Parsing the Particulars of Pollination: Ecological and Anthropogenic Drivers of Plant and Pollinator Dynamics

By

Paul Robert Glaum

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Doctoral Committee:

Professor John Vandermeer, Chair
Professor Regina Baucom
Professor Aaron King
Professor Ivette Perfecto

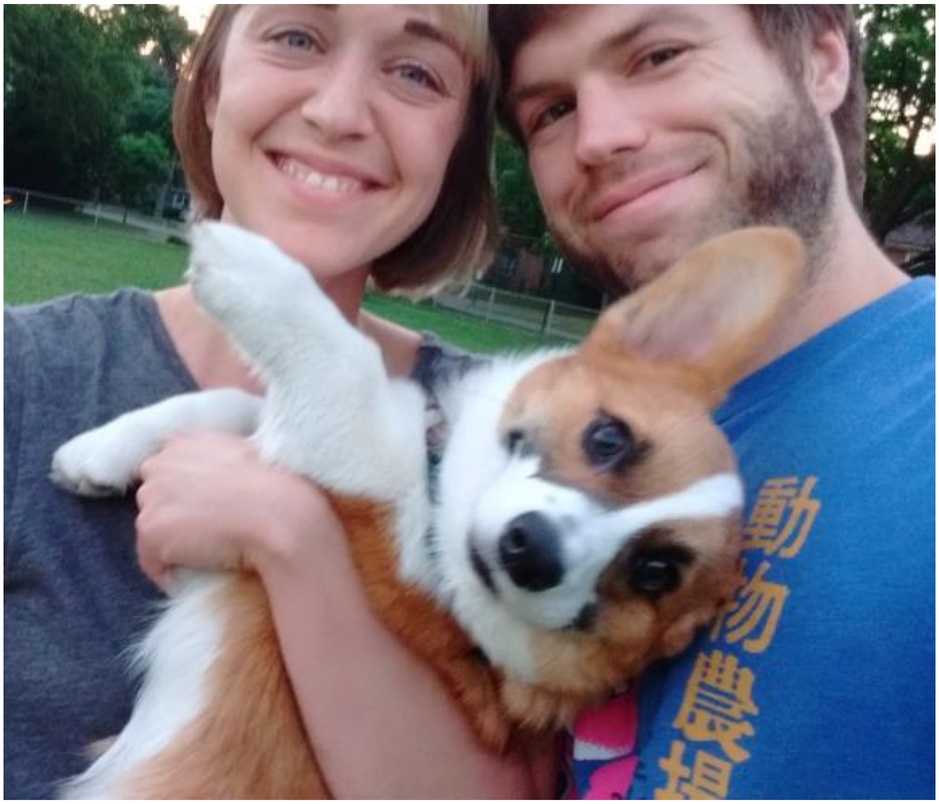
Paul Robert Glaum

prglaum@umich.edu

ORCHID iD: 0000-0002-7451-8369

Dedication

Dedicated to my colleagues, my friends, and my family. And to anyone anywhere doing anything to help fix this mess we're in, every little bit helps.



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Where in the world to possibly begin? As much as graduate school can sometimes feel like a lonely trek, no one does anything entirely alone and my time here exemplifies that.

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僕の日本の友達へありがとう！最近に会う機会はあまりないけど、僕は毎日に日本の経験を回想する。2016年にやっと日本に帰ってよかったけど、今からもっと日本に戻って、みんなに会いたい！あなた達のおかげで本当の親切を習った。それはあまり

生物学に関係ないって言えるでしょう。でも、僕にとって、関係あると思います。全部にありがとう。

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List of Abbreviations, Acronyms, and Symbols

LM – Linear model
LME – Linear mixed model
GLM – Generalized linear model
· - Statistical significance at p<0.1 level
* - Statistical significance at p<0.05 level
** - Statistical significance at p<.001 level
*** - Statistical significance at p<0.0001 level
OSR – Observed sex ratio
IT – Intertegular (IT) distance, distance between bee's wings
PLS – Partial least squares regression
FAO – Food and Agriculture Organization of the United Nations
VOCs – Volatile organic compounds
HI-VOCs – Herbivory-induced volatile organic compounds
HIPL – Herbivory-induced pollinator limitation
FHS – Flowering plant, herbivore, syrphid fly community shorthand
ODE – Ordinary differential equation

Abstract

My research focuses on wild pollinating insects and the external influences on their population dynamics in both natural and human altered settings. Pollination from wild insects (e.g. wild bees, flies, butterflies, etc.) is critically important for both agricultural systems and the maintenance of wild/native plant biodiversity. Unfortunately, similarly to honey bees, numerous wild pollinating insects are experiencing global declines in abundance and diversity. Causes for the declines are varied and far reaching with mounting evidence showing these declines manifest in both, natural and human altered environments. Accordingly, the declines in pollinator health will have similarly widespread consequences, posing a precipitous threat to biodiversity, food production, and economic stability. The breadth and severity of the global pollinator decline highlights the need to develop a thorough understanding of how wild pollinators interface with their environments in both natural and human altered settings. Specifically, my research aims to help elucidate the drivers of natural plant and pollinator dynamics as well as the causes of wild pollinator decline utilizing comprehensive interwoven empirical and theory-based approaches.

The first half of this thesis investigates the effects of urban development on wild bee communities using urban gardens as study sites in southeastern Michigan. My colleagues and I developed a large-scale multi-faceted research project sampling thousands of bees and numerous environmental variables across our sites. Results described in chapter two reveal that the negative effects of urban development on ground nesting bumble bees are driven entirely by declines in females while males show no response to urbanization. It also details a surprisingly abundant bumble bee population in the city of Detroit MI. Chapter three expands focus to the entire sampled set of bees and shows that the differential effect of urban development on females and males is apparent in all sampled ground nesting bees groupings. However, wild bees which nest in above-ground cavities have positive correlations with urban development. Chapter four uses US census data to investigate how socioeconomic conditions in urban settings can influence the location and floral quality of our study sites, urban gardens.

The second half examines wild plant and pollinator dynamics in natural settings using theoretical models informed by empirical data and observations. Chapter five investigates the direct and indirect effects of insect herbivores on pollination in a community context. When attacked by herbivores, plants mount chemical defenses which deter herbivores but also deter pollinators and consequently reduce individual plant reproduction. Using empirically vetted mathematical representations of these interactions, I show that while this defense strategy has significant costs to individual reproduction it has stabilizing effects on the population and community level. Chapter six focuses on an often overlooked pollinator, predatory syrphid flies. These flies are pollinators when adults but predators of insect herbivores when in their larval stage. While this can be beneficial, I demonstrate how this dynamic can lead to a negative feedback loop in communities isolated from background biodiversity. Chapter seven expands the consideration of ecologically distinct developmental stages to plants. Incorporating independent stages of plant development into a model framework is shown to fundamentally alter the effects certain demographic rates on both population and community dynamics.

This work presents novel findings regarding pollinator interactions with their environment in both anthropogenic and natural settings, contributing to foundational ecological information which will hopefully aid in managing and conserving pollinator biodiversity.

Chapter 1

Introduction

Animal pollination provides a critically important ecological service essential to the maintenance of both agricultural and wild plant communities. Given that plants communities serve as the basal resource level of terrestrial ecological communities, their role in supporting plant yield and reproduction extends pollinator significance in biodiversity maintenance to entire ecosystems. Wild insects are a particularly important group of pollinators given their diversity over their extensive global range. Their pollination services are responsible for the increased quantity, quality, and stability of over 60% of world crops (Garabaldi et al 2010) and worth an estimated ~200 billion dollars per year (Gallai et al 2009). Outside of human food systems, wild insect pollination is essential for supporting the reproduction and genetic diversity of thousands of plant species which make up the core of terrestrial ecosystems (Biesmeijer et al 2006; Burkle et al 2013).

These essential services are now increasingly at risk as wild pollinating insects continue to experience global declines. The sources of these declines are also widespread and varied such that they are apparent in both wild and human altered landscapes (Biesmeijer et al 2006; Potts et al 2010; Cameron 2011; Koh et al 2016). The extensive range of pollinator decline highlights the need to better understand both biotic and abiotic drivers of both plant and pollinator dynamics. Such efforts will not only aid in attributing cause to pollinator decline but they will also deepen our understanding of mechanisms of biodiversity maintenance in the wild given the central role of insect pollinators.

Wild bees in urban environments

Human land use has altered the environment wild pollinators inhabit through agricultural and urban development. Industrial agriculture limits suitable nesting sites (Kennedy et al 2013) , produces crop monocultures which reduce pollinator nutritional diversity (Williams & Kremen

2007), and uses harmful pesticides like neonicotinoids (Whitehorn et al 2012; Rundolf et al 2015; Woodcock et al 2016). In urban settings, however, the patterns have been less clear. Studies have found an array of non-significant and contradictory results when investigating overall bee communities (Winfree et al 2011; Kearns & Oliveras 2009; Pardee & Philpott 2014; Fortel et al 2014). To study wild bees in urban environments, 3 graduate collaborators and I cultivated working relationships with urban gardeners from Dexter to Detroit, MI to create a network of organic urban garden study sites across a gradient of urban development. Urban gardens have high floral densities which act as resource lures, attracting area pollinators to our traps and netting arrangements. Detailed GIS environmental profiles measure the level of urban development at each site using the National Landcover database. We amassed a large data set of wild bees representing 143 species from 30 sites across two years of sampling in 5 cities.

Chapter two focuses on bumblebees, an important generalist pollinator (Goulson 2003; Goulson et al 2008). I incorporated landscape history and behavioral traits of bumblebees to show that urbanization affects bumblebee sexes differently depending on city characteristics (Glaum et al 2017). Females nest underground and therefore their movement into cities is limited by paved surfaces or mowed lawns. Males live transiently on flowers and are not directly limited by paved surfaces meaning they can disperse into urban gardens with flowers. However, Detroit's abundance of vacant land serves as refuges for ground nesting females, reducing the negative effect of urban development on female nesting. This work is the first to show that behavioral differences between sexes are an important new dimension in landscape bee studies. It also identifies city characteristics in Detroit that may help promote sustainable pollinator populations.

Chapter three expands focus to the entire wild bee community we sampled from southeastern Michigan. My colleagues and I were again able to utilize a natural history driven analysis across the 143 species caught in our sampling efforts. This was accomplished using a large metadata set of species' traits of all our sampled species created through an exhaustive literature search and invaluable assistance from Prof Jason Gibbs. The sex difference in bumblebee response to urban development is found to be consistent with the *overall* ground nesting community, across the categories of bee sociality. This contributed to a significant decline in female ground nesters along the rural-to-urban gradient. Conversely, we found that cavity nesting bees actually *increased* in abundance along the rural-to-urban gradient. The result has direct relevance to understanding how urban development affects the overall wild communities.

Chapter four represents initial steps towards understanding some of the more direct human drivers of bee habitats produced by urban gardens/farms. Urban agriculture is, at its core, a human endeavor in which municipal and personal level decisions determines garden location and resource quality. We hypothesized that these decisions would experience some measurable influence from surrounding socio-economic conditions. Started in collaboration with students in the University of Michigan's Urban Planning department, we accumulated socio-economic data of garden locations in order to develop socio-economic profiles of our sample sites. The project was driven to its final form in collaboration with a driven undergraduate researcher. Preliminary results indicate more municipal level influences over garden location, but that local level influence may exist in the resource composition of urban agriculture (Iuliano et al 2017).

Wild pollinator and plant dynamics: theoretical considerations

My research into pollinators in natural settings is driven by incorporating data and experimentally vetted empirical realities into mathematical models. Theoretical ecologists develop mathematical models to educate the intuition and reveal the outcomes of complicated ecological interactions. The goal of this work has been to develop a fundamental knowledge of both plant and pollinator dynamics in multiple natural settings at varying levels of complexity.

Chapter five connects plant-pollinator dynamics to other important plant-insect interactions, namely plant consumption by insect herbivores (herbivory). Using field experiment data from wild insect pollinator communities in North and South America, my collaborators and I showed that increased herbivory reduces the frequency of pollinator visits to plants according to a consistent mathematical relationship dubbed herbivore-induced pollinator limitation (HIPL). Initially, this seems like a particularly potent problem for plants as herbivores directly reduce individual plant health and decrease possibilities for reproduction by limiting pollination. I integrated this relationship into a full community model of plants, pollinators, and herbivores. While HIPL does intuitively hinder individual plant and pollinator reproduction, model output shows that it can manifest into positive population effects on plants and pollinators by indirectly regulating the growth rates of the herbivore across time and space (Glaum & Kessler 2017).

Chapter six extends the modeling approach to an increasingly important but neglected pollinator, predacious syrphid flies (hover/flower flies) (Kearns 2001; Ssymank et al 2008; Kühsel & Blüthgen 2015). Syrphid flies pollinate flowers as adults but have larval stages which feed on the insect herbivores of flowering plants (Miller 1918). This double mutualism across the stages of syrphid development seems extra beneficial. However, unlike other wild pollinators, syrphids fly larvae rely on herbivores for food. Therefore, when herbivores have low abundance, it limits syrphid growth, which actually limits pollination. In other words pollination by syrphids indirectly depends on persistent herbivores and needs supplementing from other wild pollinators. This work is the first to detail this negative feedback loop and describe how syrphid flies are dependent on a background biodiversity of other pollinators and herbivores (Glaum 2017).

Chapter seven continues the modeling study of unique stages in an organisms' ontogeny to plants. The results from studying the distinct stages of syrphids in Chapter six demonstrate the importance of a stage-structured ontogeny to community dynamics. With this in mind, myself and my co-author/PI, John Vandermeer, investigate the effects of incorporating ubiquitous plant stages into dynamic models of both single populations and communities. Taking common stages in plant development, such a seed banks and/or seedlings, we show that the effect of intraspecific competition between stages can alter key assumptions about resource dynamics. Specifically, these intraspecific competitive effects induce numerous non-additive effects of model parameters on community stability. This modeling work presents initial steps towards incorporating stage structure in larger community models involving plant-pollinator interactions.

Finally, chapter eight offers summaries of key points from each of the previous chapters. Here I also describe conclusions and implications before detailing some future projects developing from the work presented in this thesis. I then end with a brief description of how I hope to build off the results and relationships I have developed over my time completing this degree.

1.1 References

Biesmeijer JC, et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. Science 313(5785):351–354.

Burkle LA, Marlin JC, Knight TM. 2013. Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function. Science. 339: 1611-1616.

Cameron SA, et al. 2011. Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Science USA 108(2):662–667.

Fortel L., Henry M, Guilbaud L, Guirao AL, Kuhlman M, Mouret H, Rollin O, Vaissiere BE. 2014. Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. Plos One 9(8): e104679.

Garibaldi LA, Aizen MA, Klein AM, Cunningham SA, Harder LD. 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. Proceedings of the National Academy of Science USA 108(14):5909–5914.

Gallai N, Salles JM, Settele J, Vaissiere BE. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68(3): 810–821.

Goulson D. 2003. Conserving wild bees for crop pollination. International Journal of Food Agriculture and the Environment, 1, 142–144.

Goulson D, Lye GC, Darvill B. 2008. Decline and conservation of bumble bees. Annual Review of Entomology, 53, 191–208.

Glaum, P. 2017. A theoretical basis for the study of predatory syrphid fly ecology. Theoretical Ecology 10(4): 391-402.

Glaum P & Kessler A. 2017. Functional reduction in pollination through herbivore-induced pollinator limitation and its potential in mutualist communities. Nature communications 8.1: 2031.

Glaum, P., Simao, M.-C., Vaidya, C., Fitch, G. & Iulinao, B. 2017. Big city Bombus: using natural history and land-use history to find significant environmental drivers in bumble-bee declines in urban development. R. Soc. Open Sci. 4, 170156.

Iuliano, B., Markiewicz, A., Glaum, P. 2017. Socio-economic Drivers of Community Garden Location and Quality in Urban Settings and Potential Effects on Native Pollinators."

Michigan Journal of Sustainability 5.1

Kearns CA. 2001. North American dipteran pollinators: assessing their value and conservation status. Conservation Ecology 5(1): 5. [online] URL: http://www.consecol.org/vol5/iss1/art5/

Kearns CA & Oliveras DM. 2009. Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. Journal of Insect Conservation 13:655-665. DOI 10.1007/s10841-009-9215-4.

Kennedy CM, et al. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters 16: 584–599.

Koh, I. *et al.* 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proc. Natl. Acad. Sci.* **113,** 140–145.

Kühsel S & Blüthgen N. 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. Nature communications 6.

Miller D. 1918. The Economic Bearing of Hover-Flies. New Zealand Journal of Agriculture 1918, September 20th Vol. 17 No. 3:129-135.

Pardee GL & Phipott SM. 2014. Native plants are the bee's knees: local and landscape predictors of bee richness and abundance in backyard gardens. Urban Ecosystems 17: 641–659.

Potts SG, et al. 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol Evol 25(6):345–353.

Rundolf M, Anderson GKS, Bommarco R, Fries I, Hedertrom V, et al. 2015. Seed coating with a neonicotinoid insecticide negatively affects wild bees. Nature. doi:10.1038/nature14420.

Ssymank A, Kearns CA, Pape T, Thompson FC. 2008. Pollinating flies (Diptera): A major contribution to plant diversity and agricultural production. *Biodiversity* 9.1-2: 86-89.

Williams NM & Kremen C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecological Applications 17(3): 910-921.

Winfree R, Bartomeus I, Cariveau DP. 2011. Native Pollinators in Anthropogenic Habitats. Annu. Rev. Ecol. Evol. Syst. 42:1-22.

Whitehorn P, Connor SO, Wackers FL, Goulson D. 2012. Neonicotinoid Pesticide Reduces Bumble Bee Colony Growth and Queen Production. Science. 336: 351-352.

Woodcock BA, Isaac NJB, Bullock JM, Roy DB, Garthwaite DG, Crowe A, Pywell RF. 2016. Impacts of neonicotinoid use on long-term population changes in wild bees in England. Nature Communications. DOI: 10.1038/ncomms12459.

Chapter 2

Big city *Bombus*: Using natural history and land use history to find significant environmental drivers in bumble bee declines in urban development

2.1 Abstract

Native bee populations are critical sources of pollination. Unfortunately, native bees are declining in abundance and diversity. Much of this decline comes from human landuse change. While the effects of large-scale agriculture on native bees are relatively well understood, the effects of urban development are less clear. Understanding urbanity's effect on native bees requires consideration of specific characteristics of both particular bee species and their urban landscape. We surveyed bumble-bee (*Bombus* spp.) abundance and diversity in gardens across multiple urban centres in southeastern Michigan. There are significant declines in *Bombus* abundance and diversity associated with urban development when measured on scales in-line with *Bombus* flight ability. These declines are entirely driven by declines in females; males showed no response to urbanization. We hypothesize that this is owing to differing foraging strategies between the sexes, and it suggests reduced *Bombus* colony density in more urban areas. While urbanity reduced *Bombus* prevalence, results in Detroit imply that 'shrinking cities' potentially offer unique urban paradigms that must be considered when studying wild bee ecology. Results show previously unidentified differences in the effects of urbanity on female and male bumble-bee populations and suggest that urban landscapes can be managed to support native bee conservation.

2.2 Introduction

Evidence is mounting that native wild bee populations have dramatically decreased (Biesmeijer et al 2006; Potts et al 2010; Caemeron et al 2001). The decline of these pollinators is a significant concern for human food systems, given that pollinators are responsible for the increased quantity, quality and yield stability of over 60% of world crops (Garibaldi et al 2011), worth an estimated approximately 200 billion dollars per year (Gallai et al 2009). While managed honeybees have received much of the attention (especially in popular media), wild bees have also experienced significant declines. The loss of wild bee pollination is a critical concern. Wild bees are often more efficient pollinators than honeybees, providing pollination services that cannot be replaced by honeybees (Garibaldi et al 2013). Furthermore, parallel declines in honeybees through colony collapse disorder reinforce the importance of wild bees to pollination services. Outside of human food systems, wild bees are essential for the maintenance of angiosperm diversity. Extirpation of bee species vulnerable to land-use change has been shown to disrupt wild plant–pollinator networks (Beismeijer et al 2006; Burkle et al 2013).

Causes for the decline in the abundance and diversity of wild bees are varied, though many of the empirically supported drivers have an anthropogenic source. Human land-use change has greatly altered the environment these wild pollinators inhabit through agricultural and urban development. Industrial agriculture reduces flowering plant biodiversity and suitable nesting sites, particularly for ground nesting species (Williams & Kremen 2007; Kennedy et al 2013). Additionally, pesticides such as neonicotinoids have been increasingly linked to declines in colony health for eusocial bees (Whitehorn et al 2012; van der Sluijs et al 2013; Goulson 2015; Rundolf et al 2015). Neonicotinoids have also been linked to the declines seen in other wild bee species with varying degrees of sociality (Woodcock et al 2016). For urban settings, often considered detrimental for various taxa (Czech 2007), the effect on wild bee communities has actually been less clear (Winfree et al 2011).

A number of published studies show no significant effects of urban development on overall wild bee abundance, richness and/or diversity (Kearns and Oliveras 2009; Sattler et al 2010; Banaszack-Cibicka & Zmihorski 2012; Pardee & Philpott 2014). There are studies which have found a significant negative effect of urban development on bee abundance and richness (Bates et al 2011), though others have found this negative effect to be significant only with small solitary bees but not larger bees (Geslin et al 2013). Still others have found that abundance declines with the highest intensities of urban development, but intermediate levels of urban development support the highest levels of species richness (Fortel et al 2014). Finally, there are researchers who similarly found no significant effects on wild bees until sampled bees were broken down into functional groups. For example, urban environments can have very different effects on ground and cavity nesting species (Cane et al 2006; Neame et al 2013). Thus, there seems to be no clear trend in the effects of urban development on overall wild bee abundance and diversity.

This lack of understanding needs to be addressed for multiple reasons. Pollinator decline is an urgent issue and global urban land area in the year 2030 is expected to be triple that of year 2000 measurements (Seta et al 2013), meaning more and more pollinating species will come into contact with urban landscapes. Furthermore, the makeup of urban spaces is becoming more diverse. While many cities continue to expand, other cities experiencing economic hardship, deemed ‘shrinking cities’, have developed high numbers of vacant lots creating pockets of unmanaged land in supposedly dense urban locations (Pallagst et al 2013). Additionally, many modern land-use strategies now advocate the expansion of forest fragments, natural reserves and urban gardens within cities, in part, to function as potential refugia supporting biodiversity (Lovell & Johnston 2009; McClintock 2010; Hodgson et al 2011; Miller et al 2015). In other words, not only are urban spaces expanding, they are becoming more diverse while changing their form and function.

Here, we propose two issues that may be restricting the research in addressing the status of wild bees in urban environments. First, wild bees as a ‘group’ have a diverse set of natural history traits and different species probably respond differently to the same variables. For example, key differentiating traits in wild bees include nesting substrate, diet preferences and effects of sociality on bee behaviour. Studies focused on investigating specific bee species or functional groups may better elucidate how different bees respond to urban spaces. Second, urbanity is an approximate term and there is heterogeneity in what urbanization means in different cities. While measures of general physical urban development are well established (Mckinney 2008), they may need to be coupled with further knowledge of land-use history and socio-economic characteristics of the landscape itself to develop a deeper understanding of the environment. For example, unique economic histories and different management of similar land types may alter the suitability of seemingly similar urban environments to wild bees.

To address these issues, we present an investigation on the effects of urban development on bees in the genus *Bombus* (bumble-bees) sampled across multiple cities in southeastern Michigan with varying degrees of urban development. Bumble-bees are important generalist pollinators considered a key-stone species (Goulson 2003; Goulson et al 2008) and are some of the most effective native pollinators (Williams et al 2012). Currently, numerous *Bombus* species are experiencing population and diversity declines (Cameron et al 2011; Williams & Osborne 2009). Therefore, there is a conservation aim to studying *Bombus*, but bumble-bees are also suitable study organisms, given the aims of this study.

The genus *Bombus* represents a distinct, well-studied set of traits that make it feasible to incorporate natural history into analysis, addressing the need to integrate species-specific traits into analysis. For example, bumble-bees' need to nest in less-disturbed areas with bare ground, tall grass or abandoned tree stumps, making them a good candidate for testing the effects of urban land development. Also, their generality as pollinators suggests less confounding effects from specific floral resources when studying *Bombus* populations across an urban gradient. Finally, the eusociality of *Bombus* means different colony members have distinct roles, behavioural and movement patterns which allows for further inference into the effects of urbanization on specific components of bumble-bee dynamics. Specifically, female workers are central place foragers, generally tied to colony location. Male drones, on the other hand, are not tied to colony location as they leave to find mates. Our study design also addresses the need to incorporate urban heterogeneity. The use of multiple city centres allows for the comparison of areas with similar general characteristics but disparate land-use histories.We contend that incorporating fundamental but potentially overlooked natural history characteristics of *Bombus* coupled with land-use history of the study sites helps present a clearer picture of the status of these bees in urban spaces.

The broad questions addressed here are:

(1) How do landscape-level variables (urbanization) and local variables (temperature, floral resources) affect measured *Bombus* abundance and diversity in sample sites?

(2) How do the effects of urbanization differ for female workers and male drones?

(3) Are the effects of urbanization on *Bombus* consistent in all sites across all cities sampled?

2.3 Study System

2.3.1 Sample sites

Sampling took place across 30 sites in southeastern Michigan, USA, across a gradient of urbanization during the summers of 2014 and 2015. Sites were located in the cities of Dexter, Ann Arbor, Ypsilanti, Dearborn and Detroit and span 110km (see Figure A1). These cities vary markedly in size and density. Detroit is a large city, but in many areas has a high proportion of vacant land, the result of decades of economic difficulty and population declines. As such - and recent economic growth notwithstanding - it, along with many other post-industrial cities experiencing population decline, has been termed a ‘shrinking city’ (Pallagst et al 2013; Ryan 2008). Other cities in the survey area are smaller, with substantially lower vacancy rates and with dense urban cores surrounded by suburban development. Across the 30 sites, three natural/reserve sites and two rural farms were included, while the remaining 25 were urban gardens/farms. Gardens/farms sampled in each city were either part of an independent managing organization or property of the University of Michigan (see Table A.1). Urban farms and gardens are good study sites because they act as resource lures and can have very different local characteristics. This makes it possible to study the effects of landscape-level variables by using gardens in distinctly widespread locations as well as any interactions between those landscape-level variables and different local variables at each particular garden. All sample sites prohibited the use of neonicotinoid pesticides. Garden sites have guidelines to use organic growing practices with some management organizations following the guidelines put forth by the Organic Crop Improvement Association.

2.3.2 Study organism: the genus Bombus

Typical bumble-bees (non-parasitic) live in colonies with a eusocial structure, including a single reproductive queen, variable numbers of non-reproductive female workers and male reproductive drones. Over-wintered, mated queens emerge, typically in spring, and begin foraging, laying eggs and producing female workers. Workers then take over the task of foraging, leaving and returning to the colony multiple times per day with pollen and nectar loads for larvae (known as central place foraging) (William et al 2012). In late summer/autumn, new virgin queens and males are produced. Both leave the colony to mate. Queens may return, but males are eventually forced out of the colony permanently. The original queen, workers and males eventually die before winter and only the newly mated queen overwinters until the next season.

Bumble-bees are generalist foragers, able to pollinate and gain sustenance from numerous plant families. Their nests are smaller than honeybee nests and are made in shaded areas within old rodent holes or self-made cavities in loose soil. There are some bumble-bees that can nest above ground in thick grass or holes in tree stumps. Bumble-bees are also strong fliers

(Greenleaf et al 2007), able to cover greater than 1km during foraging flights, with maximum measurements reaching approximately 2km (Hagen et al 2011).

2.4 Materials and Methods

2.4.1. Bee sampling and identification

Fixed effort sampling for bees across sites was completed through pan traps and active netting. Pan traps were coated with a UV light reflective paint in one of three colours: white, yellow and blue. These three colours have shown success in covering the range of attractive UV spectrum colours used by many flowering plants (Droege 2002). We used two pan traps of each colour for a total of six pan traps per site per trapping effort. This is equal to or greater than the number of pan traps used in other studies (Cane et al 2006; Neame et al 2013; Hernandez et al 2009; Philpot 2013). In sites where vegetation height was low and the ground was visible from above, pan traps were placed at ground level. In sites where vegetation covered the ground, pan traps were mounted on PVC pipes used to match the height of the vegetation line and keep them visible to flying bees. Traps were arranged in an 8m2 rectangle with pan traps at the vertices and middle of the longer sides of the rectangle. In order to cover a sufficient range of the gardens with all the pan trap colours, similar coloured pan traps were placed 2m apart.

Bumble-bees are strong fliers and can often escape pan traps (Droege 2002). Therefore, pan trapping was accompanied by monthly active netting sessions. Netting took place each month for the duration of this study between 9.00 and 12.00 and 13.00 and 14.00 at each site during clear and sunny days (wind speeds less than 4ms−1). Netting was completed using nets with a 2 ft long handle, 1 ft diameter net as well as plastic bagging when bees were stopped on flowers.

Pan trapping was performed once every second week, starting mid-May and running until mid-September for a total of nine trapping dates. Netting occurred four times throughout the sampling, once in spring, twice in summer and once at the beginning of autumn in an attempt to cover the differences in community composition linked to the major seasonal changes. Owing to permissions from managing organizations, four of the six Detroit sites had to be sampled in 2015. This additional sampling was completed in order to increase the amount of data from sites with higher urbanity. All other sites were sampled in 2014. No sites were sampled in both years. Site lists and sampling times are available in Table A.1. In general, insects are not federally regulated wildlife and no permits or permissions are required for sampling. The rusty patch bumble-bee (*Bombus affinis*) was added to the endangered species list in 2017, but this sampling took place years earlier and no *B. affinis* were collected in this dataset. Permissions for entry and sampling in sites were granted by managing organizations at each site (Table A.1). All sampled bees were returned to the laboratory and stored in 70% ethanol until they were cleaned, air-dried and pinned for identification. Initial identification to sex and species was completed using a digital microscope and the discoverlife.org online key for the genus *Bombus*. Identifications were verified by taxonomist Jason Gibbs at Michigan State University.

2.4.2 Geographical information system measurements of landscape variables: impervious surface

We used geographical information system (GIS) programmes to develop profiles of the land cover types surrounding each study site. The proxy metric for urban development in this study is impervious surfaces. Impervious surfaces are roads, buildings, parking structures or anything else that effectively blankets the surface with concrete or building material. To calculate the amount of impervious surface coverage around each site, National Land Cover Database data from 2011 (Multi-Resolution Land Characteristics Consortium, mrlc.gov) was used. In keeping with McKinney’s (2008) suggestion of defining urban landscapes as areas with more than 50% impervious surface, areas categorized as high (80–100% impervious) and medium (50–79% impervious) density development were summed to obtain the total area of impervious surface within buffer zones of radius 500 m, 1, 1.5 and 2km around each individual sampling site. Dividing that total area of impervious surface by the overall land area resulted in the proportional area of impervious surface cover for each buffer zone of each sampling site.

2.4.3 Local variables (floral resources and temperature)

Floral resources were measured in a 20m radius circle at each sampling date. The circle was centred in the centre of the pan trapping 8m^2 rectangle on trapping dates and the centre of the netting area on active netting dates giving 1256.637m2 of floral survey area per site per trapping date. Floral abundance of each species was estimated using a modified logarithmic scale (i.e. 1–10 blooms, 11–50, 51–100, 101–200, 201–500, 501–1000, greater than 1000) and species’ individual floral area was calculated by averaging a representative sampling of individual flower areas for each species (MecFrederick & Lebuhn 2006; Potter & Lebuhn 2015). The floral area of a single species at a site can then be calculated by multiplying the flower count by the average floral area for that species; flower area has been shown to be a good proxy for floral resource availability (Weiner et al 2014). Summing each species' area gives the overall floral resource area at each site per sampling date. Floral resource area per sample sitewas measured as total cumulative area across the growing season, mean area across sampling times and variance in area across sampling times. Total cumulative floral area was used as a proxy for count data to determine floral diversity per site using the Shannon–Wiener *H* index. Regressions presented here use the mean floral area per site as the site-level floral abundance, but no floral variables showed any significant effects on *Bombus* abundance or diversity in any models.

Local temperature wasmeasured by Hobo brand data loggers from the Onset Computing Corporation placed in an unshaded area at each site within the floral survey circle. Loggers were placed at sites during the first sampling effort, removed at the last sampling date. Daily average, minimum and maximum temperatures were logged every 24 h. Several data loggers were either damaged by wildlife or stolen from sites, so temperature data were only available for 22 sites (Table A.1). Temperature data across the field season were broken into three summarized subcomponents, average daily minimum temperature, average daily mean temperature and average daily highest temperature.

2.4.4 Statistical analysis

Bombus abundance per site is a cumulative sum of all individual bumble-bees sampled at a site. Males and females are summed separately when the abundance of different sexes are analysed. *Bombus* diversity per site was measured by using EstimateS (Colwell 2013) to estimate the Shannon–Wiener *H* diversity index from rarefied *Bombus* species counts. When separate female and male diversity levels are considered per site, rarefaction and Shannon–Wiener *H* estimates are completed for each sex separately.

Statistical analysis and model fitting was done using the statistical language R. *Bombus* abundance and diversity function as dependent variables in regressions, with floral resources, temperature, sampling year and the proportion of impervious surface serving as predictors. Four Detroit sites were sampled in 2015, while the remaining sites were sampled in 2014. Therefore, analysis of abundance and diversity involving the Detroit sites initially used year as a random effect in linear mixed models (LMEs) fit by maximum likelihood, with proportion of impervious surface, temperature and floral area/diversity as fixed effects. Maximum likelihood was used instead of restricted maximum likelihood in order to compare across different combinations of fixed effects (Zurr et al 2009; Fairway 2006). However, across all LMEs tested, year consistently had no effect, partially because there is very little variation in the abundance and diversity of 2015 sites. Likelihood ratio tests on LMEs and general linear models (LMs) with no year effect show no significant differences. Additionally, Akaike information criterion (AIC) values for general LMs with only fixed effects are consistently lower. Therefore, the analysis involving Detroit sites presented here shows results from LM regressions. All sites outside of Detroit were sampled in 2014, so there is no year effect. Therefore, general LMs were used when analysing abundance and diversity at sites outside of Detroit alone. Model residuals show a good match to linear regression (Figures A.3 and A.5).

Spatial autocorrelation can influence results of regressions through effects on dependent variables. We used the same metrics as Pardee & Philpott (2014) to examine the possibility of the influence of spatial autocorrelation: spatial correlograms (R package 'ncf') and the Moran's test for spatial autocorrelation in R. For correlograms, we computed 100 permutations using the 'resamp' argument in the correlog function. Moran's *I* results showed no spatial autocorrelation among dependent variables and spatial correlograms showed no spatial autocorrelation at the various buffer zone increments.

2.5 Results

Across the sample sites, we collected 520 individual *Bombus* specimens with the vast majority of the samples collected by netting (401 individuals) and a smaller subset (119 individuals) coming from pan trapping. In our sample population, 10 species/morphospecies were identified. The most abundant species sampled was *Bombus impatiens* (the common eastern bumble-bee), making up 72.12% of the sample set. Other species making up a sizeable percentage of the sample set were *Bombus griseocollis* (brown-belted bumble-bee, 11.35%) and *Bombus bimaculatus* (two-spotted bumble-bee, 9.62%), while the remaining specimens rounded out the remaining approximately 7%.

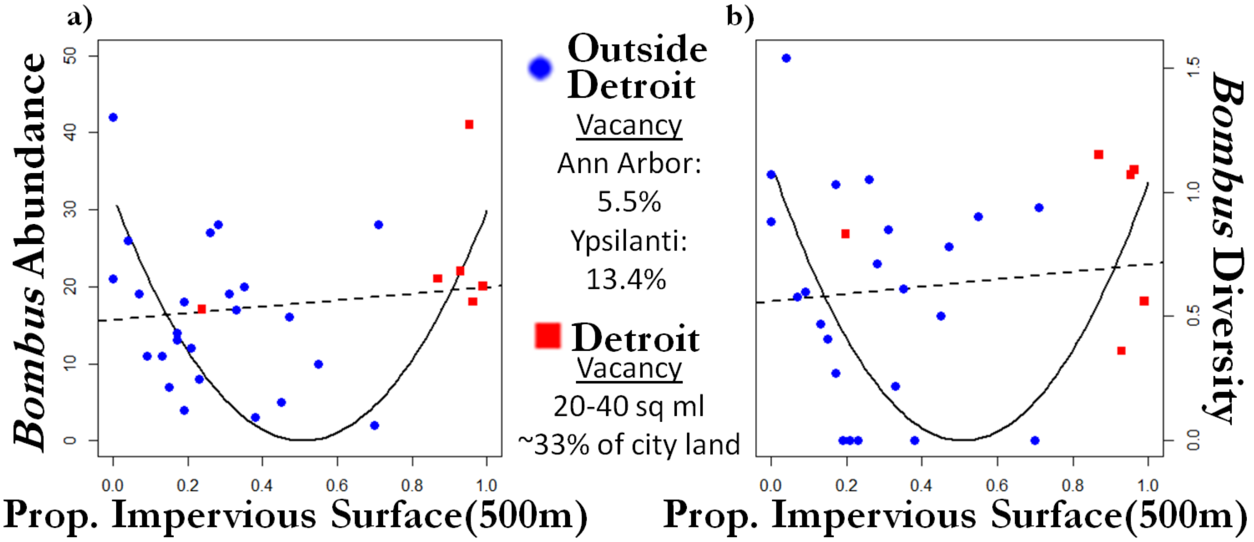

Figure 2.1- Overall Bombus abundance and diversity. Scatterplots of (a) overall Bombus abundance and (b) overall Bombus diversity with impervious surfac e measured in the 500 m radii from sites. Sites outside the city limits of Detroit are shown in blue circles and sites within the city limits of Detroit are shown in red squares. (a) Initial linear analysis shows no significant interactions between Bombus abundance and %impervious space (general linear model, dashed line, $F_{1,28}=0.513$, $p=0.48$, $R^2=-0.0171$). However, a parabolic model can be significantly fitted to the data (solid line), $y=(a \times x-i)2$; y is the overall Bombus abundance, x the proportion of impervious surface proportion at 500 m, $a=11.09$ with $p<0.001$, $i=5.632$ with $p<0.001$. Residual standard error: 11.08 on 28 d.f. (b) Initial linear analysis shows no significant interactions between Bombus diversity and % impervious space (e.g. general linear model, dashed line, $F_{1,28}=0.341$, $p=0.564$, $R^2=-0.0233$). However, a parabolic model can be significantly fitted to the data (solid line), $y=(a \times x-i)2$; y is the overall Bombus diversity, x the proportion of impervious space at 500 m, $a=2.08$ with $p<0.001$, $i=1.056$ with $p<0.001$. Residual standard error: 0.474 on 28 d.f.

2.5.1. Bombus abundance

Initial analysis into drivers of *Bombus* abundance across all sampled sites did not indicate any significant linear relationships with impervious surface (measured at all buffer zones, Figure 2.1a), floral resources (mean and total area, richness nor diversity) or temperature (low, mean nor high). However, further analysis revealed that significant parameter fits can be produced using parabolic models across proportion of impervious surface (shown at 500m buffer zone radius in Figure 2.1a). This parabolic pattern prompted investigation into the results in individual sites across the different cities along the range of impervious surface cover. Sites outside of Detroit generally aggregate on the left side of the parabola where increasing impervious surface decreases the abundance of bumble-bees sampled. Sites within Detroit, on the other hand, are located on the right side of the parabola where increased impervious surface seemingly correlates with an increase in *Bombus* abundance compared with sites with moderate impervious surface cover.

This is an initially unintuitive trend and prompted a general examination into the characteristics of the different major urban settings of the sites, Ann Arbor, Ypsilanti and

Detroit. Despite having the highest proportional area of impervious surface of any city in our study, Detroit has large amounts of vacant or idle land. Measurements of vacancy rates vary with some controversy (Davidson 2012), making them difficult to study/include in analysis. But recent estimates of vacancy classify approximately 33% of city land classified as vacant (Data Driven Detroit 2010; Detroit Works Project 2011). On the other hand, the other two major cities sampled, Ann Arbor and Ypsilanti, have comparatively small percentages of vacant/idle land at 8.9% and 13.4%, respectively (United States census 2010). Despite any uncertainty over the official amount of vacant land in Detroit (Davidson 2012), there is a clear difference in vacancy rates inside and outside Detroit. This difference in city composition (which exists despite an increase in impervious surface) signals the need for distinct analyses to be completed inside and outside of Detroit. These separate analyses serve to clarify the patterns introduced in the parabolic model fitting and help compensate for the fact that the sites with highest impervious surface were also located in the city with the highest percentage of vacant land.

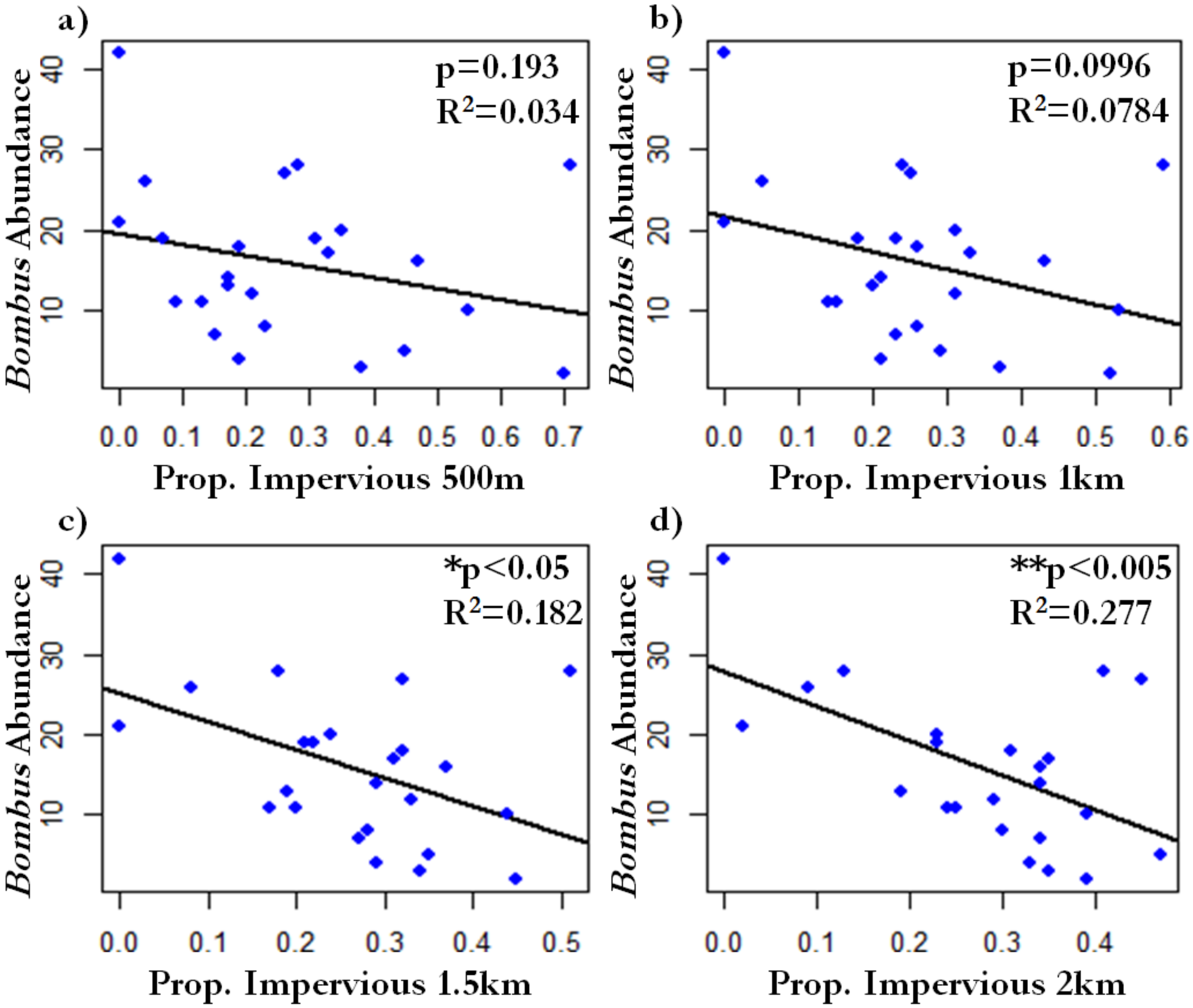

*Figure 2.2 – Bombus abundance at different radii. Scatterplots and general linear regressions of overall sampled Bombus abundance and proportion of impervious surface at sites outside of Detroit. Overall Bombus abundance is regressed against (a) 500 m buffer zone radii (F1,22 =1.81, p=0.193, R^2 =0.034, AIC=179.97), (b) 1 km buffer zone radii (F1,22 =2.96, p=0.0996, R^2 =0.0784, AIC=178.84), (c) 1.5 km buffer zone radii (F1,22 =6.10, p=0.022, R^2 =0.182, AIC=176.00) and (d) 2 km buffer zone radii (F1,22 =9.82, p=0.0048, R^2 =0.277, AIC=173.01). The significance of fit and effect size increase as the regressed buffer zone radius increases from 500mto 2 km, indicating the importance of measuring landscape variables at appropriate scales. *p<0.05; **p<0.01.*

For sites outside of Detroit, general LM show significant negative correlations between impervious space and overall *Bombus* abundance. These negative correlations become stronger as the radius of the regressed environmental profile of each site increases from 500m to 2km (Figure 2.2a–2.2d). In other words, the effect of impervious surface on bumble-bee abundance becomes apparent only when environmental variables are measured on a larger scale. Recall that bumble-bees are strong fliers; workers have been measured flying greater than 1km during foraging flights. If a foraging worker can fly greater than 1km away from the colony to a particular area of floral resources, then knowing that 500m of unsuitable habitat surrounds the floral resources does not necessarily indicate whether or not a worker will reach that resource. That is because 500m of unsuitable space would easily be traversed by a forager with greater than 1km of flight ability. Only upon measuring impervious surface at a scale in accordance with workers' flight ability do significant interactions become clear (Figure A.2). This result highlights the importance of considering the appropriate scale when measuring environmental variables at the landscape level.

Owing to the apparent importance of bumble-bee flight ability, further natural history characteristics were taken into consideration. Given the behavioural differences between female workers and male drones, we separately analysed the response of each sex to impervious surface. Splitting the data reveals that the decline in overall *Bombus* abundance shown in Figure 2.2 is entirely driven by a decrease in female workers across the impervious surface gradient (Figure 2.3a). Models of reductions in female abundance follow the same pattern detailed in Figure 2.2, becoming more significant with greater effect size as the regression considers larger buffer zone radii (Figure A.4). Removing males from the regression and focusing solely on females clearly increases the significance and effect size compared with the overall abundance results outside of Detroit. On the other hand, male abundance shows no correlation with impervious surface (Figure 2.3b) at any buffer radius (Figure A.4). This is a strikingly different pattern between male and female bumble-bees and is consistent when examining total sampled abundance or just the most prevalent species, *B. impatiens* (Table A.3).

Outside of Detroit, floral data did not seem to have an effect on *Bombus* abundance through any metric. The mean and total floral abundance per site, floral diversity and floral richness showed no significant relationships with overall *Bombus* abundance, female abundance or male abundance (Table A.2). Among the sites with a temperature data logger, there is a significant negative relationship between average daily minimum temperature and *Bombus* abundance (both overall and female only, but not with male abundance, Table A.4). This is owing to the link between increased impervious surface and a locations daily minimum temperature (e.g. $F_{1,19}$ =12.12, p=0.0025, R^2 =0.36 w/% impervious at 500 m). In past studies, moderately higher temperatures have been linked to increased bee activity and abundance (McCall & Primack 1992; Hegland et al 2009). Here however, because minimum temperature only increases with higher amounts of impervious surface, the correlation is reversed in this study for bumble-bees.

In the Detroit sites, overall abundance showed no significant interactions or consistent trends across any of the buffer zone radii measuring impervious surface. This is partially driven by the fact that five out of six Detroit sites ended up with approximately 20 individuals sampled per site, so there is little variation in a smaller sample size. Splitting Detroit abundance data into female and male categories also shows no significant relationships. Furthermore, models including floral data do not show any significance or help with model selection. Despite the lack of correlations within Detroit sites, average abundance in Detroit sites clearly breaks from trends established with impervious surface outside of Detroit.

If abundance trends from sites outside Detroit continued in Detroit sites, models would predict close to zero bumble-bees abundance at sites with the highest impervious surface cover. However, Detroit sample sites show abundance on par with low impervious surface sites. In fact, the site with the highest impervious surface coverage (an urban agriculture demonstration garden in downtown Detroit) had only one less individual sampled than the E.S. George Nature Reserve (42 individuals), the most preserved natural site with the lowest impervious surface cover proportion in the study.

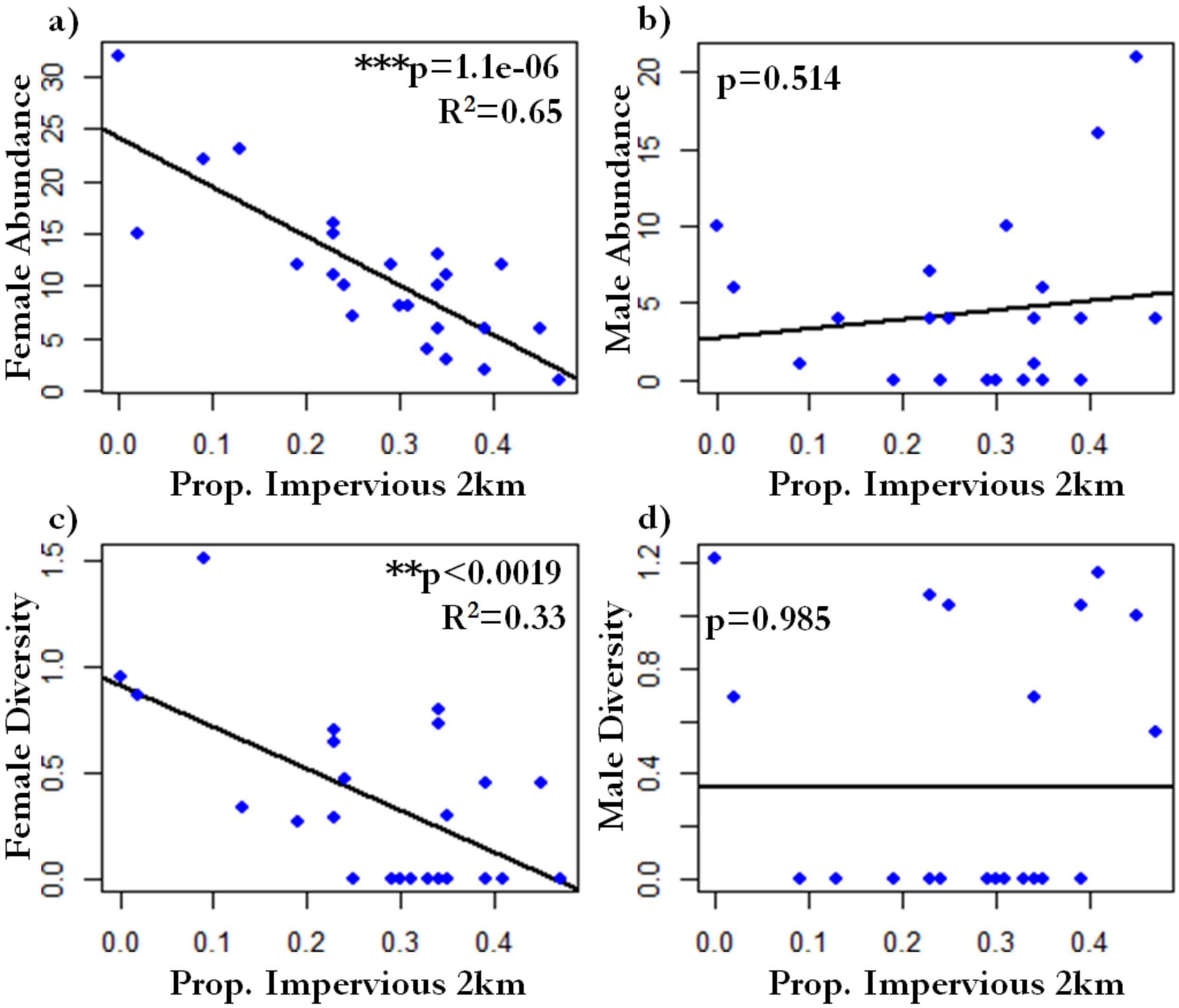

*Figure 2.3 - Differences in female and male abundance and diversity. Abundance and diversity data outside Detroit split into female worker and male drone categories regressed against site-level impervious surface measured in 2 km buffer zones. Splitting data into female workers and male drones shows the decline of Bombus abundance and diversity in high impervious surface outside Detroit is driven by decreases in female-workers. Male drones show no significant response to impervious surface. (a) Female Bombus abundance ($F_{1,22}$ =44.08, p=1.13 $\times 10^{-6}$, R^2 =0.652). (b) Male Bombus abundance ($F_{1,22}$ =0.441, p=0.5137, R^2=−0.0249). (c) Female Bombus diversity ($F_{1,22}$ =12.44, p=0.00189, R^2 =0.3323). (d) Male Bombus diversity ($F_{1,22}$ =0.0004, p=0.9852, R^2=−0.0454). **p<0.01; ***p<0.001.*

2.5.2. Bombus diversity

Similar to the initial patterns found in *Bombus* abundance, preliminary linear analysis on overall *Bombus* diversity shows no significant interactions or trends when considering all sites sampled in the survey. However, as with abundance, significant parameter fitting can be done using parabolic relationships between proportion of impervious surface and *Bombus* diversity (Figure 2.1b). Once again, the sites outside of Detroit mainly aggregate on the left side of the parabola and sites inside Detroit largely aggregate on the right side (Figure 2.1b). Given this result and the relationships found with abundance and impervious surface, separate analyses were again completed for the diversity of sites outside Detroit and sites inside Detroit.

Outside of Detroit, there are near significant declines in overall *Bombus* diversity with increased impervious surface (Table A.6). Intuitively, given the different results for female and male abundance, the significant correlation between *Bombus* diversity and increased impervious surface is driven entirely by declines in female-worker diversity (Figure 2.3c). The significance and effect size of impervious surface on female diversity generally increases with the radius of the environmental profile considered in the regression (Figure A.6). Inclusion of floral abundance, floral diversity and temperature did not increase the goodness-of-fit for any model tested (Table A.6). Male diversity, on the other hand, did not show any significant interaction with proportion of impervious surface measured at any radii (Figure 2.3d; Figure A.6), any floral data or temperature data.

For sites in Detroit, no significant effects of impervious surface were found for overall, female or male *Bombus* diversity. Furthermore, floral data and temperature did not aid in model fitting. Despite the lack of significant effects found across sites within Detroit, diversity of bumble-bees sampled within Detroit is higher than would be suggested by models only considering sites outside Detroit. For example, the mean diversity of females in Detroit sites is 0.52 while the data from sites outside of Detroit produce models which predict the diversity of 0.0 at approximately 70% impervious surface (Figure A.6a). Within Detroit sites, both *Bombus* abundance and diversity go against significant relationships established by the sampling results in the remaining sites.

Finally, in sites outside of Detroit, the abundance of bumble-bees caught at each site strongly correlated with the diversity of the bumble-bees caught ($F_{1,22}$ =18.3, p=0.0003, R^2=0.43). Sites within Detroit show no such relationship ($F_{1,4}$ =0.272, p=0.630, R^2=−0.171). This is partially caused by a smaller sample size within Detroit and the lack of variation in abundance found in Detroit sites.

2.6 Discussion

We found that increased urbanization (as measured through proportion of impervious surface area) in sample sites outside of Detroit had a significant negative effect on *Bombus* abundance and diversity. However, the decline is apparent only when impervious surface is measured at appropriate scales (Figure 2.2). Bumble-bees are large-bodied bees with large foraging ranges, so measurements of landscape level variables must be taken at scales which align with their flight ability. In fact, this study doubled the amount of land area taken into consideration of other *Bombus* studies (Ahme et al 2009). This relationship could be lost in our efforts if impervious surface was only measured at the 500m scale.

Crucially, we found that the decline in overall *Bombus* abundance and diversity was entirely driven by declines in female workers while male abundance and diversity were unrelated to urbanization. Given that workers are central place foragers, workers spend most of their time foraging close to the nest. Thus, it is reasonable to hypothesize that worker abundance is proportional to bumble-bee colony density. Then, this decline in worker abundance and diversity implies that higher impervious surface coverage could be reducing the number of viable *Bombus* colonies by reducing the availability of nesting sites. Such a conclusion has been supported by molecular work where urban development showed significant correlations with decreased nest density (Jha & Kremen 2013). Impervious surface signifies building development, concrete parking structures, asphalt roads, etc. all forms of urban development which blanket the surface of the ground with impermeable material. This would limit species that nest underground as bumble-bees cannot dig through solid concrete. It also hinders species which nest on the surface by removing necessary cover like tall grass or tree stumps.

The lack of any relationship between male abundance and diversity with urban development is also noteworthy. Male bumble-bees are not tied to their natal colony post-emergence; rather, they disperse widely in search of mates. Our findings therefore suggest that *Bombus* are able to disperse across even highly modified urban landscapes. Considering this result, it is reasonable to hypothesize that male dispersal is potentially facilitated by the presence of urban gardens like the ones in which we sampled, as well as other green spaces that interrupt the density of impervious surfaces (Jha & Kremen 2013b). This distinction between female and male responses to landscape development is an important consideration for studying *Bombus* in disturbed habitats.

In addition to the importance of natural history, these results also highlight the use of considering the socio-economic history of the landscapes studied in landscape ecology. Whereas, outside of Detroit, impervious surface strongly correlated with worker decline, sites within Detroit had higher *Bombus* abundance and diversity, despite their location in the densest urban landscape. It is important to note that we do not argue that impervious surface necessarily creates a parabolic relationship with bumblebee abundance or diversity. Instead, we argue that there is a clear negative effect of increased impervious surface on bumble-bee abundance and diversity exhibited in the 24 sites sampled outside of Detroit. The sites sampled inside Detroit, however, defy this relationship and were found to have higher abundance and diversity despite the increase in impervious surface. It was the parabolic fit that prompted splitting the analysis considering the unique context of Detroit's urban spaces.

Detroit has experienced decades of economic hardship and declining human populations. Therefore, despite its high proportional impervious surface coverage, Detroit is characterized by an abundance of vacant lots. Vacancy may make lawns more suitable as they are less frequently mowed (and compacted). They are also less likely to be treated with pesticides or herbicides. Therefore, these lots can provide various flowering plants (Harrison 2002; Robinson & Lundholm 2012) and suitable nesting substrate (Cane et al 2006). Indeed, vacant lots have been shown to support bee diversity and abundance comparable to nearby green spaces (Gardiner et al 2013). In general, our results suggest that shrinking cities present unique ecological patterns and may offer avenues for research in sustainable city development.

When addressing the decline in *Bombus* workers with increases in impervious surface outside of Detroit, it is important to consider alternative hypotheses. It is possible that impervious surfaces do not necessarily restrict the number of *Bombus* colonies, but instead correlate with a decline in the health of *Bombus* colonies such that a similar number of colonies produce fewer workers per colony than colonies surrounded by less impervious surface. However, preliminary results suggest that commercial *Bombus* colonies placed in mid and high-level impervious surface areas do not produce lower numbers of workers (C. Vaidya 2016, personal communication).

Alternatively, it could be that colony growth patterns differ systematically along the impervious surface gradient. Sampling in this study ended in September, but *Bombus* species can forage into October. If colonies in midlevel urban locations outside Detroit (where we found low *Bombus* abundance) had either later emergence time or required longer times to reach peak worker abundance, we may be underestimating *Bombus* abundance at these sites. However, the decline in *Bombus* owing to impervious surface is a consistent significant interaction across the entire sampling period, so there is no signal that this result depends on the time of year the sampling occurs (Table A.5). Also, if the low abundance sites did produce more workers after our sampling ended, it is reasonable to assume there would be a similar decline in males across the urban gradient, which is not the case.

Nothing in the analysis suggested that the measured floral resources contributed to the decline in sampled workers or any of the other results presented here. While flowering plants are obviously an important resource of any pollinator, the scale of floral resources measured for this study may not align with bumble-bee foraging behaviour. Bumble-bees can make an urban garden a single stop on a longer foraging flight. Given their flight ability, floral data may need to be measured at very large scales in order to find effects of floral resources on *Bombus* prevalence.

