ecol. Evol. Syst*. 36:419-444.

Yates, CJ, DA Norton, and RJ Hobbs. 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. *Austral Ecology* 25:36-47.

Yule KM, TEX Miller, JA Rudgers. 2013. Costs, benefits, and loss of vertically transmitted symbionts affect host population dynamics. *Oikos* 122(10):1512-1520.

Zuur A, E Ieno, N Walker, A Saveliev, G Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Verlag, New York.