Overall, these results have important implications for conservation of native bee populations and pollination services. The impervious surface-driven decline in *Bombus* worker abundance and diversity is potentially problematic on a broader scale, given that numerous native bee species are soil nesting and may experience similar declines. Perhaps most importantly though, is the lack of relationship between impervious surface and male abundance/diversity. This implies that female and male bumble-bees use and move through urban environments differently. This variation in movement behaviours is critical to understanding abundance patterns and an important consideration for landscape bee studies in general.

Finally, our results highlight the importance of heterogeneity in urban areas. In particular, we found that Detroit supported comparatively high native bee populations despite high amounts of impervious surface. This environmental heterogeneity should be considered more explicitly in future studies of the ecological effects of urban development. This study design and analysis framework would be well suited for replication in further *Bombus* studies in other shrinking and non-shrinking cities. A catalogue of *Bombus* response to urban development across different ecosystems and socio-economic land-use histories could potentially benefit sustainable city planning practices and would address the call for monitoring programmes for these important pollinators (Inouye et al 2017).

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2.8 References

Ahrné K, Bengtsson J, Elmqvist T. 2009. Bumble Bees (*Bombus* spp) along a Gradient of Increasing Urbanization. PLoS ONE 4(5): e5574. doi: 10.1371/journal.pone.0005574

Banaszack-Cibicka W & Zmihorski M. 2012. Wild bees along an urban gradient: winners and losers. Journal of Insect Conservation 16:331-343. DOI 10.1007/s10841-011-9419-2

Bates, A.J., Sadler, J.P., Fairbrass, A.J., Falk, S.J., Hale, J.D., Matthews, T.J. 2011. Changing Bee and Hoverfly Pollinator Assemblages along an Urban-Rural Gradient. Plos One 6(8): e23459.

Biesmeijer JC, et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. Science 313(5785):351–354.

Burkle, LA, Marlin, JC, Knight, TM. 2013. Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function. Science. 339: 1611-1616.

Cameron SA, et al. 2011. Patterns of widespread decline in North American bumble bees. Proc Natl Acad Sci USA 108(2):662–667.

Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H., Williams, N.M. 2006. Complex Responses within a Desert Bee Guild (Hymenoptera: Apiformes) to Urban Habitat Fragmentation Ecological Applications 16(2): 632-644.

Colwell RK. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Persistent URL <purl.oclc.org/estimates>.

Czech B, Krausman P, Devers P (2007) Economic associations among cases of species endangerment in the United States. Bioscience 50:593–601

Data Driven Detroit. 2010. Detroit Residential Parcel Survey. Published on Feb 15, 2010. http://www.detroitparcelsurvey.org/pdf/reports/DRPS_citywide_vacancy_housing.pdf.

Davidson K. 2012. Detroit has tons of vacant land. But forty square miles? Michigan Public Radio. Published on Apr 18, 2012. http://michiganradio.org/post/detroit-has-tons-vacant-land-forty-square-miles#stream/0.

Detroit Works Project. 2011 Detroit Works Project - Why Change. Published on Jan 27, 2011. http://www.slideshare.net/stranflow/detroit-works-project-why-change.

Fortel L., Henry, M., Guilbaud, L., Guirao, A.L., Kuhlman, M., Mouret, H., Rollin, O., Vaissiere, B.E. 2014. Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. Plos One 9(8): e104679.

Gallai N, Salles JM, Settele J, Vaissiere BE. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68(3): 810–821.

Gardiner, Mary M., Caitlin E. Burkman, and Prajzner SP. 2013. The value of urban vacant land to support arthropod biodiversity and ecosystem services." Environmental entomology 42(6): 1123-1136.

Garibaldi LA, Aizen MA, Klein AM, Cunningham SA, Harder LD. 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. Proc Natl Acad Sci USA 108(14):5909–5914.

Garibaldi LA et al. 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. Science 339: 1608-1611.

Geslin, B., Gauzens, B., Thebault E., Dajoz, I. 2013. Plant Pollinator Networks along a Gradient of Urbanisation. Plos One 8(5): e63421.

Goulson D. 2003. Conserving wild bees for crop pollination. International Journal of Food Agriculture and the Environment, 1, 142–144.

Goulson D, Lye GC, Darvill B. 2008. Decline and conservation of bumble bees. Annual Review of Entomology, 53, 191–208.

Goulson, D. 2015. Neonicotinoids impact bumblebee colony fitness in the field; a reanalysis of the UK's Food & Environment Research Agency 2012 experiment. PeerJ 3:e854; DOI 10.7717/peerj.854

Greenleaf SS, Williams NM, Winfree R, Kremen C. 2007. Bee Foraging Ranges and Their Relationship to Body Size. Oecologia 153(3): 589-596.

Hagen M, Wikelski M, Kissling WD. 2011. Space Use of Bumblebees (*Bombus* spp.) Revealed by Radio-Tracking. Plos One. 6(5): e19997

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. and Totland, Ø. 2009. How does climate warming affect plant-pollinator interactions?. Ecology Letters, 12: 184–195. doi:10.1111/j.1461-0248.2008.01269.x

Hernandez, JL, Frankie, GW, Thorp, RW. 2009. Ecology of Urban Bees: A Review of Current Knowledge and Directions for Future Study. Volume 2, Issue 1 Article 3

Hodgson K, Caton Campbell M, Bailkey M (2011) Urban Agriculture (PAS 563): Growing Healthy, Sustainable Places. American Planning Association, Chicago.

Jha S, Kremen C. 2013a. Bumble bee foraging in response to landscape heterogeneity. Proceedings of the National Academy of Sciences USA, 8: 555–558.

Jha S, Kremen C. 2013b. Urban land use limits regional bumble bee gene flow. Molecular Ecology. 22, 2483–2495.

Kearns C.A. and Oliveras, D.M. 2009. Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. Journal of Insect Conservation 13:655-665. DOI 10.1007/s10841-009-9215-4

Kennedy,C.M. et al. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters 16: 584–599.

Lovell, S.T.; Johnston, D.M. Designing landscapes for performance based on emerging principles in landscape ecology. Ecol. Soc. 2009, 14, 44.

Matteson, K, Achser, j. Langellotto, G. 2008. Bee Richness and Abundance in New York City Urban Gardens. Annals of the Entomological Society of America, 101(1):140-150.

McCall, C. & Primack, R.B. (1992). Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. Am. J. Bot., 79, 434–442.

McClintock, Nathan. "Why farm the city? Theorizing urban agriculture through a lens of metabolic rift." Cambridge Journal of regions, economy and society (2010): rsq005.

McFrederick QS & LeBuhn G. 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? Biological Conservation 129: 372 –382.

McKinney M. 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosystems, 11, pp.161–176.

Miller RW, Hauer RJ, Werner LP. Urban forestry: planning and managing urban greenspaces. Waveland Press, 2015.

Neame LA, Griswold T, Elle E. 2013. Pollinator nesting guilds respond differently to urban habitat fragmentation in an oak-savannah ecosystem. Insect Conservation and Diversity 6: 57–66. doi: 10.1111/j.1752-4598.2012.00187.x

Pallagst, Karina, Thorsten Wiechmann, and Cristina Martinez-Fernandez. Shrinking cities: international perspectives and policy implications. Routledge, 2013.

Pardee G.L. and Phipott, S. M. 2014. Native plants are the bee's knees: local and landscape predictors of bee richness and abundance in backyard gardens. Urban Ecosystems 17: 641–659 DOI 10.1007/s11252-014-0349-0

Philpot, S., Cotton, J, Bichier, P, Friedrich, R, Moorhead, L, Uno, S, Valdez, M. 2013. Local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats. Urban Ecosystems. DOI 10.1007/s11252-013-0333-0.

Potter A & LeBuhn G. 2015. Pollination service to urban agriculture in San Francisco, CA. Urban Ecosyst 18:885–893. DOI 10.1007/s11252-015-0435-y.

Potts SG, et al. 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol Evol 25(6):345–353.

Rundolf, M., Anderson, G.K.S., Bommarco, R., Fries, I., Hedertrom, V. et al. 2015. Seed coating with a neonicotinoid insecticide negatively affects wild bees. Nature. doi:10.1038/nature14420.

Sattler T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M.K., and, Moretti, M. 2010. Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology. 91(11): 3343–3353.

Seto, K, Güneralpa,B, Hutyrac, LR. 2013. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences. www.pnas.org/cgi/doi/10.1073/pnas.1211658109.

The State of the World's Land and Water Resources for Food and Agriculture. 2011. Food And Agriculture Organization Of The United Nations.

van der Sluijs, J., Simon-Delso, N. , Goulson, D., Maxim, L., Bonmatin, J., Belzunces, L.P. 2013. Neonicotinoids, bee disorders and the sustainability of pollinator services. Current Opinion in Environmental Sustainability 5:293–305.

Whitehorn, P, Connor, SO, Wackers, FL, Goulson, D. 2012. Neonicotinoid Pesticide Reduces Bumble Bee Colony Growth and Queen Production. Science. 336: 351-352.

Williams, N.M. and Kremen, C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecological Applications 17(3): 910-921.

Williams PH & Osborne JL. 2009. Bumblebee vulnerability and conservation world-wide. Apidologie 40: 367–387.

Williams NM, Regetz J, Kremen C (2012) Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 93(5):1049–1058.

Winfree R, Bartomeus I, Cariveau DP. 2011. Native Pollinators in Anthropogenic Habitats. Annu. Rev. Ecol. Evol. Syst. 42:1-22.

Woodcock BA, Isaac NJB, Bullock JM, Roy DB, Garthwaite DG, Crowe A, Pywell RF. 2016. Impacts of neonicotinoid use on long-term population changes in wild bees in England. Nature Communications. DOI: 10.1038/ncomms12459

Chapter 3

Urban development drives changes in observed adult sex ratio in wild bee communities

3.1 Abstract

Wild bees are indispensable pollinators, supporting global agricultural yield and angiosperm biodiversity. They are experiencing widespread declines, resulting from multiple interacting factors. The effects of urbanization, a major driver of ecological change, on bee populations are not well understood. Studies examining the aggregate response of wild bee abundance and diversity to urbanization tend to document minor changes. However, the use of aggregate metrics may mask trends in particular functional groups. We surveyed bee communities along an urban-to-rural gradient in SE Michigan, USA, and document a large change in observed sex ratio (OSR) along this gradient: female relative abundance declined as urbanity increased. Nest site preference and body size mediated the effects of urbanity on OSR. Our results suggest that previously documented negative effects of urbanization on ground-nesting bees may underestimate the full impact of urbanity, and highlight the need for improved understanding of sex-based differences in the provision of pollination services by wild bees.

3.2 Introduction

Wild bees (Apoidea: Hymenoptera) are critically important both to agricultural production and the maintenance of angiosperm biodiversity (Biesmeijer et al 2006; Garibaldi et al 2013), but populations of these bees are in widespread decline (Potts et al 2010). These declines are the result of multiple interacting factors including parasites and disease, pesticide use and habitat loss (Goulson et al 2015). Agricultural conversion and intensification, which is a major driver of both habitat loss and pesticide use (Goulson et al 2015; Schreinemachers & Tipraqsa 2012), is an important contributor to wild bee decline (Goulson et al 2015; Koh 2016).

The effect urbanization, however, another type of land use driving worldwide habitat loss, on wild bee communities is less well understood. This research gap is particularly concerning given that the amount of land occupied by urban development has increased rapidly in the past 50 years (Sleeter et al 2013), and this increase is expected to accelerate in the coming decades (Seto et al 2012).

In comparison to the effects of agricultural intensification, studies examining changes in bee communities along the rural-to-urban gradient have found relatively minor effects on overall wild bee abundance and diversity (Cane et al 2006; Banaszak-Cibicka & Zmihorski 2011; Fortel et al 2014). However, evaluating only these aggregate metrics of abundance and diversity obscures trends in particular guilds of bees. Most notably, studies have consistently found reduced abundance and/or diversity of ground-nesting bees in urban areas (Cane et al 2006; Fortel et al 2014; Matteson et al 2008; Ahrne et al 2009; Neame et al 2013). This shift has been attributed to the lack of appropriate nesting substrate for ground-nesting bees in urban areas due to ground coverage by urban structures (Glaum et al 2017). Thus, while the available evidence suggests that urban areas are capable of supporting robust bee communities, it also indicates that these communities are likely to differ systematically from those found outside cities, with, for example, an proportional decrease in ground-nesting bees.

Much like examining aggregate bee abundance and diversity without reference to nesting or feeding ecology, using ecological guild or even species as the unit of analysis may disguise important effects of urbanization on bee communities. In particular, life history differences between female and male bees seem likely to result in distinct trends in observed sex ratio (OSR) with increasing urbanization (Glaum et al 2017). There are two non-exclusive mechanisms by which urbanization may drive changes in OSR, explored in greater detail below: 1) sex-specific patterns of movement and dispersal and 2) labile sex ratios due to changes in available resources. For most of their life cycle, female bees are central-place foragers, collecting nectar and pollen in order to provision their brood; as a result, most foraging occurs close to the nest site (Osborne et al 2008). This is especially true for worker bees in eusocial species. Male bees, on the other hand, do not engage in parental care, instead dispersing in search of mates. Consequently, male bees tend to travel longer distances than foraging females (Lopez-Uribe et al 2015). Moreover, while reproductive females also disperse from their natal nest prior to establishing their own nest, females' dispersal distances have been measured to be smaller than males' (Osborne et al 2008; Ulrich et al 2009; Lopez-Uribe et al 2015).

Areas dominated by human land use tend to produce habitat patches in a fragmented landscape (Perfecto et al 2009). In industrial agriculture, habitat patches exist between plots of highly managed farm land. In urban landscapes, habitat patches are fragmented within a built structural matrix likely low in suitable nesting sites [at least for ground-nesting bees (Cane et al 2006; Jha & Kremen 2013)] and possibly appropriate floral resources (Matteson et al 2013 but see Lowenstein et al 2014). These differential movement patterns could result in overrepresentation of male bees. An additional point to consider is that sex allocation in bees is labile and dependent in part on food resource availability. Greater food abundance results in a higher proportion of female offspring (Tepedino & Porchio 1982; Kim 1999). Changes in the ability of foragers to provision their brood along the rural-to-urban gradient, resulting from changes in the abundance or distribution of suitable floral resources, could therefore also result in OSR shifts along an urbanity gradient.

While environmentally-generated spatial variation in OSR in bees has been scarcely investigated, prior work from my colleagues and myself has documented changes in relative abundance of male and female bumble bees (*Bombus* spp.) along a rural-to-urban gradient (Glaum et al 2017). The potential for urbanization to drive changes in bee sex ratios is significant for several reasons. First, changes in adult sex ratio can affect population dynamics (Bessa-Gomes et al 2004). Failing to account for deviations in adult sex ratio can therefore lead to potential underestimation of local extinction risks (Bessa-Gomes et al 2004; Eberhart-Phillips et al 2017). Second, there is evidence for sex-based differences in bee foraging behavior, including floral preferences (Ritchie et al 2016); floral constancy (i.e. the tendency to sequentially visit flowers of the same species, Ne'eman et al 2006); pollen transfer efficiency (Ostevik et al 2010); and flight distance between foraging bouts (Ne'eman et al 2006; Ostevik et al 2010). Thus, changes in bee community OSR may also have direct impacts on pollinations regimes and services.

Here, we document a shift in OSR in bee communities found in nature preserves and community gardens along a rural-to-urban gradient, where the proportion of male bees increases with increasing urbanity. We find that the observed increase in male relative abundance is due primarily to declining female abundance among ground-nesting bee species as urbanity increases, and that urbanity-associated OSR shifts only occur in medium- and large-bodied ground-nesting bees. We argue that OSR shifts are driven by a combination of reduced ground-nesting bee nest density in urban areas, leading to reductions in abundance of ground-nesting bees of local origin. This dispersal of male bees, we argue, compensates for reductions in the locally-originating population, thereby masking the negative effects of urbanity on ground-nesting bees measured as a single group.

3.3 Materials and Methods

3.3.1 Data collection

Sampling occurred May-September 2014, at 26 sites distributed along a rural-to-urban gradient in southeastern Michigan, USA. Sites spanned a distance of 110 km, with the surrounding land use ranging from dense urban core to suburban to rural-agricultural. Twenty one of 26 sites were community gardens, 3 sites were nature reserves, and the remaining 2 sites were rural farms. The gardens or farms sampled in each city were either part of an independent managing organization or property of the University of Michigan (see Table B.4). All gardens and farms included in the study observe organic growing practices prohibiting the use of synthetic pesticides and fertilizers.

3.3.2 Data Collection

Data collection in the field was implemented using the methods described in Chapter 1. All bees were identified to species and assigned to sex. Identification was accomplished using the Discoverlife key (Ascher & Pickering 2016), with additional identifications made by Dr. Jason Gibbs (University of Manitoba, Winnipeg, Canada) and Jamie Pawelek (Wild Bee Garden Design, formerly University of California Berkeley, USA).

3.3.3 Pollinator natural history and body size data

Once all specimens were identified to species, natural history profiles were compiled for each species using four characteristics: preferred nesting substrate, sociality, native status, and body size (Table B.2). Most natural history data were generously provided by Dr. Jason Gibbs, supplemented as necessary with literature searches. As a measure of body size, we used female intertegular (IT) distance, which is strongly correlated with flight ability and is therefore a proxy measurement of bee dispersal ability and foraging distance (Greenleaf et al 2007). When IT distance could not be found in the literature, we measured IT distance of 5 individuals of that species from our collection and took the mean as the species-specific IT distance. In cases where the species was represented by fewer than 5 individuals, we took measurements from all available samples; in general variance in IT distance across conspecific individuals was small (Table B.2). Bees were then classified as small (≤1.5mm), medium (>1.5–3.0mm), or large (>3.0mm) on the basis of IT span.

3.3.4 Landscape-level impervious surface measurements

We used National Land Cover Database (NLCD) data from 2011 (Homer et al 2015) to calculate the amount of urban development surrounding each study site as described in (Glaum et al 2017). Briefly, we used proportion of impervious surface cover as our measure of urbanity, and measured impervious surface cover at radii of 500m, 1km, 1.5km, and 2km around the study site. Summing cells categorized as high- or medium-intensity developed in the NLCD 2011 database gave us the total area of impervious surfaces within each buffer (Table B.5).

We used GLMs with Poisson distribution and log-link function to determine the radius at which impervious surface cover had the most explanatory power over bee observed sex ratio (OSR), and which, therefore, to include in subsequent analyses. For each radius, we fit a model with overall OSR as the response variable, and proportional impervious surface cover at the radius of interest as the sole predictor. We used AIC values to select the best radius; while the effect of impervious cover was similar regardless of radius, and goodness-of-fit varied little, the 2km radius had marginally the lowest AIC value (Table 3.4) and so was chosen for subsequent analyses.

3.3.5 Local floral resource and temperature measurements

Floral resource availability within 20m of the center of pan trap placement was measured at each pan trap sampling date. We identified all plants in flower within this circle to species or morphospecies, and recorded the number of open blooms on each species using a modified logarithmic scale (1-10 blooms, 11-50, 51-100, 101-200, 201-500, 500-1000, >1000). Species-specific flower dimensions were recorded in the field, and per-flower area calculated, as in ref. (Weiner et al 2014). Per-species floral area at a given survey was then calculated by multiplying floral abundance (mean value of the abundance bin) by flower size. Summing each species' area gives the overall floral resource area at each site per sampling date. Floral resource area mean across all surveys were calculated for each site (Table B.6), and we used these, along with species richness, as our measures of floral resource availability.

Because different classes of floral resources may be of differential importance in supporting bee populations, and the relative abundance of these classes may vary with urbanity, we additionally classified each flowering species found in our study sites as crop, ornamental, or weed. In subsequent analyses, we considered how floral resources were affected by urbanity, and affected bee abundance and OSR, using metrics of both the aggregate floral community and of each of these three classes of flowering plants.

Temperature at each site was measured by data loggers (HOBO, Onset Computing Corporation, Bourne, MA USA) placed in an unshaded area within the floral survey circle. Data loggers remained throughout the sampling season and recorded daily average, minimum and maximum temperatures every 24 hours. Because data loggers at several sites were compromised, temperature data were available for 22 of 26 sites (Table B.4). While mean minimum temperature had a significant effect on OSR (z = -2.92, d.f. = 20, p = 0.003), it was also significantly correlated with impervious cover surface (e.g. $p < 0.001$ at 2km radius). The direction and magnitude of the effects of temperature and impervious surface cover were similar, and the model including impervious surface cover had a lower AIC value (ΔAIC = 5.43). Thus, we omitted any measure of temperature from the analyses described below; including mean minimum temperature in our models had little impact on model outcomes (Table B.7).

3.3.6 Analysis

All analyses were carried out in R v.3.4.1 (R Core Team 2017). Because we were interested in the response of wild bees to urbanity, we excluded records of the managed European honey bee (*Apis mellifera*) from our analysis; *A. mellifera* represented 4.9% of collected bees (164 individuals).

The OSR was found by dividing the number of female bees collected by the total number of bees. We calculated overall OSRs for each site, as well as for each sampling bout (defined as a combination of a netting bout and the two bracketing pan trap events). To model the relationship between OSR and environmental variables, we used GLMs with Poisson distribution and log-link function. To avoid the difficulties of interpretation when modeling ratios, we used number of female bees as our response variable, with log(total bee abundance) included as an offset.

Predictor variables in the maximal model included: impervious surface cover within 2km, total floral area within 20m and floral richness within 20m. To test the relationship between OSR and each predictor, we conducted stepwise reduction of the model, beginning with the predictor showing the least explanatory power. The best model was then selected using AIC comparison. To assess the role of species attributes in determining response of OSR to environmental variables, we ran separate models for OSR response by nesting strategy (ground and cavity nesters), sociality (solitary, parasocial, and eusocial), and body size (small, medium, and large). Models were checked for overdispersion, and in all cases the dispersion parameter value was <1.4.

To determine whether OSR response to urbanity was significantly affected by species attributes (e.g. preferred nest substrate or sociality), we constructed GLMs that included urbanity, species attribute of interest, and an urbanity × species attribute interaction term as predictors; a significant interaction term indicated significant differences among species in OSR response to urbanity, mediated by the attribute of interest.

A parallel analysis was conducted for bee abundance, with model form, predictors, and model selection process as above, with two exceptions. First, because we were looking at abundance, rather than OSR, these models omitted the offset term. Second, abundance data were in all cases significantly overdispersed; to account for this overdispersion, a quasi-Poisson distribution was used in place of the Poisson distribution. Because AIC values cannot be calculated from quasi- distributions, we instead used the related quasi-AIC metric for model comparison.

We assessed the relationship between metrics of floral resource availability and urbanity using GLMs with log-link function. As with bee abundance data, floral richness and area metrics were significantly overdispersed, so quasi-Poisson distributions were used to account for overdispersion.

3.4 Results

We caught a total of 3,336 bees (Table B.1) consisting of 143 species across 28 genera (Table B.2). Of these, 2,481 (74%) belonged to species that nest underground (hereafter ‘ground nesters’), while 855 (26%) belonged to species that nest above ground in cavities or hollow stems (hereafter ‘cavity nesters’). Ground-nesting bees in the sampled population were comprised of 60.9% eusocial, 18.1% parasocial, and 18.8% solitary, while cavity-nesting bees were overwhelmingly solitary (96.0%). Neither total bee abundance nor abundance of ground-nesting bees was affected by urbanity (total: *t* = -0.36, d.f. = 24, p = 0.73; ground-nesting: *t* = -1.09, d.f. = 24, p = 0.29), but cavity nester abundance increased with urbanity (t = 2.62, d.f. = 24, p = 0.01) (Figure B.1). Local floral resource availability, as measured by total floral area or richness within 20m of the sampling point, was unrelated to total bee abundance or richness, nor did it affect the abundance of any bee nesting guild (Table 3.1).

Table 3.1 - Effects of floral resource availability on bee abundance. Floral areas represent the mean area covered by blooms at a given site, averaged over all sampling events. Richnesss similarly represents mean richness averaged over all sampling events. Crop area includes floral area for all crop species, i.e. species that are not naturally occurring and are grown for food production; non-crop includes all other flowering species.

Relationship between Floral Quality and Bee Abundance									
	Overall			Ground			Cavity		
Mean Floral Resource/Site	**Residual dev. on $DF = 24$**	t, p	β	**Residual dev. on $DF = 24$**	t, p	β	**Residual dev. on $DF = 24$**	t, p	β
Overall Flower Area	513.93	-1.51, 0.145	$-1.31\ e^{-5}$	603.77	-1.49, 0.15	$-1.67\ e^{-5}$	272.18	-0.13, 0.901	$-1.53\ e^{-6}$
Crop Area	529.14	-1.17, 0.255	$-1.96\ e^{-5}$	613.30	-1.22, 0.234	$-2.90\ e^{-5}$	271.93	0.20, 0.843	$-3.69\ e^{-6}$
Non-Crop Area	538.79	-1.08, 0.291	$-1.35\ e^{-5}$	639.05	-0.997, 0.329	$-1.59\ e^{-5}$	270.92	-0.365, 0.719	$-6.55\ e^{-6}$
Overall Floral Richness	550.7	-0.817, 0.422	-0.014	633.51	-1.1, 0.284	-0.02	266.00	0.78, 0.446	0.02

The observed sex ratio (OSR) of the sample populations changed significantly along the rural-to-urban gradient, with relative abundance of females decreasing with urbanity (*z* = -4.73, d.f. = 23, p < 0.001; Figure 3.1a). This overall change in OSR was driven entirely by changes in ground-nesting bees (*z* = -4.60, d.f. = 23, p < 0.001); in cavity nesters OSR was consistent across the rural-to-urban gradient (*z* = -1.42, d.f. = 23, p = 0.16). The change in OSR in ground nesters is the result of declining female abundance with increasing urbanity (*t* = -2.18, d.f. = 24, p = 0.04); male abundance remained essentially unchanged across the urbanity gradient (*t* = 1.41, d.f. = 24, p = 0.17; Figure 3.1b). By contrast, in cavity nesters, abundance of both sexes increased with urbanity, marginally so in females (*t* = 1.98, d.f. = 24, p = 0.06) and significantly in males (*t* = 3.36, d.f. = 24, p = 0.003; Figure 3.1c). Because provisioning female bees tend to focus foraging efforts in the vicinity of the nest, with probability of occurrence decreasing with distance from nest (Osborne et al 2008), female abundance should be correlated with local nest density. Therefore, these data suggest that urbanity reduces nest density of ground-nesting bees, consistent with findings from Chapter 2.

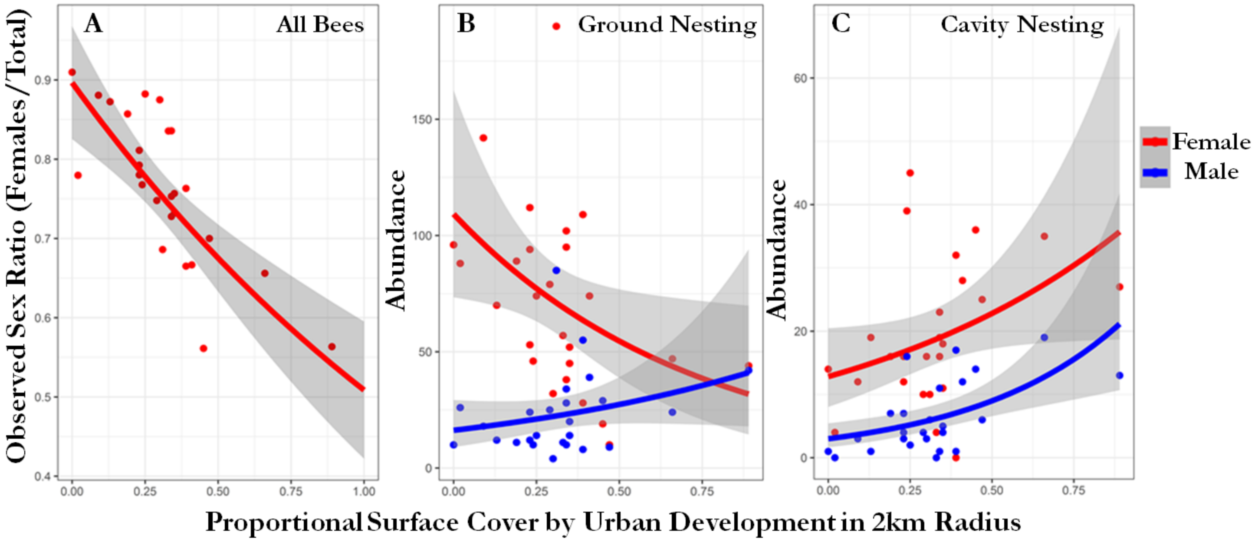


*Figure 3.1 - Effects of urbanity on wild bee community. Relationship between the level of urban development (measured as proportional impervious surface cover within 2km of the sampling site) and **A)** bee observed sex ratio per site (OSR) (z=-4.73, d.f.=23, p<0.001); **B)** ground-nesting bee abundance per site of females (red, t=-2.18, d.f.=24, p=0.04) and males (blue , t=1.41, d.f.=24,p=0.17); and **C)** cavity-nesting bee abundance per site of females (red, t=1.98, d.f.=24, p=0.06) and males(blue, t=3.36, d.f.=24, p=0.003). Fitted line in **A** represents GLM fit of female abundance offset by total abundance; in **B** and **C** lines represent GLM fit of female (red) or male (blue) abundance. Shaded regions represent standard error.*

Shifts in OSR were not related to degree of sociality. The decline in female relative abundance in ground-nesters was significant and consistent across sociality classes; this was true despite the smaller number of solitary and parasocial bees caught relative to eusocial bees (Table 3.2). Therefore, the pattern of OSR shift in ground-nesting bees was not driven exclusively by eusocial species.

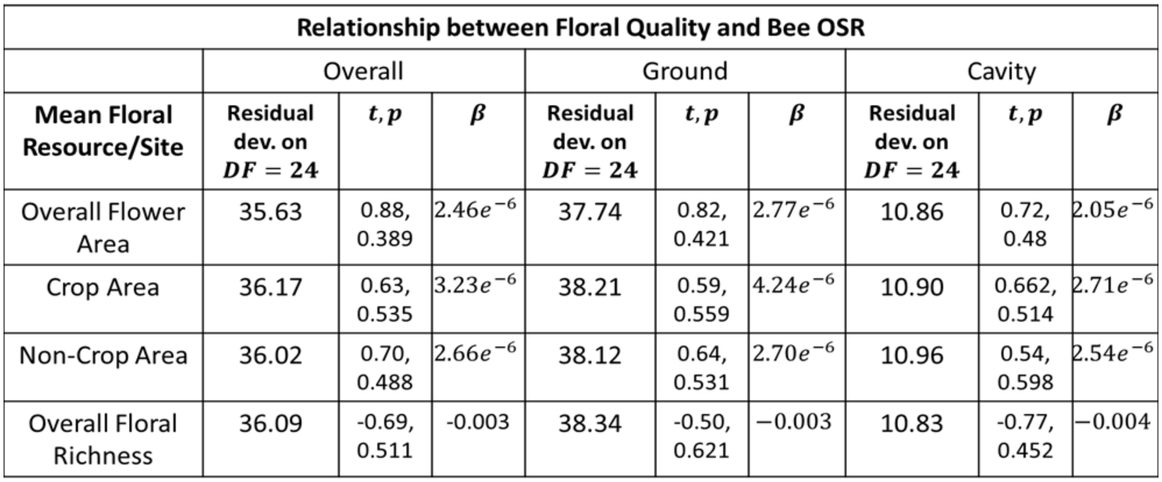
Table 3.2 - Bee observed sex ratio responses to urbanity by sociality class.

<table>
<tr><th colspan="4">Effect of Prop. Impervious Surface Coverage on OSR of Ground Nesting Bees Across Sociality Categories</th></tr>
<tr><th>Sociality Categories</th><th>Residual Deviance</th><th>Significance - p</th><th>Effect Size - β</th></tr>
<tr><td>Eusocial</td><td>19.07_{24}</td><td>0.019</td><td>-0.385 ± 0.164</td></tr>
<tr><td>Parasocial</td><td>18.66_{22}</td><td>0.048</td><td>-1.001 ± 0.507</td></tr>
<tr><td>Solitary</td><td>16.77_{24}</td><td>0.003</td><td>-0.994 ± 0.334</td></tr>
</table>

The relationship between urbanity and OSR in ground nesters is mediated by body size: there was no effect of urbanity on OSR in small ground-nesting bees (z = -0.686, d.f. = 24, p = 0.49); while both medium and large ground-nesting bees experienced decreases in female relative abundance with increasing urbanity. The effect of urbanity on OSR was stronger for large than medium bees (large: z = -4.09, d.f. = 24, p < 0.001; medium: z = -3.07, d.f. = 24, p = 0.002; Figure B.2). Though, this is complicated by the smaller sample size of small bodied ground nesting bees.

Finally, no metric of floral resource availability or species richness showed a significant relationship with OSR of either the total bee community or ground- or cavity-nesting bees (Table 3.3). Moreover, there was no relationship between within-garden floral resource metrics and urbanity (Table B.3). The best model for predicting OSR included only urbanity, excluding floral resource availability and mean minimum temperature, both when the entire bee community was considered together (Table 3.4) and when nesting guilds were considered independently. Together with the different outcomes for ground- vs. cavity-nesting bees, this strongly indicates that the observed effects of urbanization on OSR are the result of urbanization-associated changes in nest-site availability rather than floral resource availability.

Table 3.3 - Effects of floral resource availability on bee observed sex ratio. Crop Area includes floral area for all crop species, i.e. species that are not naturally occurring and are grown for food production.

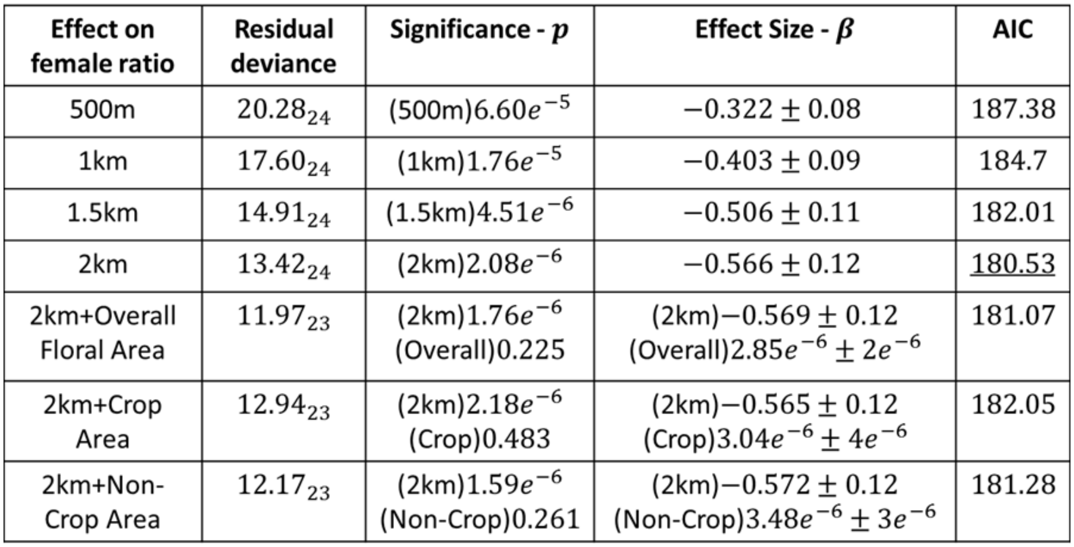


Relationship between Floral Quality and Bee OSR									
	Overall			Ground			Cavity		
Mean Floral Resource/Site	**Residual dev. on $DF = 24$**	t, p	β	**Residual dev. on $DF = 24$**	t, p	β	**Residual dev. on $DF = 24$**	t, p	β
Overall Flower Area	35.63	0.88, 0.389	$2.46e^{-6}$	37.74	0.82, 0.421	$2.77e^{-6}$	10.86	0.72, 0.48	$2.05e^{-6}$
Crop Area	36.17	0.63, 0.535	$3.23e^{-6}$	38.21	0.59, 0.559	$4.24e^{-6}$	10.90	0.662, 0.514	$2.71e^{-6}$
Non-Crop Area	36.02	0.70, 0.488	$2.66e^{-6}$	38.12	0.64, 0.531	$2.70e^{-6}$	10.96	0.54, 0.598	$2.54e^{-6}$
Overall Floral Richness	36.09	-0.69, 0.511	-0.003	38.34	-0.50, 0.621	-0.003	10.83	-0.77, 0.452	-0.004

3.5 Discussion

Here we document a shift in observed sex ratio (OSR) of wild bees along an urbanization gradient, with the relative abundance of female bees declining as urbanity increases. This trend is driven by declines in absolute abundance of female ground-nesting bees as urbanity increases; abundance of male ground-nesting bees is unaffected by urbanity. Thus, the OSR shift is likely the result of reduction in nest density of ground-nesting bees in more urbanized landscapes, with dispersal of male bees from less urban areas with higher nest density augmenting the locally originating male population. A parallel augmentation by immigrating females does not occur because 1) for most of their life cycle, female bees are central-place foragers and therefore are closely tied to existing nests, and 2) even dispersing reproductive females are unlikely to travel as far as dispersing males (Wolf et al 2012; Lopez-Uribe et al 2015; Ulrich et al 2009). Our finding that urbanity-associated changes in ground-nesting bee OSR are stronger for larger-bodied bees further supports this explanation. Movement distance in bees is strongly correlated with body size (Greenleaf et al 2007); thus, males of larger species are more likely to disperse sufficiently far from their natal nest to reach resource patches in urban landscapes. The sample of smaller-bodied bees, then, more closely reflects the makeup of the locally-originating population.

Table 3.4 - Model comparison for predicting bee observed sex ratio .The first four rows present the effect of impervious surface cover measured within circles of increasing radii (i.e. within 500m of the garden, with 1km, etc.).



Effect on female ratio	**Residual deviance**	**Significance - p**	**Effect Size - β**	**AIC**
500m	20.28_{24}	(500m)$6.60e^{-5}$	-0.322 ± 0.08	187.38
1km	17.60_{24}	(1km)$1.76e^{-5}$	-0.403 ± 0.09	184.7
1.5km	14.91_{24}	(1.5km)$4.51e^{-6}$	-0.506 ± 0.11	182.01
2km	13.42_{24}	(2km)$2.08e^{-6}$	-0.566 ± 0.12	<u>180.53</u>
2km+Overall Floral Area	11.97_{23}	(2km)$1.76e^{-6}$ (Overall)0.225	(2km)-0.569 ± 0.12 (Overall)$2.85e^{-6} \pm 2e^{-6}$	181.07
2km+Crop Area	12.94_{23}	(2km)$2.18e^{-6}$ (Crop)0.483	(2km)-0.565 ± 0.12 (Crop)$3.04e^{-6} \pm 4e^{-6}$	182.05
2km+Non-Crop Area	12.17_{23}	(2km)$1.59e^{-6}$ (Non-Crop)0.261	(2km)-0.572 ± 0.12 (Non-Crop)$3.48e^{-6} \pm 3e^{-6}$	181.28

An alternate explanation for the observed OSR shift could be urbanization-induced changes in sex allocation by bees. Specifically, it is known that sex allocation in bees is resource-dependent (Tepedino & Torchio 1982; Kim 1999). The production of female reproductives requires greater resource investment; consequently, resource limitation results in a shift towards production of males (Kim 1999). In eusocial species, production of workers (which are female but do not reproduce), is also correlated with resource availability (Pelletier & McNeil 2003). Thus, the observed decrease in female relative abundance with urbanity could be the result of reductions in floral resource availability in urban landscapes and a consequent reduction in the production of females. However, this explanation does not account for the importance of bee nesting strategy (i.e. cavity- vs. ground-nesting) in mediating the effect of urbanization on OSR. Our finding that OSR is influenced by urbanity for only medium and large bees is potentially consistent with either sex allocation or dispersal-based explanations for OSR shifts: larger bees are likely to both have larger foraging ranges (and thus be more affected by floral resource availability in the wider landscape, potentially leading to increased production of males in resource-scarce landscapes) and disperse greater distances (allowing for disproportionate concentration of dispersing males in urban habitat patches). But again, the lack of OSR shifts among larger cavity-nesting bees argues against the sex allocation hypothesis. Moreover, floral surveys revealed no relationship between urbanity and local (20m) floral resource availability. Study sites were located within community gardens, which in our study area tend to have higher floral abundance and richness relative to the surrounding landscape (Fitch 2017), so the lack of correlation between local floral resource availability and urbanity does not preclude the possibility that landscape-scale floral resource availability was negatively correlated with urbanity; we did not assess landscape-scale floral resource availability in this study. However, the high diversity and abundance of floral resources found within garden study sites likely attenuates the effect of landscape-level floral resource availability.

Our findings highlight the importance of considering sex-specific differences in bee behavior when analyzing the effects of environmental change on bee populations. They suggest, moreover, that researchers may be underestimating the negative impacts of urbanization on ground-nesting bees. While multiple studies have found reductions in ground-nesting bee populations in urban areas (Cane et al 2006; Fortel et al 2014; Matteson et al 2008), the magnitude of these reductions may be greater than total abundance measures suggest if, as we argue is the case in this study, urban ground-nesting bee populations are subsidized by males dispersing from less urban areas. Finally, these results stress the need for improved understanding of how sex-specific behavior patterns in bees, including patterns of floral preference and pollen transfer efficiency, affect pollination services. At this point, we know enough to suspect that these differences may be substantial, but too little to predict the effects of a local shift in bee sex ratio on plant communities.

3.6 Acknowledgements

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3.7 References

Ahrne, K., Bengtsson, J. & Elmqvist, T. 2009. Bumble bees (Bombus spp) along a gradient of increasing urbanization. PLoS One 4.

Ascher, J. S. & Pickering, J.2016. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila).

Banaszak-Cibicka, W. & Żmihorski, M. 2011. Wild bees along an urban gradient: winners and losers. J. Insect Conserv. 16, 331–343.

Bessa-Gomes, C., Legendre, S. & Clobert, J. 2004. Allee effects , mating systems and the extinction risk in populations with two sexes. Ecol. Lett. 7, 802–812.

Biesmeijer, J., Roberts, S. & Reemer, M. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science (80-.). 313, 351–354.

Cane, J. H., Minckley, R. L., Kervin, L. J., Roulston, T. H. & Neal, M. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. Ecol. Appl. 16, 632–644.

Eberhart-Phillips, L. J. et al. 2017. Sex-specific early survival drives adult sex ratio bias in snowy plovers and impacts mating system and population growth. Proc. Natl. Acad. Sci. 5474–5481. doi:10.1073/pnas.1620043114/-/DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1620043114

Fitch, G. M. 2017. Urbanization-mediated context dependence in the effect of floral neighborhood on pollinator visitation. Oecologia 185, 713–723.

Fortel, L. et al. 2014. Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. PLoS One 9, e104679.

Garibaldi, L. A. et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science (80-.). 339, 1608–1611.

Glaum, P., Simao, M.-C., Vaidya, C., Fitch, G. & Iulinao, B. 2017. Big city Bombus: using natural history and land-use history to find significant environmental drivers in bumble-bee declines in urban development. R. Soc. Open Sci. 4, 170156.

Goulson, D., Nicholls, E., Botías, C. & Rotheray, E. L. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science (80-.). 347, 1255957.

Greenleaf, S. S. et al. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596.

Homer, C. G. et al. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States - representing a decade of land cover change information. Photogramm. Eng. Remote Sensing 81, 345–354.

Jha, S. & Kremen, C. 2013. Resource diversity and landscape-level homogeneity drive native bee foraging. Proc. Natl. Acad. Sci. 110, 555–558.

Kim, J. 1999. Influence of resource level on maternal investment in a leaf-cutter bee (Hymenoptera: Megachilidae). Behav. Ecol. 10, 552–556.

Koh, I. et al. 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. Proc. Natl. Acad. Sci. 113, 140–145.

López-Uribe, M. M., Morreale, S. J., Santiago, C. K. & Danforth, B. N. 2015. Nest suitability, fine-scale population structure and male-mediated dispersal of a solitary ground nesting bee in an urban landscape. PLoS One 10, 1–21.

Lowenstein, D. M., Matteson, K. C., Xiao, I., Silva, A. M. & Minor, E. S. 2014. Humans, bees, and pollination services in the city: the case of Chicago, IL (USA). Biodivers. Conserv. 23, 2857–2874.

Matteson, K. C., Ascher, J. S. & Langellotto, G. A. 2008. Bee richness and abundance in New York City urban gardens. Ann. Entomol. Soc. Am. 101, 140–150.

Matteson, K. C., Grace, J. B. & Minor, E. S. 2013. Direct and indirect effects of land use on floral resources and flower-visiting insects across an urban landscape. Oikos 122, 682–694.

Neame, L. A., Griswold, T. & Elle, E. 2013. Pollinator nesting guilds respond differently to urban habitat fragmentation in an oak-savannah ecosystem. Insect Conserv. Divers. 6, 57–66.

Ne'eman, G., Shavit, O., Shaltiel, L. & Shmida, A. 2006. Foraging by male and female solitary bees with implications for pollination. J. Insect Behav. 19, 383–401.

Osborne, J. L. et al. 2008. Bumblebee flight distances in relation to the forage landscape. J. Anim. Ecol. 77, 406–415.

Ostevik, K., Manson, J. & Thomson, J. 2010. Pollination potential of male bumble bees (Bombus impatiens): movement patterns and pollen-transfer efficiency. J. Pollinat. Ecol. 2, 21–26.

Pelletier, L. & McNeil, J. N. 2003. The effect of food supplementation on reproductive success in bumblebee field colonies. Oikos 103, 688–694.

Potts, S. G. et al. 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353.

Perfecto, Ivette, John Vandermeer, and Angus Wright. Nature's matrix: linking agriculture, conservation and food sovereignty. Routledge, 2009.

R Core Team. 2017. R: a language and environment for statistical computing.

Ritchie, A. D., Ruppel, R. & Jha, S. 2016. Generalist behavior describes pollen foraging for perceived oligolectic and polylectic bees. Environ. Entomol. 45, 909–919.

Roulston, T. H., Smith, S. A. & Brewster, A. L. 2011. A Comparison of Pan Trap and Intensive Net Sampling Techniques for Documenting a Bee (Hymenoptera: Apiformes) Fauna. J. Kansas Entomol. Soc. 80, 179–181.

Schreinemachers, P. & Tipraqsa, P. 2012. Agricultural pesticides and land use intensification in high, middle and low income countries. Food Policy 37, 616–626.

Seto, K. C., Güneralp, B. & Hutyra, L. R. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc. Natl. Acad. Sci. U. S. A. 109, 16083–16088.

Sleeter, B. M. et al. 2013. Land-cover change in the conterminous United States from 1973 to 2000. Glob. Environ. Chang. 23, 733–748.

Tepedino, V. J. & Torchio, P. F. 1982. Temporal variability in the sex ratio of a non-social bee, Osmia lignaria propinqua: extrinsic determination or the tracking of an optimum? Oikos 38, 177–182.

Ulrich, Y., Perrin, N. & Chapuisat, M. 2009. Flexible social organization and high incidence of drifting in the sweat bee, Halictus scabiosae. Mol. Ecol. 18, 1791–1800.

Weiner, C., Werner, M., Linsenmair, K. & Blüthgen, N. 2014. Land-use impacts on plant-pollinator networks: interaction strength and specialization predict pollinator declines. Ecology 95, 466–474.

Wolf, S., Toev, T., Moritz, R. L. V & Moritz, R. F. A. 2012. Spatial and temporal dynamics of the male effective population size in bumblebees (Hymenoptera: Apidae). Popul. Ecol. 54, 115–124.

Chapter 4

Socio-economic Drivers of Community Garden Location and Quality in Urban Settings and Potential Effects on Native Pollinators

4.1 Abstract

Concurrent with increased urban agriculture in American cities over the past decade, questions have arisen concerning how gardens spread and what effects they have on local ecosystems. Socio-economic demographics may factor into patterns of garden placement and quality, which lead to changes that could affect biotic communities in ways urban ecologists are only beginning to understand. Some changes are potentially beneficial. For example, researchers hypothesize that increased floral resources in gardens could benefit declining pollinator species. However, the types and extent of such connections between socio-economic drivers and ecological effects are poorly understood. Here we present a case study of urban community gardens in southeast Michigan and potential effects on floral resources and native pollinator communities. We created socio-economic profiles of communities surrounding gardens using census land cover data to discern patterns in garden placement. A subset of these gardens was then sampled for floral resources and bees. In general, results show that gardens are evenly dispersed across communities with varying socio-economic characteristics, indicating that other factors, such as land availability, may be greater determinants of garden locations. However, socio-economic variables significantly correlate with garden floral qualities, which may have implications for urban pollinator support. The findings of our study have relevant policy implications: cities looking to reap the environmental benefits of gardens should consider creating policies and initiatives that support and enable the development of community gardens. Overall we present a novel combination of techniques to connect social and ecological components of sustainability.

4.2 Introduction

In recent years, urban agriculture has seen a marked increase in prevalence across the United States. According to estimates by the National Gardening Association, the number of urban gardeners increased by 29 percent between 2008 and 2013, and the number of households participating in community gardening increased by 200 percent to over three million during the same time period (National Gardening Association 2014). Such trends give rise to questions about how and why gardens spread, as well as where they get established and who stands to benefit most. Urban and community gardens have been touted for their ability to address a wide range of issues including food security, urban blight, community cohesion, public health, poverty and unemployment, and environmental sustainability (Santo et al. 2016). The purported sustainability potential of urban agriculture has been attributed to reduction of food miles and greenhouse gas emissions (Kulak et al. 2013), sequestration of air pollutants into plant tissue (Janhäll 2015), biodiversity preservation (Galluzzi et al. 2010), and other ecosystem services. Yet empirical impacts vary greatly with context and require more research (Santo et al. 2016).

Studies have also examined what effects gardens have on surrounding communities using a variety of indicators, and socio-economic effects of gardens are a common area of inquiry. For example, a 2012 review of urban community garden literature examined 11 US studies that measured the effect of gardens on surrounding property values, all of which found an increase (Guitart et al. 2012). Yet most academic studies thus far have not addressed whether particular types of communities are more prone to establish and maintain community gardens than others. In other words, it is prudent to study not only how socio-economic variables are affected by community gardens, but also how they may be determinants of community garden persistence and quality.

Socio-demographic differences across communities might affect the underlying environmental quality and resultant ecological structure of gardens. This might be especially true in decentralized community gardens managed by individual residents rather than institutions. Links between socio-economic characteristics and the biodiversity of plants (Grove et al. 2006, Kinzig et al. 2005; Hope et al. 2003) and birds (Loss et al. 2009; Kinzig et al. 2005) in US cities have been studied at a variety of scales ranging from home gardens to neighborhoods and landscapes. Plant biodiversity in itself has been demonstrated as an important determinant of the status of animal and insect communities (Knopps et al. 1999), and this might be particularly true in urban gardens (Smith et al. 2006). For example, it has been suggested that the floral resources in urban gardens might be a valuable resource for at-risk bee communities (Hernandez et al. 2009), which are suffering global declines (IPBES 2016). Yet the broader connection between socio-economic variables and the ability of gardens to support bees remains understudied.

Bees provide an indispensable service to ecosystems by pollinating plant communities so as to maintain their genetic diversity and resilience. Lack of animal pollinators is the most common proximate cause of reproductive impairment in wild flowering plants, 80 percent of which depend directly on insects for this purpose (Potts et al. 2010). Bees are also responsible for the increased quantity, quality, and stability of over 60 percent of the world's crops (Garibaldi et al. 2011). This agricultural service is appraised at nearly $200 billion annually (Gallai 2009). Beyond domesticated honeybees, wild bees are of particular interest because of their highly significant positive impact on yields. A study of 41 crop systems worldwide, found that "fruit set increased significantly with wild insect visitation in all crop systems, but with honey bee visitation in only 14 percent of the systems," and that "fruit set increased twice as strongly with visitation by wild insects as with visitation by honey bees" (Garibaldi et al. 2013).

One of the largest probable causes of global bee declines is habitat loss and fragmentation, driven in part by increasing urbanization (Goulson et al. 2015). Meta-analyses have found significant negative effect of distance from natural habitat on the richness and abundance of wild bees in particular (Potts et al. 2010). Community gardens might be considered an attractive and straightforward solution to this problem—in theory, planting more flowers should offer bees more resources in urban centers and act as corridors between fragmented natural habitats. Indeed, some studies provide evidence that this may be the case (Pardee and Philpott 2014; Potter and LeBuhn 2015), while others have found floral additions do not necessarily enhance bee abundance or richness in urban gardens (Matteson 2010). Considering aspects of garden quality besides general flower abundance may be necessary to explain the potential of urban gardens to sustain healthy urban pollinator communities. Yet this raises the question of what drives garden floral quality. Beyond ecological conditions, characteristics related to who uses the garden could be influencing factors. Assessing how socio-economic demographics affect the prevalence of gardens across different communities and their floral compositions may be important to understand the habitat connectivity and resources availability for pollinators in cities. Such understanding would be invaluable for informing desperately needed policy initiatives at local, state, and federal levels to maximize benefits to both human and pollinator communities (Inouye et al. 2017).

Here we present a case study of community gardens in Ann Arbor and Ypsilanti, Michigan to investigate the relationships among socio-economic demographics, community garden placement, garden floral quality, and bee community composition. Given the inherently interdisciplinary nature of this work, we employ a diverse set of methods spanning the natural and social sciences to analyze complex socio-ecological trends. Specifically, we ask three questions:

1. Are community gardens more prevalent in certain socio-economic conditions of urban environments? Specifically, do socio-economic variables correlate with garden placement in Ann Arbor and Ypsilanti, Michigan?
2. How do socio-economic conditions of the surrounding community correlate with community garden floral resource quality?
3. How does floral resource quality influence the pollinator abundance in urban community gardens?

4.3 Materials and Methods

4.3.1 Study Sites

Our study encompasses 30 community gardens maintained by management organizations Project Grow in Ann Arbor and Growing Hope in Ypsilanti. These particular sites are advantageous for addressing our research questions. Both management organizations maintain readily available data about community garden locations and administer consistent management regulations across garden sites. Furthermore, the Ann Arbor/Ypsilanti area encompasses significant heterogeneity of socio-economic demographics within a limited geographic range, both making our study logistically feasible and limiting the effect of confounding variables such as divergent climates.

During the summer of 2014 we received permission to sample bee communities and floral resources across a subset of 11 of the original 30 garden sites. These gardens were located at Buhr Park, Clague Middle School, the University of Michigan Campus Farm, County Farm Park, Catholic Social Services, Eastern Michigan University, Frog Island, Greenview, Normal Park, Perry Community Garden, and West Park. All gardens ban the use of neonicotinoid pesticides - which have been linked to declining bee health (Woodcock et al. 2016; Blacquière et al. 2012) - and provide guidelines to utilize organic growing practices accepted by major organic certification agencies, such as the Organic Crop Improvement Association (http:// www.ocia.org/).

4.3.2 GIS and Socio-economic Data

We used socio-economic/ demographic indicators related to wealth from the US Census Bureau's 2006-2010 American Community Survey in our analyses. These included median income, percent below the poverty line, population percent with a bachelor's degree, median property value, and median age. All of the socio-economic variables considered here are associated with wealth in Ann Arbor and Ypsilanti. Median income has significant positive correlations with age, percent bachelor's degree, and property value, and a negative correlation with poverty rate. These associations correspond to our understanding of Ann Arbor/Ypsilanti demographics. Additionally, both cities are college towns, and official census rules dictate that most college students should be counted at their college addresses (census.gov/2010census).

Profiles for each site regarding each socio-economic variable were created using Geographic Information System (GIS) programs. Garden locations were aggregated with available data from Project Grow and Growing Hope. GIS was used to create quarter-mile buffer zones around each of 30 garden sites in Ann Arbor and Ypsilanti and overlay these buffers with census tract data for each socio-economic variable. We determined the proportion of each census tract that lay within a particular buffer, multiplied the variables by this proportion, and summed the proportional values to attain the socio-economic data values associated with each garden site.

To analyze the relationship between garden location and level of urban development, we used the proxy variable impervious surfaces. Impervious surfaces are roads, buildings, parking structures, or anything else that effectively blankets the surface with concrete or building material. To calculate the amount of impervious surface around each site, National Land Cover Database data from 2011 (Multi-Resolution Land Characteristics Consortium, mrlc.gov) was used. In keeping with literature suggestions (McKinney 2008) of defining urban landscapes as areas with >50 percent impervious surface, areas categorized as high (80-100 percent impervious) and medium (50-79 percent impervious) density developed were summed to obtain the total area of impervious surface within 500-meter buffer zones around each individual sampling site. Dividing that total area of impervious surface by the overall land area resulted in the percent impervious surface for each buffer zone of each sampling site.

4.3.3 Field Sampling

Data collection in the field was implemented using the methods described in Chapter 1 and Chapter 2.

4.3.4 Statistical Analyses

Data was compiled in GIS and statistical analysis was completed using the statistical software R. In order to address question 1 of this study, socio-economic and demographic variables at garden locations were compared to areas without gardens. To accomplish this, buffer zones were created for randomly chosen non-garden locations. Then socio-economic variables and impervious surface coverage were measured within the buffer zones similarly to garden locations (see GIS section). Using non-garden locations as reference points is more applicable than simply comparing garden locations to overall city averages. Using city averages would result in a fallacious comparison: garden locations would be tested against a broader landscape also containing those same garden locations. In other words, we would be comparing something to itself.

Socio-economic variables at garden locations and non-garden locations were compared directly through t-tests. Additionally, the effect of physical urban development on garden location was investigated by considering the range of impervious surface coverage around garden and non-garden locations. The amount of impervious surface coverage around each land type was input into a logistic regression which output the probability of finding urban gardens given the amount of impervious surface coverage at any given point in the city.

In addressing question 2, we initially set out to use socio-economic variables as predictors and floral measurements as dependent variables in multivariate regression analysis. In this process we confronted the fact that the socio-economic variables in our data exhibit "multicollinearity." In other words, the income around gardens strongly and positively correlates with property value, median age, and bachelor's degree percentage. Conversely, these variables all strongly, negatively correlate with percent in poverty (see Appendix 1.2). Perhaps unsurprisingly, socio-economic variables are very often collinear (Wagner 1982). Multicollinearity can lead to particularly imprecise estimates of beta coefficients in ordinary multivariate regressions. Since tests showed our data exhibits a high degree of multicollinearity (see Appendix C.2), ordinary multivariate models had to be avoided. We proceeded with the analysis in two ways.

First, analysis of the effects of socio-economic factors on floral quality and subsequent effects on bee abundance was handled using single-variable linear models. Estimates of the beta coefficients of these more straightforward single–variable linear models were verified through residualization in multivariate models. The results presented in this work stem from this analysis, as they are more widely accessible to readers with varying degrees of statistical exposure. Given the use of linear models, skewed variables were log transformed to meet conditions of normality (see Appendix C.1 for more detail). Data was also standardized to z-scores given that each variable was measured across significantly different ranges and scales, streamlining comparison of effect size across variables. Second, to more directly address multivariate models and to corroborate coefficient estimates garnered from single variate models, we utilized partial linear square regressions (PLS regressions) to create multivariate regressions. PLS regression is often used when predictor variables are highly collinear (Mevik and Wehrens 2007). In our analysis, PLS regressions acted as a degree of authentication of the relationships found between socio-economic variables and dependent variables (see Appendix C.2 for further details).

4.4 Results

4.4.1 Garden Location

Analysis of the geographic and socio-economic patterns of communities surrounding gardens reveals a number of important quantitative and qualitative observations. Median income and percentage of Bachelor’s degrees in garden buffer areas showed no significant differences from parts of the respective city not containing gardens. In other words, the income and education demographics of neighborhoods surrounding gardens in Ypsilanti tended to reflect those of Ypsilanti as a whole, and the demographics of neighborhoods surrounding gardens in Ann Arbor was similar to Ann Arbor as a whole. Ypsilanti also showed no difference between garden and non-garden areas for the variables of poverty and age. In Ann Arbor, however, areas surrounding community gardens were significantly older (t=-2.766, df=42.344, p=0.008) and had a significantly lower poverty rate (t=2.603, df=51.111, p=0.012) than non-garden areas. These differences might be explained by the pattern of student housing in the city, which will be explicated in the discussion. Additionally, there were significant differences in garden demographics between cities, apparent in the differential shading on the maps in Figure 4.1.

One factor that was an important determinant of garden placement was available space. We looked at the prevalence of gardens along a gradient of impervious surface across garden sites and derived a model for the percent chance of finding a garden with increasing impervious surface. Community gardens were more likely to be located in places with low levels of impervious surface (Figure 4.2).

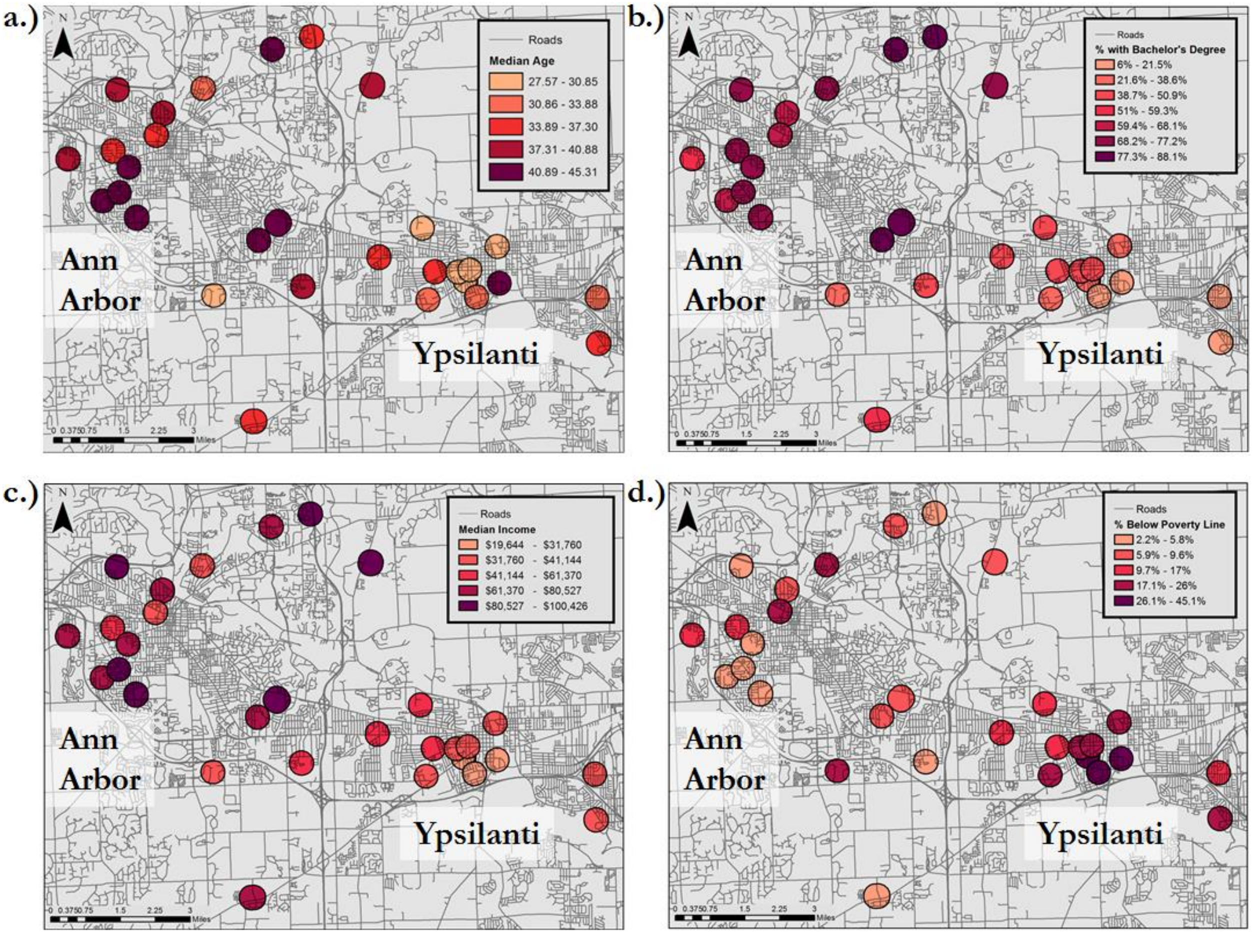


Figure 4.1 - Socio-economic demographics in garden buffer zones in Ann Arbor and Ypsilanti, MI. Circles represent buffer zones with garden at center. a) Median age b) Percent of bachelor's degrees c) Median income d) Percent below the poverty line. Original maps created by Alexandra Markiewicz and Brad Vogelsmeier with input from Paul Glaum (see Iuliano et al 2017).

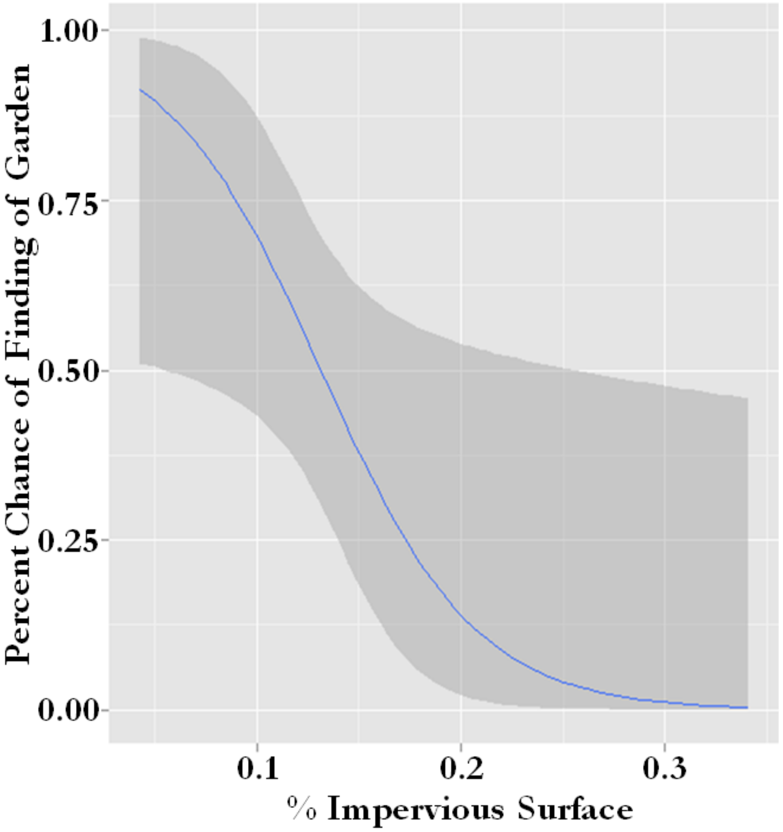


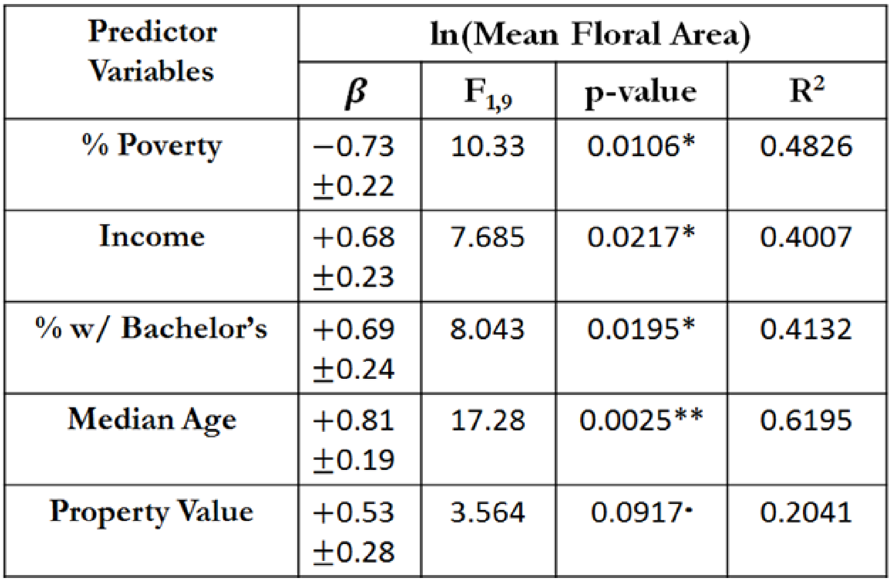
Figure 4.2 - Logistic regression of the probability of finding a garden at a particular location given the amount of urban development. Urban development is quantified as the percent of impervious surface coverage measured within the GIS-created buffer zones. There is a significant negative relationship between probability of garden placement and impervious surface coverage (estimate = -26.52, p=0.0381; residual deviance: 31.919 on 26 degrees of freedom).

4.4.2 Socio-economic Demographics and Garden Quality

Across the 11 sample sites, 2086 floral abundance measurements were taken of 316 flowering plant species. Results of linear models between mean floral area and socio-economic variables are shown in Table 4.1. Variables associated with wealth (median income, percent with bachelor’s degree, and median age), had a significant positive linear relationship with general floral resource availability in community gardens. Conversely, percent of residents below the poverty line surrounding gardens had a significant negative correlation with floral area. In general, Ann Arbor/Ypsilanti gardens in more affluent areas tended to have greater overall floral resource availability than those in lower-income communities. In contrast there was a decrease in floral resource abundance associated with poverty. This qualitative result was mirrored in the results of the PLS regression (see Appendix C.2).

We hypothesized that this increase in floral area associated with wealth did not constitute a proportional increase in all types of flowers. To investigate how floral composition changed with the increase in area, flower data was broken down into further descriptive categories and regressed against the same socio-economic variables as well as general floral area. Significant relationships were found among socio-economic variables and various garden flower composition variables (see Figure 4.3). Some of the strongest and most consistent relationships involved mean crop area, mean introduced species area, and mean weed percent, and thus these variables will be the primary focus of our analysis.

Table 4.1 Relationships with socio-economic variables as predictors and mean overall floral area as the dependent variable in separate generalized linear models. Significance of model fits is given by p-values: · <.1,<.05,**<.01,***<.001.*



Predictor Variables	ln(Mean Floral Area)			
	β	$F_{1,9}$	p-value	R^2
% Poverty	−0.73 ±0.22	10.33	0.0106*	0.4826
Income	+0.68 ±0.23	7.685	0.0217*	0.4007
% w/ Bachelor's	+0.69 ±0.24	8.043	0.0195*	0.4132
Median Age	+0.81 ±0.19	17.28	0.0025**	0.6195
Property Value	+0.53 ±0.28	3.564	0.0917·	0.2041

Significant relationships were found between mean crop area in gardens and all socio-economic variables of interest in surrounding neighborhoods. As with mean floral area, wealth-associated variables were positively correlated with crop area, and poverty was negatively correlated. The same trends held true for mean introduced species floral area: introduced flowers increased with wealth and decreased with poverty. In contrast, the percentage of floral area occupied by weeds had significant negative correlations with income and a positive trend associated with poverty (p=0.052) (see Table 4.2). It is important to note that we do not see significant changes in absolute weed area with wealth or poverty, but rather the amount of weeds relative to other types of flowers (crops and introduced species) is changing. These relationships were also corroborated in the factors derived from the PLS regression.

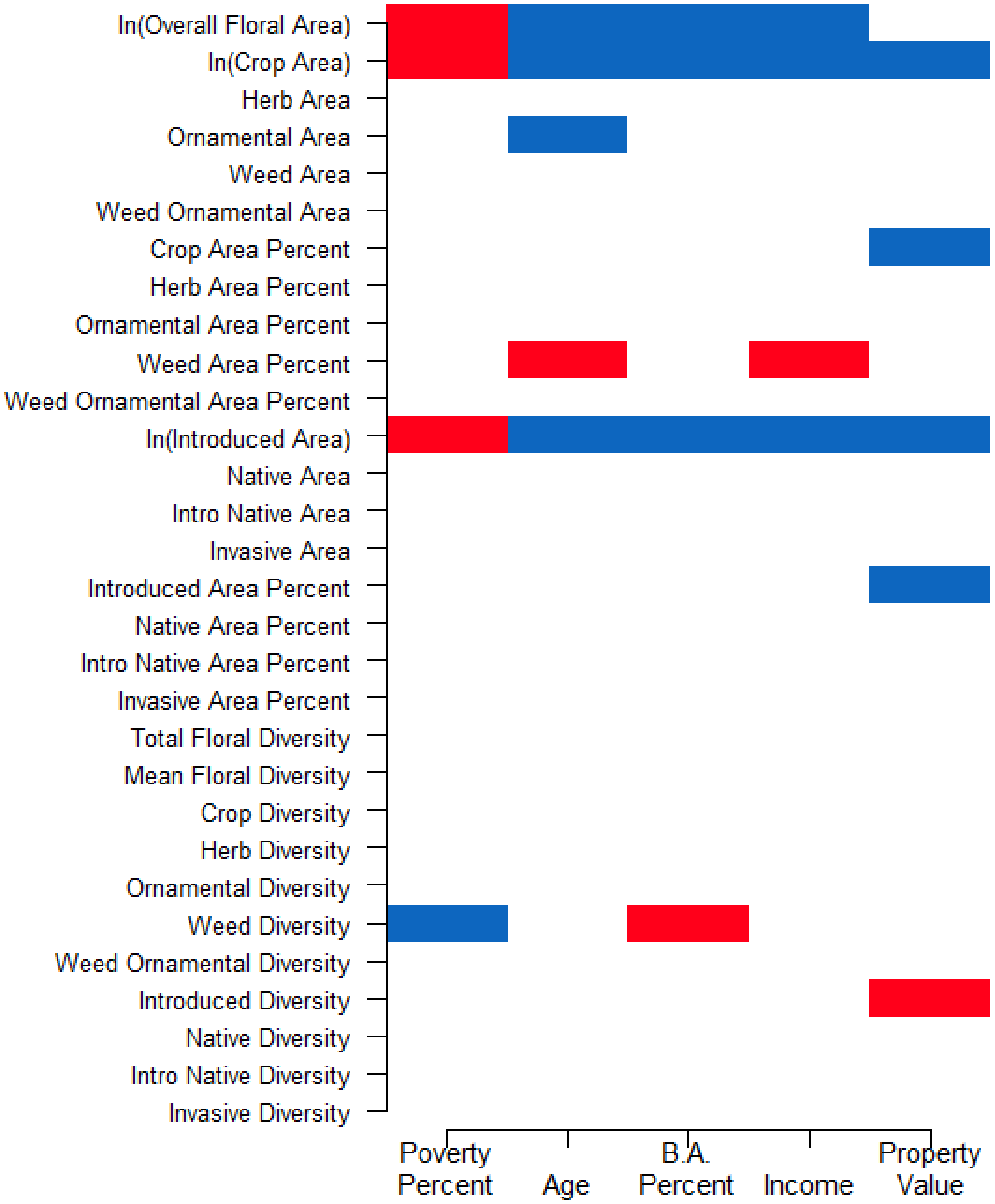


Figure 4.3- Heat map of beta estimates from statistically significant relationships between socio-economic and floral variables at the p<.05 level where socio-economic variables are the predictors .Colors represent the sign value of the beta estimates of linear regressions. Blue colors represent positive relationships; red colors represent negative relationships.

4.4.3 Garden Quality and Pollinator Communities

We collected 1,706 individual bee specimens from 112 species. The most abundant species were the bronze sweat bee (Halictus confusus) with 132 individuals, the common eastern bumble bee (Bombus impatiens) with 124 individuals, and a metallic green sweat bee species (Agapostemon virescens) with 116 individuals (Figure 4.4). General floral area did not significantly correlate with the number of bees sampled, failing to support the hypothesis that simple increases in general floral resources results in greater bee abundance. In fact, the relationship between floral area and bee abundance trended negative ($F_{1,9}$=4.76, p=0.057, adjusted R^2=0.270), the opposite of what is commonly assumed. This trend might be driven by the significant negative interaction between introduced species floral area and bee abundance (recall that the increase in general floral area was partially comprised of introduced species). On the other hand, there was a nearly significant positive trend ($F_{1,9}$=5.001 p=0.052, adjusted R^2=0.29) between percent weeds and bee abundance; number of bees tended to increase as a greater proportion of garden floral area was occupied by weeds. Finally, there was no significant relationship between crop area and bee abundance.

Table 4.2 - Relationships with socio-economic variables as predictors and mean crop area, mean introduced area, and percent weed area as dependent variables in separate GLMs. Significance of fits given by p-values: · <.1,<.05,**<.01,***<.001.*

Predictor Variables	**ln(Mean Crop Area)**				**ln(Introduced Area)**				**% Weed Area**			
	β	$F_{1,9}$	**p-value**	R^2	β	$F_{1,9}$	**p-value**	R^2	β	$F_{1,9}$	**p-value**	R^2
% Poverty	−0.65 ±0.25	6.53	0.031*	0.36	−0.69 ±0.24	8.30	0.018*	0.42	+0.60 ±0.27	5.006	0.052·	0.29
Income	+0.73 ±0.22	10.77	0.0095**	0.49	+0.71 ±0.23	9.31	0.0138*	0.45	−0.62 ±0.26	5.715	0.0405*	0.32
% w/ Bachelor's	+0.71 ±0.23	9.14	0.0144*	0.45	+0.68 ±0.25	7.57	0.02243*	0.40	−0.47 ±0.29	2.56	0.144	0.14
Median Age	+0.77 ±0.21	13.33	0.0053**	0.55	+0.82 ±0.19	18.67	0.0019**	0.64	−0.71 ±0.27	8.947	0.0152*	0.44
Property Value	+0.79 ±0.21	14.55	0.0041**	0.58	+0.67 ±0.25	7.31	0.0242*	0.39	−0.38 ±0.31	1.528	0.248	0.05

4.5 Discussion

In summary, the analysis of how socio-economic demographics correspond to community garden locations showed significant differences in Ann Arbor between median age and poverty rates in areas surrounding gardens versus non-garden areas. Such differences were not consistent in Ypsilanti, where gardens were more evenly dispersed across neighborhoods. Impervious surface was a better overall predictor of the presence or absence of gardens across both cities. On the other hand, socio-economic factors *were* closely correlated with garden floral quality and composition. Furthermore, while urban community gardens can be successful in their ability to support pollinator communities, intuitive garden traits within local control might not explain differences in this ability between gardens. In Ann Arbor and Ypsilanti community gardens, we find wealth is correlated with high floral areas, but that does not necessarily translate to more abundant bee communities. The statistical relationships leading to these conclusions are summarized in Figure 4.5.

In general, the socio-economic makeup of neighborhoods surrounding community gardens tended to reflect the socio-economic makeup of their respective cities. In Ypsilanti, there was no significant difference for any socio-economic variables. In Ann Arbor there was no difference for income, education, or property value, while there were significant differences for poverty and age. The city's much larger student population might explain these differences in Ann Arbor. Students who are not generally present during the peak growing months tend to live in the denser, centrally located neighborhoods. Ann Arbor residents participating in community gardening are likely to be older, permanent inhabitants living near lower-density residential neighborhoods that contain more open space for gardens. The large student population would thus decrease the median age in areas without gardens relative to those areas where gardens *are* located. Similarly, the presence of off-campus college students has been shown to skew census poverty rates upward (Bishaw 2013). Thus, we would expect non-garden areas occupied by students to have higher poverty rates than garden areas.

Figure 4.4 - Photographs of the three most common bee species in our sample. a) Halictus Confusus b) Bombus impatiens c) Agapostemon virescens Photo credit: Benjamin Iuliano.

More than socio-economic factors, percentage of area covered by impervious surface seems to be an important predictor of where community gardens are located in a city. This makes intuitive sense‒gardens are more likely to get established where there is more available space. The land use types in which gardens tended to occur further support this understanding qualitatively: 77 percent of gardens were on government/institutional land or in public parks/recreational space, while the remaining 23 percent were on commercial or residential land. Beyond this general trend, the maps in Figure 4.1 illustrate gardens in Ypsilanti were more centrally clustered than in Ann Arbor. The heterogeneity of spatial and demographic characteristics across even the two geographically proximate cities in this work highlights the need for similar studies to be conducted at fine scales across a diversity of locations.

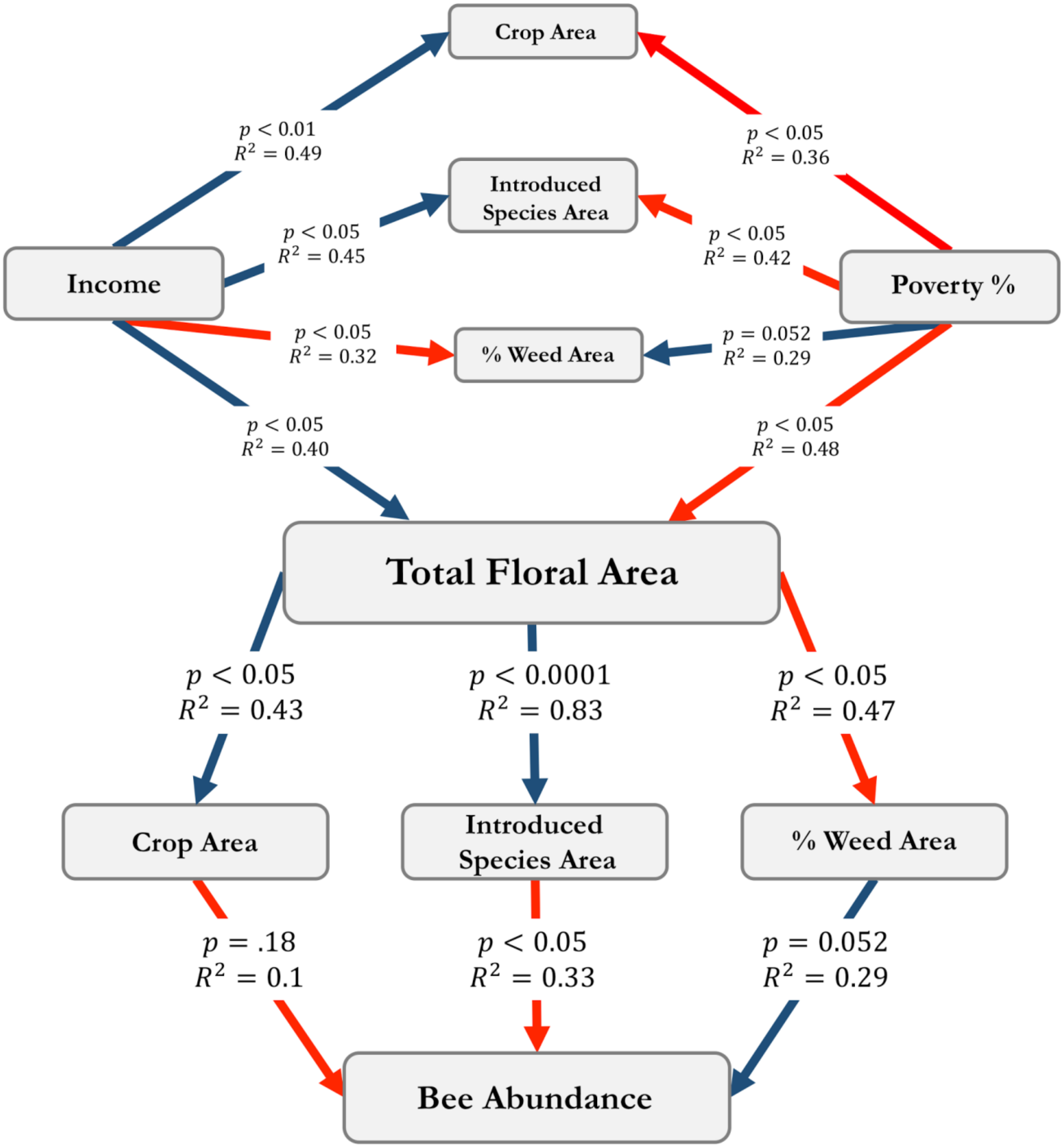


Figure 4.5 - Conceptual flow diagram of the relationships among income, poverty, garden floral qualities, and bee abundance. Lines represent linear correlations, with arrows pointing toward the dependent variable. Text along the line indicates the direction of the relationship (positive or negative), p-value to indicate significance, and adjusted R2 to show the effect size.

These findings also highlight the importance of land use patterns, city planning, and policy for urban agriculture. The gardens in Ann Arbor and Ypsilanti spanned diverse communities, demonstrating that gardens are established and persist regardless of a community's characteristics. However, the findings indicate that high presence of impervious surface and lack of available open land may be a difficult barrier to overcome in developing gardens, no matter how strong the environmental, ecological, or community-oriented incentives to do so may be. Vacant land may be unavailable or the cost of land may be insurmountable for an individual or community motivated to develop a community garden. Therefore, strengthening or expanding urban agriculture will require the attention of city planners and policy makers. Urban agriculture-friendly zoning or land use designations, along with initiatives such as providing gardens with city water access or allowing communities to develop gardens in public parks, are some ways in which municipal stakeholders can, and may need to, support community gardens.

Beyond garden location, characteristics of community garden floral quality are significantly correlated with socio-economic variables, indicating that even factors ostensibly within the purview of local or individual-level decision-making might be influenced by broader demographic trends. Our analysis found that variables associated with wealth, such as low poverty and high income, educational attainment, and age tended to positively correlate with floral area in Ann Arbor and Ypsilanti community gardens. This increase in general floral area was primarily driven by increases in crops and introduced plant species.

Furthermore, there was a negative association between income and percentage of floral area occupied by weeds. Although we do not have qualitative data such as gardener interviews to suggest a causal mechanism for these relationships, we can propose potential explanatory hypotheses. Gardens in wealthier areas, with higher incomes and lower poverty levels, plausibly attract wealthier gardeners who are better resourced and able to manage garden plots more intensively. This could explain the significant increases in crop area (i.e. wealthier gardeners purchase and plant more crops) and corresponding increase in general floral area, as well as the decrease in percent weeds (i.e. wealthier gardeners have more resources, time, and/or concern for weed management). A similar "luxury effect" has been found in other research on vegetation in urban areas, such as a 2003 study which demonstrated socio-economic drivers of plant diversity around Phoenix, AZ (Hope et al. 2003).

One might presume that these characteristics make gardens in wealthier areas "higher quality." In particular, the significantly higher floral area in affluent gardens seems likely to be more attractive and beneficial to wild bees. Yet our findings do not support this assumption. In fact, increased floral area had a nearly significant *negative* trend with bee abundance in the 11 community gardens studied. Counter to what one might expect, we found that fewer bees were present as gardens had more flowers.

Parsing general floral area into particular categories might help explain this counterintuitive result. Specifically, increased floral abundance is driven primarily by addition of crops and introduced plant species, and the latter is also negatively correlated with bee abundance. The one floral variable that had a *positive* trend on bee abundance was the proportion of the floral area occupied by weed plants ("percent weeds"). The value of weeds (non-crop flowers) to pollinators has been well documented, such as in a recent FAO review of the ecological interactions between crops, weeds, and pollinators in agricultural systems (Altieri et al. 2015). Bees tend to be attracted to particular flower types based on nutrient quality, such as pollen protein content (Hanley et al. 2008), and non-crop flowers provide pollinators with diet diversity necessary for healthy development (Alaux et al. 2010; Schmitt et al. 1995). Furthermore, various studies have demonstrated that floral morphology, color, and scent are all important components to bee foraging decisions (Harder 1985; Kunze and Gumbert 2001). It is therefore plausible that increased proportion of crop and/or introduced flowers relative to weeds in gardens "dampens the signal" of weed flowers that are attractive to wild bees. Ultimately these results suggest that while urban community gardens are capable of supporting bee communities, moving beyond a paradigm of simple floral additions is key to sustainability. The composition of the floral resources in gardens matters, and it could be valuable for urban gardeners to incorporate more non-crop, wild flowers along with crops in order to fully support bee health.

Our study design necessarily entails limitations that should be accounted for when extrapolating results. First, using census data conducted at such a broad scale is not a perfect on-the-ground measurement of the socio-economic reality of the communities surrounding urban gardens or the wealth status of gardeners themselves. Flower and bee sampling only took place over one growing season, and thus cannot account for longer-term temporal variation in community abundance and composition. Furthermore, our analyses did not account for other garden qualities besides floral resources such as nesting habitat availability. Finally, definitive causal relationships can only be inferred due to both the observational nature of our study and the small sample size in a specific local context. Yet our results suggest future research directions into similar trends in other urban contexts as well as the mechanistic interactions among socio-economic drivers, garden location and quality, and pollinator communities. Perhaps most importantly, the interdisciplinary methodology employed here exemplifies a novel and potentially useful tool for addressing complex questions associated with social and ecological sustainability in cities. If urban gardens are anticipated to have wide-reaching effects that cut across socio-cultural, economic, public health, and environmental dimensions, research methods to study these effects must be similarly broad and diverse. Our study constitutes an illustrative example of one such approach. Incorporating similar methods into future research questions could deepen understanding of the broader relationships between socio-economic characteristics, land use, and the prevalence of community gardens, and identify the best associated policy recommendations that would foster the expansion of urban agriculture *and* improve conditions for native bee populations.

4.6 Acknowledgements

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4.7 References

Alaux, C., F. Ducloz, D. Crauser, and Y. Le Conte. 2010. Diet Effects on Honeybee Immunocompetence.” *Biology Letters* 6(4): 562–565. doi:10.1098/rsbl.2009.0986.

Altieri, Miguel A., Clara I. Nichols, Mark Gillespie, Ben Waterhouse, Steve Wratten, Gualbert Gbèhounou, and Barbara Gemmill-Herren. 2015. Crops, weeds and pollinators: Understanding ecological interaction for better management." *Food and Agriculture Organization of the United Nations*. http://www.fao.org/3/a-i3821e.pdf.

Banaszak, Józef, Weronika Banaszak-Cibicka, and Piotr Szefer. 2014. Guidelines on Sampling

Intensity of Bees (Hymenoptera: Apoidea: Apiformes). *Journal of Insect Conservation* 18, no. 4 (July 26, 2014): 651–656. doi:10.1007/s10841-014-9671-3.

Bishaw, Alemayehu. 2013. Examining the Effect of Off-Campus College Students on Poverty Rates." *U. S. Census Bureau, Social, Economic & Housing Statistics Division, Poverty Statistics Branch*. http://www.census.gov/content/dam/Census/library/working-papers/2013/acs/2013_Bishaw_01.pdf

Blacquiere, T., Smagghe, G., Van Gestel, C. A., & Mommaerts, V. 2012. Neonicotinoids in bees: a review on concentrations, side-effects and risk assessment. Ecotoxicology, 21(4), 973-992. doi: 10.1007/s10646-012-0863-x

Chatterjee, S.; Hadi, A. S.; Price, B. 2000. Regression Analysis by Example (Third ed.). John Wiley and Sons. ISBN 0-471-31946-5

Fortel, Laura, Mickaël Henry, Laurent Guilbaud, Anne Laure Guirao, Michael Kuhlmann, Hugues Mouret, Orianne Rollin, Bernard E. Vaissière. 2014. Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) Along an Urbanization Gradient." Edited by M. Alex Smith. *PLoS ONE* 9, no. 8: e104679. doi:10.1371/journal.pone.0104679.

Gallai, Nicola, Jean-Michel Salles, Josef Settele, Bernard E. Vaissière. 2009. Economic Valuation of the Vulnerability of World Agriculture Confronted with Pollinator Decline. *Ecological Economics* 68(3): 810–821. doi:10.1016/j.ecolecon.2008.06.014.

Galluzzi, Gea, Pablo Eyzaguirre, Valeria Negri. 2010. Home Gardens: Neglected Hotspots of Agro-Biodiversity and Cultural Diversity." *Biodiversity and Conservation* 19(13): 3635–3654. doi:10.1007/s10531-010-9919-5.

Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, et al. 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance." *Science* 339(6127): 1608–1611. doi:10.1126/science.1230200.

Garibaldi, L. A., M. A. Aizen, A. M. Klein, S. A. Cunningham, and L. D. Harder. 2011. Global Growth and Stability of Agricultural Yield Decrease with Pollinator Dependence. *Proceedings of the National Academy of Sciences* 108(14): 5909–5914. doi:10.1073/pnas.1012431108.

Goulson, D., E. Nicholls, C. Botias, and E. L. Rotheray. 2015. Bee Declines Driven by Combined Stress from Parasites, Pesticides, and Lack of Flowers." *Science* 347(6229): 1255957–1255957. doi:10.1126/science.1255957.

Grove, Jeremiah M., Arlington R. Troy, John PM O'Neil-Dunne, W. R. Burch, M. L. Cadenasso, and S. T. A. Pickett. 2006. Characterization of households and its implications for the vegetation of urban ecosystems. *Ecosystems* 9(4): 578-597. doi:10.1007/s10021-006-0116-z.

Guitart, Daniela, Catherine Pickering, and Jason Byrne. 2012. Past Results and Future Directions in Urban Community Gardens Research. *Urban Forestry & Urban Greening* 11(4): 364–373. doi:10.1016/j.ufug.2012.06.007.

Haenlein, Michael, and Andreas M. Kaplan. 2004. A beginner's guide to partial least squares analysis. *Understanding Statistics* 3(4): 283-297.

Hanley, M. E., M. Franco, S. Pichon, B. Darvill, and D. Goulson. 2008. Breeding System, Pollinator Choice and Variation in Pollen Quality in British Herbaceous Plants. *Functional Ecology* 22(4): 592–598. doi:10.1111/j.1365-2435.2008.01415.x.

Harder, Lawrence D. 1985. Morphology as a Predictor of Flower Choice by Bumble Bees."

Ecology 66(1): 198–210. doi:10.2307/1941320.

Hernandez, Jennifer L., Gordon W. Frankie, and Robbin W. Thorp. 2009. Ecology of urban bees: a review of current knowledge and directions for future study. *Cities and the Environment (CATE)* 2(1): 3. http://digitalcommons.lmu.edu/cgi/viewcontent.cgi?article=1036&context=cate

Hope, Diane, Corinna Gries, Weixing Zhu, William F. Fagan, Charles L. Redman, Nancy B. Grimm, Amy L. Nelson, Chris Martin, and Ann Kinzig. 2003. Socio-economics Drive Urban Plant Diversity. *Urban Ecology*: 339–347. doi:10.1007/978-0-387-73412-5_21.

Inouye, David, Samuel Droege, and Jonathan Mawdsley. 2017. Words alone will not protect pollinators. *Science* 355(6323): 357-357. doi:10.1126/science.aam6132

Iuliano, B., Markiewicz, A., Glaum, P. 2017. Socio-economic Drivers of Community Garden Location and Quality in Urban Settings and Potential Effects on Native Pollinators." Michigan Journal of Sustainability 5.1.

IPBES, *The Assessment Report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on Pollinators, Pollination, and Food Production* (IPBES, Bonn, Germany, 2016). http://www.ipbes.net/sites/default/files/downloads/pdf/spm_deliverable_3a_pollination_20170222.pdf

Janhäll, Sara. 2015. Review on Urban Vegetation and Particle Air Pollution – Deposition and Dispersion.” *Atmospheric Environment* 105: 130–137. doi:10.1016/j.atmosenv.2015.01.052.

Kinzig, Ann, Paige Warren, Chris Martin, Diane Hope, and Madhusudan Katti. 2005. The effects of human socio-economic status and cultural characteristics on urban patterns of biodiversity.” *Ecology and Society* 10(1). doi:10.5751/ES-01264-100123

Kulak, Michal, Anil Graves, and Julia Chatterton. 2013. Reducing Greenhouse Gas Emissions with Urban Agriculture: A Life Cycle Assessment Perspective. *Landscape and Urban Planning* 111: 68–78. doi:10.1016/j.landurbplan.2012.11.007.

Kunze, Jan, and Andreas Gumbert. 2001. The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems. *Behavioral Ecology* 12(4): 447-456. doi:10.1093/beheco/12.4.447.

Loss, Scott R., Marilyn O. Ruiz, and Jeffrey D. Brawn. 2009. Relationships between avian diversity, neighborhood age, income, and environmental characteristics of an urban landscape. *Biological Conservation* 142(11): 2578-2585. doi:10.1016/j.biocon.2009.06.004

Matteson, Kevin C., and Gail A. Langellotto. 2011. Small Scale Additions of Native Plants Fail to Increase Beneficial Insect Richness in Urban Gardens. *Insect Conservation and Diversity* 4(2): 89–98. doi:10.1111/j.1752-4598.2010.00103.x

Matteson, Kevin C., John S. Ascher, and Gail A. Langellotto. 2008. Bee richness and abundance in New York City urban gardens. *Annals of the Entomological Society of America* 101(1): 140-150. doi:10.1603/0013-8746(2008)101[140:BRAAIN]2.0.CO;2

Mevik, Björn-Helge, and Ron Wehrens. 2007. The pls package: principal component and partial least squares regression in R. *Journal of Statistical software* 18(2): 1-24.

Pardee, Gabriella L., and Stacy M. Philpott. 2014. Native Plants Are the Bee’s Knees: Local and Landscape Predictors of Bee Richness and Abundance in Backyard Gardens. *Urban Ecosystems* 17(3): 641–659. doi:10.1007/s11252-014-0349-0.

Potter, Andrew, and Gretchen LeBuhn. 2015. Pollination Service to Urban Agriculture in San

Francisco, CA. *Urban Ecosystems* 18(3): 885–893. doi:10.1007/s11252-015-0435-y.

Potts, Simon G., Jacobus C. Biesmeijer, Claire Kremen, Peter Neumann, Oliver Schweiger, and William E. Kunin. 2010. Global Pollinator Declines: Trends, Impacts and Drivers. *Trends in Ecology & Evolution* 25(6): 345–353. doi:10.1016/j.tree.2010.01.007.

National Gardening Association. 2014. Garden to Table: A 5 Year Look at Food Gardening in America. *National Gardening Association*. https://garden.org/special/pdf/2014-NGA-Garden-to-Table.pdf

O'Brien, R. M. 2007. A Caution Regarding Rules of Thumb for Variance Inflation Factors. Quality & Quantity. 41(5): 673. doi:10.1007/s11135-006-9018-6

Santo, R., A. Palmer, and B. Kim. 2016. Vacant lots to vibrant plots: a review of the benefits and limitations of urban agriculture. *John Hopkins Center for a Livable Future*. http://www.jhsph.edu/research/centers-and-institutes/johns-hopkins-center-for-a-livable-future/_pdf/research/clf_reports/urban-ag-literature-review.pdf

Schmidt, L. S., J. O. Schmidt, H. Rao, W. Wang, and L. Xu. 1995. Feeding Preference and Survival of Young Worker Honey Bees (Hymenoptera: Apidae) Fed Rape, Sesame, and Sunflower Pollen. *Journal of Economic Entomology* 88(6): 1591–1595. doi:10.1093/jee/88.6.1591

Smith, Richard M., Philip H. Warren, Ken Thompson, and Kevin J. Gaston. 2005. Urban domestic gardens (VI): environmental correlates of invertebrate species richness. Human exploitation and biodiversity conservation, pp. 75-98. Springer Netherlands. doi:10.1007/s10531-004-5014-0

Wagner, CH. 1982. Simpson's Paradox in Real Life. *The American Statistician*. 36 (1): 46–48. doi:10.2307/2684093

Woodcock, Ben A., Nicholas JB Isaac, James M. Bullock, David B. Roy, David G. Garthwaite, Andrew Crowe, and Richard F. Pywell. 2016. Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nature Communications* 7: 12459. doi:10.1038/ncomms12459

Chapter 5

Functional reduction in pollination through herbivore-induced pollinator limitation and its potential in mutualist communities

5.1 Abstract

Plant–pollinator interactions are complex because they are affected by both interactors' phenotypes and external variables. Herbivory is one external variable that can have divergent effects on the individual and the population levels depending on specific phenotypic plastic responses of a plant to herbivory. In the wild tomato, Solanum peruvianum, herbivory limits pollinator visits, which reduces individual plant fitness due to herbivore-induced chemical defenses and signaling on pollinators (herbivore-induced pollinator limitation). We showed these herbivory-induced decreases in pollination to individual plants best match a Type II functional-response curve. We then developed a general model that shows these individual fitness reductions from herbivore-induced changes in plant metabolism can indirectly benefit overall populations and community resilience. These results introduce mechanisms of persistence in antagonized mutualistic communities that were previously found prone to extinction in theoretical models. Results also imply that emergent ecological dynamics of individual fitness reductions may be more complex than previously thought.

5.2 Introduction

Plant-animal interactions are inherently complex because they are affected by the phenotypes of the interacting species and the environment in which the interactions play out (Kessler 2015). In an attempt to reduce this complexity and develop tractable questions, numerous studies of plant‑animal interactions have focused on "single-interactions" such as herbivory, predation (carnivorous plants), seed dispersal, habitation-mutualisms, or pollination (Herrera et al 2002). Such two-dimensional studies have provided much of our mechanistic understanding of species interactions, but provide only a limited picture of the ecology and evolution of plant‑animal interactions (Poelman & Dicke 2014). In particular, herbivory-induced changes in plant secondary metabolism have been found to mediate complex dynamics in interaction networks by affecting the suitability of a host plant to other herbivore species (Kessler & Baldwin 2004; Uesugi et al 2013; Viswanathan et al 2005), as well as the attraction of third (Kessler & Heil 2011) and fourth trophic level predators and parasitoids (Poelman et al 2012) with complex effects on plant fitness. Particularly interesting in this context is the plant metabolism-mediated interaction between herbivores and pollinators, because it is here where plants are exposed to a conflict of attracting mutualists (i.e., pollinators) and repelling antagonist consumers (i.e., herbivores) of plant tissues, using similarly structured chemical information1.

Herbivory can affect plant pollinator interactions in multiple ways (Strauss & Whittall 2006). Reduction in pollinator visitation can result from altered/damaged floral displays (Karban & Strauss 1993; Strauss et al 1996; Krupnick & Weiss 1999; Krupnick et al 1999) or pollinators actively avoiding contact with herbivores on flowers (Lohman et al 1996). Moreover, herbivore attack usually results in plant metabolic changes that can affect the quality and quantity of pollinator rewards (either nectar or pollen) (Strauss et al 1999; Adler et al 2001; Adler 2008) or the chemical information that is mediating the interactions (Kessler et al 2011; Schiestl 2014).

Particularly important in this respect, are herbivory-induced volatile organic compounds (HI-VOCs) that are emitted by plants in response to herbivory and provide a cue about the plants' metabolic state and chemical defense status. This form of chemical information can attract natural enemies (predators and parasitoids) of herbivores, mediate interactions with herbivores (Kessler & Heil 2011) or induce preemptive resistance in neighboring branches and plants (Karban et al 2014). It was hypothesized that the production of this chemical information can allow plants to manipulate the entire interaction network to minimize the impact of antagonistic interactions such as herbivory (Kessler 2015; Poelman & Kessler 2016). However, multi-functionality and ubiquitous availability of chemical information in general and HI-VOC emission in particular can become problematic for the plant if the same information is mediating interactions between antagonists and mutualists of the plant. In particular, if antagonists (e.g., herbivores) and mutualists (e.g., pollinators) both consume plant tissue or metabolites and use the associated chemical information for host choice (Kessler et al 2011; Schiestl 2014; Kessler & Halitschke 2009).

In one example, the wild tomato Solanum peruvianum, herbivore-induced changes in plant metabolism and herbivore-induced volatile organic compounds (HI-VOC)-mediated information transfer reduces the attraction of bee pollinators to herbivore-attacked plants relative to undamaged plants. This negatively affected plant fitness via reduced pollen deposition when measured in the field (Kessler et al 2011; Schiestl 2014). Such interactions have been termed herbivory-induced pollinator limitation (HIPL), whereby indirect plant trait-mediated effects negatively affect interactions with a mutualist species and so reduce fitness of an individual plant. However, the broader effects on population and community dynamics and persistence of plant-induced responses, such as HIPL, have not been investigated. Herbivore-induced changes to plant metabolism, i.e., through HI-VOCs, alter how pollinators interact with flowering plants, which can be predicted to alter population dynamics and the dynamics of other interacting species within the community. Here we propose a data-driven theoretical model-based approach to address higher level effects of HIPL.

Theoretical models of the three species community flowering plant, pollinator, and herbivore (3-dimensions) have moved beyond single-interaction studies and investigated the direct effects of herbivory on mutualist populations (Jang 2002; Sánchez-Garduño et al 2014). However, many have not included indirect trait-mediated effects in their analyses. For example, considering only the direct effect of herbivory reducing plant population abundance, some of the model based studies have concluded that these 3-dimensional systems are dissipative so the mutualism is prone to extinction unless herbivore attack rates and/or efficiencies are kept low (Wang et al 2012; Wang 2013; Mougi & Kondoh 2014). In general, the extinctions predicted by these models are triggered by herbivores directly reducing plant population abundances and growth. As herbivory reduces the actual plant population size, this limits the amount of resources available to the pollinator population and causes a subsequent reduction in the pollinator population. The smaller abundance of pollinators reduces pollination services and then lowers plant reproduction, starting a feedback loop that can further reduce both mutualist populations to local extinction. These models have found extinction to be especially likely when the mutualism is an obligate or highly specialized mutualism, where each mutualist species is fairly dependent on the other for substantial growth (Wang 2013; Mougi & Kondoh 2014).

Unlike direct herbivory, herbivore-induced pollinator limitation (HIPL) is an indirect effect. HIPL does not directly reduce the actual plant population size but does lower the rate of interactions between existing plants and pollinators. In other words, HIPL can reduce the effective population of plants the pollinators interact with as a function of the strength of induced plant metabolic changes in response to herbivory. Such an indirect ecological effect mediated by herbivore-induced changes in plant metabolism will also reduce pollination services and can thus be predicted to similarly induce mutualist extinction as had been found in previous models (Wang et al 2012; Wang 2012; Mougi & Kondoh 2014). However, we show that the inclusion of mechanisms like HIPL into models generates the potential for unexpected population and community level effects that can reduce the tendency for extinction and actually support community persistence.

We generate this model using the empirical data of the effects of herbivory on pollination through HI-VOCs (Kessler et al 2011; see Methods section). This data set measured HI-VOC release and pollinator visits at different levels of herbivory to determine how bee pollination of wild tomato plants changes as a function of the amount of herbivory experienced by a plant. Since pollinator visits change as a function of the level of herbivory, we call the resulting change in pollination the "functional form of HIPL." This functional form of HIPL can then be inserted into dynamic models of a flowering plant‑pollinator‑herbivore community to ascertain its effects on community dynamics and persistence with different pollinator relationships.

There are three objectives to the research presented here. (1) Find the functional form of HIPL by determining how pollinator visitation declines as a function of herbivory intensity. (2) Measure the effects of HIPL on the persistence of the interacting community and its dynamics through time at different rates of herbivory. (3) Compare the effects of HIPL on community dynamics and persistence in both obligate/highly specialized and facultative/generalist pollination relationships

5.3 Methods

5.3.1 Study system

The data used in this work comes from a series of field experiments on the Pacific slope of the Peruvian Andes conducted by Kessler et al.2011 using a wild tomato species, Solanum peruvianum. S. peruvianum is a self-incompatible species, which is attacked by a diverse set of herbivorous insects and pollinated by bees in the Apidae, Colletidae, and Halictidae families (Chetelat et al 2009). Bees on Solanum flowers, like those on other poricidal flowers, need to be behaviorally specialized because pollen, as the only pollinator reward, can only be harvested by the bees through vibratile (“buzz”) pollination (De Luca & Vallejo-Marin 2013). Herbivory of S. peruvianum was found to significantly lower pollinator visits through HI-VOC release. This limited pollination led to notable effects on plant fitness and was found to occur in response to actual herbivore damage or to pharmacologically induced VOC emission (application of methyl jasmonate in the absence of actual tissue damage; Kessler et al 2011). Although other traits can be important in mediating complex interactions, in this system HI-VOC emission fully explained the behavior of the bees and so the effects on plant fitness.

While a number of studies have found evidence of herbivory reducing the amount of pollination individual plants receive, these studies often use categorical treatments of pollination levels measured with and without herbivore damage (Krupnick et al 1999; Kessler & Halitschke 2009; Adler & Irwin 2005). Few have studied pollination across a continuous spectrum of herbivore damage as was done in Kessler et al 2011. It is this approach that allows for the investigation into the functional form of HIPL across various levels of herbivory.

5.3.2 Statistical analysis

In order to ascertain the functional form of the negative correlation between herbivory and pollinator visitation, Kessler et al’s data has been broken into 11 sets. The first set (serving as the control) measures average pollinator visitation at 0% herbivore damage and is followed by 10 categories each grouped by taking the averages of herbivore damage and pollinator visitation in 10 percentage point steps (Fig. 5.2). This results in 11 averaged data points with standard errors on the x (herbivore damage) and y (pollination percentage) axes (Fig. 5.2). Given that the model used in this work is a spatially implicit meanfield model where parameters model average per-capita interactions across populations, the use of average effects is appropriate. Candidate models for the functional form of HIPL were fit to the data using nonlinear (weighted) least-squares estimates (nls) in the statistical software R and compared using Akaike Information Criterion (AICc) weights given their nonlinearity.

Analysis of this averaged/binned the data points presented in the Results section reveals that the Type II was the best fit candidate. This was verified by applying the same statistical analysis to the raw un-averaged data, where the Type II response was similarly found to the best fit, though with lower AICc weights (Appendix D.1). Additionally, incorporating the standard error of the original averaged 11 data points into the nls regression and giving weights to each mean value also shows the Type II response to be the best fit (Appendix D.2).

It should be noted that the functional form of visitation reduction will likely differ across systems and communities. For example, a similar data set collected by Barber et al 2012 put through the same analysis results in no conclusive support for any one response model over the others tested. See Appendix D.1 for a full account of the analysis on that data.

5.3.3 Model Background

This relationship between herbivory and pollination was first considered in theoretical models by Jang (2002). However, in Jang's analysis, no explicit functional form was ever ascribed to this relationship. It was kept as a formless term for mathematical analysis instead of taking a Type II or Type III form for simulation. Furthermore, the dynamics-based analysis was specifically focused on the number of possible equilibrium points, the stability of those points, and the qualitative categories of possible dynamics (such as dampened oscillations or sustained oscillations). Given this basis and the goals of the analysis, Jang concluded that herbivore-induced reductions in pollinator visitation rates have no effect on the "qualitative" behavior of the model. In other words, HIPL would not change the number of equilibria or the types of dynamics that the model can potentially exhibit. We do not dispute Jang's results, but instead show that important distinctions reside in the "quantitative" change in dynamics. Jang's conclusions may explain other researchers' decision to not include pollinator visitation reduction into their models (Wang et al 2012; Wang 2013; Mougi & Kondoh 2014; Georgelin & Loueille 2014). Sánchez-Garduño et al (2014) did describe the potential inclusion of a function akin to $v(c, h)$ but set it equal to 1. Sánchez-Garduño & Breña-Medina (2011) did include a sigmoidal Type III functional response rate of pollinator visitation decrease $\left(\sim \frac{1}{1+ch^2}\right)$ for a brief numeric consideration of possible types of mutualism-herbivore community dynamics. As more studies find that herbivory can produce significant plant-mediated interactive effects with other organisms (e.g., pollinators) and that it can result in significant declines in plant fitness, we must begin to delve further into the effects of this prevalent ecological relationship.

5.3.4 Mathematical Analysis

Analysis was done through Mathematica 10 using NDSolve with Explicit RungeKutta methods (Wolfram Research 2014). Large scale analysis was facilitated by University of Michigan's FLUX computing core.

5.4 Results

Best fit functional form of HIPL. We first establish the functional form that reduced pollinator attraction takes in relation to increased herbivory/herbivore presence using Kessler et al.'s data (see Methods section). The function describing pollinator visitation decline will be denoted as $v(c,h)$ where h is the percentage of herbivore-damaged leaves on a plant and c is a parameter which describes the intensity of the effect of h on pollination.

Five potential models are considered and fit against the data: (1) Type I or linear decline response, (2) Type II declining response, (3) Type III declining response, (4) Mixed saturating decline, (5) Concave declining function (Fig. 5.1). Type I, II, and III functional responses are named as such due to their dynamic similarity to functional responses seen in predation and mutualistic interactions. The Mixed Saturating model tests the effect of a response model with a scalar multiplier, c, on h and a potential non-integer exponent, b (Fig. 5.1). The Concave function allows for the testing of a potential threshold effect. These response models were chosen based on their established use in the theoretical literature (Vandermeer & Goldberg 2013), their shown applicability in other interactions [such as predation and mutualist interaction (Schnek & Bacher 2002; Essenberg 2012)] and their ability to cover potential dynamic responses to herbivory.

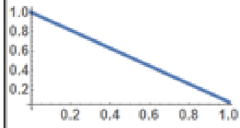
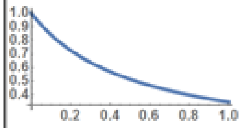
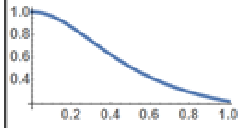
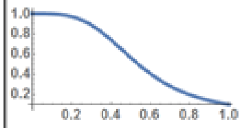
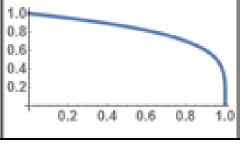
Fitted models to averages	Example of functional form	Estimated Parameters	Significance and Fit	AICc	AICc weight
1.)Type I/Linear: $\sim ch + i$		$c = -0.635,$ $i = 0.8615$	$p = (c)\mathbf{3.05e^{-6}}$ $(i)\mathbf{1.29e^{-9}}$ $R^2 = 0.9114$	-22.262	0.02995
2.)Type II: $\sim \frac{i}{1+ch}$		$c = 1.877,$ $i = 0.9565$	$p = (c)\mathbf{9.87e^{-6}}$ $(i)\mathbf{8.74e^{-10}}$	-28.649	**0.73011**
3.)Type III: $\sim \frac{i}{1+ch^2}$		$c = 2.418$ $i = 0.8419$	$p = (c)\mathbf{2.12e^{-4}}$ $(i)\mathbf{2.84e^{-9}}$	-21.524	0.02071
4.)Mixed Saturating: $\sim \frac{i}{1+ch^b}$		$c = 2.022$ $b = 1.230$ $i = 0.9240$	$p = (c)\mathbf{2.71e^{-5}}$ $(b)\mathbf{0.000111}$ $(i)\mathbf{1.19e^{-8}}$	-26.240	0.21889
5.)Concave: $\sim i * \left(1 - \frac{h}{1}\right)^c$		$c = 0.5394,$ $i = 0.8278$	$p = (c)\mathbf{0.00045}$ $(i)\mathbf{7.41e^{-10}}$	-13.279	0.00034

Figure 5.1 - Curve fitting the five candidate response models. Describing the results of the curve fitting to the five candidate response models for v(c, h): Type I/Linear, Type II, Type III, Mixed Saturating, Concave. Here h represents the level of herbivory. The parameters c and b determine the shape of the curve and i is the intercept. Equation representations of each model are given along with a pictorial example of each model. The Type II functional response has the highest Akaike Information Criterion weight of 0.73011

The Type II and Mixed Saturating response were best supported by Akaike Information Criterion (AICc) weights with the Type II being the favorite (Fig. 5.1). For the Mixed Saturating model, the estimated value of the exponent parameter b is nearly 1, making these two models very similar in overall form across the range of herbivore damage. Additionally, when the intercept (i) is set as 1 across models (presuming no HIPL effect as a control), the AICc weights for the Type II and Mixed Saturating responses are approximately 0.85 and 0.14, respectively. Finally, additional analysis corroborates the support for the Type II response (see Methods section, Appendix D.1 and D.2). Therefore, the form describing HIPL that will be used in the full model will be $v(c,h) = \frac{1}{1+ch^2}$ (Fig. 5.2). Given the appreciable support for the Mixed Saturating form, we did analyze cases where $b > 1$. We also analyzed the effects of the other functional forms of HIPL. Analysis showed consistent results with those presented here (see Discussion section).

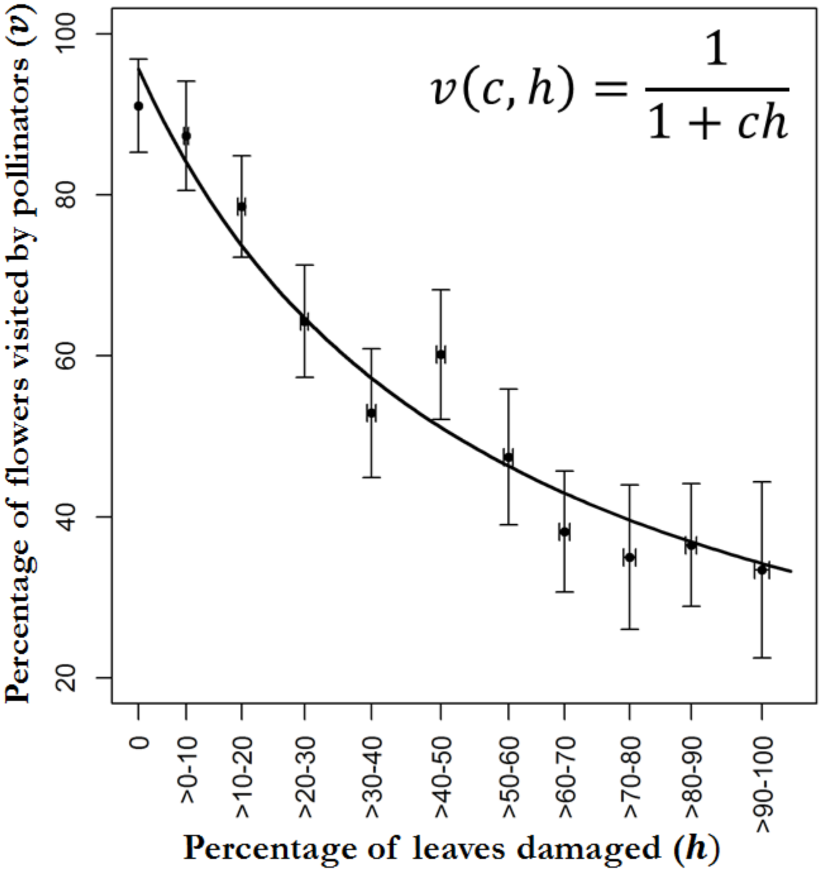


Figure 5.2 - Best fit Type II functional form. Best fit Type II functional response of pollinator visitation ($v(c,h)$) as a function of proportionate leaf damage (h). Error bars show standard error of the mean

5.4.1 Full model description

This model (Eq. 5.1) takes the form of three coupled ordinary differential equations with the following three variables: (1) population abundance of the shared flowering resource plant (F), (2) population abundance of the herbivorous insect (H), and (3) the population abundance of the insect pollinator of the flowering plant (P). Herbivory occurs through a typical Lotka‑Volte ra consumer‑resource interaction with a Type II functional response, with the rate of herbivory labeledr_H. Though studies of the functional responses of herbivores have not focused on insects, a Type II functional response has been found in numerous taxa (Spalinger & Hobbs 1992; Gross et al 1993; Durant et al 2003) and is a commonly assumed form used in many consumer‑resource models (Vandermeer & Goldberg 2013). Pollination of flowering plants by pollinators also incorporates a Type II functional response. This was first applied in Wright's 1989 modified model of stable mutualisms and has seen support from empirical studies (Essenberg 2012;

Wright 1989; Feldman 2006). Both the flowering plant and pollinator experience density-dependent growth as the populations are limited by space or nesting availability, respectively. The limitations on population growth due to density dependence scale with the parameter α.

The flowering plant and pollinator receive a reproductive benefit of b_F andb_P, respectively from pollination, which represents the conversion efficiency of the pollination visits. Baseline visitation rates, i.e., interaction rates between F and P when there is no herbivory, have a default value of 1 functioning as the visitation control value. Given that the y-intercept of the best fit form of $v(c, h)$ is approximately 0.96 (Fig. 5.1), this assumption is reasonable. Any small changes to this value would not qualitatively change the results presented below. To incorporate the functional form of HIPL, we assume that levels of herbivory are proportional to the density of herbivores. Pollination rates are therefore affected by, $v(c, H)$ where H replaces h and c represents pollinators' sensitivity to herbivore presence/damage. Additionally, because $v(c, H)$ now considers herbivore density and not the resulting percentage of leaves damaged by herbivores, tested values of parameter c will be higher than estimates in Fig. 5.1.

The flowering plant has an average rate of reproduction, independent of the focal insect pollinator population (P), represented as r_F. When $r_F$is set to 0, the flowering plant is dependent on pollination from P for fertilization so its reproduction rate is regulated by the parameter $b_F > 0$. This represents an obligate relationship with the mutualists in the model. Obligate mutualisms, while not common, are well documented (Bawa 1990; Flemming & Holland 1998; Pellmyr 2003; Kato et al 2003; Kawakita 2010) and serve as a foundation to understanding more complicated mutualistic networks in this context. Similar to obligate mutualisms, but more common (Johnson & Steiner 2000; Pauw 2006; Bluthgen et al 2007; Padysakova 2013), are specialized pollination mutualisms where some generalization exists, but the majority of visits with successful pollen deposition and fertilization is made up of a particular pollinator-plant pair. With some small positive value ϵ, such that $r_F = \epsilon$, we can model a highly specialized pollinator mutualism, where $r_F$contributes slightly to plant reproduction and the pollinator is still dependent upon F. When $r_F > 0$ by a substantial amount ($r_F > \epsilon$), the flowering plant is able to produce some average amount of viable seeds through animal pollination unaffected by insect directed HI-VOC release (e.g., bat or bird), vegetative reproduction, or self-fertilization. Self-fertilization can be common in specialized pollination systems (Fenster et al 2007; Pérez et al 2009). This condition models a generalist/facultative mutualism for the flowering plant.

Pollination specialization can often be asymmetric (Vazquez & Aizen 2004; Basilio et al 2006; Petanidou & Potts 2006; Stang et al 2007; Futuyma & Gould 1979), so in this model, only the flowering plant population's growth is allowed options outside the focal pollination mutualism with P. The full model is given in Eq. 5.1. All model parameters are listed and described in Table 5.1.

$$\begin{aligned}
\frac{dF}{dt} &= F\left(r_F + b_F v(c,H)\frac{P}{1+h_P F} - \alpha_F F \right) - \frac{r_H FH}{1+h_H F} - d_F F \\
\frac{dH}{dt} &= \frac{c_{FH} r_H FH}{1+h_H F} - d_H H \qquad \textbf{(5.1)} \\
\frac{dP}{dt} &= P\left(b_P v(c,H)\frac{F}{1+h_P F} - \alpha_P P \right) - d_P P \\
v(c,H) &= \frac{1}{1+cH}
\end{aligned}$$

The model is formulated with a specialist herbivore population that doesn't gain any metabolic energy from any other plant species. While this limits the model's application to generalist herbivore species, specialist insect herbivores are very common (Futuyma & Gould 1979; Forister et al 2015). Finally, while the model and form of $v(c, H)$ allow for a variety of mechanisms for HIPL, including HI-VOCS, this model does not include negative effects of HI-VOCS on the herbivore population, such as herbivore repellence and third trophic level interactions (De Moraes et al 2001; Kessler & Baldwin 2001; Bruce et al 2005). We argue this is acceptable, at least initially, as specialist herbivores often exhibit resistance to chemical repellence (Siemens & Mitchel-Olds 1996; Berenbaum & Zangerl 1998; Kliebenstein et al 2002) and temporary herbivore repellence or control would only reinforce the stabilizing effects of HIPL discussed in the Results sections below. Here we focus on the plant-mediated effect of herbivory on pollinator behavior and the resulting broader community dynamics.

Table 5.1 - Parameter definitions for Equation 5.1. Parameters are measured per individual per unit time. The 3 time dependent variables in the model are as follows: F-flowering plant population, H-herbivore population, P-pollinator population.

Parameter	Definition
a	Strength of density dependence. Set to .1
r_F	Intrinsic reproductive rate of the flowering plant independent from pollinator P
r_H	Rate of herbivory of herbivore consuming flowering plant
c_{FH}	Conversion rate of eaten plant biomass F into herbivore H
h_H	Handling time of the herbivore on the flowering plant
h_P	Handling time of the pollinator on the flowering plant
b_F	Reproductive benefit of pollination visit for the flowering plant
b_P	Reproductive benefit of pollination visit for the pollinator
c	Degree of pollinator visitation reduction due to effect of herbivore
d_F, d_H, d_P	Background death rates for flowering plant, herbivorous insect, the pollinator respectively

5.4.2 Model equilibria and pollination without HIPL

There are four general equilibria for the 3 species of the model (Table 5.2). The equilibrium values for the three variables F, H, and P are labeled F^*, H^*, and P^* respectively across all equilibria. Equilibria 5.1, 5.2, and 5.3 are equilibria that have been studied in well-established work and will not be of focus here. Equilibrium 5.4 is the lone equilibrium in which all three variables can persist in a positive-valued steady state. The parametric expression of F^* in Equilibrium 5.4 is $\frac{d_H}{c_{FH}r_H - d_H h_H}$. Expressions for H^* and P^* change depending upon the inclusion or exclusion of $v(c, H)$ and the status of the mutualism (see Appendix D.3 and D.4). The community can also go extinct such that all three populations in the system tend to 0. We will refer to this as the 0-equilibrium, representing full community extinction. Therefore, the two equilibria of interest are the 0-equilibrium and Equilibrium 5.4. Equilibrium 5.4 and persistent periodic oscillations for all 3 populations (stable limit cycles) will be referred to as "non-zero attractors." A non-zero attractor is any stable dynamic through time, which attracts nearby trajectories to it and results in the persistence of all populations. The full effect of HIPL and $v(c, H)$ on system persistence is made clear by first setting $c = 0$, making $v(c, H) = 1$ in Equation 5.1. This effectively eliminates the mechanism of HIPL from the model and verifies that previously described patterns (Jang 2002; Sánchez-Garduño et al 2014; Wang et al 2012; Wang 2013; Mougi & Kondoh 2014) are reproducible with our model. More specifically, it shows that obligate and highly specialized plant‑pollinator mutualisms can be destabilized and driven to extinction in their more basic theoretical formulation without trait-mediated indirect effects, such as HIPL (Appendix D.3).

Table 5.2 - All non-zero equilibria for Equation 5.1. Note the system is also stable at the 0-equilibrium, $F^* = 0, H^* = 0, P^* = 0$. *All variable and parameter descriptions are given in Table 5.1.*

Equilibrium	Description
5.1) $F^* = \frac{r_F - d_F}{a}, H^* = 0, P^* = 0$	Only possible when $r_F > d_F$. F goes to carrying capacity.
5.2) $F^* = \frac{d_H}{r_H - d_H}, H^* = \frac{-ad_H + d_F d_H - d_H r_F - d_F r_H + r_F r_H}{(d_H - r_H)^2}, P^* = 0$	Only possible when $r_F > d_F$. P is eliminated from the system and F, H community persist in a steady state as a consumer-resource system.
5.3) $F^* > 0, H^* = 0, P^* > 0$	Heliminated from the system. F and P persist in a steady state. Parametric expression too large to write here.
5.4) $F^* > 0, H^* > 0, P^* > 0$	All 3 variables persist in a steady state. Parametric expression too large to write here. See analysis in results section.

5.4.3 Obligate and specialized mutualisms with HIPL

Keeping $r_F = 0$ (obligate mutualism), but setting $c > 0$ and including the effect of the Type II functional form of $v(c, H)$, greatly alters the obligate mutualism's response to higher rates of herbivory. Most notably, the mutualism is either unaffected or more resilient to comparatively much higher values of $r_H$at the population level. In other words, the mutualism and the system overall can persist through much higher rates of herbivory. In fact, HIPL often creates a non-zero attractor where none existed before and consequently allows the mutualism to survive in systems that led to extinction when $c = 0$.

Using a bifurcation diagram with c as the bifurcation parameter, we can see that low values of c result in system extinction (Fig. 5.3a, 5.3b). Increasing the value of c, the system reaches the "rescue point," taking population trajectories from extinction to sustained oscillations (limit cycles) (Fig. 5.3a, 5.3c). The exact value of c, which becomes the rescue point depends on other parameters in the model and increases with higher rates of herbivory (Fig. 5.4). Yet, higher values of c push the system to a Hopf bifurcation which merges the maxima and minima of the oscillations to the same point leading to a locally stable Equilibrium 5.4 and steady state dynamics (Fig. 5.3a, 5.3d). Therefore, the model shows the potential for HIPL to allow for community persistence at higher rates of herbivory and stabilized systems despite further reducing interaction rates among mutualists.

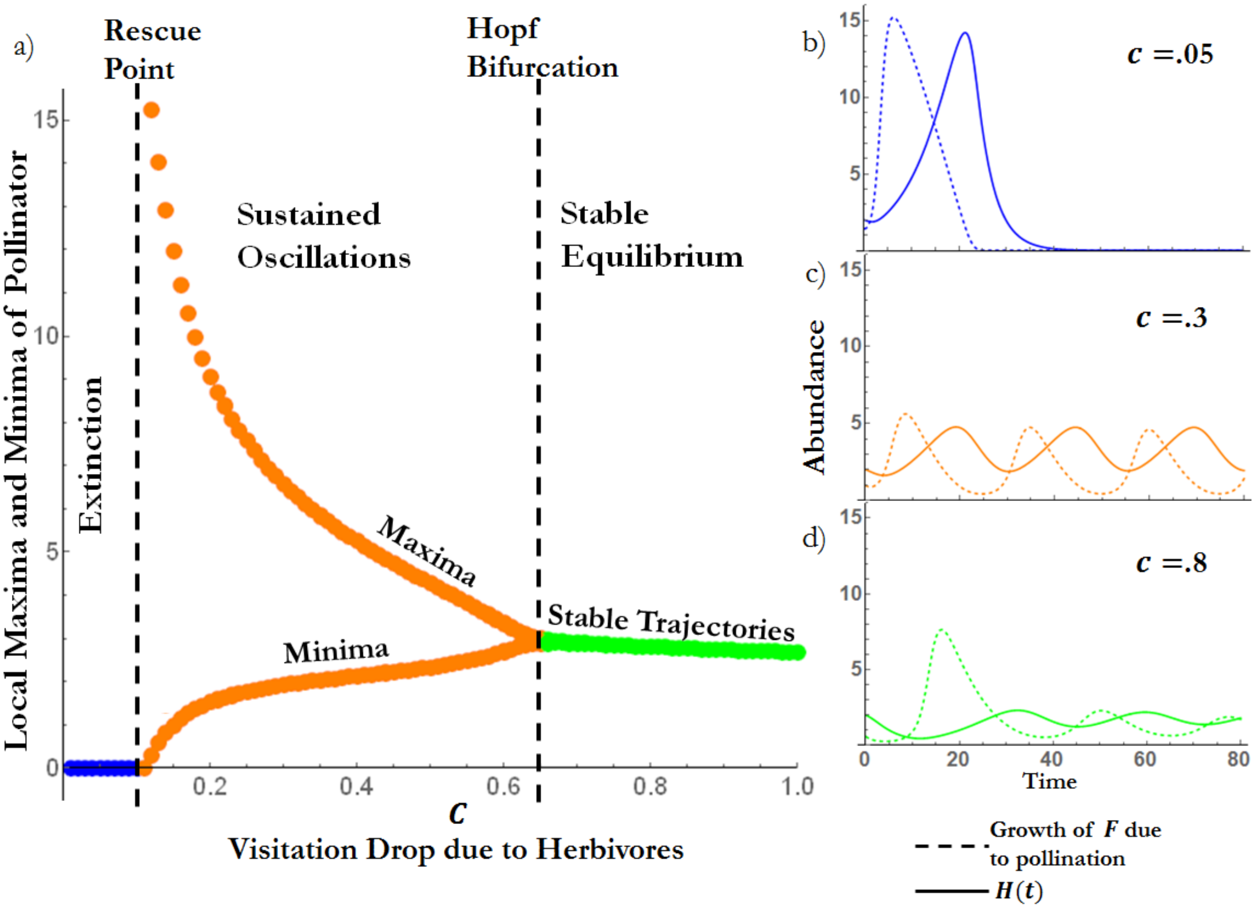


Figure 5.3 - Effects of HIPL on community dynamics within an obligate mutualism. Changing community dynamics with varying degrees of pollinator visitation reduction due to herbivory (different values of parameter c). a) A bifurcation diagram of the pollinator variable P across values of c. Values which lead to extinction, sustained oscillations, and dampened oscillations are labeled and shown in blue, orange, and green respectively. The "rescue point" and Hopf bifurcation are marked with dashed lines. b) Time series curves of growth of flowering plant population F due to pollination ($Fb_F v(c,H)\frac{P}{1+h_P F}$, dashed lines) and subsequent saturation of system with herbivores H (solid lines) leading to extinction. c) HIPL reduced growth of F (orange dashed) and subsequently attenuated growth of H (orange solid). d) Highest level of visitation reduction leading to dampened oscillations and stable equilibria F growth is shown in the green dashed line while the H is shown in the solid green line. $d_F = 0.2$; $d_H = 0.28$; $d_P = 0.2$; $c_{FH} = 1$; $b_F = 1.565$; $b_P = 1.865$; $r_F = 0$; $r_H = 0.445$; $h_F = 1$; $h_P = 1$; $\alpha = 0.1$, all initial conditions =2.

The mechanism of system persistence is apparent by considering the form of $v(c,H)$. Given that $v(c,H) = \frac{1}{1+cH}$ when $c > 0$, $v(c,H)$ and H will oscillate asynchronously through time. In other words, pollination rates will only reach maximum levels when herbivore densities are low (Appendix D.4 and Fig. D.5). We can see the results of this asynchronicity by plotting the growth in F due to pollination and the subsequent effect on the herbivore population at different levels of visitation reduction (Fig. 5.3b‑5.3d). When c is below the rescue point (Fig. 5.3a, 4b), HIPL is weak and per-capita pollinator visitation rates are roughly steady despite high herbivore densities. Herbivory does not reduce pollination received by individual plants in this case. This causes a sharp increase in F population growth, followed by a sharp rise in H (Fig. 5.3b). This saturates the system with herbivores and the mutualism cannot recover. Therefore, despite the immediate benefit of the reproduction of individual plants, the subsequent increase in herbivores is substantial enough to eliminate the plant population and consequently the pollinator.

After the rescue point (Fig. 5.3a, 5.3c), pollinator visitation begins to decrease in response to higher H loads. This reduces the initial growth of F as plants receive less immediate pollinator visits (Fig. 5.3c). In turn, this reduces $\frac{dH}{dt}$ and the peak value of H (Fig. 5.3c), keeping the population level of H low enough for the system to persist in oscillations. Finally, past the Hopf bifurcation point, (Fig. 5.3a, 5.3d) pollinator visitation drops quickly even with moderate herbivory. This causes pollination-induced growth of F to stay low and the H population cannot continue to grow (Fig. 5.3d). The asynchronicity of $v(c,H)$ and H creates a stabilizing effect, which rescues the system and induces sustained oscillations or stable equilibria depending on the level of pollinator aversion to herbivores/herbivory. In this case, the decrease in immediate plant reproduction is mitigated by the indirect control of the herbivore population. Limitation of pollinator visitation then actually has a net benefit to the plants and pollinators at the population and community level.

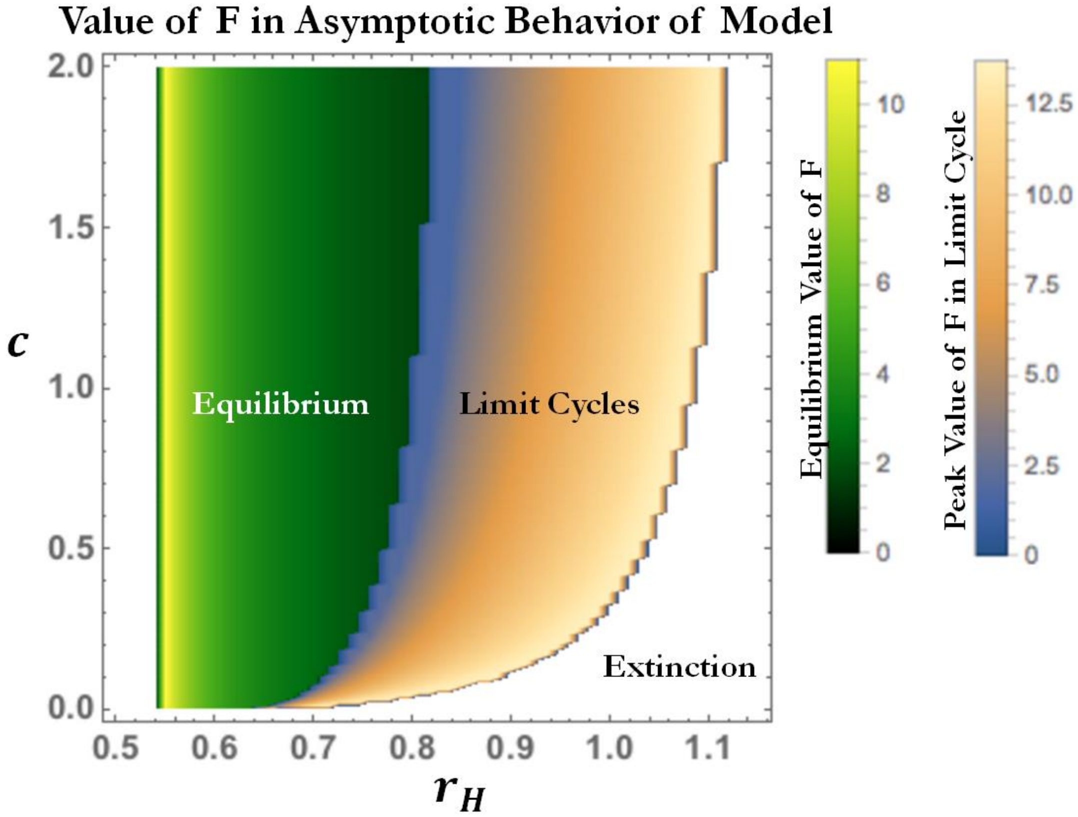


Figure 5.4 - Effects of HIPL on community dynamics across parameter space. A two-dimensional bifurcation heatmap showing the abundance of F (flowering plant) in the asymptotic behavior of the model shown as different colors across the $\{r_H, c\}$ parameter space in the obligate model. Where parameter combinations create stable equilibria, F abundance is shown in the green color scale. Where values create stable limit cycles, F abundance is shown in the sunset color scale. The switch between the two color schemes represents the Hopf bifurcation shown in Fig 5.3. Values which lead to either extinction of H ($r_H < 0.55$) or full system extinction (lower right portion of figure) are shown in white. $r_F = 0$; $b_F = 1.665$; $b_P = 1.695$; $c_{FH} = 1$; $d_F = 0.2$; $d_H = 0.5$; $d_P = 0.2$; $h_F = 1$; $h_P = 1$; $\alpha = 0.1$.

There is a clear expansion of the rate of herbivory (value of r_F), which the mutualism can withstand as the value of c increases (Fig. 5.4, a two-dimensional bifurcation heat-map). In this particular formulation of the model, at the highest value of c tested, the range of r_H, which the mutualism can withstand increases by ~4.33 times compared to the initial system, where $c = 0$ and $v(c, H) = 1$ (Fig. 5.4, see Fig. D.6 for H and P). The highest sustainable value of r_H reaches nearly double that of a system, where $c = 0$. Note, that the degree of this increase is also affected by the values of other parameters (e.g., reproductive benefit of pollination to the mutualist populations).

Analogous rescue effects and community dynamics are producible in the highly specialized case where $r_F = \epsilon$ for some small positive value $\epsilon > 0$. Examples are available in Appendix D.5. Finally, while $c > 0$ can induce system persistence, it is not without some potential cost. Both rates of herbivory (r_H) and pollinator aversion to herbivory (c) can have significant effects on the volume of the basin of attraction of non-zero attractors. In other words, HIPL ($c > 0$) can create the potential for system rescue, but higher values of c reduce the amount of initial system conditions which move toward non-zero attractors (Appendix D.6).

4.4.4 Facultative mutualism with HIPL

This section examines a system where the shared plant resource F has a substantial non-zero growth rate independent from P ($r_F > \epsilon > 0$) and there is visitation reduction ($c > 0$). This creates a system where the mutualism is obligate for the pollinator, but facultative/generalist for the flowering plant. In this case, while visitation reduction can still save the system from extinction, simulations show that the benefits of visitation reduction (especially for the pollinator, P) are dependent upon how much plant growth occurs independent from P (i.e., the value of r_F).

When the value of r_F is low and relatively small compared to the reproductive benefit of pollination, then HIPL can still indirectly control herbivore populations and rescue the system from extinction in a similar manner to the highly specialized case described above. However, when the system exists under a sufficiently high rate of herbivory (r_H) and a sufficiently high degree of visitation reduction (c) then higher values of r_F can decrease pollinator abundance and push P to a crash point. Again, these effects are displayed in a bifurcation diagram, this time across different values of r_F (Fig. 5.5). For $0 \leq r_F \leq 0.73$ the system supports a stable pollinator population at Equilibrium 5.4 but with a monotonically decreasing abundance of P^* as r_F increases (Fig. 5.5a). While the idea that higher growth rates of one mutualist would limit its mutualistic partner seems unintuitive, the reason for this is the relationship between herbivore and pollinator populations when the system is stable at Equilibrium 5.4. Analysis shows that $P^* \sim \frac{1}{H^*}$ (Appendix D.4) due to herbivory reducing flower numbers and the effect of $v(c, H)$ (Fig 5.5b). Also, H^* was found to increase over this same range of r_F (Fig 5.5b). Moreover, in Equilibrium 5.4, $F^* = \frac{d_H}{c_{FH} r_H - d_H h_H}$, so while higher r_F supports larger H populations in equilibrium, there is no corresponding increase in the population of F. As the abundance of herbivores increases, so does the effect of HIPL. High effects of HIPL limit pollination interactions between F and P decrease the population growth of the pollinator. While this would cause both P and F to decline when r_F is low, the high values of r_F allow the plant-herbivore system to persist without the pollinator. In other words, the population level effects of HIPL on the plant and pollinator populations become decoupled in a more generalist/facultative mutualism. Therefore, increased intrinsic growth from the flowering plant can actually reduce pollinator abundance through the mechanism of HIPL. Sufficiently high values of r_F increase H^* to a level which pushes the pollinator population to extinction by pushing P^* to 0 (Fig. 5.5a, 5.5b).

Further increases in r_F induce limit cycles, as they would in a classic Lotka–Volterra system. As F and H oscillate, the amplitude of these oscillations can allow for windows of time where the pollinator population can grow. This occurs because higher r_F creates larger, more dramatic oscillations in the plant-herbivore system. These large oscillations create higher peaks in H but consequently result in lower minima values (bifurcation diagram of H in Fig. 5.5c). Lower minima values mean longer recovery times from low population abundances. This result in longer periods of time, where herbivore abundance is low in-between oscillatory population peaks. Heuristically, this can be shown by measuring the amount of time $H < 0.5$ as r_F increases (Fig. 5.5c, red line). This increased time with low H abundance increases the time P can grow unencumbered by HIPL. This creates higher oscillatory peaks in P abundance (Fig. 5.5a, Appendix D.7).

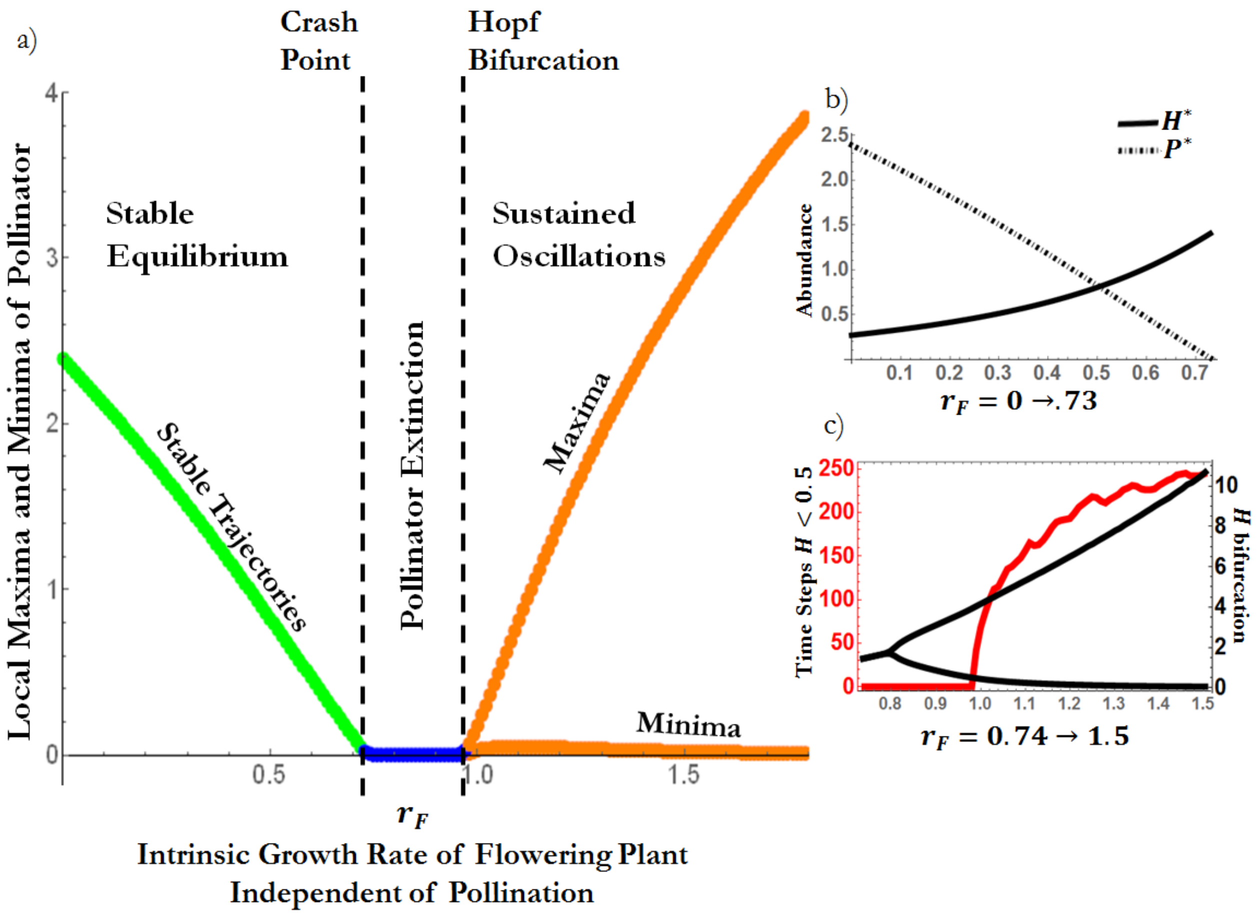


Figure 5.5 - Effects of HIPL on community dynamics within a facultative mutualism. Changing community dynamics with increasing values of the parameter r_F (intrinsic growth of F). a) A bifurcation diagram for P (pollinator) across values of the intrinsic growth rate of the flowering plant population (r_F). Values which lead to extinction, sustained oscillations, and dampened oscillations are shown in blue, orange, and green respectively. The "crash point" and Hopf bifurcation are marked with dashed lines. b) Changes in H^* (solid lines) and subsequent changes in P^* (dashed lines) for $r_F = 0 \rightarrow 0.73$. c) Black lines and right y-axis represent a bifurcation diagram of H. As r_F increases past 0.8, the system and H populations begin to oscillate with increasing amplitude. Red line and the left y-axis show the increase in the amount of time per simulation that $H < 0.5$. Results shown for $r_F = 0.74 \rightarrow 1.5$. The value of r_F which marks longer times with lower H abundance ($r_F \approx 1$) correspond to the value of r_F which facilitates higher P maxima shown in Fig 5.5a. Other parameter values: $c = 1.44$; $r_H = 0.7$; $c_{FH} = 1$; $d_F = 0.2$; $d_H = 0.5$; $d_P = 0.2$; $h_F = 1$; $h_P = 1$; $b_F = 1.04$; $b_P = 0.85$; $\alpha = 0.1$.

5.5 Discussion

Understanding the functional responses of interacting organisms has been critical to the development and extension of theoretical foundations to empirical studies of herbivory (Hobbs et al 2003), mutualisms (Wright 1989; Feldman 2006), and especially predation (Holling 1959; Abrams 1982). However, the functional response of mutualist interactions (e.g., pollinators) across levels of antagonistic interactions (e.g., herbivory) has only recently become a research focus within the plant‑herbivore interaction and community dynamics context. This increased interest largely rests on two conceptual pillars. First, interactions among members of a plant community are complex and removal or addition of players can have dramatic differential consequences (Stam et al 2014). Second, many of the interactions are mediated by plant metabolic responses to environmental stressors (e.g., herbivory) which broaden the arena in which plant-organismal interactions occur and further affects context dependency of functional links mediating interactions1. Measuring functional responses between ecological variables accounts for the fact that rates of interaction between species are not constant. In the case of HIPL, the functional response is particular in that the change in interaction rates between mutualists is mediated by a third party (the herbivore) interacting with the host plant. This is somewhat similar to trait-mediated indirect interactions, or TMII (Werner & Peacor 2006). Here we show support for the hypothesis that pollinator visitation rates may decrease as a Type II function in response to herbivory. It had already been experimentally verified that this effect can be primarily driven by a plant response to herbivory, HI-VOCs (Kessler et al 2011; Kessler & Halitschke 2009). Understanding how pollination changes due to broader interactions within communities will be an important component in the study of pollination services (Pierik et al 2014).

When an antagonistic species limits the interaction rate and therefore the reproduction of individuals in a mutualistic species pair, it is not unreasonable to consider this a fitness loss for each of the mutualists. However, the model presented here suggests that indirect population and community effects in a flowering plant, herbivore, and pollinator community can present various challenges to this conclusion. HIPL is dynamic across time, increasing or decreasing in intensity with herbivore abundance. In numerous cases, HIPL limits population growth of both mutualists thereby temporarily and indirectly limiting herbivore abundance. This allows for the persistence of plant and pollinator populations despite the temporary decrease in individual fitness due to phenotypically plastic plant traits. These indirect effects leading to persistent mutualist populations occur across much of the parameter space tested here, though some caveats should be noted. Even when pollination is reduced due to herbivory ($c > 0$), system persistence depends on relatively high values of reproductive benefit per pollinator visit for both the plant and/or the pollinator (b_F and/or b_P). Also, sufficiently high herbivore attack rates (r_H) and/or low death rates (d_H) can still crash the system, though this can be counteracted by simply lowering herbivore conversion rates. Regardless of these limits in parameter space however, adequately high values of c can expand the range of r_H that the system can withstand (Fig. 5.4), creating non-zero attractors where none existed before. Sufficiently high c can even lower the level of reproductive benefits of the mutualists (b_F and b_P) required for community persistence (Fig. D.7). Mainly though, it is noteworthy that there is the potential for a decrease in mutualist interaction rates and a subsequent decrease in population growth of one or both mutualists (plant and pollinator) to function as a mechanism for system persistence in the face of an antagonistic interaction. However, the results from the generalist/facultative model indicate that the effects of HIPL will become more complex when embedded into more complicated mutualistic networks.

Because herbivores and pollinators interacting with a particular plant species use the same information space1 it was long hypothesized that plant traits are under conflicting selection to repel herbivores while still attracting pollinators (Strauss et al 1999). The HIPL found in S. peruvianum was driven by HI-VOC-mediated information transfer between plants, herbivores and pollinators. The relatively strong negative ecological effect on plant fitness, poses the question why plants maintain such a strong induced, seemingly costly VOC emission in response to herbivory? Two principal hypotheses were suggested: (A) inducible volatile emission has additional functions in mediating interactions such as repelling herbivores, attracting natural enemies of herbivores or reducing plant damage through within plant signal transduction (Kessler et al 2011). Alternatively (B) HIPL and the resulting reduced investment in seed production may be a mechanism for the plant to reduce opportunity costs potentially resulting from high seed production when herbivory limits resources. While this study does not specifically address these hypotheses, it offers an additional alternative hypothesis. We contend that plant-induced responses with ecological consequences like HIPL have broader indirect effects in a population or community context. Indirect effects can reduce the risk of extinction as well as the strength of natural selection against HI-VOC release because they limit reproductive ability of individual organisms such that population growth rates are maintained at sustainable levels in the community context, resulting in a net benefit for the individual interactors. Ecologically this has been hypothesized to be driven by two mechanisms. First, induced plant metabolic changes affect the carrying capacity of the system and so influence the system's potential for population cycles and outbreaks (Kessler et al 2012). Second, chemical information transfer between organisms allows for behavioral responses in all interacting organism, which, in turn prevents populations from reaching critical densities (Rubin et al 2015).

Notably, the Type II form of $v(c, H)$ used in this model is not asserted to be the definitive functional form HIPL will take in nature. Other populations, species, or systems may react to herbivory in a Type I or Concave form. For example, the curve fitting analysis done with the data from Barber et al (2012) did not produce a single best fit functional response and may result in a different form with more data points (see Appendix A.1). The HIPL displayed in these data did not originate from HI-VOCs, but from direct physical effects of herbivory on flower attractiveness and mycorrhizal fungi colonization. Perhaps other mechanisms of visitation reduction may be prone to different functional forms. Additionally, the Barber et al. study system was a less specialized pollination system, and the two major pollinators were both well-known generalists (bumble bees and honey bees). This may also affect the functional form of HIPL and indicates there is a need to study these effects in more pollination mutualisms along the full degree of specialization and generalization.

Prompted by the possibility of other functional forms, we analyzed model dynamics using alternate functions for $v(c, H)$. Overall, these analyses show that other functional forms can consistently indirectly control herbivore population growth when used in Eq. 5.1 (Appendices D.8–D.11). Only the Concave functional form was found to noticeably limit the range of community persistence in tested parameter space. This occurred because the Concave function leads to long delays in the reduction of pollination services until herbivores reach comparatively high abundances, consequently, eliminating the indirect control of herbivore population growth. It would reasonable to assume that such a dynamic would also occur in the Mixed Saturating case when $b > 1$. While there is a similar delay in HIPL when $b > 1$, it's relatively limited and is followed by such a steep decline in pollinator visitation that the effective indirect control of herbivore populations can occur at lower values of c as the value of b increases (Appendix D.10). Moving forward, our results show that developing an understanding of the ecological consequences of metabolic changes in plants may require incorporating a fuller range of ecological complexity.

5.6 Acknowledgements

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5.7 References

Abrams, PA. 1982. Functional responses of optimal foragers. American Naturalist: 382-390.

Adler LS, Karban R, and Strauss SY. 2001. Direct and indirect effects of alkaloids on plant fitness via herbivory and pollination. Ecology 82:2032–2044.

Adler LS. 2008. Selection by pollinators and herbivores on attraction and defense. Pages 162–173 in K. J. Tilmon, editor. Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects. University of California Press, Berkeley, California, USA.

Adler LS & Irwin RE. 2005. Ecological costs and benefits of defenses in nectar Ecology. 86(11): 2968–2978.

Barber N, Adler LS, Theis N, Hazzard RV, Kiers ET. 2012. Herbivory reduces plant interactions with above- and belowground antagonists and mutualists. Ecology 93(7): 1560-1570.

Basilio AM, Medan D, Torretta JP, Bartoloni NJ. 2006. A year-long plant–pollinator network. Austral Ecol., 31, 975–983.

Berenbaum MR & Zangerl AR. 1998. Chemical phenotype matching between a plant and its insect herbivore. Proceedings of the National Academy of Sciences, USA 95: 13743–13748.

Bruce TJA, Wadhams LJ, Woodcock CM. 2005. Insect host location: a volatile situation. Trends in plant science 10(6): 269-274.

Cunningham SA. 1995. Ecological constraints on fruit initiation by Calyptrogyne ghiesbreghtiana (Arecaceae): floral herbivory, pollen availability, and visitation by pollinating bats. American Journal of Botany 82:1527–1536.

De Clercq P, Mohaghegh J, Tirry L. 2000. Effect of host plant on the functional response of the predator Podisus nigrispinus (Heteroptera: Pentatomidae). Biological Control 18(1): 65-70.

De Moraes CM, Mescher MC, Tumlinson JH. 2001. Caterpillar-induced nocturnal plant volatiles repel conspecific females. Nature 410(6828): 577-580.

Durant D, et al. 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. Journal of Animal Ecology 72(2): 220-231.

Essenberg CJ. 2012. Explaining variation in the effect of floral density on pollinator visitation. The American Naturalist 180(2): 153-166.

Feldman TS. 2006. Pollinator aggregative and functional responses to flower density: does pollinator response to patches of plants accelerate at low densities? Oikos 115(1): 128-140.

Fenster CB & Martén-Rodríguez S. 2009. Reproductive Assurance and the Evolution of Pollination Specialization. International Journal of Plant Sciences 168(2): 215-228.

Forister ML et al. 2015. The global distribution of diet breadth in insect herbivores. Proc Natl Acad Sci USA 112(2); 442-447.

Futuyma DJ & Gould F. 1979. Associations of Plants and Insects in Deciduous Forest. Ecological Monographs 49(1): 33-50.

Georgelin E & Loueille N. 2014. Dynamics of coupled mutualistic and antagonistic interactions,and their implications for ecosystem management. Journal of Theoretical Biology 346:67–74.

Gross JE, et al.1993. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. Ecology 74(3): 778-791.

Herrera CM., et al. 2002. Interaction of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualism-and antagonism-related traits. Proceedings of the National Academy of Sciences 99(26): 16823-16828.

Hobbs NT, et al. 2003. Herbivore functional response in heterogeneous environments: a contest among models." Ecology 84(3): 666-681.

Holling CS. 1959. Some characteristics of simple types of predation and parasitism." The Canadian Entomologist 91.07: 385-398.

Jang, SR. 2002. Dynamics of herbivore-plant-pollinator models. Journal of mathematical biology 44(2): 129-149.

Johnson SD & Steiner, KE. 2003. Specialized pollination systems in southern Africa. South African Journal of Science 99.7(8): 345-348.

Karban R & Strauss SY. 1993. Effects of herbivores on growth and reproduction of their perennial host Erigeron glaucus. Ecology 74:39–46.

Karban R, Yang LH and Edwards KF. 2014 Volatile communication between plants that affects herbivory: a meta ‐ analysis. Ecology letters 17(1): 44-52.

Kawakita A. 2010. Evolution of obligate pollination mutualism in the tribe Phyllantheae (Phyllanthaceae). Plant Species Biology 25(1): 3–19. DOI: 10.1111/j.1442-1984.2009.00266.x

Kessler A & Baldwin IT. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. Science 291(5511): 2141-2144.

Kessler A & Baldwin IT. 2004. Herbivore ‐ induced plant vaccination. Part I. The orchestration of plant defenses in nature and their fitness consequences in the wild tobacco Nicotiana attenuata. The Plant Journal 38(4): 639-649.

Kessler A & Halitschke R. 2009. Testing the potential for conflicting selection on floral chemical traits by pollinators and herbivores: predictions and case study. Functional Ecology 23: 901–912.

Kessler A & Heil M. 2011. The multiple faces of indirect defenses and their agents of natural selection. Functional Ecology 25(2): 348-357.

Kessler A, Halitschke R, and Poveda K. 2011. Herbivory-mediated pollinator limitation: negative impacts of induced volatiles on plant–pollinator interactions. Ecology 92(9): 1769–1780.

Kessler A, Poveda K, Poelman E. 2012. Induced plant responses and herbivore population dynamics. In P. Barbosa, D. L. Letourneau, A. Agrawal (eds.) Insect Outbreaks Revisited, John Wiley & Sons Ltd. Chichester, UK, pp 91–112.

Kessler A. 2015. The information landscape of plant constitutive and induced secondary metabolite production. Current Opinion in Insect Science 8: 47-53.

Kliebenstein D, Pedersen D, Barker B, Mitchell-Olds T. 2002. Comparative analysis of quantitative trait loci controlling glucosinolates, myrosinase and insect resistance in Arabidopsis thaliana. Genetics 161: 325–332.

Krupnick GA & Weis AE. 1999. The effect of floral herbivory on male and female reproductive success in Isomeris arborea. Ecology 80:135–149.

Krupnick GA, Weis AE, and Campbell DR. 1999. The consequences of floral herbivory for pollinator service to Isomeris arborea. Ecology 80:125–134.

Lohmann D J, Zangerl AR, Berenbaum MR. 1996. Impact of floral herbivory by parsnip webworm (Oecophoridae: Depressaria pastinacella Duponchel) on pollination and fitness of wild parsnip (Apiaceae: Pastinaca sativa L.). American Midland Naturalist 136:407–412.

Mougi A. & Kondoh M. 2014. Instability of a hybrid module of antagonistic and mutualistic interactions. Population Ecology. 56:257–263. DOI 10.1007/s10144-014-0430-9

Pauw A. 2006. Floral syndromes accurately predict pollination by a specialized oil-collecting bee (rediviva peringueyi, melittidae) in a guild of South African orchids (Coryciinae). American Journal of Botany 93(6): 917–926.

Pellmyr O. 2003. Yuccas, yucca moths, and coevolution: a review. Annals of the Missouri Botanical Garden 90: 35–55.

Pérez F, Arroyo MTK, Armesto JJ. 2009. Evolution of autonomous selfing accompanies increased specialization in the pollination system of Schizanthus (Solanaceae). American Journal of Botany 96(6): 1168–1176.

Petanidou T & Potts SG 2006. Mutual use of resources in Mediterranean plant–pollinator communities: how specialized are pollination webs? In: Plant–pollinator Interactions: from Specialization to Generalization (eds Waser, N.M. & Ollerton, J.). University of Chicago Press, Chicago, IL, pp. 220–244.

Pierik R, Ballare CL, Dicke M. 2014. Ecology of plant volatiles: taking a plant community perspective. Plant, Cell & Environment 37(8): 1845-1853.

Poelman EH., et al. 2012. Hyperparasitoids use herbivore-induced plant volatiles to locate their parasitoid host. PLoS Biol 10(11): e1001435.

Poelman EH & Dicke M 2014. Plant-mediated interactions among insects within a community ecology perspective. In book, Insect plant interactions. pp 309-337.

Poelman EH & Kessler A. 2016. Keystone Herbivores and the Evolution of Plant Defenses. Trends in plant science. doi:10.1016/j.tplants.2016.01.007

Rubin I, Ellner SP, Kessler A, Morell K. 2015. Informed herbivore movement and plant-plant communication determine the effects of induced plant resistance in an individual-based model. Journal of Animal Ecology 84(5): 1273-1285.

Sánchez-Garduño F & Breña-Medina VF. 2011. Searching for Spatial Patterns in a Pollinator–Plant–Herbivore Mathematical Model. Bull Math Biol 73: 1118–1153. DOI 10.1007/s11538-010-9599-z.

Sánchez-Garduño F, Castellanos V, Quilantán I. 2014. Dynamics of a nonlinear mathematical model for three interacting populations. Bol. Soc. Mat. Mex. 20:147–170.

Schenk D & Bacher S. 2002. Functional response of a generalist insect predator to one of its prey species in the field. Journal of Animal Ecology 71: 524-531.

Schiestl FP. 2014. Herbivory and floral signaling: phenotypic plasticity and tradeoffs between reproduction and indirect defense. New Phytologist 203(1): 257-266.

Siemens DH & Mitchel-Olds T. 1996. Glucosinolates and herbivory by specialists (Coleoptera: Chrysomelidae, Lepidoptera: Plutellidae): consequences of concentration and induced resistance. Environmental Entomology 25: 1344–1353.

Spalinger DE & Hobbs NT. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist: 325-348.

Stam JM, et al. 2014. Plant interactions with multiple insect herbivores: from community to genes. Plant Biology 65(1): 689.

Stang MP, Klinkhamer GL, van der Meijden E. 2007. Asymmetric specialization and extinction risk in plant-flower visitor webs: a matter of morphology or abundance? Oecologia, 151, 442–453.

Stieha CR, Abbott KC, Poveda K. 2015. The Effects of Plant Compensatory Regrowth and Induced Resistance on Herbivore Population Dynamics. The American Naturalist 187(2):000-000.

Strauss SY. 1997. Floral characters link herbivores, pollinators, and plant fitness. Ecology 78(6): 1640-1645.

Strauss S, Conner J, Rush S. 1996. Foliar herbivory affects floral characters and plant attractiveness to pollinators: implications for male and female plant fitness, American Naturalist 147, 1098–1107.

Strauss SY, et al. 1999. Ecological costs of plant resistance to herbivores in the currency of pollination. Evolution 53: 1105–13.

Strauss SY, & Whittall JB. 2006. Non-pollinator agents of selection on floral traits. Pages 120–138 in L. D. Harder and S. C. H. Barrett, editors. Ecology and evolution of flowers. Oxford University Press, Oxford, UK.

Strogatz SH. 1994. Nonlinear dynamics and Chaos: With applications to physics, biology, chemistry, and engineering. Westview Press. 11 Cambridge Center, Cambridge, MA 02142.

Uesugi A, Poelman EH, Kessler A. 2013. A test of genotypic variation in specificity of herbivore-induced responses in Solidago altissima L.(Asteraceae). Oecologia 173(4): 1387-1396.

Vandermeer JH & Goldberg DE. 2013. Population Ecology: First Principles. Second Edition. Princeton University Press.

Vázquez DP & Aizen MA. 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. Ecology 85(5): 1251-1257.

Viswanathan DV, Narwani AJT, Thaler JS. 2005. Specificity in induced plant responses shapes patterns of herbivore occurrence on Solanum dulcamara. Ecology 86(4): 886-896.

Wang Y, DeAngelis DL, Holland JN. 2012. Uni-directional Interaction and Plant–Pollinator–Robber Coexistence. Bull Math Biol 74:2142–2164. DOI 10.1007/s11538-012-9750-0

Wang Y. 2013. Dynamics of plant–pollinator–robber systems. J. Math. Biol. 66:1155–1177.

Werner EE & Peacor SD. 2006. Lethal and nonlethal predator effects on an herbivore guild mediated by system productivity." Ecology 87(2): 347-361.

Wolfram Research, Inc., Mathematica, Version 10.0, Champaign, IL (2014).

Chapter 6

A theoretical basis for the study of predatory syrphid fly ecology

6.1 Abstract

Predacious syrphid fly species, also known as flower flies or hover flies, are cosmopolitan diptera that play two important ecological roles: predator and pollinator. In decades past, syrphid flies were studied by agricultural researchers due to their larvae's ability to function as a biological control agent. In recent years, the global decline in both honey bees and various important wild bee species has led ecological researchers to investigate the role of syrphid fly pollination in both natural systems and agriculture. While these two roles have often been considered separately, they are rarely considered together in single studies. Syrphid fly population fluctuations in natural and agricultural systems are understudied, prompting calls for further study into the fundamental drivers of population dynamics of syrphid communities. In order to develop a deeper understanding of the fundamental dynamics of syrphid ecology, the present study offers a community model where both syrphid predation and pollination are incorporated into a single dynamic model. Using populations of predacious syrphid flies, herbivorous insects, and a shared resource flowering plant, the model is used to investigate community dynamics and persistence across different levels of plant reproductive dependence on syrphid pollination. Results indicate distinct levels of community viability across different pollination relationships as well as a tendency toward chaotic dynamics inherent to the trophic interactions of the community.

6.2 Introduction

Syrphid flies (aka hover flies, flower flies) are a cosmopolitan group of diptera which occupy a unique ecological position in insect communities, often acting as both pollinators and predators. Numerous syrphid fly species have larval stages which eat soft bodied insects such as aphids, thrips, leafhoppers, caterpillars, and other small phytophagous pest insects. Particularly, aphid-feeding (aphidophagous) species in the subfamily Syrphinae are known to have voracious larvae. Individual larvae have been observed consuming up to 400 aphids during development (Berry 1998). Predictably, significant syrphid predation of aphids has been found in laboratory settings (Hopper et al 2011), natural communities (Otto et al 2008), and agricultural settings (Tamaki et al 1967; Tenhumburg & Poehling 1995; Bargen et al 1998; Van Rijn 2006; Smith et al 2008). It's no surprise, then, that syrphids have been marked as economically important bio-control agents since the early 20th century (Miller 1918; Bahmeier et al 1918).

In recent years, the global declines in both honey bees and various wild bee species (Biesmeijer et al 2006; Potts et al 2010; Cameron et al 2011) signal that pollination for numerous wild plants and agricultural cultivars may come to depend more on syrphid flies. Consequently, research into the maintenance, importance, and effectiveness of syrphid pollination has been increasing with studies of cultivars/agriculture (Jauker & Wolters 2008; Haenke et al 2009; Haenke et al 2014), wild systems (Bingham & Orthner 1998; Bischoff et al 2013; Iler et al 2013), and experimental systems (Fontaine et al 2006). Such trends are likely to continue given the increase in the area cultivated with flowering crops compared with nonflowering crops (Aizen et al. 2008; Aizen & Harder 2009) and a continued decline in bee populations. Even without the bee decline, syrphid pollination is worth studying as it is observed across the globe on numerous flowers (Ssymank et al 2008) and is the dominate insect pollinator in the arctic and high altitudes (Kevan 1972; Primack 1983; Kearns 1992; Elberling and Olesen 1999).

Despite the historically recognized importance of syrphids as biological control agents and the growing focus on syrphids as pollinators, general syrphid ecology is still poorly studied and relatively unknown (Kearns 2001; Ssymank et al 2008; Kühsel & Blüthgen 2015). This is partially because few studies have considered the effect that each of these ecological roles has on the other, instead focusing solely on either interaction. While this is necessary to establish first principles (especially in application), a deeper understanding of syrphid ecology requires considering both ecological interactions and their effects on each other. The pollination regime of predatory syrphids, especially in unmanaged settings, depends on the predation dynamics of their larvae. Likewise, syrphid larvae predation on soft-bodied insects indirectly depends on syrphids adults promoting host plant recruitment through successful pollination. Larvae production also depends on pollination to promote healthy adults who can produce larvae in the first place. With the aim of generating a better understanding of the fundamental ecology of syrphid flies, I develop a theoretical basis on which to model their population and community dynamics. Currently, there is no such foundational framework developed for predatory syrphids. There are model based investigations into predicting levels of aphid predation by syrphids, but these are optimization models for biological control and do not include the pollination aspect of syrphid ecology (Gosselke et al 2001; Tenhumberg 2004).

In developing a theoretical basis to syrphid fly ecology, there are certain complexities to account for in model development. Recognizing these complexities will also aid in directing the analysis of the model. The first complexity is that the two different ecological roles of syphids, are driven by two separate life stages: adults for pollination and larvae for predation. Therefore from a community dynamics stand point, syrphid populations are split into two distinct but linked dynamical variables: syrphid larvae, which rely on predation of herbivores, and syrphid adults, which rely on pollen and nectar.

A second source of complexity in these systems stems from the degree of reproductive benefit flowering plant species receive from syrphid pollination. Different syrphid species have been found to cover the range from specialist to generalist (Haslett 1989 & vander Kooi 2016) and there is a spectrum of reproductive benefit that syrphid pollination confers across the different flowering plants they pollinate. At the most basic level, due to their shorter mouth parts, syrphids are unable to effectively pollinate certain flower morphologies. Among flowers syrphids can pollinate, past findings and texts pointed to syrphids as insignificant and poor pollinators (Faegri & van der Pijl 1979, Richards 1986). Other work has found that syrphids have lesser pollinator ‘quality’ and/or seed set efficiency when compared to Hymenoptera (Herrera 1987; Sahli & Conner 2007). Concurrent declines in the diversity of insect-pollinated wild plants in areas with declining wild bees in the UK and Netherlands also suggest that syrphids contribute comparatively little to seed set (Biesmeijer et al. 2006). Some work has pointed to frequency of syrphid pollination visits compensating for low single visit efficiency (Kearns & Inouye 1994), but there are studies that have found that isn’t always the case (Rush et al 1995; Bischoff et al 2013). Their efficacy as pollinators can also increase depending on the plant species pollinated. In agricultural settings, syrphids can be effective pollinators of certain cultivars (esp. those in the Brassicaceae family) (Nye and Anderson 1974; Jarlan 1997; Jauker & Wolters 2008). Experimental set ups have also shown sryphid pollination to result in comparatively high seed sets in wild strains of open flowering plants (Fontaine et al 2006).

Regardless of the reproductive benefit of syrphid pollination, flowering plants can still receive the indirect benefits of syrphid larval predation on herbivores. Therefore, there is a spectrum of different syrphid-flowering plant pollination relationships that need to be considered in connection with syrphid larvae predation of insect herbivores. Using the model developed here I will investigate the dynamics of the 3-species system consisting of a flowering plant population, an herbivorous insect population, and a syrphid fly population. Given the range of syrphid pollination importance to seed production/plant reproduction, I will examine how community dynamics change across 3 different types of pollination relationships:

1.) Specialist-obligate: The flowering plant species' seed production and reproduction is entirely based on an obligate mutualism with the syrphid fly population.

2.) Nominal: The plant population effectively gains no reproductive benefit from syrphid pollination and reproduces through other means (vegetative growth or self-fertilization).

3.) Facultative: The plant population reproduces through other means but also receives a facultative reproductive benefit from syrphid pollination.

6.3 Model Development

The model developed here will investigate the 3-species community using coupled ordinary differential equations (ODEs). Given the hierarchical nature of the community, the syrphid, herbivore, flowering plant community resembles the 3 trophic level model developed in Hastings and Powell 1991 which creates the well-known teacup chaotic attractor given a functional response term. However, in contrast to the Hastings and Powell system, this system has stage structure at the top trophic level (syrphid). Also the lowest trophic level (plant population) can depend on one of these top trophic stages and vice versa. With this alteration, the community interaction web can be established (see Figure 6.1). Similar to the Hastings and Powell model, the flowering plant forms the base of the community and is eaten by the herbivorous insect population. The herbivore, in turn, is predated by the syrphid larvae. Syrphid larvae pupate into syrphid adults. Finally, the pollination interactions between the syrphid adults and flowering plants result in the production of syrphid larvae and can also provide some reproductive benefit to the plant.

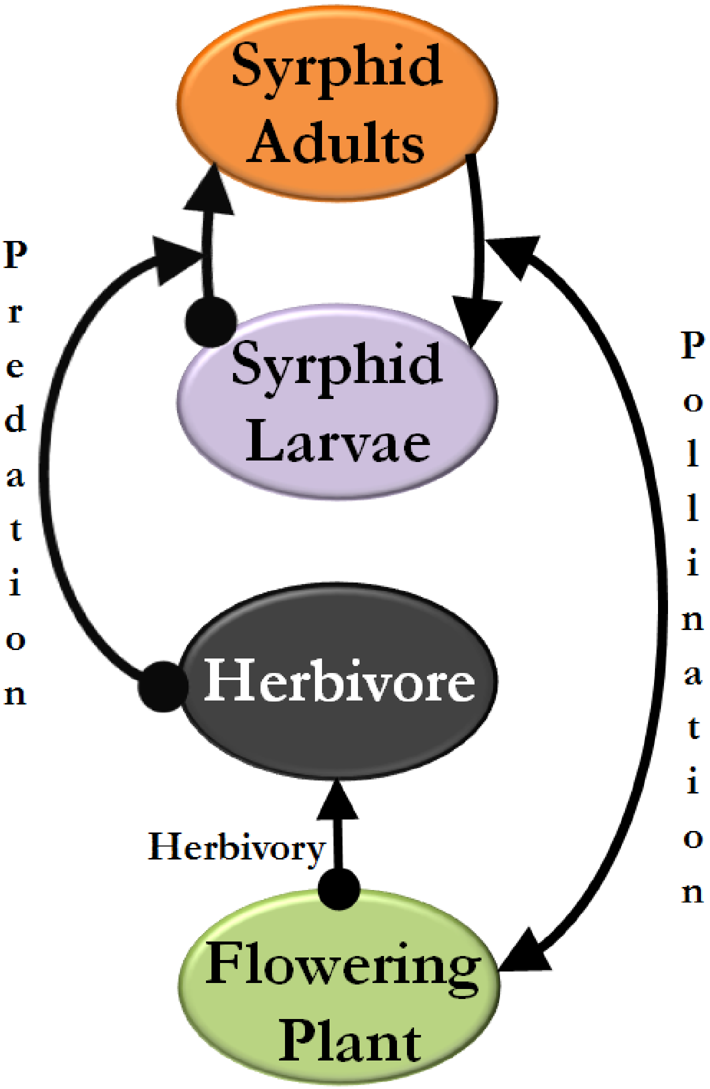

Figure 6.1 - Conceptual flow diagram of the key ecological connections between the time dependent variables: flowering resource plant, insect herbivore, and syrphid fly larvae and adults. Lines show the connections between the populations. Arrows represent the direction of positive energy flow. Black dots represent the direction of negative energy flow. Line ends with no arrow or dot show zero energy flow in that direction. Lines which represent energy flow between species are labeled. Colors used for variables here will be used to represent each variable in all 2-D time series graphs.

This structure produces a community where syrphid larvae (S_L) specialize on a particular insect herbivore (H) which is a specialist herbivore on the main nectar source (F) for the adult syrphid larvae (S_A). While this is somewhat specific, it is a reasonable first step in studying these systems. Specialist herbivorous insects are common (Futuyma & Gould 1979; Forister et al 2015) and numerous cases exist where syrphid larvae specialize on specialist herbivorous insects. For example, *Heringia calcarata* specializes on the apple specialist wooly apple aphid in Virginia (Bergh & Short 2008), *Episyrphus balteatus* specializes on the rosy apple aphid

(*Dysaphis plantaginea*) (Dib et al 2011), and syrphids in the genus *Parasyrphus* specialize on the beetle *Chrysomela lapponica* (a specialist on willows) (Gross et al 2004). Syrphid larvae can also more functionally specialize on aphids in agricultural settings where specific aphids become the dominant prey in agricultural plots (Sunderland et al 1989). These agricultural environments can also provide the settings for herbivores to specialize on the major locally available nectar resource for syrphids given large scale monoculture planting (van Rijn et al 2006). For example, *Brassicaceae* cultivars make good sources for aphid herbivory as well as syrphid pollination given their wide shallow flowers (Jauker & Wolters 2008). Herbivores can also attack the single locally available nectar resource for syrphids in natural settings when the focal floral resource reaches a dominant abundance. The effect of local availability is an important consideration in syrphids because many syrphids (especially syrphid larvae) have limited dispersal ability (Chase 1969; Cowgill et al 1993; Lovei et al 1998; Wratten et al 2003; Verheggen et al 2008).

With the above conceptual framework, the four time dependent variables are: the population density of the flowering plant (F), the population density of the insect herbivore (H), the population density of syrphid larvae (S_L), and the population density of syrphid adults (S_A). For shorthand, I will abbreviate the whole community as the FHS system. To create 3-dimensional figures of time series I will occasionally use the label S_R to denote $S_L + S_A$ which represents the entire syrphid population (both larvae and adults). The four interacting populations are cast in the well-mixed form commonly assumed for community interactions in theoretical ecology. The full four equations which make up the model are:

Equation 6.1:

$$\frac{dF}{dt} = F(r_F + b_F v S_A - \alpha F) - a_H F H$$

$$\frac{dH}{dt} = a_H c_{FH} F H - a_S H S_L - d_H H$$

$$\frac{dS_L}{dt} = b_S v F S_A - a_S c_{HS} H S_L - d_{SL} S_L$$

$$\frac{dS_A}{dt} = a_S c_{HS} H S_L - d_{SA} S_A$$

The flowering plant population is assumed to experience density dependent growth through the parameter α (set to 0.1). The parameter α models logistic growth because it's indirectly proportional to the carrying capacity, so larger α means lower carrying capacity (Glaum 2014). Positive growth for F is split into an intrinsic growth rate r_F and a pollination dependent term, $b_F vFS_A$. The intrinsic growth term can represent vegetative growth or self-fertilization leading to successful recruitment. The intrinsic growth term could represent the average pollination services of other pollinators if pollination services are very consistent for a generalist plant. The pollination dependent term, $b_F vFS_A$, confers some reproductive benefit, b_F, to the flowering plant population dependent on the pollination interactions between F and S_A which occur at a visitation rate v. The overall positive growth of the flowering plant population can be thought of as recruitment in a natural setting or a farmer's planting rate proportional to the yield amount of saved viable seeds. While seed saving is rare in industrialized nations, it's more common in certain crop industries and much more common in developing nations (Howard 2009).

Growth in the syrphid larvae population is modeled by the interaction term $b_S vFS_A$ as larvae are produced after pollination interactions between syrphid adults and flowers which occur at the same visitation rate v. Syrphid visitation can be high compared to bees (Kearns & Inouye 1994), with syrphids visitation increasing to cover higher flower abundance (Conner & Rush 1996). Therefore, as a preliminary generalization, v will initially be set to one unless otherwise noted. The reproductive benefit of pollination interactions for the syrphid is represented by the parameter b_S.

Predation in the model takes the Lotka-Volterra formulation with different attack rates for herbivores and syrphid larvae. Direct growth of syrphid larvae into the syrphid adult population is the result of predation of S_L (larvae) on H (insect herbivore) at a rate a_S with a conversion rate of c_{HS}. Therefore the flow of syrphid larvae into syrphid adults is governed by the term $a_S c_{HS} HS_L$. Growth in the insect herbivore population is the result of herbivory of H on F at a rate a_H with a conversion rate of c_{FH}. Herbivore and syrphid populations both experience a background death rate. Field studies find a higher mortality rate in syrphid larvae (Kan 1988; Michaud 1999), so the model sets $d_{SL} > d_{SA}$. All time independent parameter definitions are given in Table 6.1.

Table 6.1 - The time independent parameters of Equation 6.1 and their definitions.

Parameter	**Definition**
r_F	Intrinsic growth rate of flowering plant.
b_F	Reproductive benefit of pollination for flowering plant.
b_S	Reproductive benefit of pollination for syrphid adult.
v	Visitation rate of syrphid adults on flowers.
a_H	Attack rate of the herbivore on the flowering plant.
a_S	Attack rate of the syrphid larvae on the herbivore.
c_{FH}	Conversation rate of eaten plants into herbivores.
c_{HS}	Conversation rate of eaten herbivores into syrphid adults.
α	Strength of density dependence (set to .1)
d_H, d_{SL}, d_{SA}	Death rates for the herbivore and the syrphid (larvae and adult). $d_H = .13, d_{SL} = .2$, and $d_{SA} = .05$

Initially, this system will be studied with linear interactions between populations (Type I functional responses). While there is some evidence of Type II saturating non-linear functional responses in the pollination and predation tendencies of certain syrphid species (Feldman 2006; Khan et al 2016), the goal of this work is to develop a thorough understanding of the fundamental community dynamics of the FHS community. Full analysis of non-linear additions to the model is advisable only after developing this understanding of the fundamental basis upon which new dynamics would emerge with further additions. However, in order to test the consistency of certain results, the effects of non-linear interactions (Type II and III functional responses) are considered in a preliminary analysis for particular cases (Appendix E.4).

6.4 Methods of Analysis

Both numerical and analytical analysis was facilitated through Mathematica 10. Numerical analysis of model dynamics was completed across numerous parameter value combinations in parameter space to describe the fullest extent of possible behaviors. Analysis of the local stability of equilibria was done through traditional linear stability analysis. When analyzing local stability across parameter space, the amount of stable parameter space was determined, in part, by finding the volumes of 3-dimensional parameter spaces ($\{a_H, b_S, a_S\}$) which supported stable point equilibria. Volumes of irregular spaces were approximated using methods from Zhang and Chen (2001). The magnitudes of these volumes in parameter space were then determined across a range of values for a fourth parameter (r_F) to present a picture of how stability changes across 4 dimensional parameter space (Fig 6.4). For a more in-depth description of the volume finding process, please see the Appendix E.2.2. Time series were used to study asymptotically stable oscillatory (limit cycle) dynamics.

Various subsections of the parameter space investigated here were found to induce chaotic behavior in time series. Upon further exploration through the use of bifurcation diagrams, the parameter combinations which generated chaotic behavior were found to be widely dispersed across parameter space. Therefore, in order to more thoroughly determine the distribution and degree of chaotic behavior in parameter space, leading Lyapunov Exponents (λ) of Equation 6.1 were approximated numerically based on time series from model simulations (Wolf et al. 1985). This method was modified to 4-dimensions and vetted for accuracy in past work (Glaum 2014). When $\lambda > 0$, the system exhibits chaotic dynamics. When $\lambda \leq 0$, the system exhibits non-chaotic dynamics (dampened oscillations or limit cycles). Larger positive λ indicate a "more" chaotic system. For a more detailed description, please see Strogatz (1994). Lyapunov Exponents (λ) were approximated in Equation 6.1 with different levels of pest attack rate, syrphid larvae attack rate, and reproductive benefit of pollination to syrphids (i.e. at different combinations of parameter values of $\{a_H, a_S, b_S\}$). All of the model behaviors listed here, stable equilibria, steady oscillations, chaotic oscillations are examples of "attractors." The analysis below will use the term attractors to reference different types of behavior.

The analysis of the model is divided into three sections in order to address a range of pollination relationships between F and S_R (the syrphid fly). The first section sets $r_F = 0$ and $b_F > 0$. This models an obligate-specialist pollination relationship. Setting $r_F = 0$ eliminates intrinsic plant reproduction from the system, making seed production entirely dependent on syrphid fly pollination through the interaction term $b_F vFS_A$ ($b_F > 0$). The second section sets $r_F > 0$ and $b_F = 0$. This models an FHS community in which syrphid pollination is of nominal importance to F growth. This more closely models a situation where syrphids are utilized only for biological control with a cultivar that does not benefit from syrphid pollination or when a syrphid can obtain pollen from a flower, but its low pollination efficiency offers little to no benefit to the plant. It is also an important step to studying a system with both pollination driven and intrinsic plant growth. Model dynamics would not qualitatively change with some negligibly small positive value for b_F. The third section sets $r_F > 0$ and $b_F > 0$. This models the likely scenario that F receives some reproductive benefit from syrphid pollination while still having a substantial non-zero intrinsic reproductive rate. In all three analyses, $b_S > 0$.

6.5 Results

6.5.1 Plant Reproduction Obligate on Syrphid Pollination ($r_F = 0, b_F > 0$)

This section addresses the question: can the linear FHS system (Eq 6.1) persist if F reproduction is entirely obligatorily dependent on syrphid pollination? I start this analysis with a description of possible equilibrium solutions. Given that each time dependent variable depends (either directly or indirectly) on the other three variables, there is no subset of any three variables or two species that can persist without the full community. If $F = 0$, then there are obviously no resources for H and S_R. If $H = 0$, there is no sustenance for S_L. Finally, if S_L and S_A are locally extinct then there is no pollination which eliminates F and indirectly H. Therefore this equilibrium analysis is necessarily restricted to examining the dynamics of the full 4-variable/3-species FHS system. There are three possible biologically feasible equilibria: the trivial 0-equilibrium and two potential non-zero equilibria. These two potential non-zero equilibria are labeled Equilibrium 6.1 (Eqm 6.1) and Equilibrium 6.2 (Eqm 6.2). Both can exist or disappear in positive-real valued phase space dependent on model parameter values (Figure E.1). Parametric representations of the non-zero equilibria are quite large and presented in Appendix E.1.

Local stability analysis on all three equilibria was conducted across combinations of parameters $b_F, v, a_H, b_S, a_S, c_{FH}$, and c_{HS} for values from 0 to 1. Both non-zero equilibria (Eqm 6.1 and Eqm 6.2) were found to be unstable for every single parameter combinations tested. The 0-equilibrium, however, was shown to be locally stable across every single parameter combination tested. Stability analysis done on the 0-equilibrium indicated linear stability in 3 of the 4 dimensions of the system, with the last dimension exhibiting quadratic stability. Quadratic stability results in slower convergence to equilibria than linear stability, but despite the "slower" quadratic stability in the 4th dimension, the 0-equilibrium is the only equilibrium which is locally stable in all of the parameter combinations tested.

This is a somewhat striking result which implies that the obligate version of Eq 6.1 is intrinsically unsustainable. However, this result, by itself, does not indicate that the obligate FHS system's only stable asymptotic behavior is extinction. There is still the question of community persistence through permanent oscillatory dynamics (limit cycles) in the obligate system.

Numerical simulations across parameter space found numerous instances of oscillatory trajectories in the basin of attraction of the 0-equilibrium but did not uncover any sustained oscillations, limit cycles or chaotic oscillations. Ideally, demonstrating global stability for the 0-equilibrium would prove that no persistent oscillatory attractors exist. However, the existence of the positive non-zero equilibria, even if unstable, means that global stability would only be a parametric condition like any other ecological model. While analytical proofs of the existence or non-existence of sustained oscillatory attractors are normally difficult, in this case, it is possible to forgo the mathematical proof in favor of ecological arguments and biological intuition to describe the impossibility of sustained oscillations in the linear, obligate FHS system.

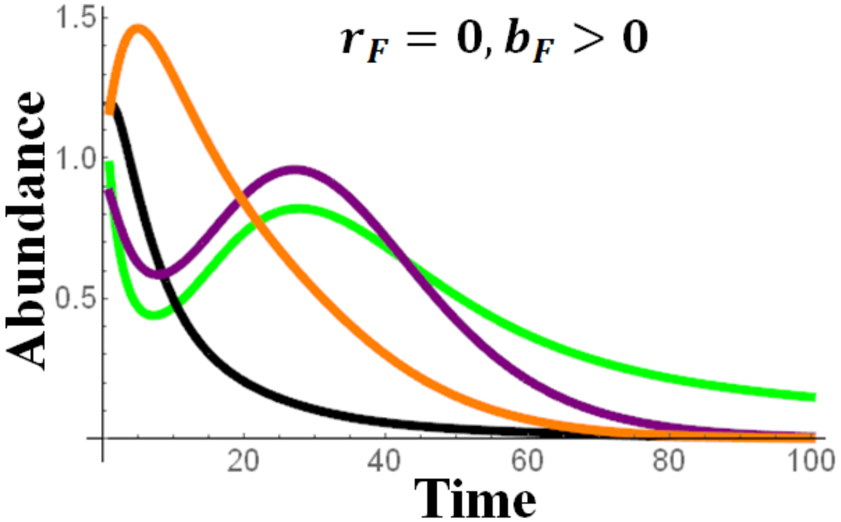

Figure 6.2 - An example of the unstable oscillations leading to the 0-equilibrium in the obligate pollination FHS model. Time dependent variables F, H, S_L, and S_A are shown in green, black, purple, and orange respectively. Parameter values: $c_{FH} = c_{HS} = 1, r_F = 0, v = 1, a_H = 0.39, b_F = 0.22, b_s = 0.256, a_S = 0.266$. $F(0) = 1.355, H(0) = 1.1, S_L(0) = 0.925, S_A(0) = 1$.

In this obligate version of the model, F is indirectly dependent on a persistent H population for reproduction and this creates a delayed negative feedback. Take for example, the Hastings & Powell three trophic level model (1991), when predators drive herbivore abundance low, this should normally be when the resource of the herbivore (F in this case) is able to reproduce and increase in abundance. Since herbivores are in low abundance, the predator population decreases, and the herbivores attack the newly abundant resource and the cycle continues. This process is critical to any sustained oscillation with 3 trophic levels. However, in the obligate FHS system, as syrphid larvae (S_L) drive herbivore (H) abundance low and pupate into syrphid adults (S_A), there is a period where flowering plants (F) are being pollinated by syrphid adults and syrphid adults continue to produce offspring. This means that despite a low abundance of herbivores (H), the predators of herbivores (e.g. the larvae, S_L) are still being produced by pollinating syrphid adults who do not need larvae for sustenance. Therefore, predation on herbivores does not decrease as directly as it would in the Hastings & Powell model (1991). This drives H to very low abundance such that the ability of larvae (S_L) to pupate into adults (S_A) eventually becomes limited. Limiting the pupation of larvae into adults begins to limit the number of syrphid adults, restricting pollination and plant (F) reproduction. Lingering syrphid larvae (S_L) and reduced plant growth restrict herbivore reproduction. This further limits the number of S_L developing into S_A. The reduction in S_A abundance causes pollination rates to stay low, further reducing F in growth and abundance. This means H cannot recover and the negative feedback leads to system extinction. Figure 6.2 shows an example of the negative feedback process apparent in the model in a time series where $r_F = 0$ and $b_F > 0$.

The implications of this result demand testing its consistency with different model assumptions, namely non-linear functional responses. Preliminary analysis shows that this negative feedback persists if the Type I functional responses are replaced with Type II saturating responses (Appendix 5.4.1). Numerical analysis produced neither persistent oscillations nor stable equilibria across tested parameter space. However, when Type I interaction s are replaced with sigmoidal Type III interactions, the system can potentially persist (Appendix 5.4.2). This is because the sigmoidal form of Type III functional responses reduces/delays herbivory or predation rates in the troughs of oscillating plant and herbivore populations respectively. Temporarily reducing herbivory or predation rates at low abundances allows plant and herbivore populations to more easily recover from low abundances. This then limits the intensity of the negative feedback loop which drives extinction in the Type I and Type II framework. This dynamic supports system persistence through stable oscillations or stable equilibria if herbivory and/or predation is sufficiently reduced at low abundances (Figure E.6).

The negative feedback loop could also be interrupted, even with Type I or II functional responses, through additional herbivore diversity or alternative host plants for either the syrphid or herbivore. Such additions would allow for host switching and will be important components in future work. For now, however, this result highlights the importance of redundant functional diversity in syrphid systems.

6.5.2 Nominal Syrphid Pollination, non-Syrphid Dependent Growth ($r_F > 0, b_F = 0$)

Given the tendency of the mutually obligate pollination FHS model to go extinct and the empirical evidence claiming syrphid pollination to be of lesser importance to seed production, it is prudent to consider a FHS system where plant reproduction is not directly tied to syrphid pollination. For that purpose, I analyze the model with $b_F = 0$ and $r_F > 0$. The analysis here was initially done with conversion rates ($c_{FH},\ c_{HS}$) equal to 1 in order to limit the parameter space for analysis to four dimensions (r_F, a_H, b_S, and a_S) and to focus the analysis on the parameters which most directly govern species interactions. However, the effects of $c_{FH}, c_{HS} < 1$ are considered as well.

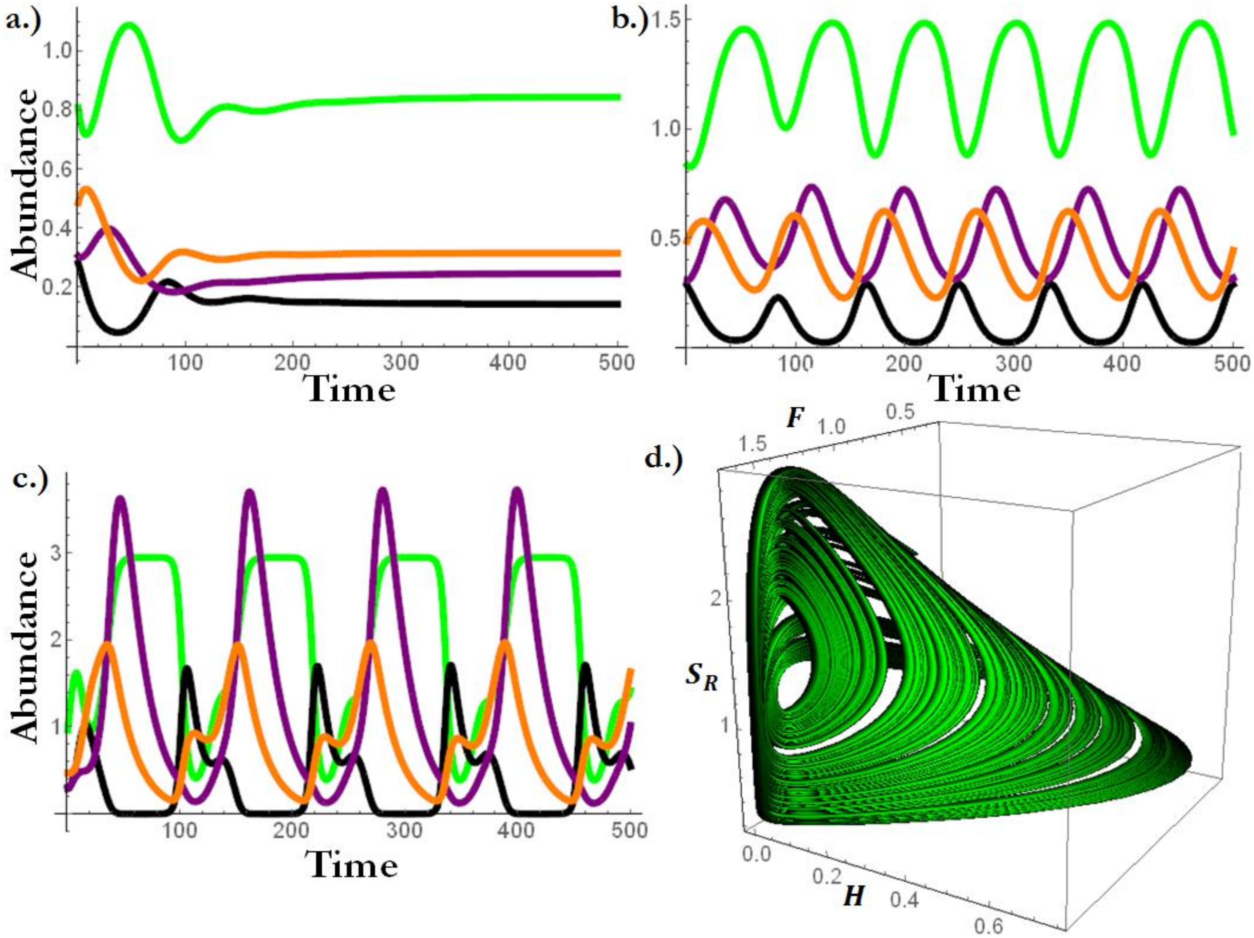

Figure 6.3 - Examples of model dynamics across parameter space for the nominal pollination FHS model. Time dependent variables F, H, S_L, *and* S_A *are shown in green, black, purple, and orange respectively. Parameters* c_{FH} *and* c_{HS} *equal 1 for all results pictured. a) Stable Equilibrium 6.1/Dampened Oscillations:* $r_F = 0.125, a_H = 0.285, b_S = 0.244, a_S = 0.45, b_F = 0, v = 1$. *b) 2-point Limit Cycle:* $r_F = 0.156, a_H = 0.285, b_S = 0.244, a_S = 0.45, b_F = 0, v = 1$. *c) 4-point Limit Cycle:* $r_F = 0.295, a_H = 0.23, b_S = 0.186, a_S = 0.265, b_F = 0, v = 1$. *d) Chaotic dynamics in a parametric plot:* $r_F = 0.165, a_H = 0.392, b_S = 0.6, a_S = 0.42, b_F = 0, v = 1$. S_R *represents* $S_L + S_A$ *to make a viewable 3D graph of the chaotic attractor. The Lyapunov Exponent of the attractor shown in Fig 6.3d is* $\lambda = 0.00986142$.

Due to the positive r_F, the system is able to persist as a classical 2-dimensional F, H consumer resource community should the syrphid population go extinct. However, $r_F > 0$ also enables F (and therefore the system) to recover from lower abundances and the full 4-variable community can exhibit an array of dynamical behaviors dependent on parameter values (Fig 6.3). Similar to the pollination-obligate system, the nominal pollination system has two potentially real positive-valued biologically feasible equilibria (see Appendix E.2.1 parametric expressions). For ease of notation, I will again refer to these positive equilibria as Equilibrium 6.1 and Equilibrium 6.2. Similar to the obligate FHS system, Eqm 6.1 and Eqm 6.2 do not exist across all parameter space. It is possible for parameter combinations to result in models which only have one equilibrium (Eqm 6.1 alone, Fig 6.4b) or two equilibria (both Eqm 6.1and 6.2, Fig 6.4c). Linear stability analysis shows that, similar to the pollination obligate system, Equilibrium 6.2 is never locally stable across any parameter combination tested. Linear stability analysis on Eqm 6.2 was conducted across $\{r_F, a_H, b_S, a_S\}$ space for values from 0 to 1 for all parameters. Equilibrium 6.1, however, does show the potential for local stability across a range of parameters space (Fig 6.3a).

Figure 6.4a represents parameters which generate a locally stable Equilibrium 6.1 in $\{a_H, b_S, a_S\}$ parameter space at $r_F = 0.1$ shown in green. Parameter space where only Equilibrium 6.1 exists is shown in blue (Fig 6.4b) and parameter space where both Equilibrium 6.1 and 6.2 exist is shown in magenta (Fig 6.4c). Notice how Equilibrium 6.1 can be stable when it is the lone equilibrium or when both Equilibrium 6.1 and Equilibrium 6.2 exist (Fig 6.4d). Results broadly indicate that higher interaction rates (a_H and a_S) or growth rates (b_S) seem to cause Eqm 6.1 to become unstable (Fig 6.4d). It's not surprising then, that higher values of r_F generally decrease the volume of $\{a_H, b_S, a_S\}$ space which is stable (Fig 6.4e). This can be thought of as the green region in Fig 6.4a shrinking in size as r_F increases. While the trend shown in Fig 6.4e is correct, the values of the volumes are only approximations of the actual volumes (see Appendix E.2.2). Overall Fig 6.4 shows that the existence and stability of equilibria is dependent on all model parameters tested. Generally, increases in any singular growth rate or interaction rate seem to reduce stable parameter volume or cause Eqm 6.1 to become unstable. Interestingly, higher r_F (either as a proxy for alternant pollinators or intrinsic growth) does not aid in system stability. It seems higher plant growth induces higher herbivore and therefore syrphid growth which destabilizes the system. Additionally, this means the predation offered by the syrphids can seemingly destabilize the FHS system similarly to a classical paradox of biocontrol situation, despite the unique connection to the plant population through adult reliance on pollen/nectar.

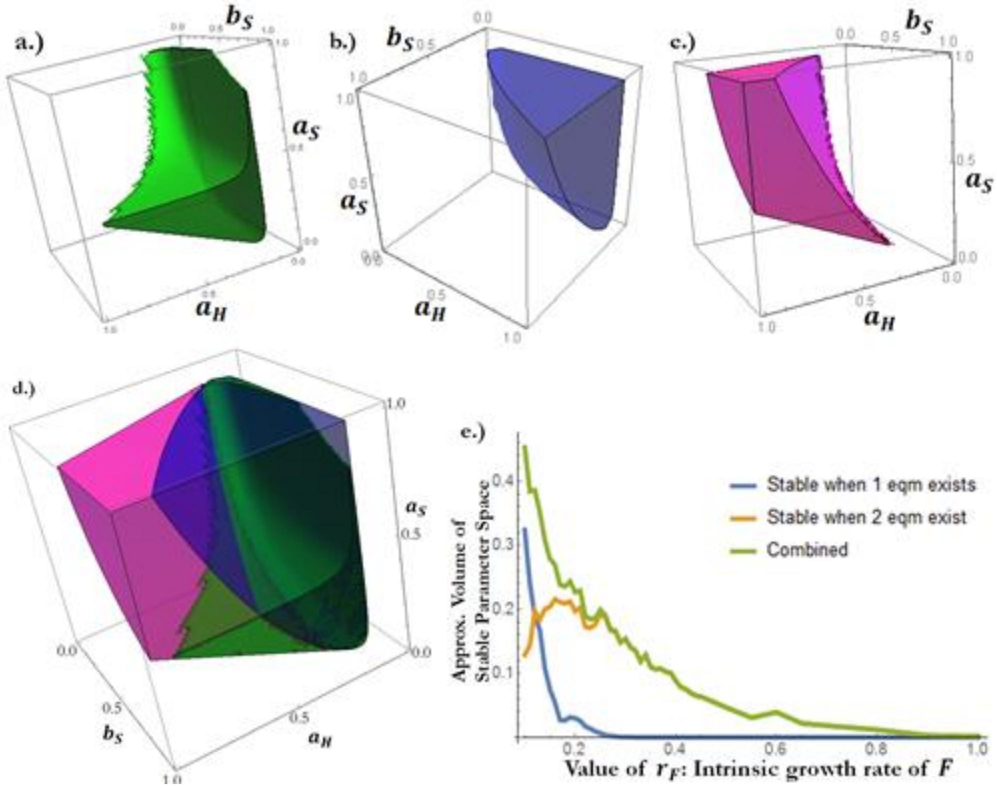

Figure 6.4 - An investigation of the local stability of Equilibrium 6.1 across parameter space $\{a_H, b_S, a_S, r_F\}$ *for the nominal FHS model. a) Results of linear stability analysis of Eqm 6.1 across parameter values of* $\{a_H, b_S, a_S\}$ *when* $r_F = 0.1, b_F = 0, v = 1$. *Green regions represent where Eqm 6.1 is stable. b) Blue regions represent combinations which only create Eqm 6.1 when* $r_F = .1, b_F = 0, v = 1$. *c) Magenta regions represent combinations which create both Eqm 6.1 and Eqm 6.2 when* $r_F = 0.1, b_F = 0, v = 1$. *d) A combination of a)-c) to show the overlap of different equilibria counts and stability of Eqm 6.1 when* $r_F = 0.1, b_F = 0, v = 1$. *Non-colored space has no 4-variable equilibria. e) The decrease in the volume of stable* $\{a_H, b_S, a_S\}$ *parameter space across values of* r_F *The volume of Eqm 6.1 stability inducing* $\{a_H, b_S, a_S\}$ *parameter space is shown when Eqm 6.1 alone exists (blue), when both Eqm 6.1 and Eqm 6.2 exist (orange), combined (green).*

Altering these parameter values ($\{r_F, a_H, b_S, a_S\}$) and transitioning out of the stable parameter space for Eqm 6.1 (Fig 6.4a) occurs dynamically through a supercritical Hopf bifurcation. This causes a stable limit cycle to emerge out from Eqm 6.1 while Eqm 6.1 itself becomes unstable. These stable oscillatory dynamics range from simple 2-period and multi-period limit cycles (Fig 6.3b, 6.3c) to chaotic attractors (Fig 6d). The stability of these oscillations was analyzed across parameter space using the numerical approximations of the Lyapunov Exponents.

Results from the analysis of Lyapunov Exponents in $\{a_H, b_S, a_S\}$ parameter space when $r_F = 0.35$ are displayed in Figure 6.5. Recall that $\lambda \leq 0$ denotes a non-chaotic system while

$\lambda > 0$ signifies chaotic oscillations. As a reference, the Lyapunov Exponent of the attractor shown in Fig 6.3d is $\lambda = 0.00986142$. Upon visual inspection of Fig. 6.5 some distinct patterns are clear. Some of the parameter space tested resulted in negative λ values. Lower values for all three parameters result in the least chaotic dynamics (Fig 6.5a), with the minimum being $\lambda = -0.026$. Much of the parameter space tested resulted in positive λ values (chaotic dynamics), with the max value being $\lambda = 0.016$. In fact, 52.7% of the 6859 parameter combinations tested resulted in $\lambda > 0$. Higher values of λ (most chaotic dynamics) were mostly clustered at higher values of a_H and b_S but across the full range of a_S (Fig 6.5b). Ecologically then, the model indicates that even low syrphid attack rates can lead to chaotic oscillations.

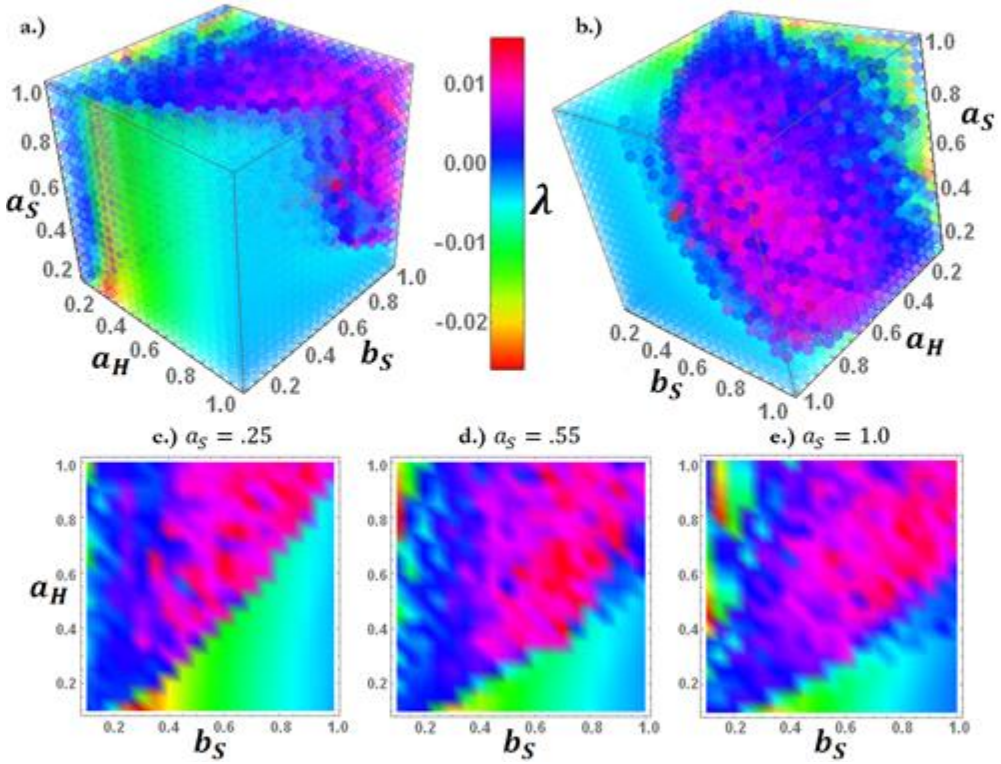

Figure 6.5 - Numerical approximations of λ across $\{a_H, b_S, a_S\}$ parameter space when $r_F = 0.35, b_F = 0, v = 1$ (nominal pollination FHS model). The value of λ, and consequently the degree chaos in the system, at each parameter combination is shown using the color spectrum shown. Initial conditions were chosen heuristically to be within the basin of attraction for the 4-variable attractor. Figure 6a and 6b are different views of λ across $\{a_H, b_S, a_S\}$. Figure 6c, 6d, and 6e show slices of the λ approximations across $\{a_H, b_S\}$ at $a_S = 0.25, 0.55, 1.0$ respectively.

However, these oscillations can be stabilized when the model considers lower conversion rates of predation interactions (c_{FH} and/or c_{HS}). An example is shown in Figure 6.6. When only one conversion rate is lowered, the reduction required to eliminate chaotic dynamics may need to be substantial (Fig 6.6), but if conversion and visitation rates are reduced, oscillations are less likely to be chaotic. Chaotic oscillations can also be stabilized with Type III functional responses, especially in the syrphid predation term (Appendix E.4.2). Type II functional responses, on the other hand, were not found to stabilize chaotic oscillations (Figure E.7a).

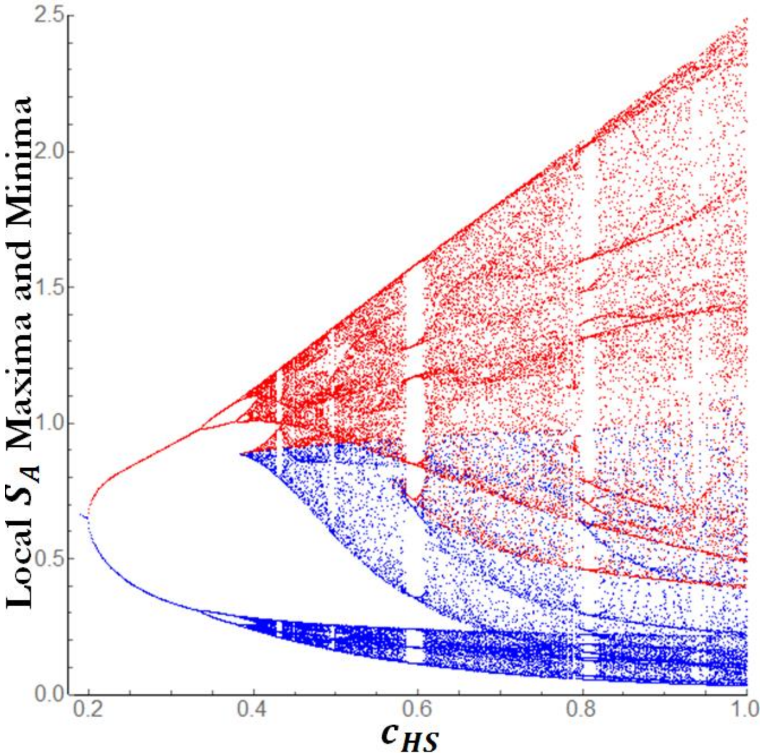

Figure 6.6 - A bifurcation diagram of S_A local maxima and minima across values of c_{HS} in the nominal pollination FHS model. Red dots represent local maxima and blue dots represent local minima. $r_F = 0.304, a_H = 0.54, as = 0.325, bs = 0.57, v = 1, b_F = 0, c_{FH} = 1$.

6.5.3 Facultative Pollination ($r_F > 0, b_F > 0$)

By setting both $b_F > 0$ and $r_F > 0$, I model the likely scenario that the flowering plant population (F) receives some reproductive benefit from syrphid pollination (b_F) while still having a non-zero intrinsic reproductive rate (r_F). Including both pollination and intrinsic means of F reproduction does not change the number of positive-real-valued equilibria, there are still two (Eqm 6.1 and Eqm 6.2) and only Equilibrium 6.1 was found to have the potential for stability (see Appendix E.3.1 for parametric expressions). With both $b_F > 0$ and $r_F > 0$, the parameter space to analyze is quite large, but there are consistent effects that allow for general conclusions.

When $b_F > 0$, the population growth of the flowering plant (F) experiences syrphid dependent increases when adult syrphids (S_A) are abundant. In turn, higher F abundance then supports higher populations of herbivores and syrphids. When Equilibrium 6.1 is stable, this can increase equilibrium values for all 4 variables $\{F, H, S_L, S_A\}$. However, these increases in equilibrium values are accompanied by larger dampened oscillations and longer periods of transience as the reproductive benefit of pollination (b_F) increases. Sufficiently high values of b_F, will cause the pollination induced increase in flowering plant abundance to be large enough that oscillations never dampen and stability of Equilibrium 6.1 is lost (again through a super critical Hopf bifurcation). The level of b_F required to destabilize Equilibrium 6.1 decreases with higher intrinsic plant reproduction (r_F) (see Appendix E.3.2). An example of b_F destabilizing Eqm 6.1 can be seen in the bifurcation diagram displayed in Figure 6.7b at $b_F \approx 0.05$.

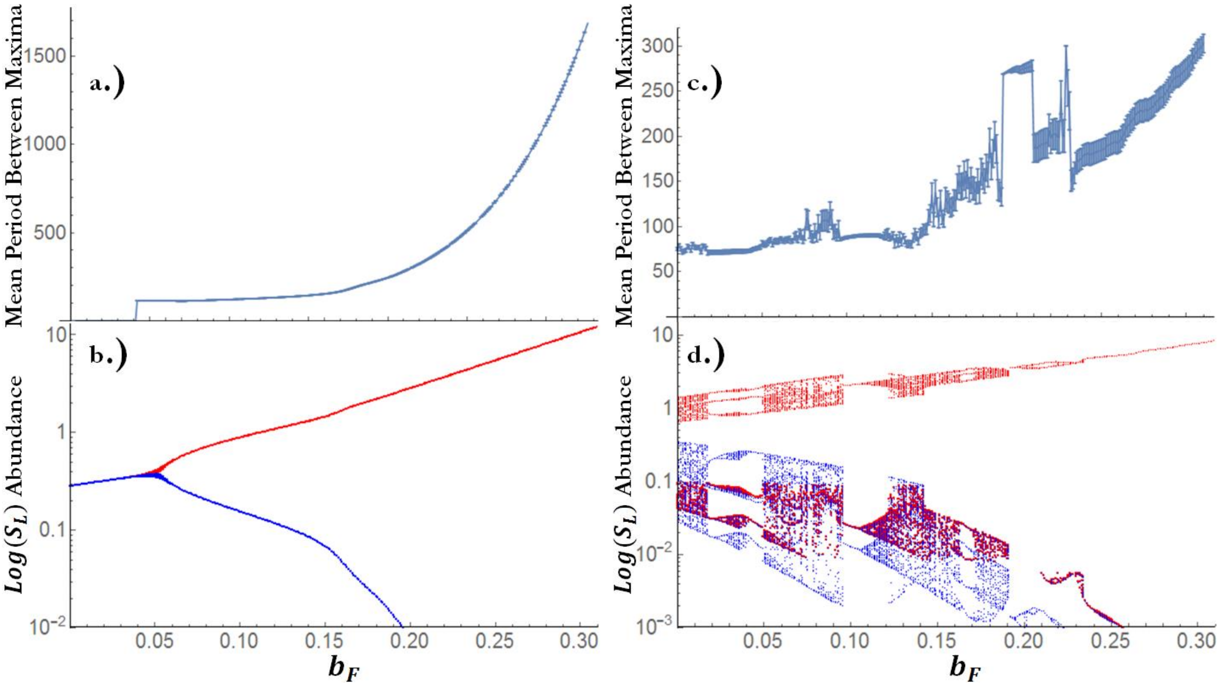

Figure 6.7 - Measures of the mean period between S_L maxima in simulations at different levels of b_F in the facultative pollination FHS model. Each sweep across different values of b_F is accompanied by a bifurcation diagram to show system dynamics. Bifurcation diagrams are shown on a log scale with limited y-axis range to account for high values of local maxima which obscure minima values. a.) and c.) Change in the period of limit cycles or the mean period between chaotic oscillations with higher b_F values. Standard error is shown with error bars. Timing between maxima in chaotic attractors shown in Figure 6.7c and 7d was measured by taking the mean time between maxima of simulations with different levels ofb_F. b.) and d.) Bifurcation diagram of $Log(S_L)$ maxima (red) and minima (blue). a.) and b.): Parameter values: $r_F = 0.13, r_H = 0.2, b_S = 0.32, a_S = 0.3, v = 1$. Initial conditions: $F(0) = 1.95, H(0) = 0.255, S_L(0) = 0.466, S_L(0) = 0.385$. c.) and d.): Parameter values: $r_F = 0.156, r_H = 0.352, b_S = 0.452, a_S = 0.7, v = 1$. Initial conditions: $F(0) = 0.505, H(0) = 0.325, S_L(0) = 0.665, S_L(0) = 0.68$.

Upon inducing persistent oscillatory dynamics, further increases in b_F steadily increases the local maxima of stable limit cycles. Again, this is caused by the greater reproductive benefit of syrphid pollination to flowering plant reproduction. This, in turn, supports more herbivores, which is then of benefit to syrphid larvae and syrphid adults which further pollinate a growing F population. In contrast to the obligate case, this causes a temporary positive feedback until syrphid larvae reach high enough levels to sharply decrease herbivore abundance (H). Through this dynamic, higher values of b_F cause the population variables to reach higher values in the maxima of their oscillations. This causes more dramatic population crashes which therefore lead to longer times to population recovery and longer periods in limit cycles (Fig 6.7a&6.7b). This result is not confined to stable limit cycles with consistent periods between maxima. Even when the system exhibits irregularly timed oscillations in chaotic attractors, the average amount of time between population oscillation maxima increases with higher b_F (Fig 6.7c&6.7d). These results were found to be consistent with the addition of Type II or III functional responses. For further analysis of the Type I facultative model please see Appendix E.3.3.

6.6 Discussion

Analysis shows that the type of pollination relationship between the syrphid and flowering plant population can be critical to the persistence of a FHS community. Under both Type I and II functional responses, the pollination mutualism is unable to sustain positive growth when the plant population depends solely on syrphid pollination for reproduction in an obligate mutualism. This is due to a negative feedback loop which hinders the pollination dependent growth of the plant population when herbivore abundances are low enough to significantly restrict syrphid population growth and pollination ability.

While the system can persist when the flowering plant has some other means of reproduction, the negative feedback loop implies that predatory syrphids may have inherent difficulties maintaining flowering plant abundance (beyond lower pollination efficiency).The continuing decline in both bees and other Hymenopteran pollinators means losing effective pollinators that do not rely on herbivores as prey. If a plant population increasingly comes to depend on predacious syrphids as a source of pollination due to losses in other pollinators, the community potentially risks the reproductive restrictions of this negative feedback loop. Therefore, even if a flowering plant does receive some reproductive benefit from syrphid pollination, the negative feedback inherent in the system hinders its long term persistence unless either the plant or syrphid fly populations have other means of reproduction. While low pollination efficiency is often pointed to as a problem for syrphid maintenance of plant biodiversity, this model offers another potential explanation as to why syrphid flies may not be able to support certain wild flower species after the bee decline (Biesmeijer et al 2006).

On the other hand, these results indirectly speak to the importance of general insect and plant biodiversity. When a high diversity of insect herbivores and/or wild plants is available, predacious syrphid populations (especially generalist species) will have more options for pollination and predation. In practice, this will be less common in large scale industrial monocultures, but this concept is applied at less industrialized agricultural operations which utilize wild/native flower hedgerows adjacent to commodity crops under aphid attack (Haenke et al 2009). Other additional ecological factors, such as syrphid pupation, create time delays in interactions that may also serve to support system persistence. Finally, given preliminary results involving Type II and Type III functional responses, further research is warranted regarding the effects of handling times and functional responses.

When the pollination relationship between syrphid and the flowering plant populations does support community persistence, the model generates chaotic dynamics across large portions of parameter space. Compared to the Hastings & Powell (1991), the added mutualistic interaction between the lowest and highest trophic level induces chaotic dynamics without incorporating predatory functional responses. Current understanding of syrphid population fluctuations is limited (Kearns 2001; Ssymank et al 2008), though the available data does point to high amounts of spatio-temporal variation (Toft 1983; Herrera 1988; Pellmyr & Thompson 1996). Given that the model points to unpredictability inherent in syrphid fluctuations through chaotic community dynamics, further analysis is recommended. While Type III functional responses and reduced conversion efficiency were shown to reduce chaotic interactions, further potential mitigating factors of the chaotic dynamics will also be of interest as chaotic population fluctuations are considered undesirable from a biological control perspective.

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6.8 Reference

Aizen MA & Harder LD. 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Current Biology 19: 915–918.

Aizen MA., Garibaldi LA, Cunningham SA, Klein AM. 2008. Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. Current Biology 18: 1572–1575.

Bahmeier FA, Bernardino CS, Bradley JC. 1918. Official Organ American Association Of Economic Entomologists. Journal of Economic Entomology 11: 275.

Bargen H, Saudhof K, Poehling H. 1998. Prey finding by larvae and adult females of Episyrphus balteatus. Entomologia Experimentalis et Applicata 87: 245–254.

Bergh JC & Short BD. 2008. Ecological and life-history notes on syrphid predators of woolly apple aphid in Virginia, with emphasis on Heringia calcarata. BioControl 53:773–786 DOI 10.1007/s10526-007-9114-0

Berry RE. 1998. Insects and Mites of Economic Importance in the Northwest. 2nd Ed. 221 p.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J and Kunin WE. 2006. Parallel declines in pollinators and insect- pollinated plants in Britain and The Netherlands. Science 313(5785): 351–354.

Bingham RA & Orthner AR. 1998. Efficient pollination of alpine plants. Nature 391.6664: 238-239.

Bischoff M. et al. 2013. The relative importance of solitary bees and syrphid flies as pollinators of two outcrossing plant species in the New Zealand alpine. Austral Ecology 38(2): 169-176.

Cameron SA, et al. 2011. Patterns of widespread decline in North American bumble bees. Proc Natl Acad Sci USA 108(2):662–667.

Conner JK. & Rush S. 1996. Effects of flower size and number on pollinator visitation to wild radish, Raphanus raphanistrum. Oecologia 105(4): 509-516.

Cowgill SE, Wratten SD, Sotherton NW. 1993. The effects of weeds on the numbers of hoverfly (Diptera: Syrphidae) adults and the distribution and composition of their eggs in winter wheat. Ann. Appl. Biol. 123:499–515.

Dibbs H, Jamont M, Sauphanor B, Capowiez Y. 2011. Predation potency and intraguild interactions between generalist (Forficula auricularia) and specialist (Episyrphus balteatus) predators of the rosy apple aphid (Dysaphis plantaginea). Biological Control 59: 90–97.

Elberling H & Olesen JM. 1999 The structure of a high latitude plant-flower visitor system: The dominance of flies. Ecography 22: 314–323.

Feldman TS. 2006. Pollinator aggregative and functional responses to flower density: does pollinator response to patches of plants accelerate at low-densities? Oikos 115: 128-140.

Fontaine C, Dajoz I, Meriguet J, Loreau M. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. Plos Biology 4(1): 1029-1035.

Forister ML.et al. 2015. The global distribution of diet breadth in insect herbivores. Proceedings of the National Academy of Sciences. 112(2): 442-447.

Futuyma DJ & Gould F. 1979. Associations of Plants and Insects in Deciduous Forest. Ecological Monographs 49(1): 33-50.

Glaum PR, 2014. Dual Invasion Analysis: A General Model of Novel Ecological Dynamics due to Bt Product and Resistant Pests in Wild Settings. Theoretical Ecology 7(2): 181-194.

Gosselke U, Triltsch H, Roßberg D, Freier B. GETLAUS01—the latest version of a model for simulating aphid population dynamics in dependence on antagonists in wheat. Ecological Modelling 145(2): 143-157.

Gross J, Fatouros NE, Neuvonen S, Hilker M. 2004. The importance of specialist natural enemies for *Chrysomela lapponica* in pioneering a new host plant. Ecological Entomology 29: 584–593.

Haslett JR. 1989. Interpreting patterns of resource utilization: randomness and selectivity in pollen feeding by adult hoverflies. Oecologia 78: 433–442.

Hastings A & Powell T. 1991. Chaos in a Three Species Food Chain. Ecology. 72(3): 896-903.

Haenke S, Scheid B, Schaefer M, Tscharntke T, Thies C. 2009. Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. Journal of Applied Ecology 46: 1106–1114.

Haenke S. 2014. Landscape configuration of crops and hedgerows drives local syrphid fly abundance. Journal of applied ecology 51(2) 505-513.

Herrera CM. 1987. Components of pollinator" quality": comparative analysis of a diverse insect assemblage. Oikos: 79-90.

Herrera CM. 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. Biological Journal of the Linnean Society 35:95-125.

Hopper JV, Nelson EH, Daane KM, Mills NJ. 2011. Growth, development and consumption by four syrphid species associated with the lettuce aphid, Nasonovia ribisnigri, in California. Biological Control 58(3): 271-276.

Howard PH. 2009. Visualizing Consolidation in the Global Seed Industry: 1996–2008. Sustainability. 1(4): 1266-1287. doi:10.3390/su1041266

Iler AM., et al. 2013. Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. Global change biology 19(8): 2348-2359.

Jarlan A & Gingras J. 1997. Pollination by Eristalis tenax (Diptera: Syrphidae) and seed set of greenhouse sweet pepper. Journal of economic entomology 90(6):1646-1649.

Jauker F & Wolters V. 2008. Hover flies are efficient pollinators of oilseed rape. Oecologia 156: 819-823.

Kan E. 1988. Assessment of Aphid Colonies by Hoverflies. II Pea Aphids and 3 Syrphid Species; Betasyrphus serarius (Wiedemann), Metasyrphus frequens Matsumura and Syrphus vitripennis (Meigen) (Diptera: Syrphidae). Journal of Ethology 6(2): 135-142.

Kearns CA. 1992. Anthophilous fly distribution across an elevation gradient. Am. Midl. Nat. 127: 172-182.

Kearns CA. 2001. North American dipteran pollinators: assessing their value and conservation status. Conservation Ecology 5(1): 5. [online] URL: http://www.consecol.org/vol5/iss1/art5/

Kearns CA & Inouye DW. 1994. Fly pollination of Linum lewisii (Linaceae). American Journal of Botany 8:1091-1095.

Khan AA, Shah MA, Majid S. 2016. Functional response of four syrphid predators associated with green apple aphid (Hemiptera: Aphididae) in laboratory. Journal of Economic Entomology 109 (1): 78-83.

Kühsel S & Blüthgen N. 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. Nature communications 6.

Lövei GL, Macleod A, Hickman JM. 1998. Dispersal and effects of barriers on the movement of the New Zealand hover fly Melanostoma fasciatum (Dipt., Syrphidae) on cultivated land. Journal of Applied Entomology 122.1(5): 115-120.

Michaud JP. 1999. Sources of mortality in colonies of brown citrus aphid, Toxoptera citricida. BioControl 44: 347-367.

Miller D. 1918. The Economic Bearing of Hover-Flies. New Zealand Journal of Agriculture 1918, September 20th Vol. 17 No. 3:129-135.

Nye WP & Anderson JL. 1974. Insect pollinators frequenting strawberry blossoms and the effect of honeybees on yield and fruit quality. J Am Soc Hortic Sci 99:40–44

Otto SB, Berlow EL, Rank NE, Smiley J, Brose U. 2008. Predator diversity and identity drive interaction strength and trophic cascades in a food web. Ecology 89(1): 134-144.

Pellmyr O, & Thompson JN. 1996. Sources of variation in pollinator contribution within a guild: the effects of plant and pollinator factors. Oecologia 107:595-604.

Potts SG, et al. 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol Evol 25(6):345–353.

Primack RB. 1983. Insect pollination in the New Zealand mountain flora. New Zealand journal of botany 21(3): 317-333.

Richards AJ. 1986. Plant Breeding Systems. 529 pp. George Allen & Unwin, London.

Rush S, Conner JK, Jennetten P. 1995. The Effects of Natural Variation in Pollinator Visitation on Rates of Pollen Removal in Wild Radish, Raphanus raphanistrum (Brassicaceae). American Journal of Botany 82(12): 1522-1526.

Sahli FS, & Conner JK. 2007. Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, *Raphanus raphanistrum* (brassicaceae). American Journal of Botany 94(2): 203-209.

Ssymank A, Kearns CA, Pape T, Thompson FC. 2008. Pollinating flies (Diptera): A major contribution to plant diversity and agricultural production. *Biodiversity* 9.1-2: 86-89.

Sunderland KD, Crook NE, Stacey DL, Fuller BJ. 1987. A Study of Feeding by Polyphagous Predators on Cereal Aphids Using Elisa and Gut Dissection. Journal of Applied Ecology 24(3): 907-933.

Tamaki G, Landis BJ, Weeks RE. 1967. Autumn Populations of Green Peach Aphid on Peach Trees and the Role of Syrphid Flies in Their Control. Journal of Economic Entomology 60(2): 433-436. DOI: http://dx.doi.org.proxy.lib.umich.edu/10.1093/jee/60.2.433 433-436.

Tenhumberg B & Poehling HM. 1995. Syrphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. Agriculture, Ecosystems and Environment, 52,39–43.

Tenhumberg B. 2004. Predicting predation efficiency of biocontrol agents: linking behavior of individuals and population dynamics. Faculty Publications in the Biological Sciences. Paper 184. http://digitalcommons.unl.edu/bioscifacpub/184.

Toft, CA. 1983. Community patterns of nectivorous adult parasitoids (Diptera, Bombyliidae) on their resources. Oecologia 57:200-215.

Van Der Kooi, CJ, Pen I, Staal M, Stavenga DG, Elzenga JTM. 2016. Competition for pollinators and intra-communal spectral dissimilarity of flowers. Plant Biology. 18(1) 56-62. doi:10.1111/plb.12328.

van Rijn, PCJ, Kooijman J, Wackers, FL. 2006. The impact of floral resources on syrphid performance and cabbage aphid biological control." IOBC wprs Bulletin 29.6: 149.

Wolf A, Swift JB, Swinney HL, Vastano JA., 1985. Determining Lyapunov exponents from a time series. Physica D 16: 285–317.

Wratten SD, Bowie MH, Hickman JM, Evans AM, Sedcole JR, Tylianakis JM. 2003. Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. Oecologia 134(4): 605-611.

Zhang C & Chen T. 2001. Efficient feature extraction for 2d/3d objects in mesh representation. 2001 International Conference on Image Processing: 935-938(3). DOI: 10.1109/ICIP.2001.958278.

Chapter 7

Stage-structured ontogeny in resource populations generates non-additivity in stabilizing and de-stabilizing forces in populations and communities

7.1 Abstract

The importance of a stage-structured ontogeny to community dynamics has become increasingly clear across a number of studies focused on trophic interactions at higher trophic levels. To develop deeper understanding of the role stage structure in an organism's ontogeny might have on community dynamics, it is also necessary to consider the basal resource level for terrestrial ecosystems, plants. Plants have distinct ontogenetic stages that can readily be incorporated in a modeling framework. While single-stage population growth equations average out demographic rates across all individuals, a multi-stage approach can more easily incorporate the difference between seeds and reproductive adults. Additionally, since the different stages across a plant's development will have different trophic and ecological dynamics, this multi-stage approach allows me to study the effects of stage-specific ontogeny on both population and community levels. Here we show that the incorporation of distinct ontogenetic stages in plant development produces non-additivity in the drivers of dynamic stability.

7.2 Introduction

The ontogeny of numerous organisms involves distinct demographic stages creating a compartmentalized structure across development. These stages can refer to changes in size, age, and/or definite demographic phases with distinct morphologies and metabolic properties/rates. The unique qualities of each stage can have profound effects on the internal population dynamics of the species. These demographic stages will also frequently have unique ecological connections to the greater ecological network, through different feeding habits, predators, habitat requirements, etc. (de Roos & Persson 2013). Understanding the specific characteristics of each stage of a species' development and their ecological interactions is critical to understanding how the biotic and abiotic environment affects a species' internal population dynamics. Incorporation of this facet of organismal development has a legacy in the study of internal population dynamics, e.g. Leslie/Lefkovitch matrices (Leslie 1945; Lefkovitch 1965) and integral population matrices (IPM; Easterling et al 2000). Not only does this stage structure determine how the environment shapes the internal population dynamics of a species, but on a broader community scale, the unique ecology of each stage across development can also influence how a species affects its surrounding community dynamics (Wollrab et al 2012; deRoos & Perrson 2013; Glaum 2017). A well-known example: distinct ontogenetic stages in a prey species can allow multiple predator species specialized on different development stages to coexist on a single prey species (Haigh & Smith 1972; Schoener 1974), a potential avoidance of the competitive exclusion principle (Gause 1934).

Plant species developing from compact seeds to their reproductive stages represent an important example of such distinct stage structure at the foundational level of ecological communities. By incorporating effects on specific stages in plant development by density dependence (Germer & Venable 2016), abiotic environmental stochasticity (Westoby 1981; Ellner 1985a,b, 1987b; Tielborger & Valleriani 2005), and herbivore pressure (Eckberg et al 2014), researchers have studied various external drivers of internal plant population dynamics. However, it has been noted that despite this wealth of research on the external drivers of stage-structured demography of plants, the role of plant stage structure in influencing greater community dynamics has seen a relative scarcity of attention (Miller & Rudoph 2011). Despite a number of years passing since this observation, this scarcity remains.

Recently, the incorporation of the stage structure of ontogeny has provided novel explanations into the mechanisms of coexistence in ecological communities in other systems, particularly fisheries (deRoos & Perrson 2003; de Roos et al 2008). In light of these advances, we propose that the inclusion of developmental stages of plant populations is necessary in addressing the broader study of species coexistence and community dynamics. To that end, we develop a model framework which explicitly incorporates major plant life stages. Considering the full complexity of any plant species' complete ontogeny makes choosing the level of resolution in stage structure to study a daunting task. However, similar to numerous past stage structure studies (de Roos et al 2008), focusing on ubiquitous characteristics across species allows us to limit the number of stages to a manageable initial list (Table 7.1).

Beyond being functionally unique as distinct stages within a plant species, the stages considered in this work are uniquely connected to other species in an ecological network. In particular, it is almost universal among vascular plants that seeds and vegetation are preyed upon by distinct organisms. Rarely is the niche that is called "seed predator" occupied by the same species as the niche called "consumer of vegetation," yet almost all vascular plants are attacked by consumers both on the seeds and the vegetation, only rarely the same species. In large part, this is because of the different mouth parts required to feed on these different stages (especially in insects). Incorporating these different consumers into the model framework allows us to address the effects of plant stage structure on plant population dynamics and broader community dynamics, as recommended (Miller & Rudolph 2011).

Using the model developed here, we address the following key questions: (1) What are the baseline dynamics of a stage-structured plant resource without consumer pressure? (2) How do the distinct consumers of the different stages of the plant individually affect community dynamics? (3) What are the dynamics of consumer coexistence and/or competitive exclusion when consumers are split between different plant development stages? In addressing these questions, we show that consideration of the stage-structure of plant ontogeny presents various non-additive drivers in community dynamic stability.

7.3 Methods

7.3.1 Model Development

The model takes the form of coupled ordinary differential equations (ODEs). At the base of the community is the seeding plant population. For the purposes of this work, we do not consider plant species capable of significant vegetative growth. Given the interest in the effects of ontogeny through stage structure, we only consider recruitment through seed production and seed germination. The plant population is split into different stages: mature reproductive/fecund adults (F), immature seeds in the seed bank (S_1) considered removed from the parent plant, post dispersal, and a non-reproductive seedling stage (S_2). There are two consumers of the plant population: one which feeds upon the leaf /stem tissue of the adult reproductive plants hence referred to as the herbivore (H_F), and one which feeds on the seeds of the plant, referred to as the seed predator (H_S). Population dynamics of the community are governed by the equations shown in Table 7.1.

Seed production occurs at rate r_F and the population experiences density dependent reproduction with a strength a_F. In a typical consumer-resource system, the density dependence is included in the production of the single resource equation/variable. However, the resource exists in two basic stages here. Density dependence acts on reproduction, which occurs through seed production. Therefore, the density dependent effects on reproduction are felt in the production of seeds and included in the seed equation. This requires the inclusion of a simple control factor $x(S_1) = \frac{S_1}{\omega+S_1}$ for some small ω. This control factor $x(S_1)$ is effectively 1 until $S_1 \to 0$ when it becomes 0. This stops any density dependent effects on seed bank biomass when the seed bank approaches zero abundance, thereby eliminating the potential for negative seed biomass. Seeds germinate at a rate g_1 which is functionally attenuated due to density dependent effects of all the stages at rate a_g. The negative density dependent effects of adults, which can shade and better compete for resources, is higher than any experienced by other stages, so the competitive effects of seeds and seedlings on seed germination/maturation is limited by a factor ϵ. Finally, all stages experience a background death rate d_F or d_S.

Consumption for the herbivore (H_F) and seed predator (H_S) occurs at an attack rate a_{HF} and a_{HS} with conversion rates c_{FH} and c_{SH} respectively. Rates of attack are regulated by a Type II functional response where the handling times are h_{HF} and h_{HS} for the herbivore and seed predator respectively. There is no overlap in the consumption of the two stages between the two consumers. Finally, the functional rate of loss of seeds and plants due to consumer pressure is not necessarily equal. An attacked seed is assumed lost, but an attacked stem of a plant does not necessarily result in a lost reproductive adult. The parameter kr marks the differential in consumer loss of plants and seeds. Death rates for the herbivore and seed predator are d_{H_F} and d_{H_S} respectively. Note, $x(S_1)$ is shown separately for clarity. The model is, at most, 4 dimensional. The overall model framework is presented in Table 7.1 with specific function definition given in Table 7.2. Parameter descriptions are given in Table 7.3.

Table 7.1 - Description of model. The time dependent equations represent fecund plants (F), seedling (S_2), seed bank (S_1), herbivore (H_F), and seed predator (H_S).

Description	Dynamic Equation
Dynamics of Fecund/Adult Plants (F)	$\frac{dF}{dt} = \overbrace{\begin{cases}\gamma_{1F}, S_2 = 0 \\ \gamma_{2F}, S_2 > 0\end{cases}}^{maturation} - \overbrace{k_r\theta_{HF}}^{consumption} - \overbrace{d_F F}^{\substack{background \\ mortality}}$
Dynamics of non-Fecund Seedlings (S_2)	$\frac{dS_2}{dt} = \overbrace{\gamma_{12}}^{maturation} - \overbrace{\gamma_{2F}}^{maturation} - \overbrace{d_S S_2}^{\substack{background \\ mortality}}$
Dynamics of Seed Bank (S_1)	$\frac{dS_1}{dt} = \overbrace{\delta}^{seed\,production} - \overbrace{\begin{cases}\gamma_{1F}, S_2 = 0 \\ \gamma_{12}, S_2 > 0\end{cases}}^{maturation} - \overbrace{\theta_{HS}}^{consumption} - \overbrace{d_S S_1}^{\substack{background \\ mortality}}$
Dynamics of Plant-Tissue Herbivore (H_F)	$\frac{dH_F}{dt} = \overbrace{c_{FH}\theta_{HF}}^{consumption} - \overbrace{d_{H_F}H_F}^{\substack{background \\ mortality}}$
Dynamics of Seed Predator Herbivore (H_S)	$\frac{dH_S}{dt} = \overbrace{c_{SH}\theta_{HS}}^{consumption} - \overbrace{d_{H_S}H_s}^{\substack{background \\ mortality}}$

Table 7.2 – Model function descriptions.

Function	Model 1	Model 2	Model 3	Model 4	Description
δ	$F(r_F - x(S_1)\alpha_F F)$	$F(r_F - x(S_1)\alpha_F F)$	$F(r_F - x(S_1)\alpha_F F)$	$F(r_F - x(S_1)\alpha_F F)$	Seed Production
γ_{1F}	g_1S_1	$\frac{g_1S_1}{1+\alpha_g(F+\epsilon S_1)}$	0	$\frac{g_1S_1}{1+\alpha_g(F+\epsilon S_1)}$	Seed Germination
γ_{12}	0	0	$\frac{g_1S_1}{1+\alpha_{g1}\left(F+\epsilon(S_1+S_2)\right)}$	0	Seed Germination
γ_{2F}	0	0	$\frac{g_2S_2}{1+\alpha_{g2}\left(F+\epsilon(S_1+S_2)\right)}$	0	Seedling Maturation
θ_{HF}	0	0	0	$\frac{a_{HF}FH_F}{1+a_{HF}h_{HF}F}$	Consumption by Herbivore
θ_{HS}	0	0	0	$\frac{a_{HS}S_1H_S}{1+a_{HS}h_{HS}S_1}$	Consumption by Seed Predator
$x(S_1)$	$\frac{S_1}{\omega+S_1}$	$\frac{S_1}{\omega+S_1}$	$\frac{S_1}{\omega+S_1}$	$\frac{S_1}{\omega+S_1}$	Density Dependence Monitor

Table 7.3 - Parameter names and definitions for Tables 7.1 and 7.2. All parameters are positive and real valued, measuring rates per individual per unit time.

Parameter	Definition
r_F	Intrinsic reproduction (seed) rate of resource plant population.
g_1	Germination rate of seeds into seedlings or reproductive adults depending on model.
g_2	Maturation rate of seedlings into reproductive adults.
a_{H_F}	Attack rate of the herbivore on the plant population.
$a_{\mathrm{H_S}}$	Attack rate of the seed predator on seeds.
c_{F_H}	Conversation rate of eaten plants into herbivores.
c_{S_H}	Conversation rate of eaten seeds into seed predators.
$\alpha_F, \alpha_{g1}, a_{g2}$	Strength of density dependence affecting seed production, seed germination, and seedling maturation respectively.
ω	Parameter regulating density dependence of reproductive adults on seed production.
ϵ	Parameter mitigating density dependent attenuation of seeds on germination (set to 0.2).
$d_{\mathrm{F}}, d_S, d_{H_F}, d_{H_S}$	Death rates for the flowering plant, seeds/seedlings, herbivore, and the seed predator. $d_F = 0.1, d_S = 0.1$, and $d_{H_F} = d_{H_S} = 0.2$.
h_{H_F}, h_{H_S}	Handling times for herbivory on reproductive adults (h_{HF}) and seed predation (h_{HS}).
k_r	Kill rate of herbivore attack on plant individuals.

7.3.2 Modes of analysis

Numerical analysis was conducted using Mathematica 10 and the University of Michigan's FLUX computing core to facilitate large parameter sweeps. Parameter sweeps allowed for the dynamics of the model to be tested across the range of pertinent parameter combinations. We examined the model for stable equilibria, stable limit cycles, and persistent chaotic oscillations.

Stability of equilibria was tested using traditional linear stability analysis. When the model did not produce stable equilibria, model runs were completed and measured for asymptotic behavior after 6000 time steps. Much of the results are presented through pictorial representations of asymptotic model behavior across parameter space. This is represented in heatmap bifurcation diagrams (e.g. Figure 7.3a) where different model dynamics (stable equilibrium, limit cycles, etc.) are displayed across parameter space. Stable equilibria are represented by the green/avocado gradient where the colors correspond to the value of state variable at stable equilibrium. Limit cycles are shown in the sunset color gradient where the colors represent the value of variable at maxima in the oscillations.

7.4. Results

7.4.1 Internal Plant Population Dynamics (Model 1, 2, and 3)

First, we address the stage-structured plant population dynamics in the absence of consumers. The relatively simple act of splitting the classic logistic growth equation into two stages, F and S_1 in Model 1, alters the dynamics of population growth in the model such that density dependence has affects across stages. In this case (Model 1), density dependence alters the rate of seed production (δ). This alone introduces oscillatory behavior (through dampened oscillations) not present in the single dimension logistic growth model (Fig F.1a). These oscillations form the basis of the non-additivity in stabilizing and de-stabilizing forces seen below. Model 1 is used here to show how the stage-structure itself infuses the population dynamics with oscillatory behavior. The density dependent germination rate γ_{1F} of Model 2 will be used as the basis for further additions to the model.

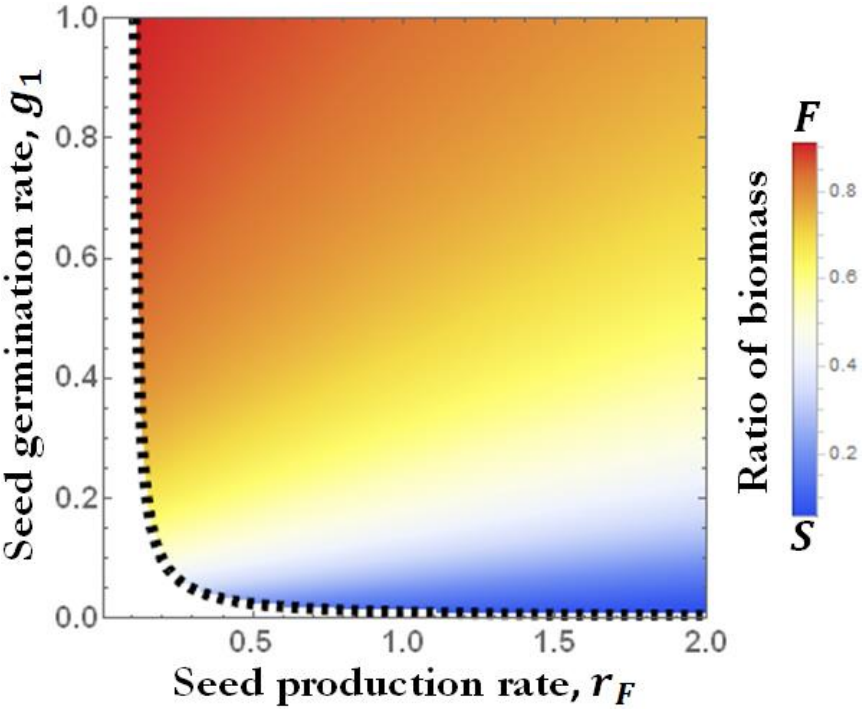


Figure 7.1 - Ratio of equilibrium biomass for the seeding plant's two stages (reproductive adults and seeds) with no consumers across rates of seed production (r_F) and seed germination (g_1). Both seed and reproductive adult variables go to equilibrium in the absence of consumer pressure. Colors represent the relative composition of the plant population biomass across different values of r_F and g. The ratio is created by taking $\frac{F}{F+S_1}$, so higher values ("hotter" colors) represent a plant population with a smaller seed bank and higher contingency of reproductive adults. Lower values ("colder" colors) represent a plant population with a larger seed bank. The dashed line represents the conditions for plant population persistence, $g_1 > \frac{d_F d_S}{r_F - d_F}$. Other parameters: $a_F = a_g = 0.1, \epsilon = 0.2, \omega = 0.001$.

Model 2 exhibits the same dampened oscillatory behavior taking the plant population to its carrying capacity (Fig F.1b). This carrying capacity is > 0 contingent upon $g_1 > \frac{d_F d_S}{r_F - d_F}$ or $r_F > \frac{d_F d_S}{g_1} + d_F$ (Figure 7.1, Appendix F.1). Beyond providing conditions for persistence, the rates of seed germination (g_1) and seed production (r_F), also change the absolute (Fig F.2) and relative (Fig F.1) composition of the plant population's biomass. Lower seed germination rates (or longer periods of seed dormancy) mean a larger seed bank relative to reproductive adults. This change is largely due to increases in the seed bank biomass, while the final abundance of adults (F) is relatively less effected (Fig F.2). Increases in relative seed biomass can also occur with higher seed production rates (r_F), but this also increases the absolute number of reproductive adults, so the effect is not as pronounced. Notably, the stable stage distribution of the plant population is not invariant to demographic rates, a strong indication that the inclusion of ontogeny through stage structure will have strong community level effects (Miller & Rudolf 2011).

The dampened oscillations exhibited by Model 2 provide the first indication of non-additivity in the effect of a single parameter, seed production rate r_F. Dependent upon intrinsic demographic parameters, increasing seed production rates can raise or lower the time taken to reach stable equilibrium through dampened oscillations (Fig F.3). Increasing r_F can even have the effect of raising the time taken to reach equilibrium before eventually lowering it (Fig F.3). This tendency is amplified by considering a third stage in the plant population as in Model 3. The additional stage magnifies the cross-stage density dependent effects allowing for persistent oscillatory dynamics driven solely by internal demographic processes with sufficiently high seed production. These oscillations occur when density dependent restrictions on maturations of lower stages and seed production temporarily limits stage transitions or reproduction during intervals of high abundance. Similar to the system dynamics across r_F seen in Model 2, further increasing seed production rates in Model 3 when the system is exhibiting persistent oscillations will actually *re-stabilize* the system (Fig 7.2a). This growth driven transition from dampened to persistent to dampened oscillations is found in various tested sections of parameter space (Fig F.4). The dampening of oscillations once the growth rate is high enough that the effect of the aforementioned density dependence is relatively consistent across time instead of temporarily reaching restricting levels.

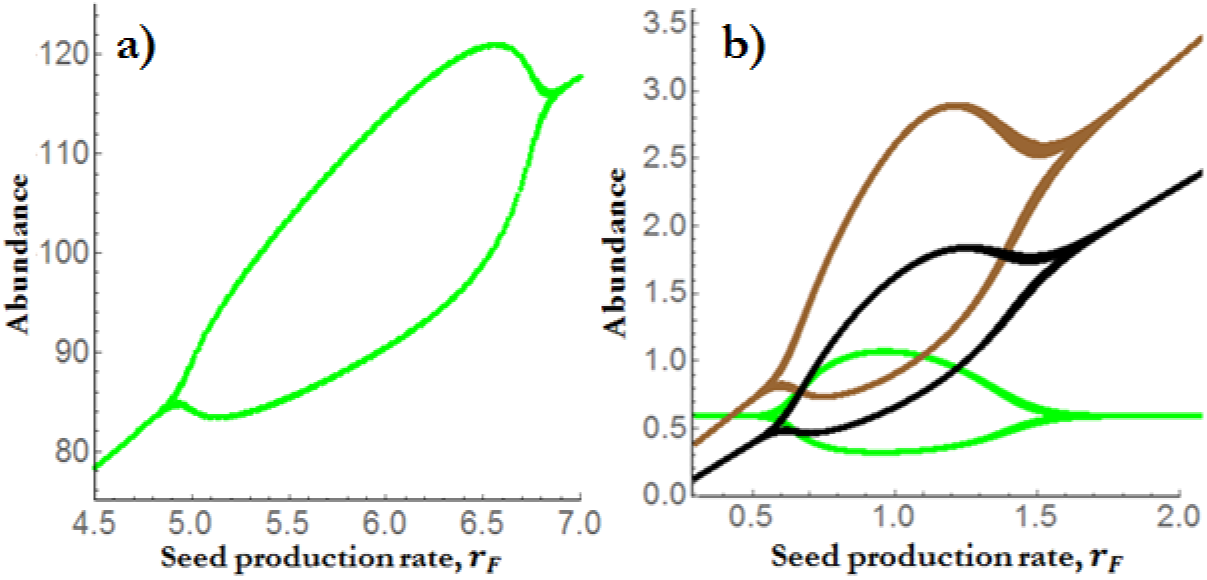


Figure 7.2 - Bifurcation diagrams showing the period bubble caused by increasing seed production in the stage-structured plant population. a) Bifurcation diagram from Model 3. With increasing growth, the plant population exhibits limit cycles until the

increased intra-specific competition limits the fluctuations. Parameter values: $g_1 = 0.738$*;* $g_2 = 0.832$*;* $a_F = 0.054$*;* $a_{g1} = 0.045$*;* $a_{g2} = 0.045$*;* $\epsilon = 0.2$*;* $d_F = d_{S1} = d_{S2} = 0.1$*;* $w = 1.0$*. b) Bifurcation diagram from Model 4 (*$H_F > 0, H_S = 0$*).* F *is shown in green,* S *is shown in brown,* H_F *is shown in black. Similar to a single stage consumer-resource system, higher growth induces oscillations. But the stage structure controls maturation rates such that actual adult abundance is limited by intra-specific competition instead of herbivory. This stabilizes the system despite higher growth. Parameter values:* $g = 0.288$*;* $a_g = a_F = 0.1$*;* $h_{H_F} = 1.0$*;* $c_{FH} = 0.6$*;* $a_{H_F} = 0.85$*;* $\epsilon = 0.2$*;* $d_F = d_S = 0.1$*;* $d_{H_F} = 0.2$*;* $\omega = 0.01$*.*

7.4.2 Herbivore-consumer system (Model 4 with $H_F > 0, H_S = 0$)

Next, we analyze the consumer-resource system in Model 4 with only the herbivore H_F, excluding the seed predator *(*Model 4 w/ $H_F > 0, H_S = 0$*)*. Note that Model 4 only has two stages in the resource plant population. Similar to a classic Lotka-Volterra consumer-resource system, the herbivore consumer system exhibits both dampened oscillations to stable equilibria and consistent oscillations through limit cycles. As expected given this similarity, higher herbivore attack rates (a_{H_F}) destabilize the system and cause persistent oscillations through a Hopf bifurcation destabilizing the equilibrium. However, lower rates of seed germination (g_1) can stabilize the system, with lower g required for stability with higher a_{HF} (Fig 7.3a).

The stabilizing effect of lower germination rates stems from the changes in demographics it causes in the plant population. First, as shown in Fig 7.1, lower g_1 values shift the overall plant population to a more seed bank dominate ratio. This occurs because the seed bank population grows as lower g_1 values mean less seeds transitioning into reproductive adults per unit time. Slower germination leads to reduced growth rates of reproductive adults (Fig 7.4a), which consequently means a larger seed bank (Fig 7.4b) and reduced resources for the herbivore consumer (Fig 7.4c). This implies that a robust seed bank may stabilize population fluctuations in the face of herbivore pressure.

The stabilizing effect of a robust seed bank can emerge through other less intuitive processes, namely through the seed production parameter r_F. Analogous to the non-stage Lotka-Volterra consumer-resource system, higher seed production rates can destabilize the community by inducing higher growth rates in the consumer population. However, similar to the dynamics shown in Models 2 and 3, further increases in seed production rates can actually *re-stabilize* the population and community (Fig 7.2b). This re-stabilization occurs because sufficiently high seed production means that the number of new reproductive adults is not limited by the herbivore, but by the increased intra-specific competition to germinate (a_g). This means the plant population's growth rate will experience comparatively less pronounced oscillations in relation to the herbivore population, which will in turn stabilize the system (Fig 7.4d-7.4f).

Reduced growth rates in basal resource populations have been shown to have stabilizing effects in other systems (McCann et al 1999, Glaum & Kessler 2017). However, the results presented here suggest that the stabilizing effect of lowered growth rates may depend on the mechanisms of intra-specific competition emergent from the internal population structure in the basal level of the community. These results also indicate that the non-additive effects seen in demographic rates of the plant population dynamics have the potential scale up to broader community dynamics.

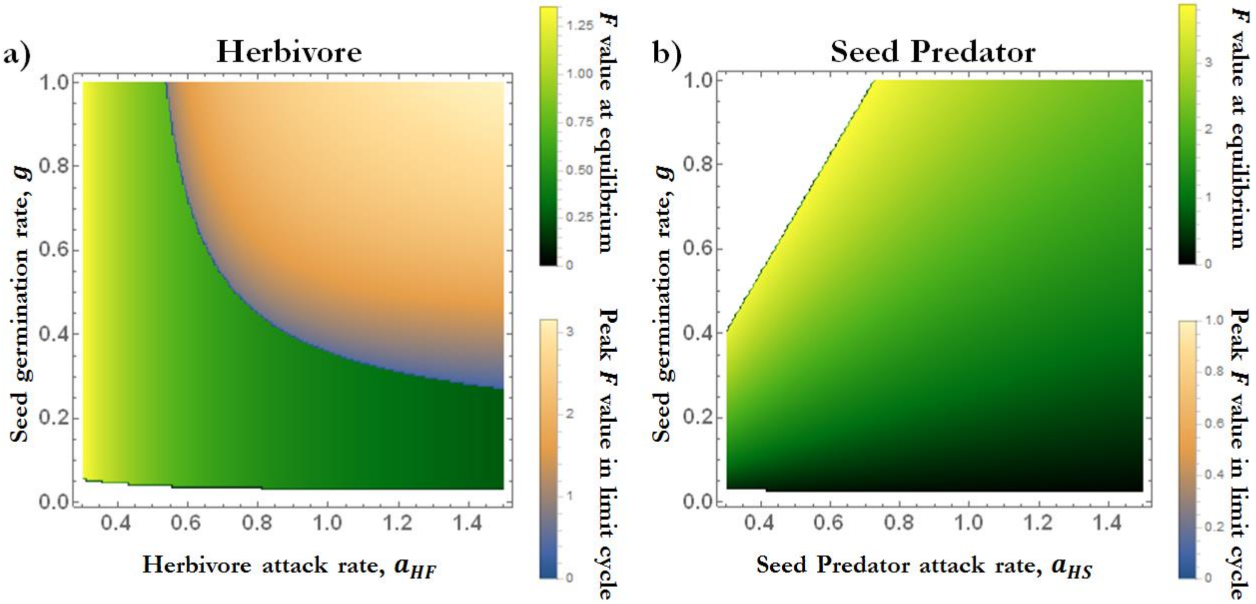


Figure 7.3 - Two dimensional heatmap bifurcation diagram showing the dynamics of the herbivore and seed predator systems from numerical analysis of Model 4. Colors represent the values of F from the time series. The avocado color scale shows values F^* when the system is at stable equilibrium. The sunset color scale shows F at peak values in oscillations when the system supports stable oscillations. White represents parameter space leading to the extinction of the consumer (the plants persist). Figures show dynamics across different combinations of values for the seed germination rate (g) and the attack rates of each consumer (a_{HF} and a_{HS}). a) Dynamics in the herbivore consumer system. b) Dynamics in the seed predator consumer system. There were no limit cycles found in the seed predator system with the parameter space explored here. Other parameters: $r_F = 0.5, kr = 0.7, c_{FH} = c_{SH} = 0.6, h_{HF} = h_{HS} = 1, \omega = 0.001$.

7.4.3 Seed Predator-consumer system (Model 4 with $H_F = 0, H_S > 0$*)*

Here we analyze the consumer-resource system in Model 4 with only the seed predator H_S *(*Model 4 w/ $H_F = 0, H_S > 0$*)*. Note that Model 4 only has two stages in the resource plant population (F and S_1). Given the stabilizing effect of lower g_1 in the herbivore-consumer system by keeping plant biomass in an inaccessible stage, it would be reasonable to predict that higher

g_1 can stabilize a seed predator-consumer system. In other words, given a similar parameter set up, the seed predator system would produce a similar dynamical pattern to Fig 7.2a, but with the y-axis roughly flipped. Following the reasoning detailed above in the herbivore-consumer system, changes in the seed germination rate (g_1) can change the biomass composition of overall plant population and the effective growth rate of the population. Lower g_1 increases the available seed bank resource for the seed predator creating initially high growth in the seed predator population as seed germination rates fall (Fig 7.4d). Such high initial growth in the consumer population can have destabilizing effects in a more traditional consumer-resource system with no stage structure. However, by feeding on the seed bank (S_1), the seed predator eliminates the reproductive product of the adults before those seeds can mature and reproduce themselves. This is akin to effectively lowering the intrinsic population growth rate r in the traditional Lotka-Volterra consumer-resource system. This has a stabilizing effect on the system. Furthermore, this seed predation consequently limits the growth of new fecund adults (F), such that the initial surge in seed biomass is never replenished (Fig 7.4d-7.4f), further dampening oscillations until a steady state is reached.

This stabilizing dynamic of limiting maturation of seeds into reproductive adults means that higher seed predator attack rates (a_{H_S}) also dampen oscillations (Fig 7.4g-7.4i). This is direct contrast to the traditional non-stage structured consumer-resource system and Model 4 with just the herbivore ($H_F > 0, H_S = 0$). These dynamics lead to a consistently stable system across values of g_1 and $a_{H_S}$when only the seed predator is present (Fig 7.3b).

While the seed predator-consumer system is more prone to produce stable equilibria across the parameter space tested here, it should be mentioned that the initial hypothesis of stabilization realized at higher germination rates is viable with particular parameter combinations. It is possible to generate stable oscillations in the seed predator-consumer system with large handling times for the seed predator ($h_{H_S} \approx 2$), coupled with weak density dependence in the resource ($a_F, a_g \leq 0.01$) and higher attack rates (Fig F.6). This is an intuitive result as handling times greater than 1 can often lead to oscillatory dynamics through delays in effective consumer attack rates (Holling 1959; Oaten & Murdoch 1975).

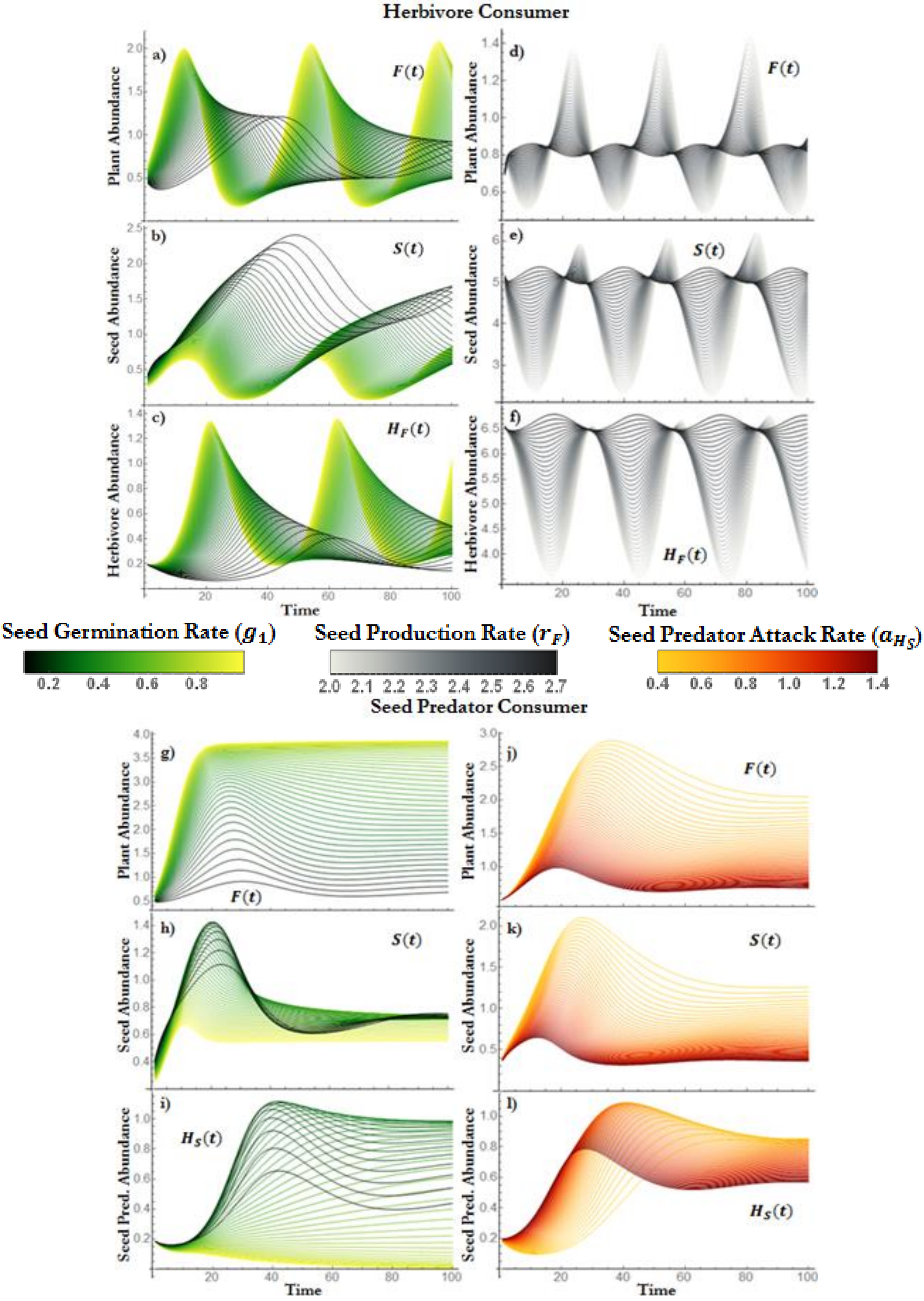


Figure 7.4 - Representations of model dynamics in single consumer communities, the herbivore alone (7.4a-7.4f) and the seed predator alone (7.4g-7.4l). Model dynamics are shown across gradients of values for parameters g (7.4a-7.4c, 7.4g-7.4i), r_F

(7.4d-7.4f), and a_{HS} *(7.4j-7.4l) with line color corresponding to the value of the parameters shown in the color legend. Changes in the value of* g *are represented by the "avocado" color gradient, changes in the value of* r_F *are represented by the gray scale color gradient, and changes in the value of* a_{HS} *are shown in the solar color gradient. Other parameters are as follows. Figures 7.3a-7.3c:* $r_F = 0.5, a_{H_F} = 0.7, k_r = 0.7, c_{FH} = 0.6, h_{H_F} = 1, \omega = 0.001, \alpha_g = \alpha_F = 0.1$. *Figures 7.3d-7.3f:* $g_1 = 0.378, a_{H_F} = 0.615, k_r = 0.7, c_{FH} = 0.6, h_{H_F} = 1, \omega = 0.001, \alpha_g = \alpha_F = 0.1$. *Figures 7.3g-7.3i:* $r_F = 0.5, a_{H_S} = 0.7, k_r = 0.7, c_{SH} = 0.6, h_{H_S} = 1, \omega = 0.001, \alpha_g = \alpha_F = 0.1$. *Figures 7.3j-7.3l:* $r_F = 0.5, g_1 = 0.2, k_r = 0.7, c_{SH} = 0.6, h_{H_S} = 1, \omega = 0.001, \alpha_g = \alpha_F = 0.1$.

7.4.4 Two consumer system (Model 4 with $H_F > 0, H_S > 0$)

The competitive exclusion principle dictates that two consumers competing for the same resource cannot coexist (Gause 1934) barring some mitigating factor. Having the two consumers attacking separate stages in the resources life cycle is one potential mechanism for the persistence of both consumers, as attacking distinct stages of the resource is akin to consuming distinct (but related) resource populations (Haigh & Maynard-Smith 1972). Intuitively, the distinct consumers across the stage structure of the plant population can support coexistence of both H_F and H_S.

Despite coexistence brought on by the attacking separate stages, there is still a degree of exploitative competition between consumers. The effects of this competition can be seen, not only in the relative abundance of each consumer, but also in the resultant community dynamics of the overall system. Recall that low or high rates of seed predation (a_{H_S}) can actually reinforce stability in the system dynamics while herbivory (a_{H_F}) can induce oscillations. Simulations reveal that the consumer with the larger attack rate can instill its characteristic dynamic on the system (Fig 7.5a). Examining the relative abundance of each consumer from these same simulations across the attack rate parameter space reveals that each consumer's relative dominance in the system can drive this change in community dynamics (Fig 7.5b). Therefore, the results of consumer competition can mean more than just one consumer's abundance over its competitor, it can also have distinct qualitative effects on the type of community dynamics.

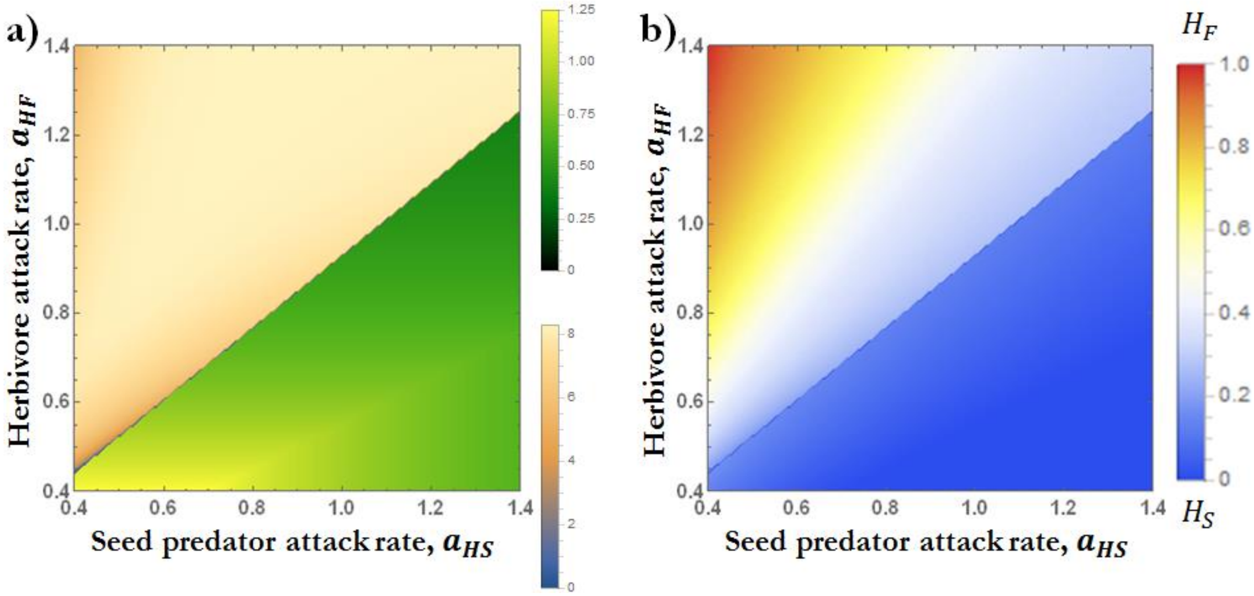
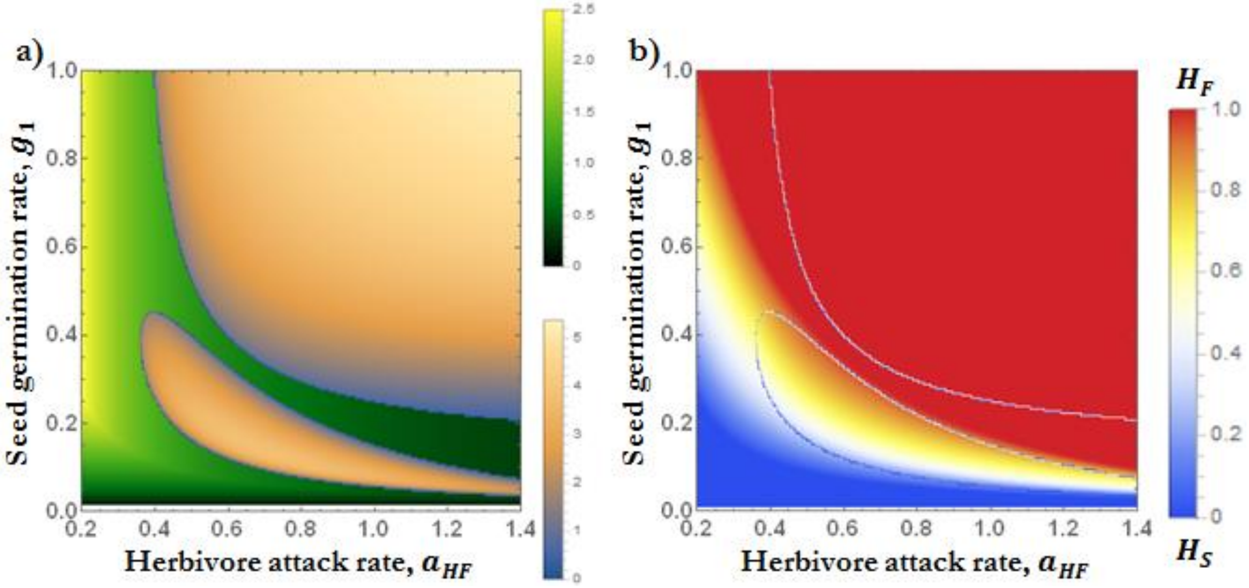


Figure 7.5 - Simulation results with both herbivore and seed predator present. Figure shows the asymptotic model dynamics of the model after 6000 time steps across $\{a_{HS}, a_{HF}\}$ *parameter space. a.) The "avocado" color gradient represents* F *values when the system produces equilibrium dynamics. The "sunset" color gradient represents the maximum values of* F *when the system produces limit cycles. b.) Blue to red temperature gradient shows the ratio of* H_S *to* H_F*. A value of 1 indicates high* H_F *and low* H_S *and a value of 0 indicates high* H_S *and low* H_F*. Other parameter values:* $r_F = 1.1, g = 0.2, kr = 0.7, c_{FH} = c_{SH} = 0.6, h_{HF} = h_{HS} = 1, \omega = 0.001, \alpha_g = \alpha_F = 0.1$.

However, the effects of this competition on dynamics are not always so clear cut. While much of the tested parameter space shows the consumer with the higher functional growth rate (attack rate*conversion) dictating community dynamics (i.e. Fig 7.5), coexistence can also decouple relative consumer abundance from the resultant dynamics. For example, lower g_1 values have stabilizing effects against herbivore consumer pressure (Fig 7.2a). Additionally, seed predation has a stabilizing effect (Fig 7.3b, Fig 7.4g-7.4i). However, combining these two qualitatively different stabilizing forces does not necessarily result in an additive stabilizing effect (Fig 7.6).

In the presence of stabilizing seed predation, incisions of unstable parameters are found in previously stable parameter space (Fig 7.6a). The destabilizing effect of this consumer coexistence is confirmed by matching the unstable parameter space (Fig 7.6a) with the corresponding region of coexistence (Fig 7.6b). Consequently, both the herbivore attack rate (a_{H_F}) or the germination rate (g_1) now have non-monotonic effects on dynamic stability. We can observe a similar result when viewed from the perspective of seed predator (Fig 7.6c & Fig 7.6d).

Such incisions are sometimes referred to as period bubbling and, in this model, are the result of consumer coexistence exerting sufficient and simultaneous pressure on each stage in the plant's life cycle. The seed predator's (H_S) consumer pressure lowers seed biomass such that plant populations experience a deeper trough in oscillations as they experience consumer pressure from herbivores and smaller influxes of new adults due to seed consumers. This eventually causes crashes in the consumer populations, leading to an eventual burst of consumer free growth of the plant population before the consumers recover. This boom-bust cycle can keep oscillations from diminishing over time. Sufficient differences in the attack rate of either consumer will push the system into either consumer's dominant dynamic as they become the dominant consumer (see how outside of the incision of instability, the consumer ratios quickly become dominated by either H_S or H_F, Fig 7.6b & Fig 7.6d). However, coexistence of consumers can take distinct dynamic processes that were stabilizing when separate and combine them in ways that destabilize equilibria and support oscillations instead. Such results indicate one cannot necessarily assume additive effects of stability across different species interactions and ecological processes.



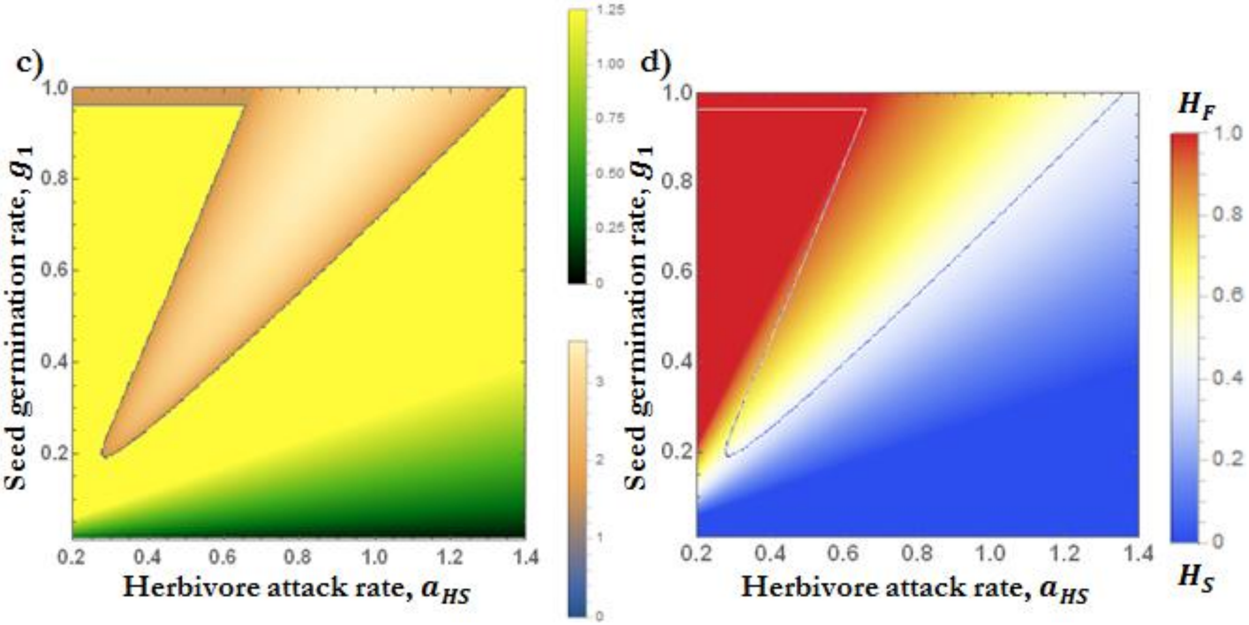


Figure 7.6 - Results from Model 4 with both herbivore and seed predator. Figure shows the asymptotic model dynamics of the model across $\{g, a_{HF}\}$ *parameter space after 6000 time steps. a.) The "avocado" color gradient represents* F *values when the system produces equilibrium dynamics. The "sunset" color gradient represents the maximum values of* F *when the system produces limit cycles. b.) Blue to red temperature gradient shows the ratio of* H_F *to* H_S*. A value of 1 indicates high* H_F *and low* H_S *and a value of 0 indicates high* H_S *and low* H_F*. The feint lines represent the switches between stable equilibria and stable limit cycles. Other parameter values:* $r_F = 0.7, a_{HS} = 0.4, kr = 0.7, c_{FH} = c_{SH} = 0.6, h_{HF} = h_{HS} = 1, \alpha_g = \alpha_F = 0.1, \epsilon = 0.2, \omega = 0.001$.

Non-additive dynamic effects by parameters are not limited to cases of exploitative competition between consumers. In is also possible in situations of emergent facilitation between stage-specialized consumers. Emergent facilitation occurs when one stage-specialized consumer is *required* to alter the stage ratios of the shared resource such that a separate stage which functions as the resource of the second consumer becomes prevalent enough for the second consumer to persist (de Roos 2008). Specifically, this dynamic can occur when consumption of one stage alleviates competitive effects on a second stage to the point that the second stage can become more abundant as a resource to its consumer.

In Model 4, the density dependent intraspecific competition between fecund adults (i.e. the effect of α_F on r_F) can lower the average rate of seed production at high abundances. This competition can limit reproduction enough that the seed bank abundance is too low to sustain the seed predator. However, the presence of the herbivore can reduce the population abundance of F such that the intraspecific competition is alleviated and seed bank abundance can rise to levels that can support a seed predator population. This emergent facilitation allows both consumers to coexist and is a subject to the same potential for non-additive effects on community dynamics as before (Fig 7.7). While H_S requires some presence of H_F to persist, high enough consumer pressure from the herbivore can return the consumers' interaction to exploitative competition and oust the seed predator. Though, the property of emergent facilitation of the seed predator by the herbivore was wide spread in the tested parameter space (Fig F.7).

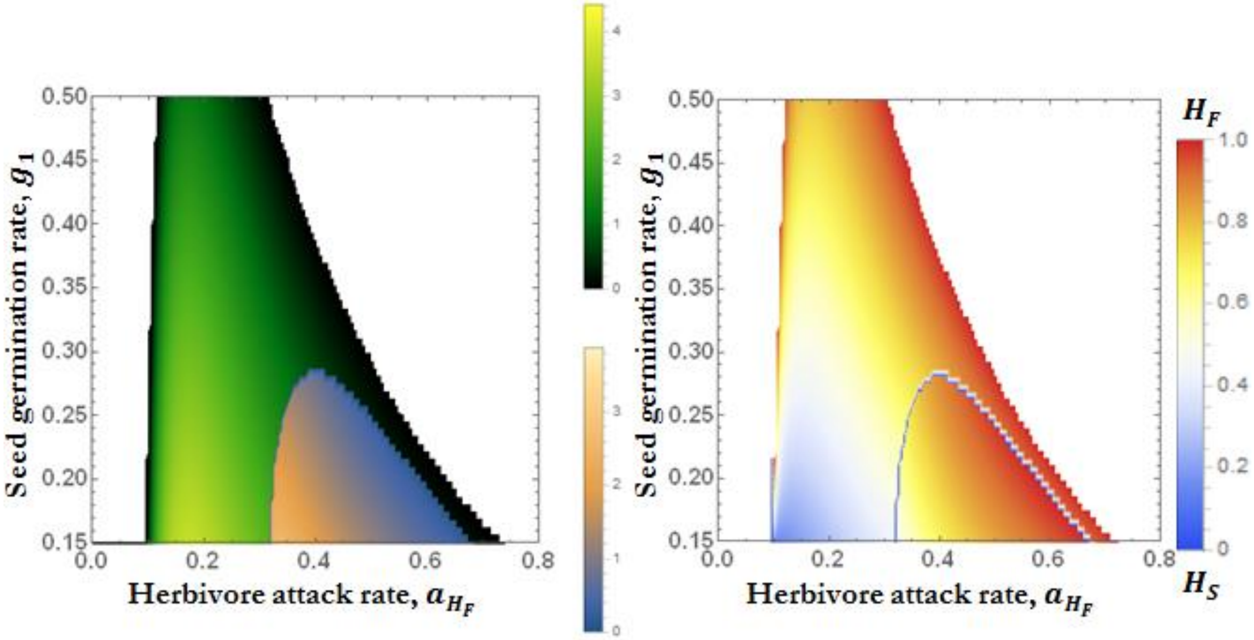


Figure 7.7 - Two-dimensional heatmap bifurcation diagrams showing the emergent facilitation of the seed predator population by the herbivore in Model 4 across $\{\alpha_{H_F}, g_1\}$ *parameter space. Colors represent the values of* H_S *from the time series. a) The avocado color scale shows* H_S^* *values when the system is at stable equilibrium. The sunset color scale shows* H_S *at peak values in oscillations when the system supports stable oscillations. b) The temperature map colors represent the relative abundance of each consumer type. White areas represent local extinction of the seed predator* H_S*. Other parameters:* $r_F = 1.32$; $\alpha_{H_S} = 0.19$; $\alpha_F = 0.2$; $\alpha_{g1} = .01$; $d_F = d_S = 0.1$; $d_{H_F} = d_{H_S} = 0.2$; $k_r = 0.7$; $h_{H_F} = h_{H_S} = 1$; $c_{FH} = 0.546$; $c_{SH} = 0.552$; $\omega = 0.01$; $\epsilon = 0.2$.

7.5. Discussion

The incorporation of stage structure in plants and autotrophs introduces non-additive nuances into various drivers of population and community dynamics. In a plant population isolated from consumer pressure, a two-stage structure alone can induce population oscillations through the mechanism of intraspecific competition and its effects on demographic rates. In a three-stage population model we found that the oscillations can persist into limit cycles when seed production rates increase. However, further increases in seed production (and therefore growth) in the 3-stage population can actually re-stabilize the population trajectories into dampened oscillations to stable equilibrium. This presents, not only the first example of non-additive dynamic drivers resulting from stage structure, but also the impetus for reconsidering the effects of higher basal resource growth rates on community dynamics.

Numerous studies have found that lower growth rates in the basal resource level of a food web can have a stabilizing effect on consumer-resource dynamics (McCann et al 1999). However, the stabilizing effect of high growth rates in the stage structured plant community was consistent with the addition of the herbivore consumer to the system. Additionally, higher growth rates also did not necessarily destabilize dynamics when consumer pressure was applied by a seed predator population (unless $h_{H_S} > 1$). Both of these results stem from the stage structure of the plant population limiting oscillatory behavior in single consumer situations. In the case of the herbivore, the higher growth rate causes density dependence to control growth instead of the herbivore. In the case of the seed predator, high growth in the plant population necessitates high seed production which immediately feeds the seed predators and limits population spikes in the plants.

Interestingly, both single-consumer systems can also be stabilized by effectively lowering plant population growth rates as well. In the herbivore system, low germination rates reduce the rate at which plants mature and therefore the rate at which herbivore resources are replenished, thereby controlling herbivore population growth (Fig 7.4a – 7.4c). In the case of seed predation ($h_{H_S} \leq 1$), the very act of predating seeds limits successful recruitment thereby regulating plant population and seed predator growth (Fig 7.4g – 7.4l).

Combining stabilizing effects from each single-stage resource system does not necessarily produce an additive effect on dynamic stabilization. For example, adding a low attack rate seed predator to a stable herbivore consumer-resource system has the potential to destabilize the overall community (Fig 7.6). A further consequence of this non-additivity of combining two qualitatively different stabilizing forces is that now additional parameters show a non-additive effect on stability, namely attack germination rates (Fig 7.6). Coexistence of the two stage specific consumers can result in parametric non-additive stabilizing effects even in instances of emergent facilitation (Fig 7.7).

Some potential caveats to the pertinence of this model framework to certain systems exist. First, some species of plant produces seeds which germinate after digestion by a consumer. Such a dynamic would add a complicating change in relationship between the plant and seed predator populations. Incorporating that kind of interaction would require a new development in modeling consumer-resource relations. Additionally, certain plants have been known to alter their seed production rates in the face of herbivory. This can take the shape of increasing seed production to produce offspring before consumption or restricting seed production to instead focus on plant defenses. Either dynamic would certainly drive noteworthy distinctions in community dynamics.

Finally, despite any caveats, there is further room to explore the results of the models presented here. First, the role of the seed bank is interesting. Delayed germination has been described as a mechanism to avoid intraspecific competition or stochastic environmental changes (Gremer 2016). Here we describe a related potential benefit in avoiding consumers. However, many seeds require some level of consumption in order to have the best chance at germinating. This would be an interesting addition to this modeling framework. Second, seed production is commonly tied to interactions with pollinator communities who themselves have intricate relationships with herbivore activity on plants (Glaum & Kessler 2017). The addition of pollination driven seed production in this stage-structured framework is an important consideration in developing a deeper understanding of the dynamics of consumer-resource systems and communities in general.

7.6. Acknowledgements

Thank you to my PI and co-author John Vandermeer for helping me develop and frame these ideas. And thank you to whatever series of circumstances happened to come together to cause me to fall into this project through a series of other temporarily stalled projects that will give me more to do later.

7.7. References

de Roos, AM., & Persson L. *Population and community ecology of ontogenetic development*. Princeton University Press, 2013.

de Roos AM, Schellekens T, Kooten TV, Persson L. 2008. Stage-specific predator species help each other to persist while competing for a single prey. Proc Natl Acad Sci 105(37): 13930–13935.

Easterling M, Ellner S, Dixon P. 2000. Size-specific sensitivity: applying a new structured population model. Ecology 81: 694–708

Ebenman, B. & Persson L, eds. *Size-structured populations: ecology and evolution*. Springer Science & Business Media, 2012.

Eckberg JO, Tenhumberg B, Louda SM. 2014. Native insect herbivory limits population growth rate of a non−native thistle. Oecologia 175: 129–138.

Ellner, S. 1985a. ESS germination strategies in randomly varying environments 2. Reciprocal yield-law models. Theor. Popul. Biol.s, 28: 80–116.

Ellner, S. 1985b. ESS germination strategies in randomly varying environments. 1. Logistic-type models. Theor. Popul. Biol., 28: 50–79.

Ellner, S. 1987b. Competition and dormancy - a reanalysis and review. Am. Nat., 130, 798–803.

Gause GF. 1934. The Struggle for Existence (Williams and Wilkins, Baltimore).

Gerner JR & Venable DL. 2014. Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. Ecology Letters 17: 380–387.

Glaum P & Kessler A. 2017. Functional reduction in pollination through herbivore-induced pollinator limitation and its potential in mutualist communities. Nature communications 8.1: 2031.

Haigh J & Maynard-Smith J. 1972. Can there be more than predators than prey? Theoretical Population Biology 3: 290-299.

Holling C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91:293–320.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrika 35: 183 –212.

Leslie, P.H. 1945. The use of matrices in certain population mathematics. Biometrika, 33(3), 183–212.

McCann K, Hastings A, Huxel GR. 1998. Weak trophic interactions and the balance of nature. Nature. 395: 794-798.

Miller TEX & Rudolph VHW. 2011. Thinking inside the box: community-level consequences of stage-structured populations. Trends in Ecology and Evolution 26 (9): 457-466.

Oaten A, Murdoch W.W. 1975. Functional response and stability in predator–prey systems. Am. Nat. 109: 289–298. 10.1086/282998

Schoener TW. 1974. Resource partitioning in ecological communities. Science 185: 27–39.

Tielborger, K. & Valleriani, A. 2005. Can seeds predict their future? Germination strategies of density-regulated desert annuals. Oikos, 111: 235–244.

Wollrab, S., de Roos A.M., Diehl, Sebastian. 2013. Ontogenetic diet shifts promote predator‐mediated coexistence. Ecology 94(12): 2886-2897.

Westoby, M. 1981. How diversified seed-germination behavior is selected. Am. Nat. 118: 882–885.

Chapter 8

Conclusion

This work examined the environmental drivers of pollinator dynamics in both urban landscapes and wild ecological communities.

In southeastern Michigan, my colleagues and I developed an extensive research program across numerous sites covering over a 100 km range. We sought out and developed working relationships with gardeners/farmers across numerous city centers while establishing longer term connections which continue currently. Through these connections my colleagues and I gave multiple yearly public popular talks to community members in Detroit and Ann Arbor. These connections also helped us establish or join outreach opportunities such as the Bioblitz activities in D-Town Farms through the Detroit Black Community Food Security Network or the A2 Summerfest Kids Biology Tent in Ann Arbor. These were invaluable experiences that I am grateful for and will serve as lessons in future outreach activities.

The sites described in this work served not only as the location of the research presented in this thesis, but also to multiple other individual projects between my colleagues and myself. This range of projects provided research experience for more than ten undergraduates across three years. Some of these undergraduates have gone on to their own professional scientific careers and/or graduate studies. The data and results garnered from this work present valuable insights into the effect of urban landscapes on wild bee communities.

In chapter two, over 500 bumble bee specimens were identified to species. Bumble bees provided an advantageous starting point as they are more widely studied than other wild bees, which eased the process of integrating their natural history into analysis. Using landscape level GIS data surrounding each of the study sites we found that urban landscapes showed different effects on male and female abundance and diversity. Analysis found that female *Bombus*, which nest underground, are limited by paved surfaces and were significantly negatively affected by urbanization (Glaum et al 2017). Males live transiently on flowers and are not directly limited by paved surfaces, meaning they can disperse into urban gardens with flowers. Additionally, results showed that this effect was lessened in Detroit, possibly due to a higher degree of vacant land limiting the negative effects of paved urban surfaces.

These results captured media and public attention through the publication of a number of stories. Focus of each publication ranged from interest mainly in the ecological aspects of the findings to a deeper interest of the city planning implications. Some of these publications include PBS, The Scientist Magazine, Discover Magazine, The Detroit Metro Times, and PLOS News.

In chapter three, longer-term identification efforts of our entire sampled bee community showed that the uneven effects of urbanity on female and male bumble bees extends to the entire ground nesting wild bee community. Results showed that urban development correlated with a significant decline in female ground nesting bees while the males showed no significant effects. This led to a pronounced change in the overall sex ratio among ground nesting bees and, given that ground nesting bees make up the majority of wild bees in North America, a similar change in the entire wild bee community observed sex ratio (OSR).

On the other hand, bees that nest in cavities saw a significant increase in abundance, for both males and females. We are currently unable to determine if this increase stems from an increase in cavity nesting spaces available for cavity nesters or competitive release due to the decline in ground nesters. Either way, these results indicate a significant shift in wild bee community composition due to urban development and again insinuate urban development may limit nesting opportunities for ground nesting bees.

These changes in community composition have potential effects on pollination services as male and female bees of the same species often pollinate the same plant with different behaviors/efficiencies (Ne’eman et al. 2006; Ulrich et al. 2009; Ostevik et al. 2010) or pollinate completely different species of plants (Powell & Powell 1987). Additionally, ground nesting and cavity nesting bees do not necessarily pollinate the same species of plants, though there is work to be done on understanding the full range of pollinator hosts in Northern America. Finally, the uneven effects between males and females have the potential to affect mating success and, consequently, genetic diversity. Despite the fact that overall/total bee abundance showed no relationship with urbanity, these sex-specific effects indicate a possible underestimation of the negative effect of human development on wild bees.

My fourth chapter was the culmination of a project started early in my PhD with students in The A. Alfred Taubman College of Architecture and Urban Planning. The surveys of wild bee communities in urban environments were built on the use of urban gardens and farms as resource centers for bees. This led to discussions of what drives garden location and resource quality in cities. Drivers of local level city qualities can come from a complex combination of socio-economic factors (Batty 2007). As an initial investigation of into some of these drivers, my graduate collaborators and I used GIS census data from the Census' American Community Survey to develop socio-economic profiles of 30 garden sites in Ann Arbor and Ypsilanti Michigan, USA. Working with a driven undergraduate researcher, the end result was compiled using data from sites that overlapped with wild bee surveys.

Analysis showed that garden locations did not differ from surrounding city environments in any of the socio-economic variables used in our analysis. In fact, each city's gardens were in neighborhoods that closely matched the averages of the city they are located (Ann Arbor or Ypsilanti). The only significant predictor of garden location was available space in municipally owned lots (Iuliano et al 2017). We did, however, find significant relationships with location wealth and certain garden floral qualities; gardens in wealthier neighborhoods have greater floral resource abundance. This increase in floral abundance however was made up mainly of introduced cultivars and did not correlate with higher pollinator abundance. Gardens with a higher percentage of weeds did show a trend toward supporting more abundant bee communities, but weed percentage correlated more with a lack of wealth in surrounding neighborhoods.

Finding and cataloguing the direct effects of human development on wild pollinators, or any taxa, is an important step in developing sustainable management strategies and forecasting possible future scenarios of land use change. However, conservation and management does not rest solely on the focus of one group of taxa, even one as diverse and important as wild bees. These pollinators are an interdependent part of a community of organisms full of interactions which influence each other. Conserving and managing pollinators means developing thorough understanding of their role in ecological systems and there are still clearly numerous unresolved questions regarding pollinator dynamics in wild settings.

Starting with chapter five I use the tools provided by ecological theory to develop mathematical models of plant and pollinator interactions with their surrounding biotic community. Pollinators' interactions with flowering plants have numerous barriers to overcome, from changing phenology (Abrol 2012) to habitat fragmentation (Jha & Kremen 2013a) limiting interaction rates. However, sometimes, plants themselves can limit pollinator interactions. Various plants defend themselves with volatile chemical compounds meant to deter insect herbivores (Kessler et al 2012). However, these same chemicals have been shown to similarly deter insect pollinators, limiting pollination interactions (Kessler et al 2011). This obviously limits the individual reproductive success of pollinators and plants in the presence of herbivory. Consequently this puts strain on mutualistic interactions and begs the question how this defense mechanism is maintained if it further limits individual reproductive success.

Using field data of pollination interaction in the presence of herbivory (Kessler et al 2011), my co-author André Kessler and I were able to show that pollinator visitation declines according to set functional form. I then input this functional form of herbivory-induced pollinator limitation (HIPL) into a model framework. In this framework we showed that, in a community setting, these limitations restricted plant reproduction, which indirectly limits herbivore reproductive potential and ultimately introduces a stabilizing force to the system (Glaum & Kessler 2017). This result provides a novel answer to the questions posed above and suggests that the benefit of certain traits may be more readily apparent at levels larger than the individual.

Wanting to consider multiple pollinators, in chapter six, I used a modeling approach to consider the community dynamics of predacious syrphid flies. These pollinating flies are unique in that many species have predacious larvae which feed on the soft bodied insects that attack plants syrphids pollinate as adults (Miller 1918; Kühsel & Blüthgen 2015). Recognizing the distinct ecological role of each stage in syrphid development I compartmentalize this stage structure into the model framework. Then by considering various syrphid pollination syndromes found in the literature, I investigated the dynamics of communities dependent on syrphid pollination (Glaum 2017).

Results indicated that predacious syrphid pollination alone may present a negative feedback loop. Unlike other wild pollinators, syrphids fly larvae rely on herbivores for food. Therefore, when herbivores have low abundance, it limits syrphid growth, which actually limits pollination. In other words pollination by syrphids indirectly depends on persistent herbivores and needs supplementing from other wild pollinators.

Given the significant effect of incorporating distinct ontological stages on greater community dynamics, I investigated further how explicitly including distinct demographic stage structure can change central ecological assumptions. With chapter seven, I focused instead on plant demographics, as the ubiquity of distinct stages like seeds made it easier to develop a general, first-principles model. Taking these common stages in plant development, such a seed banks and/or seedlings, my co-author/PI and I show that the effect of intraspecific competition between stages can alter key assumptions about resource dynamics. Specifically, these intraspecific competitive effects induce numerous non-additive effects of model parameters on community stability. This modeling work presents initial steps towards incorporating stage structure in larger community models involving plant-pollinator interactions.

In completion of this thesis, I come to what I can only assume is the same recognition of every other biologist and researcher to date. The answers garnered from this work beget more questions and set up the prospect of numerous future projects. Some of these projects have already been initiated. For instance, the effects of HIPL were seen to scale up to unexpected results in Chapter five, yet further scaling is certainly possible. Preliminary modeling work done in explicit space implies that HIPL has a prominent role to play in spatial population dynamics. Additionally, HIPL needs to be incorporated into larger food webs involving numerous plant-pollinator interactions and herbivore consumer-resource interactions. Such steps are necessary to understand how the stabilizing effects of HIPL interact with competitive effects at the pertinent trophic levels. In its fullest form, these modeling approaches will eventually need to include both non-bee pollinators like syrphid flies and consequently, some degree of distinction in the ecologically unique developmental stages. These are large scale projects requiring long term work which I look forward to contributing to.

The need to extend scope is also apparent in the empirical study of pollinators and is already being considered in our sample sites across southeastern Michigan. Sampling efforts produced large numbers of non-bee flying insects, many of them pollinators. Collaborators and I are currently in the midst of processing and analyzing this data in order to better understand the effect of urban development on broader insect communities. Of course, empirical work is necessary outside of areas of the most direct human development. I am currently working with collaborators to develop less harmful, longer term sampling methods using remote sensing devices in natural settings. The better success found in this work, the better our ability to measure plant-pollinator interactions across a range of landscapes and the better our ability to integrate these empirical measurements in theoretical work.

Ideally, the integrated use of these diverse research tools will merge into an ever-increasing understanding of pollinator dynamics which can be better used to conserve and manage this critical ecological service. I hope the work presented here contributed to this effort in some way. I am excited to continue my own efforts with the dedicated scientists, teachers, gardeners, farmers, policy makers, and citizens who endeavor to produce some positive changes in our relationship with the natural world and each other.

8.1. References

Abrol, D P. 2012. Climate change and pollinators. *Pollination Biology*. Springer Netherlands, 479-508.

Batty, M. 2007. Cities and complexity: understanding cities with cellular automata, agent-based models, and fractals. The MIT press.

Glaum, P. 2017. A theoretical basis for the study of predatory syrphid fly ecology. Theoretical Ecology 10(4): 391-402.

Glaum P & Kessler A. 2017. Functional reduction in pollination through herbivore-induced pollinator limitation and its potential in mutualist communities. Nature communications 8.1: 2031.

Glaum, P., Simao, M.-C., Vaidya, C., Fitch, G. & Iulinao, B. 2017. Big city Bombus: using natural history and land-use history to find significant environmental drivers in bumble-bee declines in urban development. R. Soc. Open Sci. 4, 170156.

Iuliano, B., Markiewicz, A., Glaum, P. 2017. Socio-economic Drivers of Community Garden Location and Quality in Urban Settings and Potential Effects on Native Pollinators." Michigan Journal of Sustainability 5.1

Jha S, Kremen C. 2013a. Bumble bee foraging in response to landscape heterogeneity. Proceedings of the National Academy of Sciences USA, 8: 555–558.

Kessler A, Halitschke R, and Poveda K. 2011. Herbivory-mediated pollinator limitation: negative impacts of induced volatiles on plant–pollinator interactions. Ecology 92(9): 1769–1780.

Kessler A, Poveda K, Poelman E. 2012. Induced plant responses and herbivore population dynamics. In P. Barbosa, D. L. Letourneau, A. Agrawal (eds.) Insect Outbreaks Revisited, John Wiley & Sons Ltd. Chichester, UK, pp 91–112.

Kühsel S & Blüthgen N. 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. Nature communications 6.

Miller D. 1918. The Economic Bearing of Hover-Flies. New Zealand Journal of Agriculture 1918, September 20th Vol. 17 No. 3:129-135.

Ne'eman, G., Shavit, O., Shaltiel, L. & Shmida, A. 2006. Foraging by male and female solitary bees with implications for pollination. J. Insect Behav. 19, 383–401.

Ostevik, K., Manson, J. & Thomson, J. 2010. Pollination potential of male bumble bees (Bombus impatiens): movement patterns and pollen-transfer efficiency. J. Pollinat. Ecol. 2, 21–26.

Powell, AH & Powell GVN. 1987. Population dynamics of male euglossine bees in Amazonian forest fragments." Biotropica: 176-179.

Ulrich, Y., Perrin, N. & Chapuisat, M. 2009. Flexible social organization and high incidence of drifting in the sweat bee, Halictus scabiosae. Mol. Ecol. 18, 1791–1800.

Appendix A – Appendices to Chapter 2

Appendix A.1

Table A.1 - Table listing sample site names, shorthand initials, location by city group, and managing organization from Chapter 1. All sites listed were sampled in 2014 except for ACG, BM, BS, and FF which were sampled in 2015. The remaining sites could not be resampled in 2015 due to separate studies being run with bumble bees and management turnover at the sites.

Site Name	Initials	City Group	Managing Organization	Temperature Data Logger
Nichols Arboretum	A	Ann Arbor	U of Michigan	Yes
Boehnke Household	BH	Ann Arbor	Independent	Yes
Buhr Park	B	Ann Arbor	Project Grow	No
Cultivating Community	CC	Ann Arbor	U of Michigan	Yes
Clague Elementary	CE	Ann Arbor	Project Grow	Yes
Campus Farm	CF	Ann Arbor	U of Michigan	Yes
County Farm Park	CFP	Ann Arbor	Project Grow	Yes
Ellsworth	E	Ann Arbor	Project Grow	Yes
Greenview	GV	Ann Arbor	Project Grow	Yes
Leslie Science Center	LSC	Ann Arbor	Project Grow	Yes
Platt	P	Ann Arbor	Project Grow	Yes
Scio Church	SC	Ann Arbor	Independent	Yes
School of Public Health Garden	SPH	Ann Arbor	U of Michigan	Yes
West Park	WP	Ann Arbor	Project Grow	Yes
UM-Old Field	OF	Dearborn	U of M-Dearborn	No
UM-Organic Garden	OG	Dearborn	U of M-Dearborn	Yes
Art Center Community Garden	ACG	Detroit	Midtown Gardens	No
Brightmoor Foodway	BM	Detroit	Independent	No
Burnside Community Garden	BS	Detroit	Independent	No
Food Field	FF	Detroit	Independent	No
Lafayette Greens	LG	Detroit	Greening of Detroit	Yes
N. Cass Community Garden	NC	Detroit	Midtown Gardens	No
Dexter Community Garden	DCG	Dexter	Independent	Yes
E.S. George Reserve	ESG	Dexter	U of Michigan	Yes
M'Lis Farm	MF	Dexter	Independent	Yes

Catholic Social Services	CSS	Ypsilanti	Growing Hope	Yes
EMU - The Giving Garden	EMU	Ypsilanti	Growing Hope	Yes
Frog Island Community Garden	FI	Ypsilanti	Growing Hope	Yes
Normal Park Community Garden	NP	Ypsilanti	Growing Hope	Yes
Perry / Parkridge Community Garden	PCG	Ypsilanti	Growing Hope	No

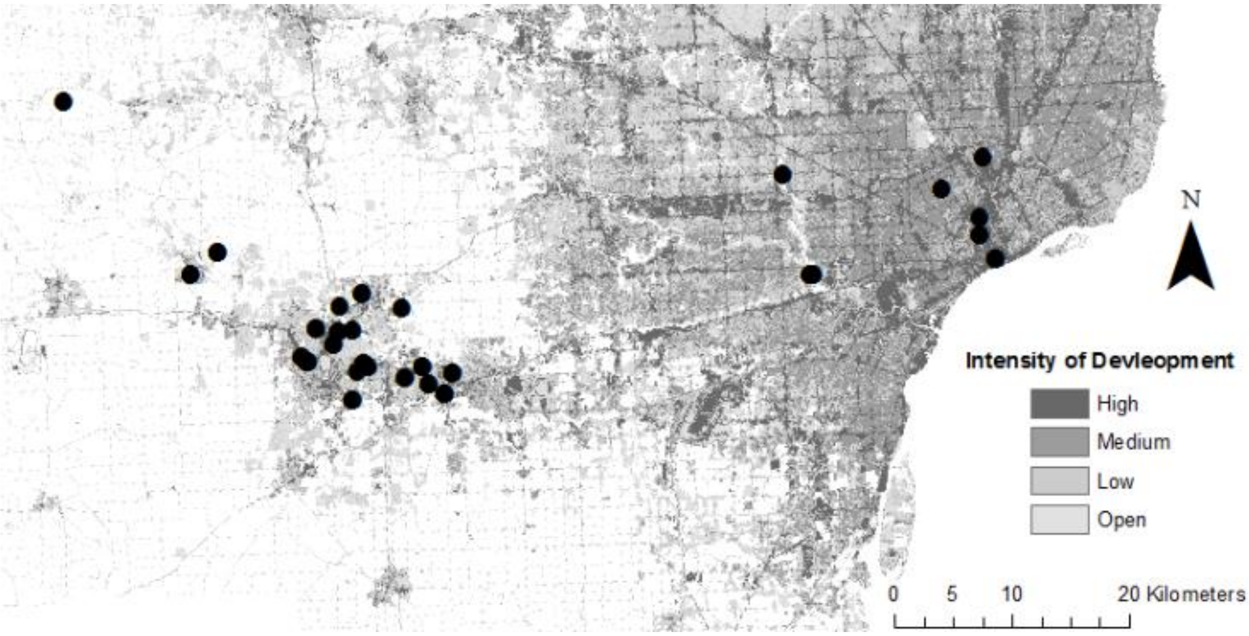


Figure A.1 - GIS map of southeastern Michigan. Black dots represent sites where sampling occurred. The proportion of impervious surface coverage (Intensity of Development) at a given location (see Methods) is given by the grayscale gradient. Landscape data sourced from 2011 National Landcover Database Multi-Resolution Land Characteristics Consortium (MRLC) mfc.gov. Original map created by Maria-Carolina Simao with input from Paul Glaum (see Glaum et al 2017).

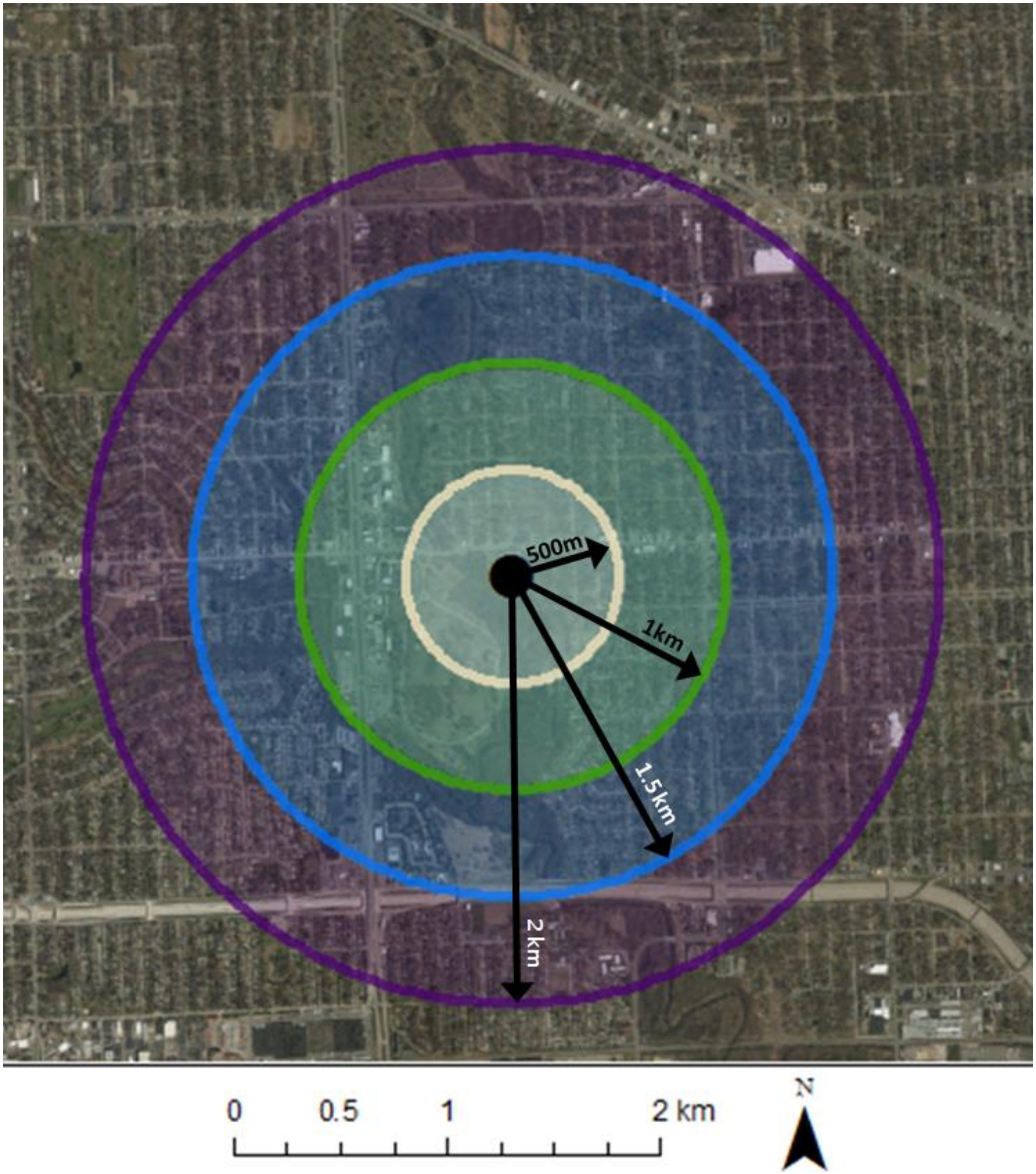
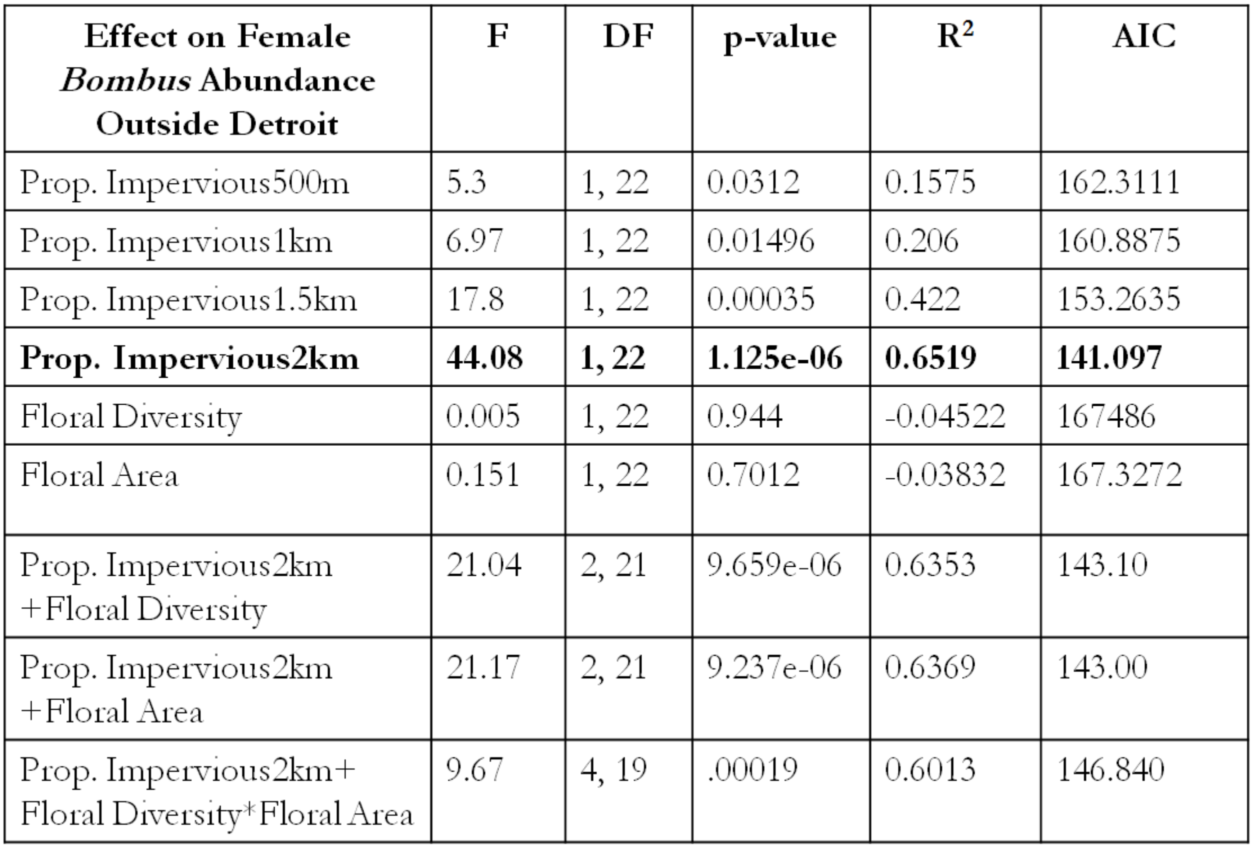


Figure A.2 - Figure representing the four buffer zones inside of which the proportion of impervious surface was measured around each site. The four buffer zones had distinct radii of 500m (white circle), 1km (green circle), 1.5km (blue circle), and 2km (purple circle). The significance of the regressions shown in Figures 2.2 (in the main paper), Fig A.4, and Fig A.6 increased as the buffer zone radius increased. For example, in Figure 2.2, when impervious surface coverage was measured within 2km of each site, the regression produced most significant model output with the highest effect size. Measuring impervious surface at only 500m provided an insufficient measurement of impervious surface and consequently the signal was lost. Original map created by Maria-Carolina Simao with input from Paul Glaum (see Glaum et al 2017).

Appendix A.2: Abundance

Table A.2 - Summary stats of the effects of all measured independent variables on female Bombus abundance outside of Detroit from general linear models. All sites outside of Detroit were measured in 2014 so use of a mixed model is not required. The linear effect of Proportion of Impervious 2km is clearly the best fit model.



Effect on Female *Bombus* Abundance Outside Detroit	**F**	**DF**	**p-value**	**R^2**	**AIC**
Prop. Impervious500m	5.3	1, 22	0.0312	0.1575	162.3111
Prop. Impervious1km	6.97	1, 22	0.01496	0.206	160.8875
Prop. Impervious1.5km	17.8	1, 22	0.00035	0.422	153.2635
Prop. Impervious2km	**44.08**	**1, 22**	**1.125e-06**	**0.6519**	**141.097**
Floral Diversity	0.005	1, 22	0.944	-0.04522	167486
Floral Area	0.151	1, 22	0.7012	-0.03832	167.3272
Prop. Impervious2km +Floral Diversity	21.04	2, 21	9.659e-06	0.6353	143.10
Prop. Impervious2km +Floral Area	21.17	2, 21	9.237e-06	0.6369	143.00
Prop. Impervious2km+ Floral Diversity*Floral Area	9.67	4, 19	.00019	0.6013	146.840

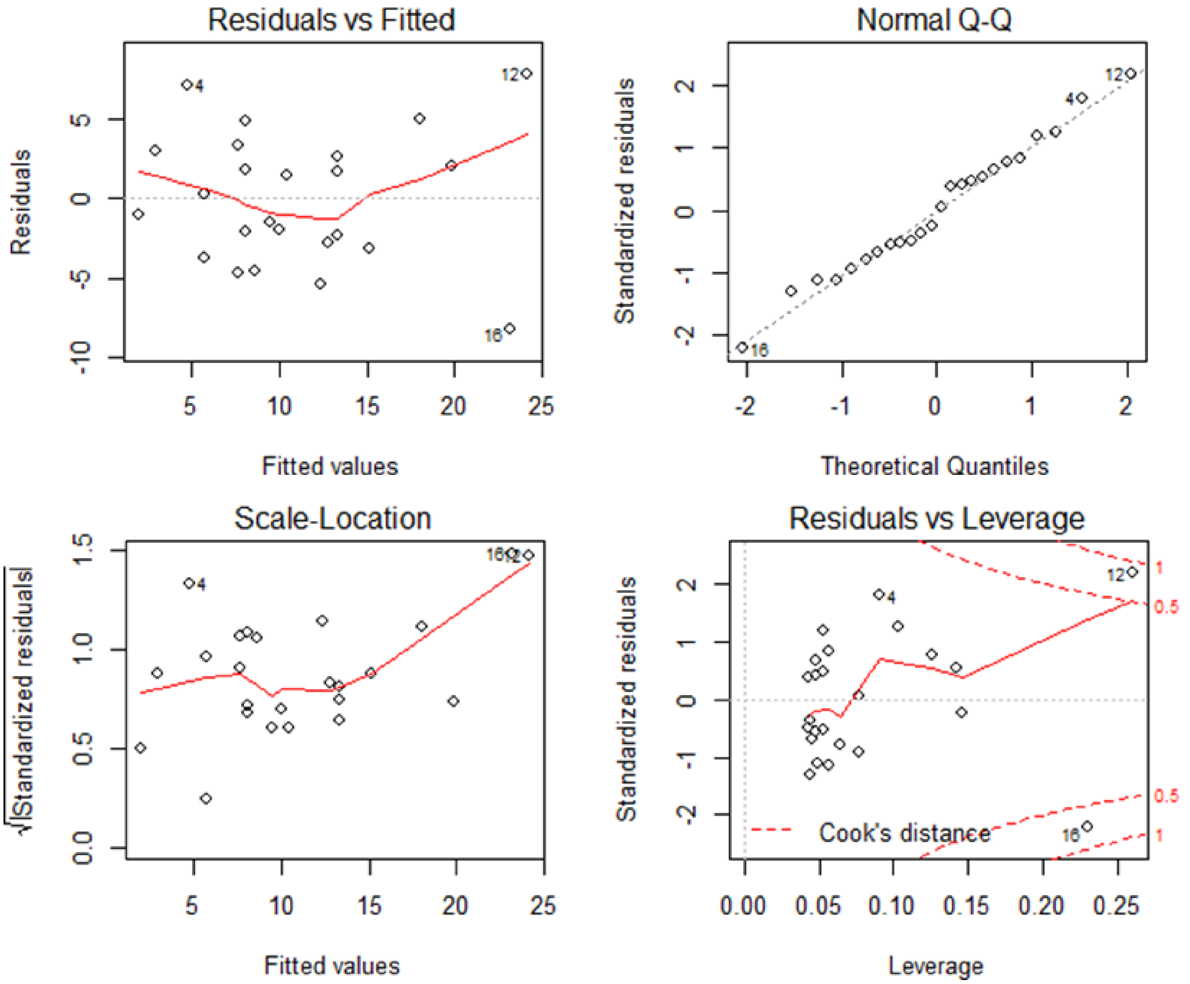


Figure A.3 - Summary plots for the linear model female Bombus abundance ~ %Impervious 2km from Table A.2. Only sites outside of Detroit considered here.

Table A.3 - The different effect of impervious surface on the overall females and males communities is also apparent when looking only at the most abundant species (B. impatiens). There is a strong negative relationship for females and no significant patterns for males. Only sites outside of Detroit considered here.

Effect on Female *B. impatiens* Abundance	**F**	**DF**	**p-value**	**R^2**	**AIC**
Prop. Impervious500m	2.9	1, 22	0.1052	0.0747	151.0575
Prop. Impervious1km	3.34	1, 22	0.08131	0.0923	150.5966
Prop. Impervious1.5km	9.404	1, 22	0.00565	0.27	145.445
Prop. Impervious2km	**25.56**	**1, 22**	**4.604e-05**	**0.5164**	**135.484**
Effect on Male *B. impatiens* Abundance	**F**	**DF**	**p-value**	**R^2**	**AIC**
Prop. Impervious500m	0.0002	1, 22	0.9902	-0.04545	127.2781
Prop. Impervious1km	0.0010	1, 22	0.9749	-0.04541	127.2772
Prop. Impervious1.5km	0.103	1, 22	0.7513	-0.04058	127.1662
Prop. Impervious2km	0.5149	1, 22	0.4806	-0.02155	126.723

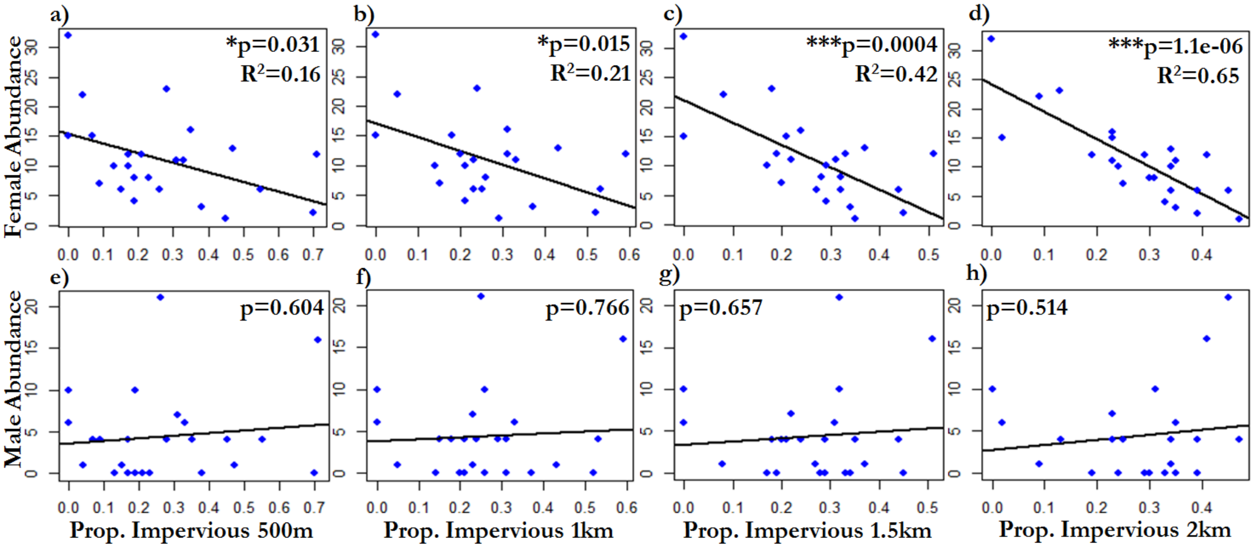
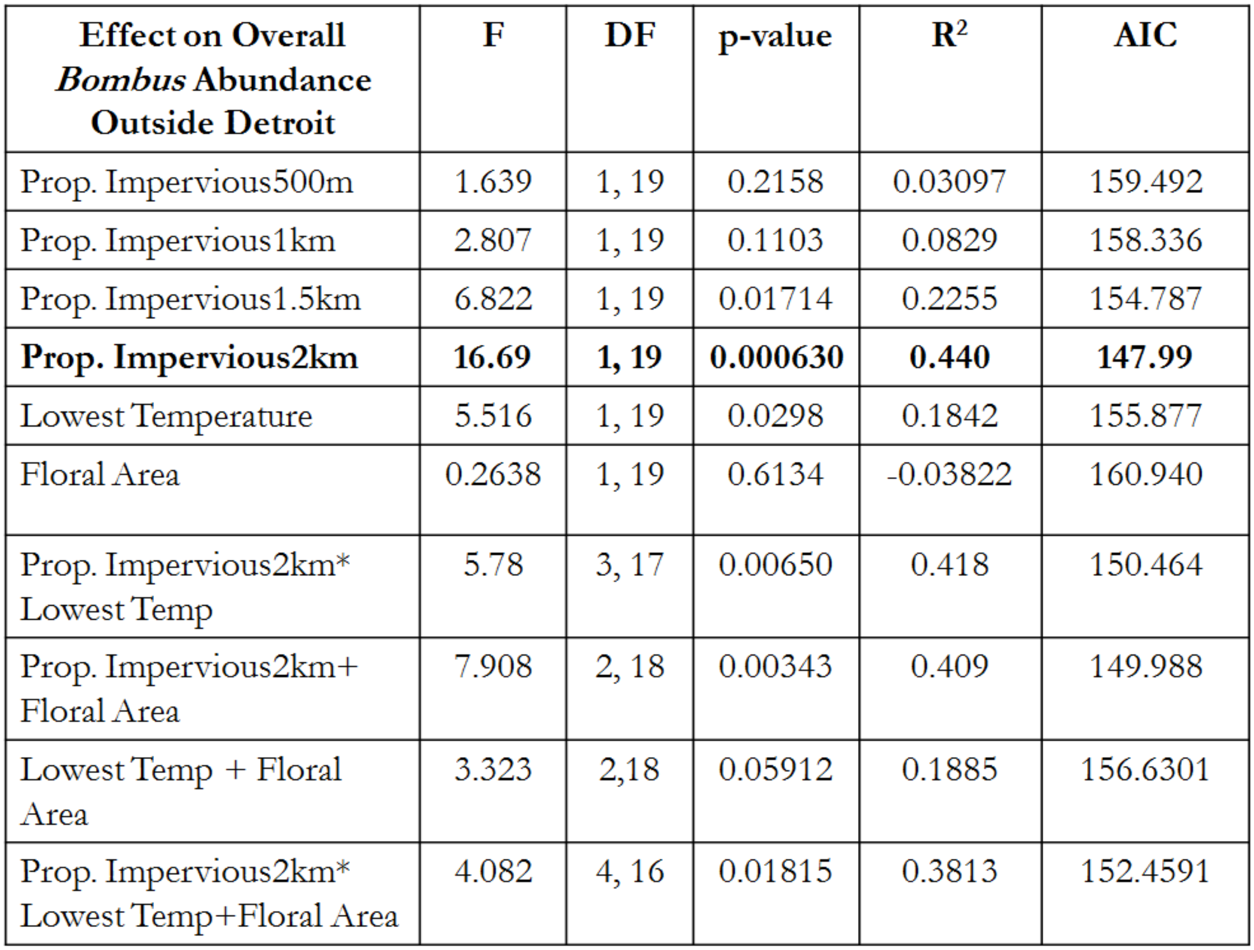


Figure A.4 - Abundance data outside of Detroit split into female worker and male drone categories regressed across the impervious surface gradient with general linear models. Splitting abundance data into female workers and male drones shows the decline of Bombus abundance in high impervious surface is driven by decreases in female-worker abundance outside of Detroit. Female abundance regressed against a) 500m ($F_{1,22}$ = 5.3, p= 0.0312, R^2 = 0.158), b) 1km ($F_{1,22}$ = 6.97, p= 0.01496, R^2 = 0.206), c) 1.5km ($F_{1,22}$ = 17.8, p= 0.00035, R^2 = 0.422), d) 2km ($F_{1,22}$ = 44.08, p= 1.125e^{-6}, R^2 = 0.652). Male abundance regressed against e) 500m ($F_{1,22}$ = 0.28, p= 0.604, R^2 = -0.0325), f) 1km ($F_{1,22}$ = 0.091, p= 0.766, R^2 = -0.0412), g) 1.5km ($F_{1,22}$ = 0.202, p= 0.657, R^2 = -0.0359), h) 2km ($F_{1,22}$ = 0.441, p= 0.514, R^2 =-0.0249).

Appendix A.3: Temperature

Increases in impervious surface are highly correlated with an increase in the lowest daily temperature measured at sites. Urban centers are heat islands which tend to trap heat from day time temperatures. This causes locations with higher amounts of impervious surface to have higher minimum temperatures across the span of a day. Without impervious surfaces, heat is not trapped in concrete structures and is released, therefore leading to a lower minimum daily temperature.

Table A.4 - Model output from sites where temperature was recorded with a data logger. The best model including the temperature data is still %Impervious surface at 2km for Bombus abundance.



Effect on Overall *Bombus* Abundance Outside Detroit	**F**	**DF**	**p-value**	**R^2**	**AIC**
Prop. Impervious500m	1.639	1, 19	0.2158	0.03097	159.492
Prop. Impervious1km	2.807	1, 19	0.1103	0.0829	158.336
Prop. Impervious1.5km	6.822	1, 19	0.01714	0.2255	154.787
Prop. Impervious2km	**16.69**	**1, 19**	**0.000630**	**0.440**	**147.99**
Lowest Temperature	5.516	1, 19	0.0298	0.1842	155.877
Floral Area	0.2638	1, 19	0.6134	-0.03822	160.940
Prop. Impervious2km* Lowest Temp	5.78	3, 17	0.00650	0.418	150.464
Prop. Impervious2km+ Floral Area	7.908	2, 18	0.00343	0.409	149.988
Lowest Temp + Floral Area	3.323	2,18	0.05912	0.1885	156.6301
Prop. Impervious2km* Lowest Temp+Floral Area	4.082	4, 16	0.01815	0.3813	152.4591

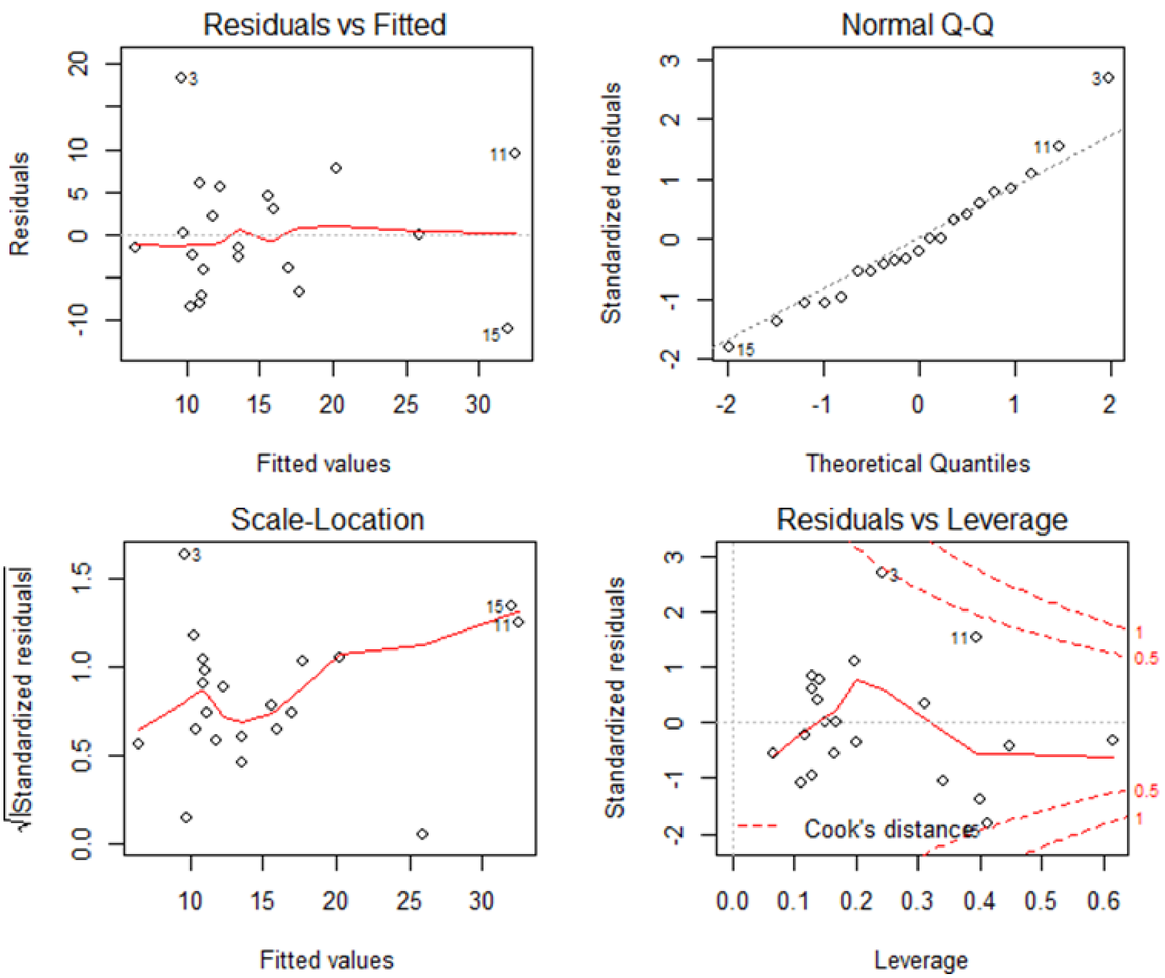


*Figure A.5 - Summary plots for the model Bombus abundance ~ lowest temp * %Impervious 2km + floral area from Table A.4. Only sites outside of Detroit considered here.*

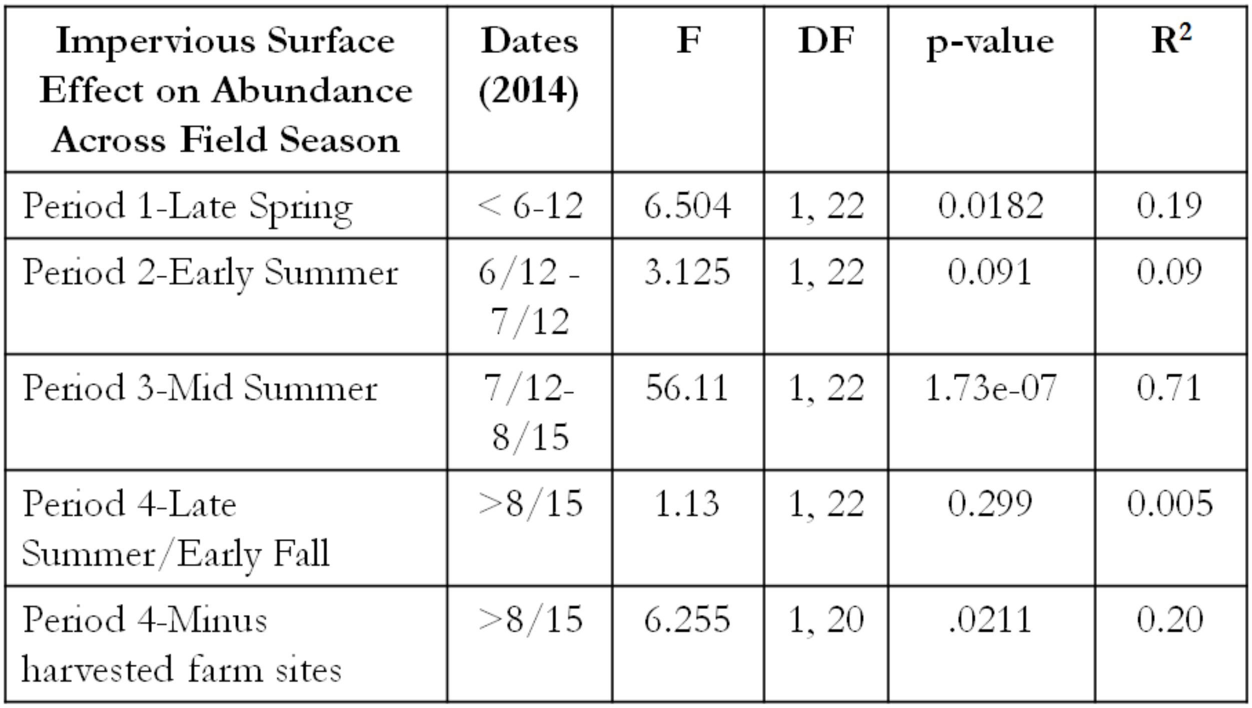
Appendix A.4: Addressing alternative hypotheses

In addressing alternate hypotheses for the decline in worker abundance and diversity outside of Detroit, we consider the possibility that the sampling schedule of this study missed a potential delayed emergence or growth rate of *Bombus* in mid-level impervious surface coverage. If this was the case, then it is likely that the measured decrease in *Bombus* with higher impervious surfaces would be limited to earlier times of the year and become insignificant later in the year. To test this, the overall *Bombus* sampling data was split into four distinct periods across the field season to align with the four netting dates instead of the cumulative sum over the entire growing as was used in the main analysis. This was done because the vast majority of samples came from netting efforts. Each period then also included the samples from the trapping prior to the netting date and the trapping immediately after the netting date. This then allowed us to test the consistency of the impervious surface induced worker decline across smaller subsections of the overall field season. The four periods are titled P1, P2, P3, and P4.

Worker decline with impervious space is significant in P1 and P3 and the decline is very nearly significant in P2 (Table A.5). The decline initially seemed to disappear in P4, but this was found to be an artifact of sampling in farms post crop harvest. The two farms included in this study (MF and CF) had been harvested and cleared prior to final netting date. This removed nearly all floral resources from each site and limited sampling efficacy as workers did not land in our sampling area. While measured floral resources in this study were found to not significantly affect *Bombus* abundance, a complete absence of flowers is enough to eliminate any ability to lure and catch foraging workers. Removing those two sites from the analysis shows that the decline in *Bombus* with impervious surface is still significant in P4.

While there is certainly variation in the effect size and significance, but all periods analyzed show the same decline in relation to impervious surface and there is no consistent weakening of the trend across the summer. Therefore, the significant decline in *Bombus* workers due to impervious surface seems to be a consistent result across the entire sampling season. There is no evidence of a later increase in *Bombus* activity that disrupts the signal.

Table A.5 - This table shows the consistent significance of the negative effect of impervious surface on female Bombus abundance outside of Detroit across the growing season. Periods represent the sum total female abundance of trappings and nettings from 4 distinct periods in growing season instead of the entire growing season. Each period contains one netting date and two pan trapping dates. Impervious surface is measured in the 2km buffer.



Impervious Surface Effect on Abundance Across Field Season	**Dates (2014)**	**F**	**DF**	**p-value**	**R^2**
Period 1-Late Spring	< 6-12	6.504	1, 22	0.0182	0.19
Period 2-Early Summer	6/12 - 7/12	3.125	1, 22	0.091	0.09
Period 3-Mid Summer	7/12-8/15	56.11	1, 22	1.73e-07	0.71
Period 4-Late Summer/Early Fall	>8/15	1.13	1, 22	0.299	0.005
Period 4-Minus harvested farm sites	>8/15	6.255	1, 20	.0211	0.20

Appendix A.5: Diversity

Table A.6 - Summary stats of the effects of all measured independent variables on overall Bombus diversity outside of Detroit.

Effect on Overall *Bombus* Diversity Outside Detroit	F	DF	p-value	R^2	AIC
Prop. Impervious500m	0.589	1, 22	0.4511	-0.01822	32.3214
Prop. Impervious1km	1.77	1, 22	0.197	0.03241	31.090
Prop. Impervious1.5km	3.1	1, 22	0.0922	0.0837	29.784
Prop. Impervious2km	2.867	1, 22	0.1045	0.07508	30.008
Floral Diversity	1.432	1, 22	0.2441	0.01845	31.434
Floral Area	0.5778	1, 22	0.4553	-0.0187	32.3254
Prop. Impervious2km+ Floral Diversity	2.205	2, 21	0.1351	0.0949	30.372
Prop. Impervious2km+ Floral Area	1.814	2, 21	0.1876	0.06611	31.1227
Prop. Impervious2km+ Floral Diversity*Floral Area	1.254	4, 19	0.3224	0.04224	33.3263

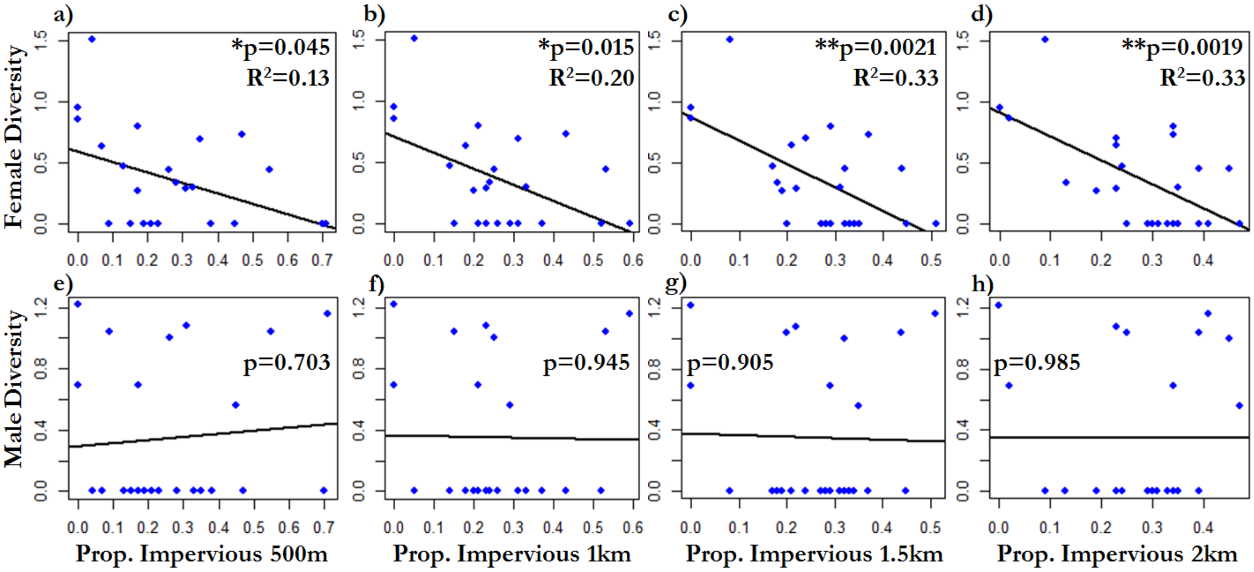


Figure A.6 - Diversity data outside of Detroit split into female worker and male drone categories regressed across the impervious surface gradient with general linear models. Splitting diversity data into female workers and male drones shows the decline of Bombus diversity in high impervious surface is driven by decreases in female-worker diversity outside of Detroit. Female diversity regressed against a) 500m ($F_{1,22}$ = 4.53, p = 0.0448, R^2 = 0.134), b) 1km ($F_{1,22}$ = 6.895, p = 0.0154, R^2 =

0.204), c) 1.5km ($F_{1,22} = 12.2$, $p = 0.0021$, $R^2 = 0.326$), d) 2km ($F_{1,22} = 12.44$, $p = 0.0019$, $R^2 = 0.332$). Male diversity regressed against e) 500m ($F_{1,22} = 0.150$, $p = 0.703$, $R^2 = -0.0384$), f) 1km ($F_{1,22} = 0.00049$, $p = 0.945$, $R^2 = -0.0452$), g) 1.5km ($F_{1,22} = 0.0148$, $p = 0.905$, $R^2 = -0.0448$), h) 2km ($F_{1,22} = 0.00035$, $p= 0.985$, $R^2 =-0.0454$).

Appendix B– Appendices to Chapter 3

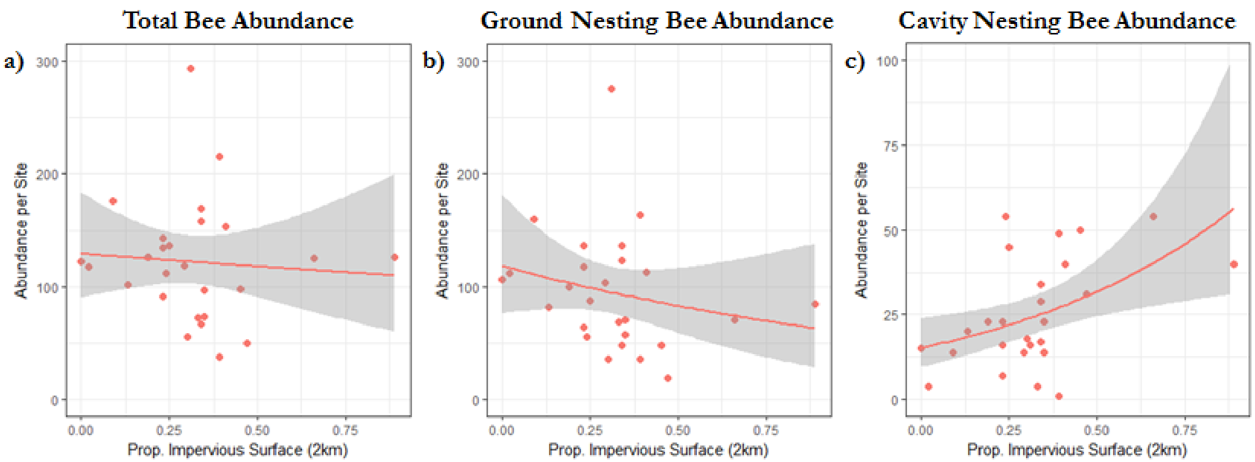


Figure B.1 - Relationship between urbanity and bee abundance. Urbanity was measured through proportional impervious surface coverage within a 2km radius of study site. Regressions were done using GLM with quasi-Poisson distribution. a) Total bee abundance: t= -0.357, df=24, β= -0.1796, p=0.724. b) Ground nesting bee abundance: t= -1.087, df=24, β= -0.7033, p= 0.288. c) Cavity nesting bee abundance: t= 2.712, df=24, β= 1.470, p=0.012.

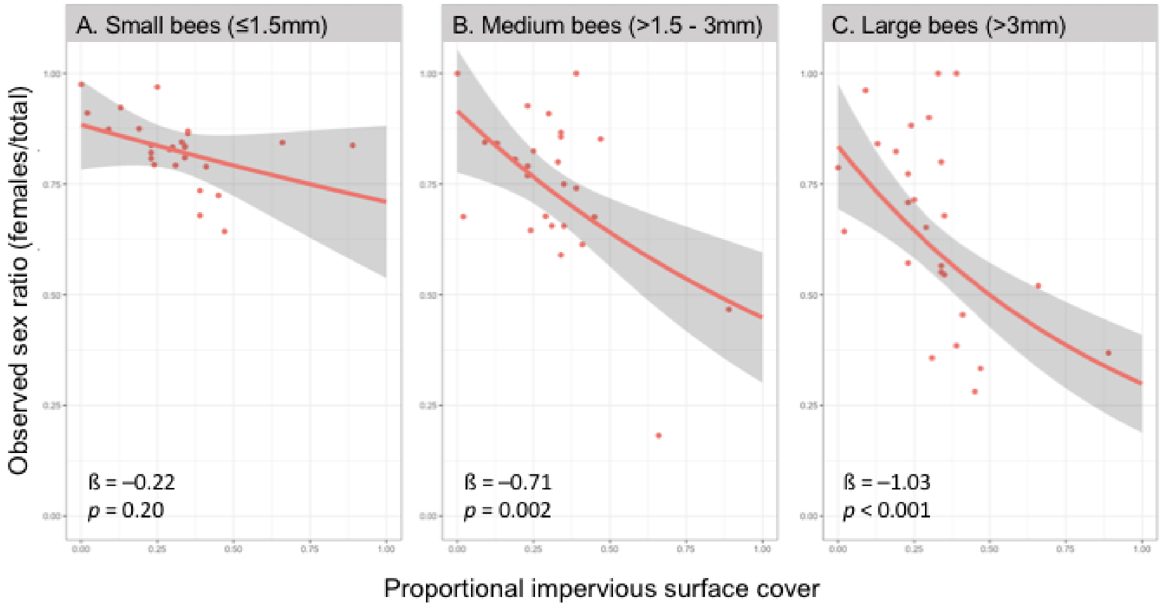


Figure B.2 - Relationship between urbanity and bee observed sex ratio as mediated by body size. Body size was measurements are taken from the intertegular distance, which is a proxy for flight distance. Urbanity measured as proportional impervious surface cover within 2km of the study site. Line represents best fit for GLM model of number of female bees offset by total number *of bees, using Poisson distribution and log-link; shaded area represents standard error. z-scores for each size class are as follow: a) small bees, z = –1.28; b) medium bees, z = –3.09; c) large bees, z = –4.06; in all cases d.f. = 24.*

Table B.1: **List of individual bee specimens.** (see https://www.researchgate.net/profile/Paul_Glaum)

Table B.2: **List of bee species collected with natural history information.** (see https://www.researchgate.net/profile/Paul_Glaum)

Table B.3 - Relationship between urbanity and floral resource availability.

Relationship between Impervious Surface (2km) and Floral Quality			
Category of Mean Floral Resource/Site	**Residual dev. on $DF = 24$**	t	p
Overall Flower Area	186657	0.478	0.637
Crop Area	149704	0.528	0.602
Non-Crop Area	131500	0.25	0.805
Overall Floral Richness	529.75	-0.387	0.702

Table B.4 - Site characteristics.

Site Name	Initials	City Group	Managing Organization	Temperature Data Logger
Arboretum	A	Ann Arbor	U of M	Yes
Boehnke Household	BH	Ann Arbor	Independent	Yes
Buhr Park	B	Ann Arbor	Project Grow	No
Cultivating Community	CC	Ann Arbor	U of M	Yes
Clague Elementary	CE	Ann Arbor	Project Grow	Yes
Campus Farm	CF	Ann Arbor	U of M	Yes
County Farm Park	CFP	Ann Arbor	Project Grow	Yes
Ellsworth	E	Ann Arbor	Project Grow	Yes
Greenview	GV	Ann Arbor	Project Grow	Yes
Leslie Science Center	LSC	Ann Arbor	Project Grow	Yes
Platt	P	Ann Arbor	Project Grow	Yes
Scio Church	SC	Ann Arbor	Independent	Yes
SPH Garden	SPH	Ann Arbor	U of M	Yes
West Park	WP	Ann Arbor	Project Grow	Yes
Organic Garden	OG	Dearborn	U of M	Yes
Old Field	OF	Dearborn	U of M	No
Lafayette Greens	LG	Detroit	Independent	Yes
N. Cass Community Garden	NC	Detroit	Independent	No
Dexter Community Garden	DCG	Dexter	Independent	Yes
E.S. George Reserve	ESG	Dexter	U of M	Yes
M'Lis Farm	MF	Dexter	Independent	Yes
Catholic Social Services	CSS	Ypsilanti	Growing Hope	Yes
EMU - The Giving Garden	EMU	Ypsilanti	Growing Hope	Yes
Frog Island Community Garden	FI	Ypsilanti	Growing Hope	Yes
Normal Park Community Garden	NP	Ypsilanti	Growing Hope	Yes
Perry / Parkridge Community Garden	PCG	Ypsilanti	Growing Hope	No

Table B5: **List of proportional impervious surface coverage around each site.** (see https://www.researchgate.net/profile/Paul_Glaum)

Table B6: **List of floral metrics used from data measured at each site.** (see https://www.researchgate.net/profile/Paul_Glaum)

Table B.7 - Regressions against observed sex ratio at sites with temperature measurements.

Effect on female ratio	**Residual deviance**	**Significance - p**	**Effect Size - β**	**AIC**
500m	12.99_{20}	(500m) 0.0014	-0.300 ± 0.09	155.01
1km	10.79_{20}	(1km) $4.4e^{-4}$	-0.400 ± 0.11	152.81
1.5km	9.67_{20}	(1.5km) $2.2e^{-4}$	-0.504 ± 0.14	151.69
2km	10.52_{20}	(2km) $3.2e^{-4}$	-0.553 ± 0.15	152.54
Temperature	15.01_{20}	(Temp)0.004	-0.015 ± 0.01	157.12
2km + Temperature	10.47_{19}	(2km)0.032 (Temp)0.820	(2km)-0.511 ± 0.24 (Temp)$-0.002 \pm 8e^{-3}$	154.49
2km+Overall Floral Area	9.54_{19}	(2km)$2.36e^{-4}$ (Overall)0.320	(2km)-0.565 ± 0.15 (Overall)$2.58e^{-6} \pm 2e^{-6}$	153.57
2km+Crop Area	10.23_{19}	(2km)$2.94e^{-4}$ (Crop)0.584	(2km)-0.557 ± 0.15 (Crop)$2.43e^{-6} \pm 4e^{-6}$	154.25
2km+Non-Crop Area	9.62_{19}	(2km)$2.47e^{-4}$ (Non-Crop)0.339	(2km)-0.563 ± 0.15 (Non-Crop)$3.41e^{-6} \pm 4e^{-6}$	153.64

Appendix C– Appendices to Chapter 4

Appendix C.1 Data Transformations

Given the use of linear models in this analysis, variables were tested for normality using the Shapiro Wilks test. Upon passing the Shapiro Wilks test, skewed variables with non-normal distributions were log transformed. All transformed variables were reexamined using normal Q-Q plots and the Shapiro Wilks test to verify better fits to normality.

Appendix C.2 Addressing Multicollinearity

Socio-economic variables are often related to each other. This is intuitive given that an area's general income levels are inversely proportional to poverty rates but directly proportional to property values. When such socio-economic variables are used as predictors in multivariate regression analysis, this can lead to issues of multicollinearity. In general, this means that the predictor variables (the socio-economic data in our case) are all linearly correlated with each other. An example of what this multicollinearity looks like is displayed in Figure C.1 with our data; notice the consistent linear relations between all the predictor variables. Multicollinearity must be recognized because it obfuscates the precision in multivariate models using ordinary least squares regression to estimate coefficients.

When multicollinear variables are used as predictors in ordinary multivariate regressions, it can be a considerable problem because multicollinearity can make coefficient estimates imprecise. Additionally, multicollinearity increases the standard errors of the estimated coefficients (Chatterjee et al 2000). Increased standard errors, in turn, mean that coefficients for some predictor variables may be found not to be significantly different from 0. In other words, by over-inflating the standard errors, multicollinearity makes some variables statistically insignificant when they should be significant. Without multicollinearity (and thus, with lower standard errors), those coefficients may be significant. Therefore, before proceeding we tested for multicollinearity in our models.

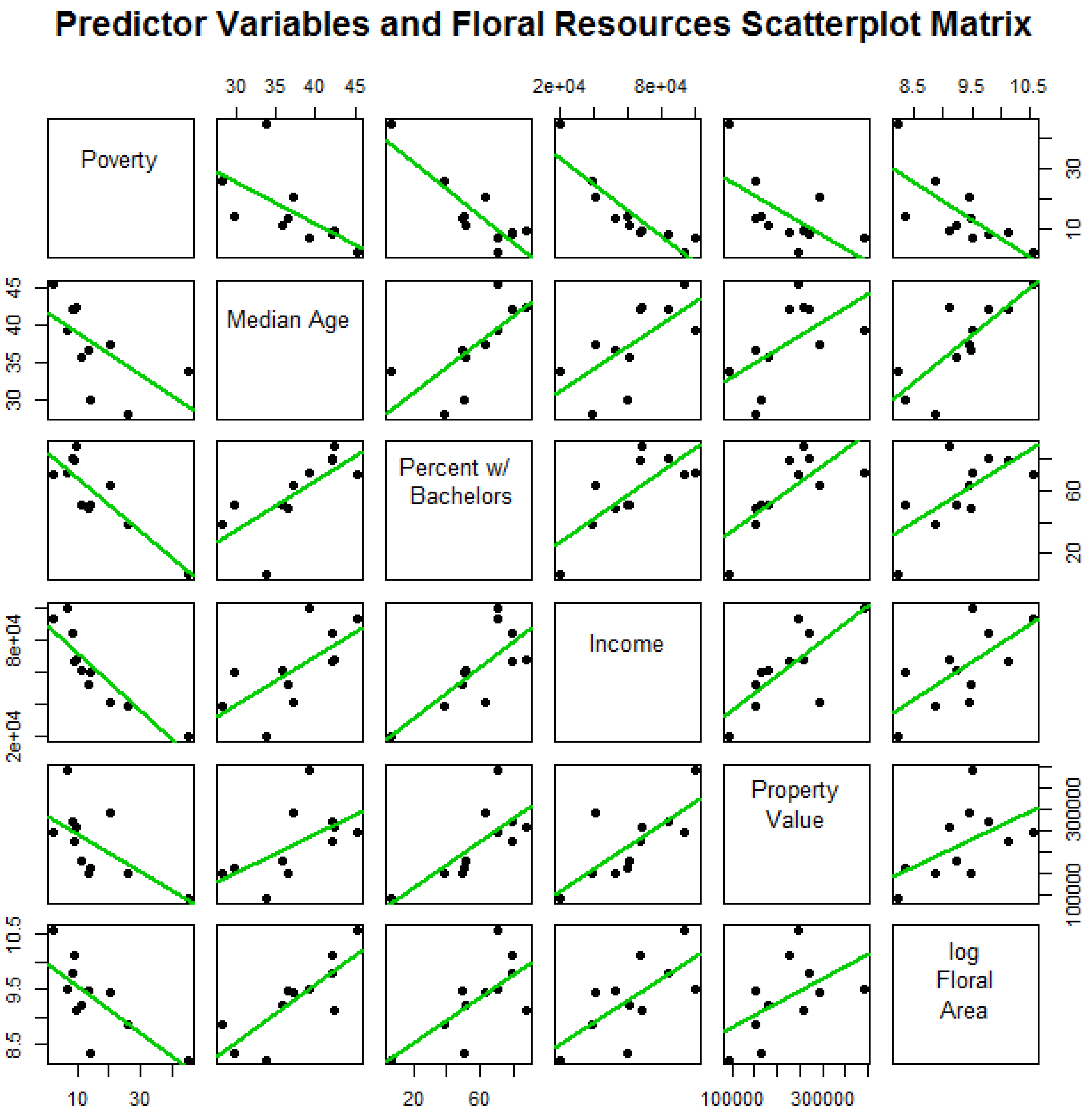


Figure C.1 - A scatterplot matrix showing the collinear relationships between the socio-economic predictor variables.

To test the degree of multicollinearity in our data, we measured variance inflated factors (VIF). VIF values larger than 5 indicate multicollinearity problems that must be addressed (O'Brien 2007). Our data set produced VIF values as high as 25 without interactions between predictor variables and as high as 160 when interaction s were directly accounted for in models (e.g. Poverty*Income in linear regressions). We can conclude then, that our data exhibits a high degree of multicollinearity and ordinary multivariate statistics/regressions are not appropriate for analysis in this case.

One method of analysis we used to avoid the issues of multicollinearity was partial least squares regression (PLS regression). PLS regressions create estimates using partial least squares and not ordinary least squares (as the name implies). This helps avoid the issues of collinearity between predictors. PLS regression is often used when predictor variables are highly collinear (Mevik and Wehrens 2007). PLS regressions work in a similar manner to principal component analysis (PCA) in that it finds independent linear combinations of the predictor variables (our socio-economic data) that best predict the dependent variable (e.g. floral data). These combinations are called factors or components. The elements of these factors/components are regression coefficients for each predictor variable. We chose the appropriate number of components per regression using cross-validation. For more in-depth explanations on PLS, see Haenlein (2004). For the purposes of this work, PLS was used to find the appropriate factors using and their regression coefficients which we could then compare to the more common beta coefficients obtained from our single-variate models. This acted as a degree of authentication of the relationships found between socio-economic variables and dependent variables.

For example, when using PLS we can run the following model in R:

pls(ln(Mean Floral Area) ~ (Poverty) + (Income) + (BA Percentage) + (Median Age)+(Property Value))

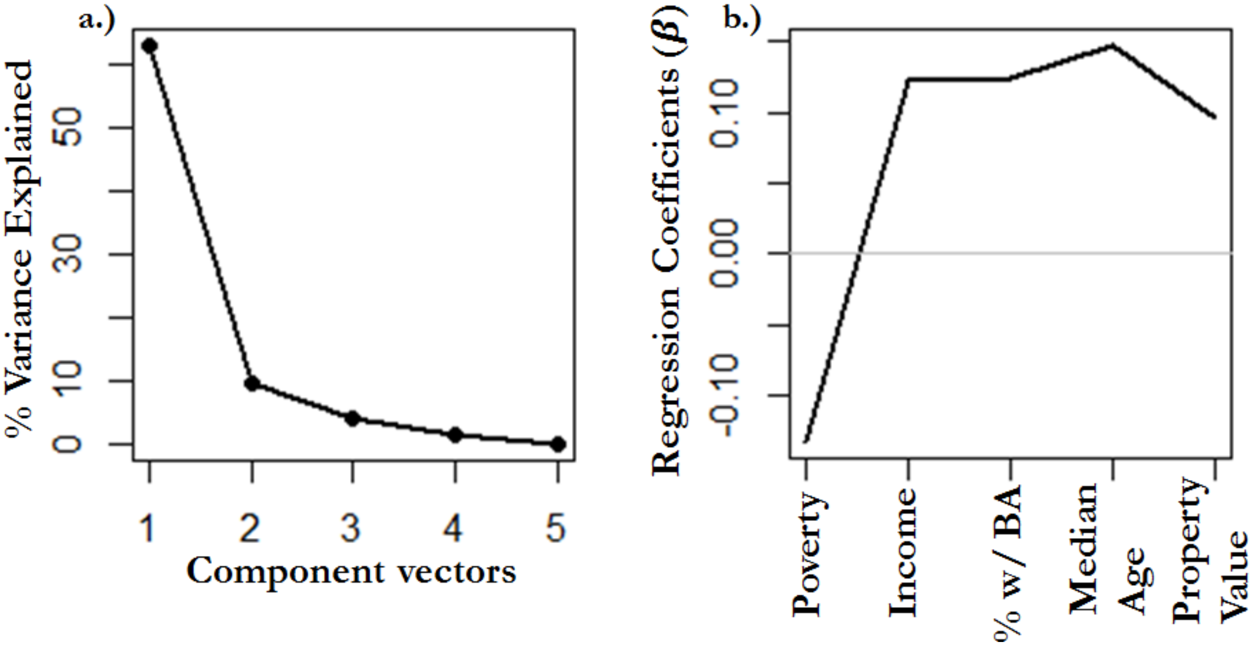


Figure C.2 - Output from PLS regression of socio-economic variables against ln(Mean Floral Area). a.) Graph showing the percent of the variance explained by each component vector of the PLS regression. Component vector 1 explains approx. 65% of the variance while other vectors explain much less comparatively. b.) Regression coefficients of each socio-economic predictor variable on ln(Mean Floral Area) from component vector 1. Poverty shows a negative relationship while all other variables show a positive relationship.

This produces 5 component vectors/factors that each explain a certain amount of the variance. As is visible in Figure C.2a, component 1 explains the most variance by far. The other component vectors add little to explanative power of the regression. The coefficients of each predictor variable are shown in Figure C.2b. Poverty shows a negative relationship while all other variables associated with wealth show a positive relationship. These coefficients correspond in their +/- sign from those detailed in Table 3.1. Similar corresponding PLS component vectors can be produced for all results detailed in Table 3.2.

Appendix D– Appendices to Chapter 5

Appendix D.1 –Curve Fitting Against Raw Data

In this work, two data sets were used from studies which investigated the effects of herbivory on pollinator visitation across a continuous spectrum of herbivory: Kessler et al 2011 and Barber et al 2012 (Kessler et al 2011; Barber et al 2012). While a number of studies have found evidence of herbivory reducing the amount of pollination individual plants receive, those studies often use categorical treatments of pollination measured with and without herbivore damage (Krupnick et al 1999; Adlet & Irwin 2005; Kessler & Halitschke 2009). Few have studied pollination across on a continuous spectrum of herbivore damage as was done in these two studies. This data was used to curve fit and find the best possible support for the form of functional response of pollinator visitation rates to different levels of herbivory. As written in the main paper, the functional response is labeled $v(c, h)$ where h is the percentage of herbivore damaged leaves and c is parameter which describes the intensity of the effect of h.

Statistics on the raw data from each study can be found below. Each data was fitted against 6 models.: 1.) Type I or linear decline response, 2.) Type II declining response, 3.) Type III declining response, 4.) Mixed Saturating decline, 5.) Concave declining function, 6.) a generalized Poisson fit. Type I, II, and III functional responses are named as such due to their dynamic similarity to functional responses seen in predation and mutualistic interactions. The Mixed Saturating model tests the effect of a response model with a scalar multiplier on h and a potential non-integer exponent (see Table D.1). The concave function allows for the testing of a potential threshold effect. These response models were chosen based on their established use in the theoretical literature, their shown applicability in other interactions (such as predation and mutualist interaction), and their ability to cover potential dynamic responses to herbivory. Finally, the Poisson fit allows us to compare the functional response to a more traditional test of this type of count data. Models were fit to the data in the statistical software R and compared using AICc weights given their nonlinearity.

D.1.1 Fitting raw data from Kessler et al 2011

Experiments in Kessler et al 2011 were conducted in Peru. This field study measured the proportion of flowers with pollination marks as a proxy for pollinator visitation and as a function of herbivore damage in the wild tomato *Solanum peruvianum*. Pollination marks were measured in relation to herbivore leaf damage experienced by individual *S. peruvianum* plants. *S. peruvianum* is attacked by a diverse set of herbivorous insects and pollinated by specialist bees in the *Apidae*, *Colletidae*, and *Halictidae* families. For more information, please see the original paper[1].

The results of curve fitting the 6 candidate models to Kessler's raw data are displayed in Table D.1. This shows no entirely definitive support for a single model. The Linear, Type II, and Mixed Saturating models are all shown to have some comparable support. However, as with the results shown in the main paper, the Type II response has the highest support and the Mixed Saturating Model has a very similar form to the Type II ($b = 1.196$). We also note that the shape of the Poisson predicted fit does mimic the exponential decay relationship modeled by the Type II functional response (Figure D.1). While the level of support in the raw data for the Type II form is more limited, the above reasoning and the results described in the main paper lead us to argue that the Type II response is the best suited functional response form from this data set. It should also be noted that not allowing the y-intercept to vary and fixing it to 100% increases the AICc weight of the Type II functional response to 0.85 and 0.62 in the averaged data fit and raw data fit respectively.

Table D.1 - Curve fitting results from Kessler et al 2011 raw data. Model fitting to original data from *Solanum peruvianum* field experiments in Peru. Curve fittings of six candidate response models to Kessler et al 2011 raw data[1]: Type I/Linear, Type II, Type III, Mixed Saturating, Concave, Poisson fit. Here h represents the level of herbivory. The parameters c and b determine the shape of the curve and i is the intercept. Estimated parameters that are significant have their p values bolded. The Type II functional response has the highest Akaike Information Criterion weight of 0.46021.

Fitted models to real data w/ intercepts	Estimated Parameters	Significance and Fit	AICc	AICc weight
1.)Linear: $\sim ch + i$	$c = -0.64,$ $i = 0.8583$	$p = (c)\mathbf{6.98e^{-13}}$ $(i)\mathbf{2e^{-16}}$ $R^2 = .2049$	168.3532	0.21497
2.)Type II: $\sim \frac{i}{1 + ch}$	$c = 1.7577,$ $i = 0.9440$	$p = (c)\mathbf{7.3e^{-7}}$ $(i)\mathbf{2e^{-16}}$	166.8308	$\underline{\mathbf{0.46021}}$
3.)Type III: $\sim \frac{i}{1 + ch^2}$	$c = 2.3514$ $i = 0.8282$	$p = (c)\mathbf{6.1e^{-6}}$ $(i)\mathbf{2\ e^{-16}}$	169.8738	0.10050
4.)Mixed Saturating: $\sim \frac{i}{1 + ch^b}$	$c = 1.8948$ $b = 1.1964$ $i = 0.9164$	$p = (c)\mathbf{1.68e^{-5}}$ $(b)\mathbf{.000163}$ $(i)\mathbf{2e^{-16}}$	168.3841	0.21167
5.)Concave: $\sim i * \left(1 - \frac{h}{100}\right)^c$	$c = 0.6062,$ $i = 0.8396$	$p = (c)\mathbf{4.52e^{-9}}$ $(i)\mathbf{2e^{-16}}$	174.0195	0.01265
6.) Poisson fit on count data:	Intercept$= 0.9190$ $\beta = -0.9983$	$p =$(Intercept)0.154 $(\beta)\mathbf{1.43e^{-12}}$	798.8534	2.6362 e^{-138}

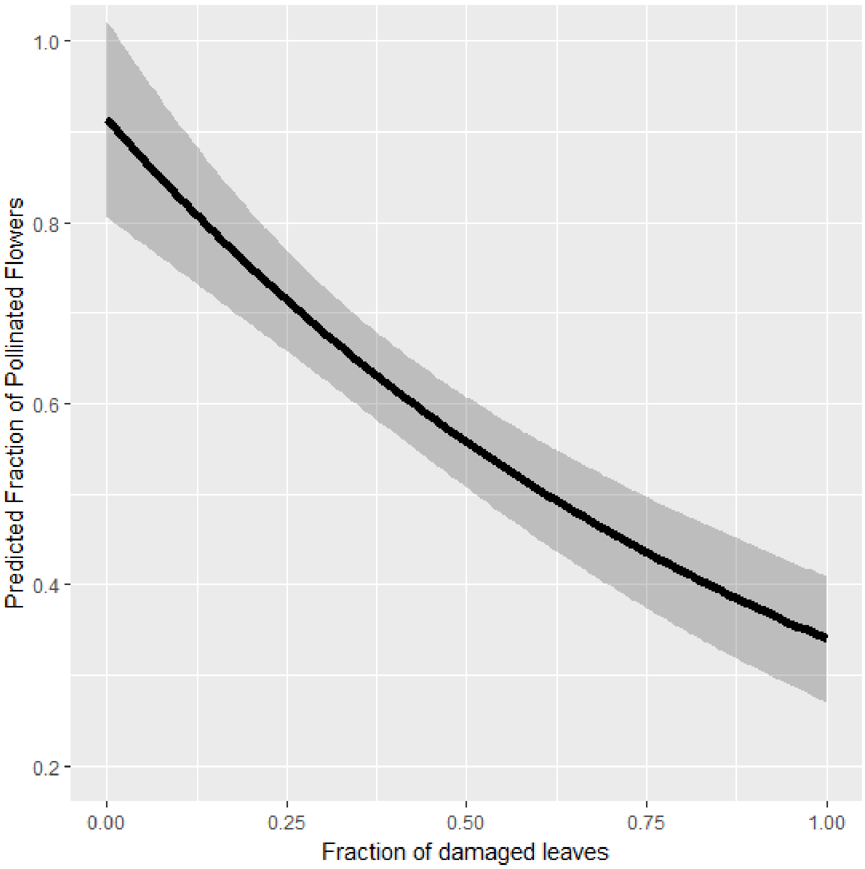


Figure D.1 - Plotted fit of the Poisson fit. Plotting the predicted relationship between herbivore damage and pollinator visited flowers derived from the generalized Poisson fit using the raw count data.

D.1.2 Fitting raw data from Barber et al 2012

The flowering plant used in this was *Cucumis sativus* (cucumber, *Cucurbitaceae*), a widely cultivated annual, monoecious herb reliant on pollinators to vector pollen between male and female flowers. *Cucumis sativus* is pollinated by a numerous insects, including generalist bees (honey bees and bumble bees), a variety of solitary bees, butterflies, and hover-flies (*Syrphidae*). The herbivorous insect of interest was *Acalymma vittatum*, a common specialist herbivore and agricultural pest of *Cucurbitacea* in the northeast United States. Herbivory occurs by adults feeding on stems and leaves above as well as larvae eating roots below ground. At various levels of herbivory, per replicate plant, pollinator visits were recorded. For more information, please see the original paper (Barber et al 2012). In this data set, all pollinators listed above are grouped together in observations. Data for just honey bees and bumble bees was also tested separately, but is not displayed here. This data and the six fitted models are displayed in Figure D.2. Data was not averaged in this case as the coverage across leaf damage percent was not even across the full spectrum.

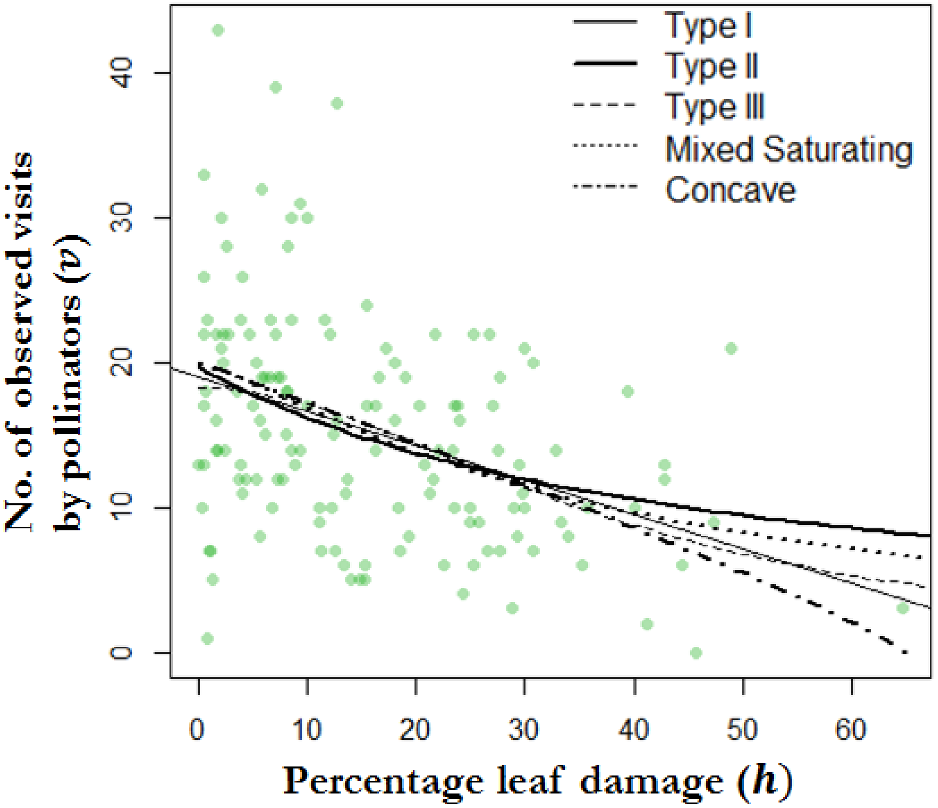
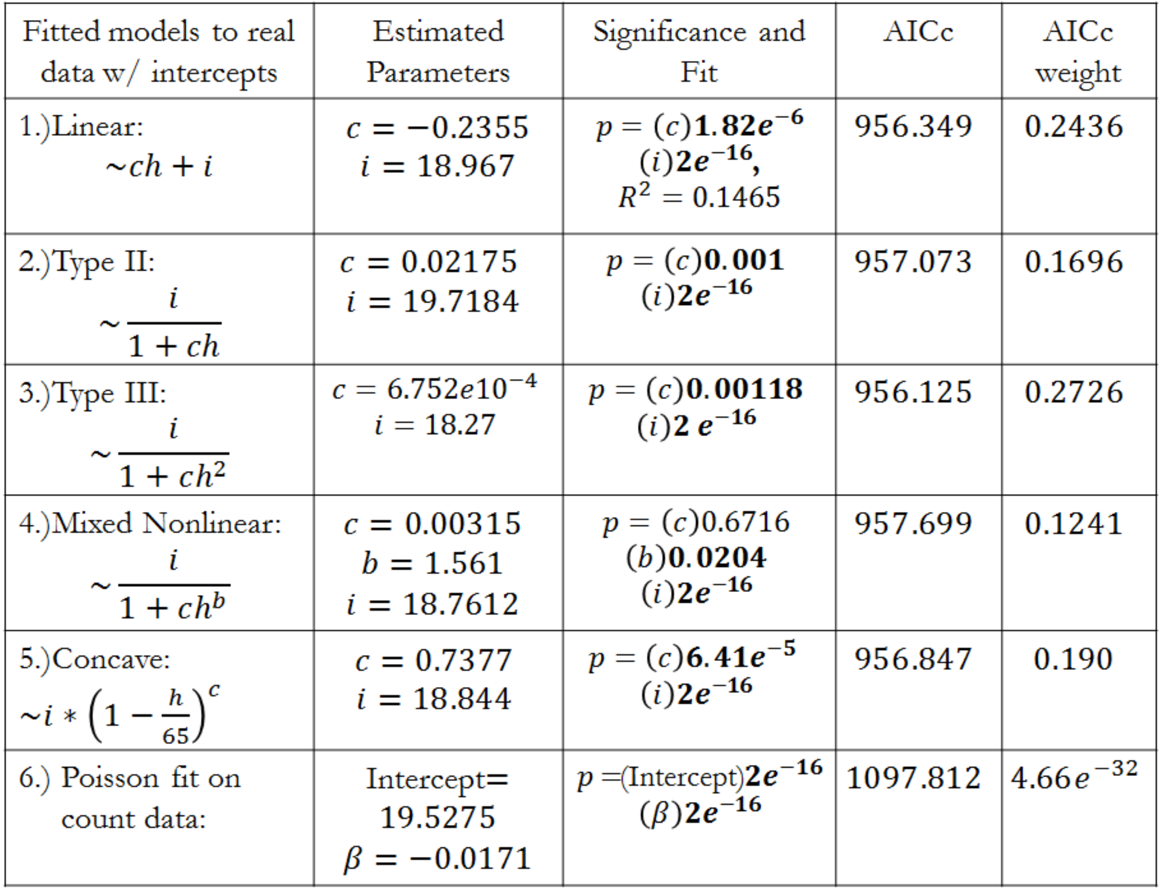


Figure D.2 - Fits of candidate models to Barber et al 2012 data. Effects of herbivore damage (h) on number of observed visits by pollinators (v) on *Cucumis sativus*. Individual data points are shown as green dots. While there is a significant negative effect of herbivory on pollinator visits, none of the five candidate models are shown to have noticeably better fits than any others. The fits of five of the candidate models are overlaid over the data as different lines. The legend describes which line represents which model. The lack of any singular best fit model is reflected in the fact all five models overlap a great deal.

The results of curve fitting the six candidate models to Barber's data are displayed in Table D.2. While the negative effect of increased levels of herbivory is significant, this data set shows no support for any one out of the six candidate models tested here. The AICc weights are particularly even across all six models. Given that the bulk of the pollinators observed in this study are large generalists (honey bees and bumble bees), it is reasonable to expect different results than those garnered from Kessler et al's 2011 paper, where the bees were smaller specialists[1]. While there are numerous speculative reasons for these differences, what this result shows is that the form of $v(c, H)$ is likely different across species and systems. This may be an important component when considering interactions among multiple pollinators on shared resource flowers.

Table D.2 - Curve fitting results from Barber et al 2012 data. Model fitting to original data from *Cucumis sativus* field experiments from Barber et al 2012[2]. Curve fittings of six candidate response models: Type I/Linear, Type II, Type III, Mixed Saturating, Concave, and Poisson. Here h represents the level of herbivory. The parameters c and b determine the shape of the curve and i is the intercept. Estimated parameters that are significant have their p values bolded. While the Type III functional response has the highest Akaike Information Criterion weight of 0.2726, no one model has the clear advantage.

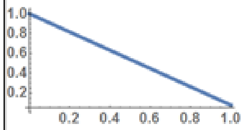
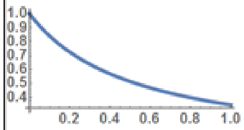
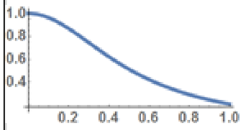
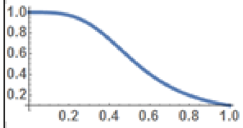
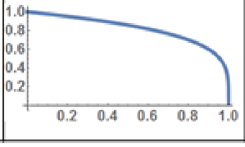


Fitted models to real data w/ intercepts	Estimated Parameters	Significance and Fit	AICc	AICc weight
1.)Linear: $\sim ch + i$	$c = -0.2355$ $i = 18.967$	$p = (c)\mathbf{1.82e^{-6}}$ $(i)\mathbf{2e^{-16}}$, $R^2 = 0.1465$	956.349	0.2436
2.)Type II: $\sim \frac{i}{1 + ch}$	$c = 0.02175$ $i = 19.7184$	$p = (c)\mathbf{0.001}$ $(i)\mathbf{2e^{-16}}$	957.073	0.1696
3.)Type III: $\sim \frac{i}{1 + ch^2}$	$c = 6.752e10^{-4}$ $i = 18.27$	$p = (c)\mathbf{0.00118}$ $(i)\mathbf{2\ e^{-16}}$	956.125	0.2726
4.)Mixed Nonlinear: $\sim \frac{i}{1 + ch^b}$	$c = 0.00315$ $b = 1.561$ $i = 18.7612$	$p = (c)0.6716$ $(b)\mathbf{0.0204}$ $(i)\mathbf{2e^{-16}}$	957.699	0.1241
5.)Concave: $\sim i * \left(1 - \frac{h}{65}\right)^c$	$c = 0.7377$ $i = 18.844$	$p = (c)\mathbf{6.41e^{-5}}$ $(i)\mathbf{2e^{-16}}$	956.847	0.190
6.) Poisson fit on count data:	Intercept= 19.5275 $\beta = -0.0171$	$p =$(Intercept)$\mathbf{2e^{-16}}$ $(\beta)\mathbf{2e^{-16}}$	1097.812	$4.66e^{-32}$

Appendix D.2 – Fitting binned data from Kessler et al 2011 with weighted bins

In using the binned data, it is reasonable to also consider the effects of standard errors of the mean values from the bins in estimation and comparison of the curves. This can be done by counting the number of observations per bin and using them as weights with the “weights” argument provided in the nls function in R. When we do so, we see no change in the main result, the Type II functional form is still the best supported model from the analysis (Table D.3). However, there is more comparable support for the Type I/Linear form and still appreciable support for the Mixed Saturating form. These results provided additional prompting to study the effects of the other functional forms on the model results (see Appendix D.8 – Appendix D.11).

Table D.3 - Curve fitting results considering bin weights. Table describing the results of the curve fitting to the 5 candidate response models: Type I/Linear, Type II, Type III, Mixed Saturating, Concave when including the weights in each bin. Here h represents the level of herbivory. The parameters c and b determine the shape of the curve and i is the intercept. Equation representations of each model are given along with a pictorial example of each model. Estimated parameters that are significant have their p values bolded. The Type II functional response has the highest Akaike Information Criterion weight of 0.587.

Fitted models to averages	Example of functional form	Estimated Parameters	Significance and Fit	AICc	AICc weight
1.)Type I/Linear: $\sim ch + i$		$c = -0.654,$ $i = 0.864$	$p = (c)\mathbf{4.13e^{-6}}$ $(i)\mathbf{8.43e^{-10}}$ $R^2 = 0.911$	-315.09	0.215
2.)Type II: $\sim \frac{i}{1+ch}$		$c = 1.807,$ $i = 0.953$	$p = (c)\mathbf{2.77e^{-5}}$ $(i)\mathbf{1.89e^{-9}}$	-317.10	$\underline{\mathbf{0.587}}$
3.)Type III: $\sim \frac{i}{1+ch^2}$		$c = 2.491$ $i = 0.838$	$p = (c)\mathbf{3.57e^{-4}}$ $(i)\mathbf{2.86e^{-9}}$	-312.59	0.062
4.)Mixed Saturating: $\sim \frac{i}{1+ch^b}$		$c = 2.000$ $b = 1.243$ $i = 0.920$	$p = (c)\mathbf{1.13e^{-4}}$ $(b)\mathbf{0.242e^{-4}}$ $(i)\mathbf{2.62e^{-8}}$	-313.90	0.119
5.)Concave: $\sim i * \left(1 - \frac{h}{100}\right)^c$		$c = 0.606,$ $i = 0.842$	$p = (c)\mathbf{2.58e^{-4}}$ $(i)\mathbf{2.36e^{-8}}$	-310.16	0.018

Appendix D.3 - Obligate mutualism without functional HIPL

The full effect of $v(c, H)$on system persistence is made clear by first setting $c = 0$, making $v(c, H) = 1$. This effectively eliminates the mechanism of herbivore-induced visitation reduction from the model. Doing this also allows us to quickly verify previous theoretical work and show the fragile nature of antagonized mutualisms in their most basic theoretical formulation. The categories of possible dynamics are relatively short. The system can be sustained by both stable equilibria and stable limit cycles. However, the two different dynamics of system persistence are mutually exclusive across parameter space such that no parameter combination creates a phase space with both a stable equilibrium and a stable limit cycle. Antagonized obligate-mutualisms function dynamically similar to a predator-prey system with the prey split into two mutually dependent populations. Classic Lotka-Volterra predator-prey systems also result in only one dynamic category of persistence per parameter combination. Therefore, the lack of overlapping in dynamical categories of persistence has reasonable precedence in this and other models.

The range of parameter space which creates dynamics that support persistence is quite narrow. Figure D.3 shows the results of a Jacobian stability analysis across $\{b_F , b_P , r_H\}$ parameter space. The results of the stability analysis are visualized as colors across parameter space. Parameter combinations which create locally stable equilibria are shown in green, while the blue represents space where equilibria are unstable and result in system extinction. The actual equilibrium values are written out parametrically in Equations D.1-D.3. The slim orange space represents the space which creates unstable equilibria but stable limit cycles (sustained oscillations). The parameter space which supports limit cycles had to be compiled in a list of data because the surface was too thin for the available software, Mathematica, to render.

$$\boldsymbol{F}^* \rightarrow \frac{d_H}{c_{FH} r_H - d_H h_H} \tag{Eq D.1}$$

$$\boldsymbol{H}^* \rightarrow c_{FH} \left(\begin{array}{c} \frac{-a d_H + d_F d_H h_H - c_{FH} d_F r_H}{(d_H h_H - c_{FH} r_H)^2} \\ + \frac{b_F d_P v}{a d_H h_H - a d_H h_P - a c_{FH} r_H} \\ + \frac{b_F b_P d_H v^2}{a(d_H(h_P - h_H) + c_{FH} r_H)^2} \end{array} \right) \tag{Eq D.2}$$

$$\boldsymbol{P}^* \rightarrow \frac{-d_P + \left(\frac{b_P d_H v}{d_H(h_P - h_H) + c_{FH} r_H} \right)}{a} \tag{Eq D.3}$$

It is readily apparent that, in this simple form, the system can only potentially persist at very low levels of herbivory (Figure D.3). Values of both b_P and b_F have minimal effects on the mutualism's ability to persist across different levels of herbivory (i.e. different values of r_H). Overall, this simple version of the system has a narrow range of parameter space where all three variables can coexist without going extinct due to herbivory.

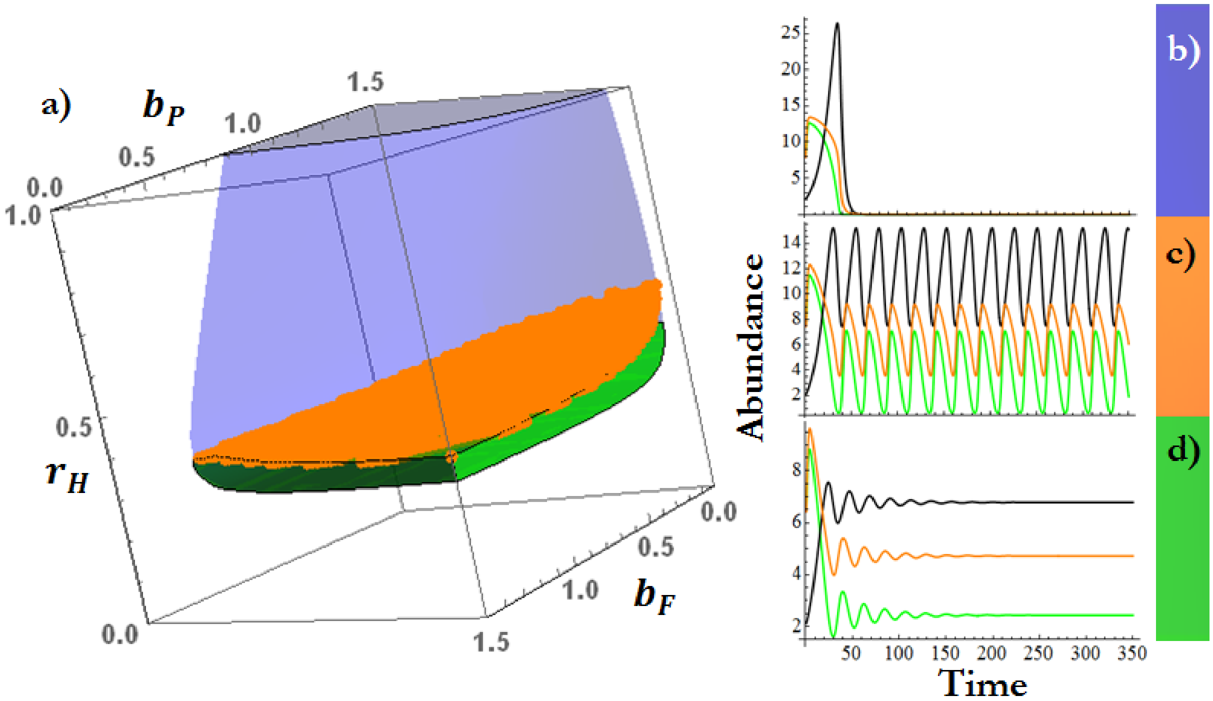


Figure D.3 - Dynamics across parameter space for Equation 5.1 without HIPL. Exploration of the different type of model behaviors/dynamics across different parameter values in the obligate model with no HIPL ($r_F = 0, c = 0$). a) A representation of different dominant asymptotic dynamics across $\{b_F, b_P, r_H\}$ parameter space. Parameter b_F represents the reproductive benefit of pollination to the flowering plant population. Parameter b_P represents the reproductive benefit of pollination to the pollinator population. Parameter r_H represents the attack rate of the herbivore. The green space represents parameter combinations where the non-zero equilibrium is locally stable. The thin orange space represents combinations where the non-zero equilibrium is unstable but a stable limit cycle exists. The parameter space which supports limit cycles had to be compiled in a list of data because the surface was too thin for the available software, Mathematica, to render. Both limit cycles and stable equilibria represent system persistence. The blue space represents space where the non-zero equilibrium exists, but is unstable resulting in the system going extinct. Fig D.3b-D.3d represent example simulations/time series from each different parameter grouping in Fig D.3a. In the time series, green lines represent F, orange lines represent P, and black lines represent H. b) An example simulation from the extinction producing region of parameter space (blue region in Fig D.3a). c) An example simulation from the limit cycle producing region of parameter space (orange region in Fig D.3a). c) An example simulation from the stable equilibrium producing region of parameter space (green region in Fig D.3a). The other parameter values are as follows: $d_H = 0.25$, $d_P = d_F = 0.2$, $r_F = 0$, $c_{FH} = 1$, $c = 0$, $h_H = h_P = 1$. See Table 1 in the main text for parameter and variable definitions.

In addition to the limited amount of parameter space which creates persistent systems, systems which do have a potential dynamic of system persistence (either equilibrium or limit cycle) can be perturbed into phase space which leads to system collapse. This can happen when trajectories are moved out of the basin of attraction of either the stable equilibrium or limit cycle and into the basin of attraction of the 0-equlibrium absorbing state in phase space. An example of this is given in Figure D.4. For more detailed descriptions of the basin of attraction see Strogatz 1994. Figure D.4 shows that the basin of attraction of the stable equilibrium is limited, mainly in the H direction, such that higher H values means trajectories are caught in the basin of the 0-equlibrium and the communities goes extinct. This exercise corroborates past work which describes the seemingly fragile nature of these systems under base model formulation.

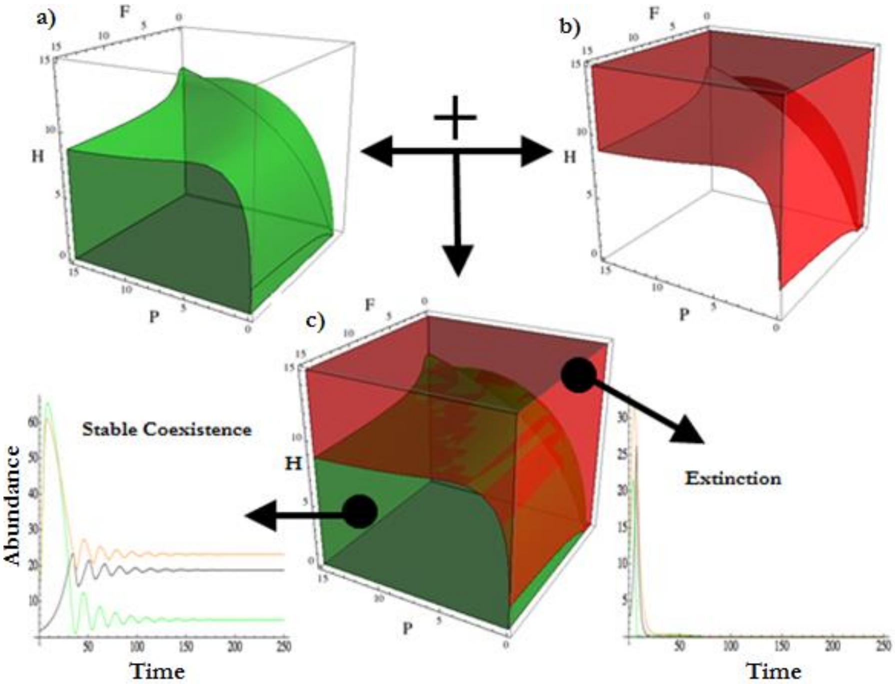


Figure D.4 - Basins of attraction for Equilibrium 5.4 and the 0-equilibrium. Examples of basins of attraction in $\{F, H, P\}$ phase space and their resulting model behaviors. F-flowering plant population, H-herbivore population, P-pollinator population. a) The basin of attraction for a stable equilibrium where $F^*, H^*, P^* > 0$ shown in green. All initial conditions inside this basin lead to stable equilibria. b) The basin of attraction for the 0-equilbrium, (0,0,0), shown in red. All initial conditions in this basin lead to extinction. c) Combining a) and b) shows that the basins completely fill the phase space. Asymptotic model behavior is shown to depend on which basin of attraction initial conditions start in. When initial conditions start in the green (basin of attraction of the stable equilibrium), trajectories experience dampened oscillations and the system persists in stable coexistence. However, when initial conditions start in the red (basin of attraction of the (0,0,0) state, trajectories are pulled to extinction due to saturation with herbivores. In the time series, green lines represent F, orange lines represent P, and black lines represent H. See Table 1 in the main text for parameter and variable definitions.

Appendix D.4 - Obligate mutualism with functional HIPL

This section studies Equation 5.1 when $r_F = 0$ and $c > 0$. The expression for F^* is written below. Parametric expression for H^* and P^* are too large for print. Please use the following Mathematica code to examine the equilibria.

$$\begin{aligned}\text{FHPSol} = \text{Solve}[&F * ((\text{bf}/(1 + c * H)) * (P/(1 + hp * F)) - a * F) \\ &- (\text{rh} * F * H)/(1 + hh * F) - \text{df} * F = \\ &= 0\&\&cfh * \text{rh} * F * H/(1 + hh * F) - \text{dh} * H = \\ &= 0\&\&P * ((\text{bp}/(1 + c * H)) * (F/(1 + hp * F)) - a * P) - \text{dp} * P = \\ &= 0, \{F, H, P\}];\end{aligned}$$

The addition of HIPL expands the range of herbivory levels that the mutualism can withstand. The mechanism of this expansion and increased resilience comes from the asynchronous oscillations of herbivore populations ($H(t)$) and $v(c, H) = \frac{1}{1+cH}$ through time (Figure D.5). When $c > 0$ increased herbivore abundance dynamically lowers the interaction rate between flowers and pollinators. While this does obviously reduce the population growth of both the flowering plant and the pollinator, this indirectly lowers $\frac{dH(t)}{dt}$ and causes the herbivore population growth to slow so that it never saturates the system as it did when $c = 0$. The greater the value of c, the quicker high H abundance lowers visitation rates and consequently, the more controlled the herbivore population (Figure 5.3).

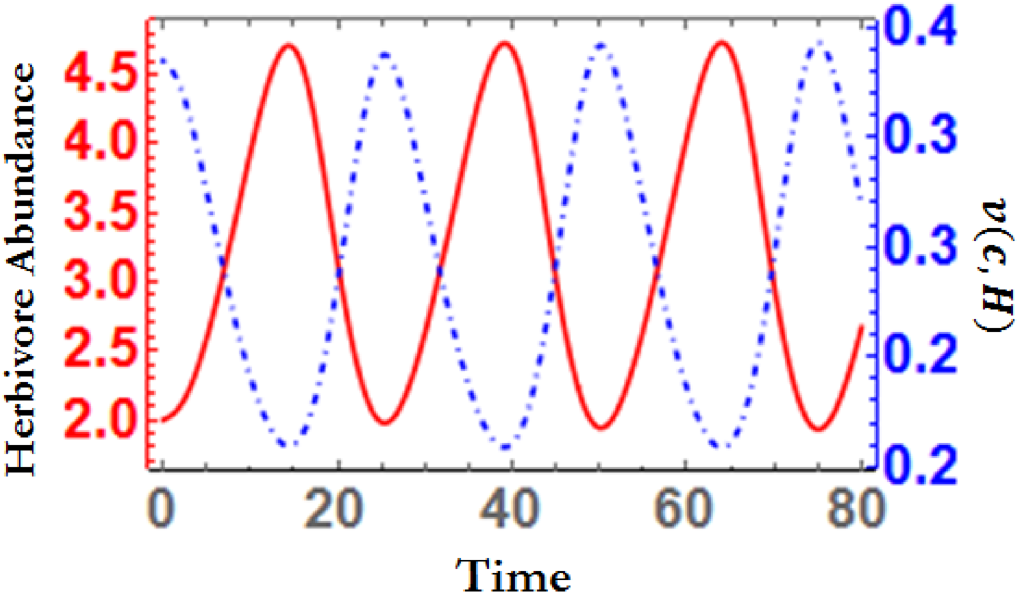


Figure D.5 - Dynamics of herbivore abundance and v across time. Asynchronous oscillations of herbivore abundance (red, left axis) and pollinator visitation rates (blue/dashed, right axis). These asynchronous oscillations come from the form of $v(c, H) = \frac{1}{1+cH}$.

Analysis of this version of the model started with analysis of available equilibria and their stability. Unfortunately, the seemingly modest addition of function $v(c, H)$ to the model creates analytically incalculable equilibria. Simple algebraic manipulation of $\frac{dH}{dt}$ can show that: $F^* = \frac{d_H}{c_{FH}r_H - d_H h_H}$. On the other hand, both P^* and H^* cannot be written completely parametrically in a length that would fit within reasonably sized manuscript. Therefore, using the Jacobian and eigenvalues to identify all general relationships between parameter values and stability in the model was not feasible. However, it is possible to find an inverse relationship that exists between the values of the equilibria of P^* and H^*. Starting with $\frac{dP}{dt} = 0$ it is possible to show that:

$$\frac{dP}{dt} = P^* \left(\frac{b_P v(c) F^*}{1 + h_P F^*} - \alpha_P P^* \right) - d_P P^* = 0 \tag{D.4}$$

$$P^* \left(\frac{b_P v(c) F^*}{1 + h_P F^*} - \alpha_P P^* \right) = d_p P^* \tag{D.5}$$

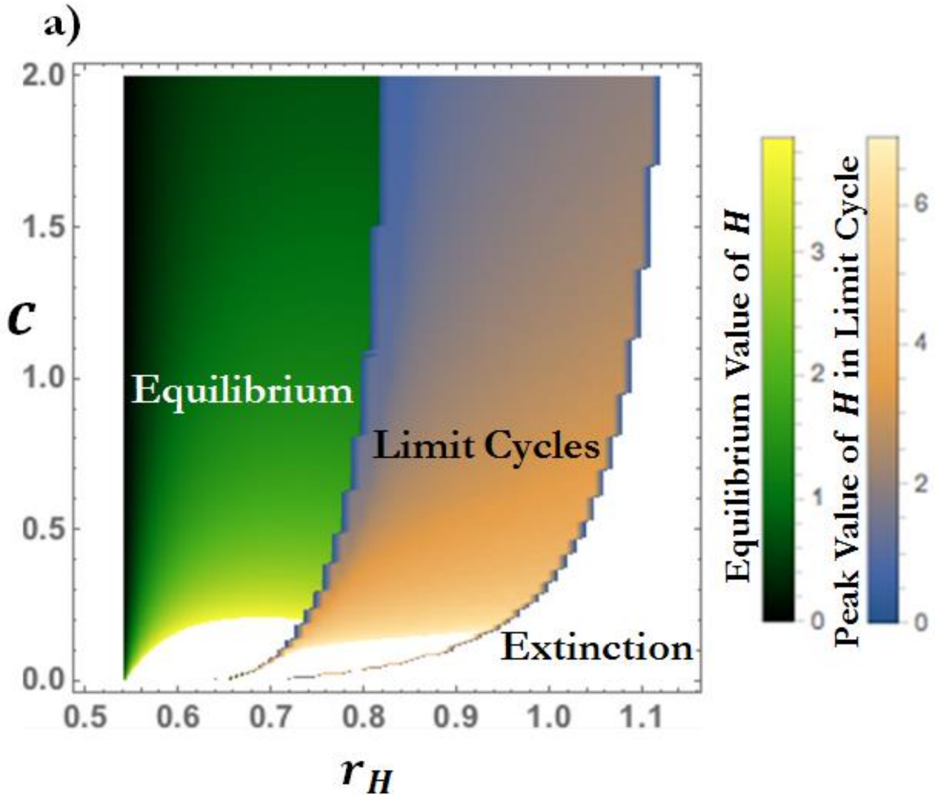
$$\text{substitute: } F^* = \frac{d_H}{(c_{FH} r_H - d_H h_H)} \rightarrow P^* \left(\frac{b_P v(c) \frac{d_H}{(c_{FH} r_H - d_H h_H)}}{1 + \frac{h_P d_H}{(c_{FH} r_H - d_H h_H)}} - \alpha_P P^* \right) = d_p P^* \quad \text{(D.6)}$$

$$\left(\frac{b_P v(c) \frac{d_H}{(c_{FH} r_H - d_H h_H)}}{\frac{(c_{FH} r_H - d_H h_H) + h_P d_H}{c_{FH} r_H - d_H h_H}} - \alpha_P P^* \right) = d_p \quad \text{(D.7)}$$

$$\left(b_P v(c) \frac{d_H}{(c_{FH} r_H - d_H h_H)} \left(\frac{c_{FH} r_H - d_H h_H}{(c_{FH} r_H - d_H h_H) + h_P d_H} \right) - d_p \right) = \alpha_P P^* \quad \text{(D.8)}$$

$$\frac{1}{\alpha_p} \left(\frac{b_p v(c) d_H}{(c_{FH} r_H - d_H h_H) + h_P d_H} - d_p \right) = P^* \quad \text{(D.9)}$$

Since $v(c) = \frac{1}{1+cH}$ it is clear to see that $P^* \sim \frac{1}{H^*}$ (Eq D.9). While this is an intuitive result, the lack of full parametric expressions of equilibria means numeric approaches must be taken to understand the effect of changing model parameters. This was done using 2-dimensional bifurcation heatmaps for H and P respectively as was shown in Figure 5.4 for F (Figure D.6). The expanded resilience to higher values of r_H as c increases is clear. Despite c representing a necessary decline in interaction between the mutualists, it is actually the herbivore population which has the most apparent population decline with higher values of c.



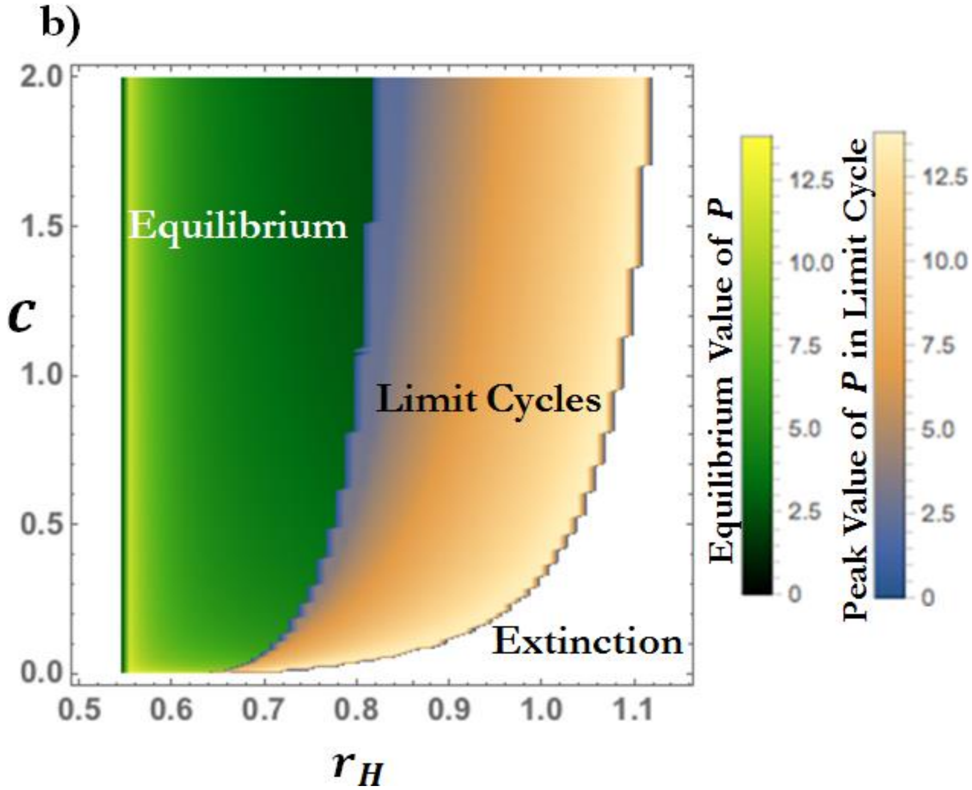


Figure D.6 - 2-D heatmaps for H and P in obligate mutualism community. 2-dimensional bifurcation heatmap showing the abundance for a) H (herbivore population) and b) P (pollinator population) across values for parameters c and r_H in the asymptotic behavior of the model. Parameter c represents the degree of herbivore-induced pollinator limitation. Parameter r_H represents the herbivore attack rate. This figure corresponds to Figure 5.4 in the main text. Where parameter combinations create stable equilibria, abundance is shown in the green color scale. Where values create stable limit cycles, abundance is shown in the sunset color scale. The switch between the two color schemes represents the Hopf bifurcation shown in Figure 5.3. Values which lead to system extinction are shown in white. a.) Value of H in the asymptotic behavior of the model. b.) Value of P in the asymptotic behavior of the model. $r_F = 0$; $b_F = 1.665$; $b_P = 1.695$; $d_F = 0.2$; $d_H = 0.5$; $d_P = 0.2$; $a = 0.1$, $c_{FH} = 1$, $h_H = h_P = 1$. See Table 1 in the main text for parameter and variable definition.

It is worth noting that an increase in c (decrease in pollinator visitation), does not necessarily result in a negative effect on F abundance. When the system produces a stable Equilibrium 5.4, there is no cost to F as c increases (Figure 4.4). This can be analytically verified by recalling that the parametric expression for $F^* = \frac{d_H}{c_{FH} r_H - d_H h_H}$ has no reliance on the value of c. Additionally, it is also possible to show that both P^* and H^* are inversely proportional to the value of c. However, the examples given in Figure 5.3a and Figure D.6b show that the effect of c on P^* is small. The effect of visitation reduction on H^* is much more pronounced (Figure D.6a). Potential costs in oscillating populations due to reduction in pollinator visitations (reduced interaction with the mutualist) are also limited. While higher c values decrease the maximum abundance in F and P (Figure 5.3a, Figure 5.5) when the system produces sustained population oscillations, the minima of these oscillations increase (Figure 5.3a). This reduces the system's tendency to produce small population sizes during its cycles, thereby keeping a higher minimum population number of the two mutualistic interactors (e.g. plant and pollinator). This limits periods of exceptionally low population growth when one of the mutualists has low abundances.

Finally, we have shown that higher levels of c can cause the system to persist in a non-zero attractor despite higher levels of herbivory. Additionally, for any given value of r_H, higher levels of visitation reduction can also expand the range of mutualism growth the system can support. Another source of system failure besides increased levels of herbivory is higher growth rates of the mutualists. In the same way that high r_H can saturate the system with herbivores, high b_F and b_P can also lead to more available resources for herbivores, leading to herbivore saturation and system failure. Herbivore induced pollinator visitation decline attenuates this indirect saturation effect and expands the range of b_F and b_P which doesn't lead to system failure. Perhaps more intuitively, sufficiently low mutualism growth rates can also lead to system failure. If growth rates of the pollinator or flowering plant are too low, the mutualism may not be able to recover herbivore induced low population numbers. Higher levels of pollinator visitation decline allow the mutualism to recover from low population numbers while reducing the growth rate when herbivores are too abundant. An example of these effects is shown in Figure D.7. Here it is clear that as c increases from 0, the range of b_F and b_P parameter space which leads to a non-zero dynamic (persistent communities) expands.

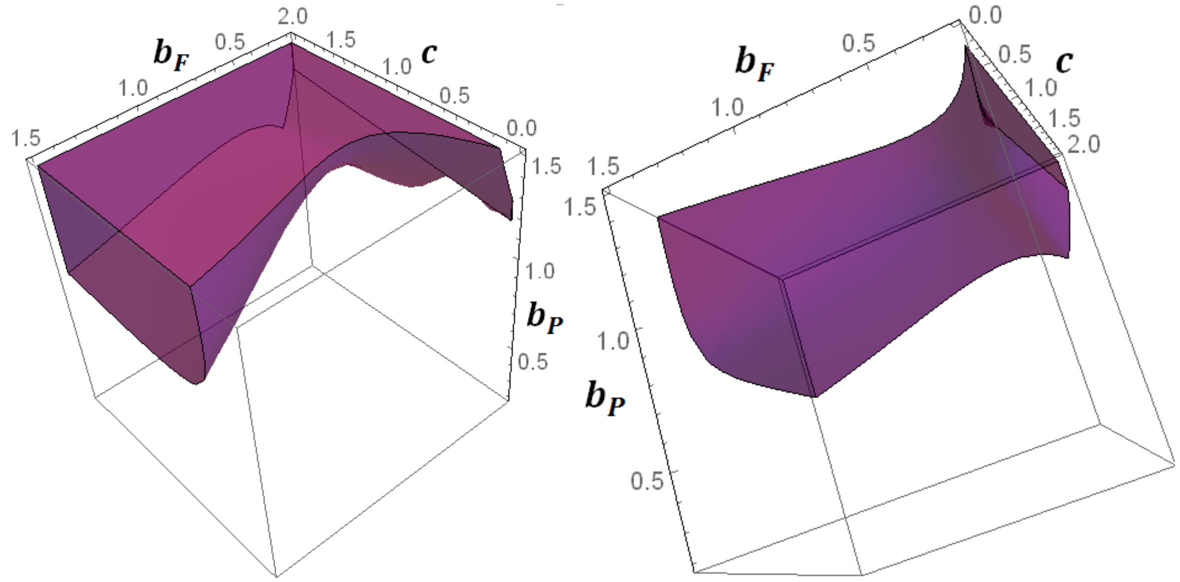


Figure D.7 - Parameter space supporting persistence. Parameters space which supports persistence in all three populations across $\{c, b_F. b_P\}$ parameter space is shown in translucent purple. Parameter c represents the degree of herbivore-induced pollinator limitation. Parameter b_F represents the reproductive benefit of pollination to the flowering plant population. Parameter b_P represents the reproductive benefit of pollination to the pollinator population. Persistence is not distinguished between equilibria and limit cycles in this case. Simulations were run with r_H at the relatively high value of 1. Other parameters were as follows: $r = 0$, a=0.1, $d_F = 0.2$, $d_H = 0.5$, $d_P = 0.2$, $c_{FH} = 1$, $c = 0$, $h_H = h_P = 1$. See Table 1 in the main text for parameter and variable definitions.

Appendix D.5 – Highly specialized mutualism with HIPL

When r_F is near zero but still positive (for some small value ϵ such that $r_F \approx \epsilon$), the model can represent a highly specialized pollination mutualism between F and P. In this case, the pollinator is dependent on the flowering plant population, but the flowering plant population is able to maintain some average positive growth independent of pollinator P. The model produces similar rescue and stabilization dynamics compared to the obligate mutualism in the Results section (Figure D.8).

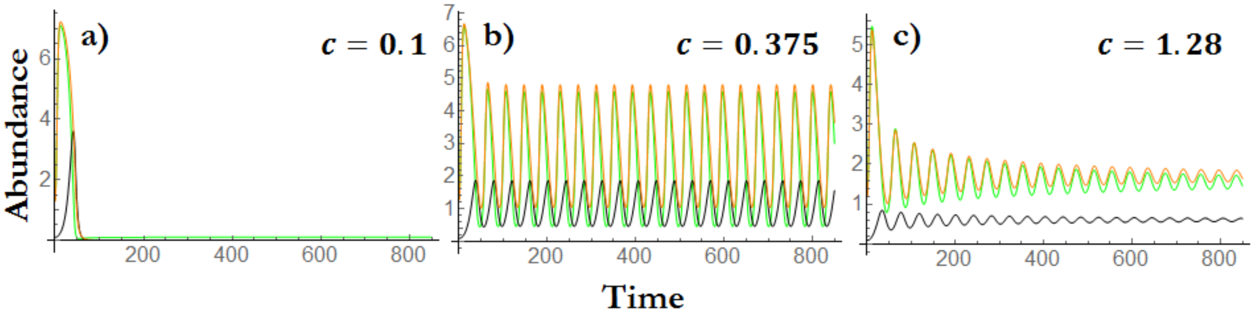


Figure D.8 - HIPL rescue effect in specialized mutualism Example of similar rescue and stabilization dynamic driven by HIPL with higher c values in a highly specialized system where r_F is slightly greater than 0 (i.e. $r_F = \epsilon$ such that $\epsilon > 0$). In this case $r_F = 0.21$. a) System failure with low influence of HIPL, $c = 0.1$. b) Past the rescue point and establishment of sustained oscillation with more influence from HIPL ($c = 0.375$). c) Oscillations dampen and approach stable equilibrium with higher c values ($c = 1.28$). All other parameters: $r_F = 0.21$; $r_H = 0.71$; $b_f = 0.83$; $b_p = 1.08$; $c_{FH} = 0.58$; $h_H = 1$; $h_P = 1$; $d_F = 0.2$; d_H = 0.25; $d_P = 0.2$; $\alpha = 0.1$.

Appendix D.6 – Approximating the Volume of the Basin of Attraction in Obligate Model

While c values greater than 0 can induce system persistence, both rates of herbivory (r_H) and pollinator aversion to herbivory (c) have significant effects on the volume of the basin of attraction of non-zero attractors (Figure D.9). In other words, non-zero c values can create the potential for system rescue, higher values of c reduce the amount of initial conditions which move toward non-zero attractors. Recall that non-zero attractors in this case are the attractors (equilibria & limit cycles) which allow for system persistence instead of extinction (the 0-equilibrium). The basin of attraction for an attractor is the set of initial conditions in phase space that will eventually be iterated into the attractor over time. When the basin of attraction of the non-zero attractor is small, there are more initial conditions which will push the system into the 0-equilibrium, leading to extinction. When the basin of attraction of the non-zero attractors is larger, there are more initial conditions which will push the system into the non-zero attractor and the community will persist. For further description, see Strogatz 1994 and Figure D.4.

We determined the approximate volume of the basin of attraction in phase space for both Equilibrium 5.4 and limit cycles (sustained oscillations) across $\{c, r_H\}$ parameter space. There is no analytical method to study the size of the basin of attraction so it must be investigated through numerical simulations. Through an extensive numerical survey of 2.7 $x10^7$ initial conditions in phase space simulated across 2800 parameter combinations we compiled a 7.56$x10^{10}$ point data set which develops a full understanding of how the size of the basin of attraction changes with different values of c and r_H. Stable equilibria were found using standard Jacobian stability analysis on Equilibrium 5.4. There is no set method to analytically determine the existence of limit cycles. Therefore, limit cycles were verified using numerical means. We determined an approximate volume of the basin of attraction in phase space for both Equilibrium 5.4 and limit cycles (sustained oscillations) across $\{c, r_H\}$ parameter space (Figure D.9).

Reduction in pollinator visitation (higher c) causes a sharp initial decrease in the volume of the basin, but then begins to have a smaller effect. Whereas the effect of increased rates of herbivory (r_H), cause a more consistently steep decline in basin volume over less parameter space. This result suggests that while visitation reduction can facilitate 3-variable coexistence at r_H levels that would otherwise cause system extinction, the basins of attraction for the non-zero attractors are smaller with higher r_H. In other words, the potential for persistence offered by pollinator visitation reduction comes with the caveat of susceptibility to perturbations. There is also a clear continuation of the non-zero attractors' basin volume across the bifurcation from stable equilibrium to limit cycles. With this result, we can say that the prominent dynamic (equilibria or oscillations) in the model does not affect the basin volume of the non-zero attractor. Instead, it is the parameter values themselves which lead to changes in volume.

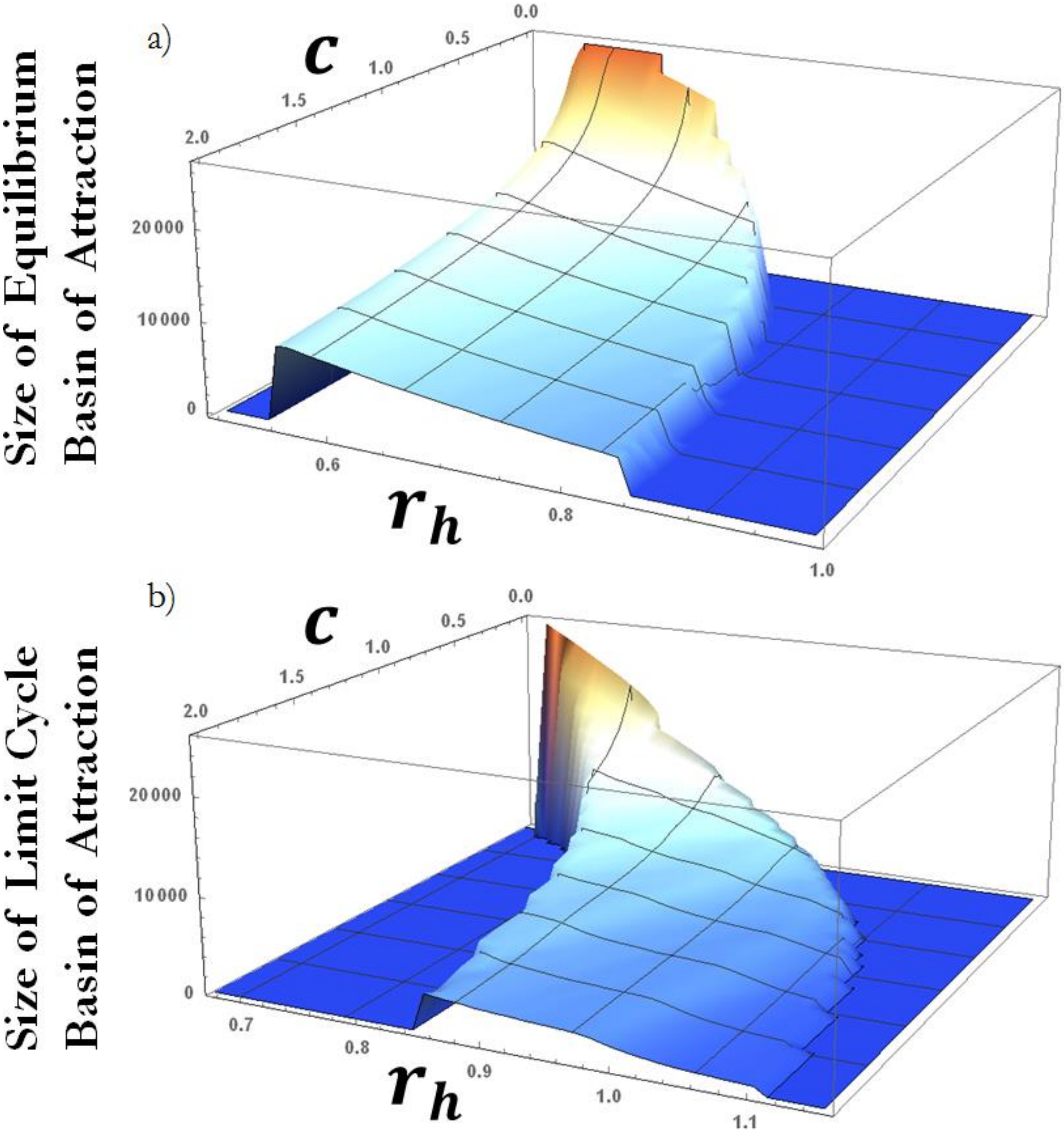


Figure D.9 - Size of Equilibrium 4's Basin of Attraction across parameter space. Numerical approximation of the phase space unit volume of basins of attraction as a function of r_h (the rate of herbivory) and c (the degree of pollinator visitation reduction due to herbivory) for a) the stable equilibria and b) the stable limit cycles. The volume was approximated through testing asymptotic system behavior across all initial conditions from 0 to 15 for each variable. This was repeated across different combinations of c and r_h values. The number of initial conditions which result in equilibrium behavior is a suitable approximation of the basin of attraction's unit area in phase space. $r_F = 0$; $b_F = 1.665$; $b_P = 1.695$; $d_F = 0.2$; $d_H = 0.5$; $d_P = 0.2$; $h_F = 1$; $h_P = 1$; $c_{FH} = 1$; $\alpha = 0.1$.

Appendix D.7 - Facultative mutualism with HIPL

Setting r_F substantially greater than 0 (r_F greater than some small value ϵ, $r_F > \epsilon > 0$) leads to complications in the effects of visitation reduction. As shown in the main paper, non-zero values of r_F can lead to a population crash for the pollinator. The potential for a high growth rate of one facultative mutualist to crash its obligate partner has to do with the growth of the antagonist (in this case the herbivore). When the system is stabilized in equilibrium by visitation reduction and r_H is low, with an overall growth rate of $(r_H - d_H)$ of roughly 0.3, increasing r_F can keep the system in equilibrium while pushing $P^* \rightarrow 0$ (Figure D.10 and Figure 5.5). As was shown in the main paper, inducing oscillations and increasing their amplitude by further increasing r_F can create windows of time where r_H is low and P is allowed time to grow. Additionally, the 2-parameter bifurcation diagram in Figure D.10 shows a similar effect is possible when r_H is increased. As r_H is increased, we can see an initial drop in equilibrium values of P^* and an eventual rebound in peak values after the induction of limit cycles. The reasoning here is similar to when pollinator populations are saved by higher r_F. The fast growth of herbivore populations will induce limit cycle behavior in the plant-herbivore Lotka-Volterra consumer-resource system. This will cause high peaks in herbivore abundance that will lead to prolonged troughs in flowering plant populations. This will consequently drop the population of herbivore long enough for the small populations of pollinators to begin to grow in the interim. The result described here is similar to that described in Figure 5.5c.

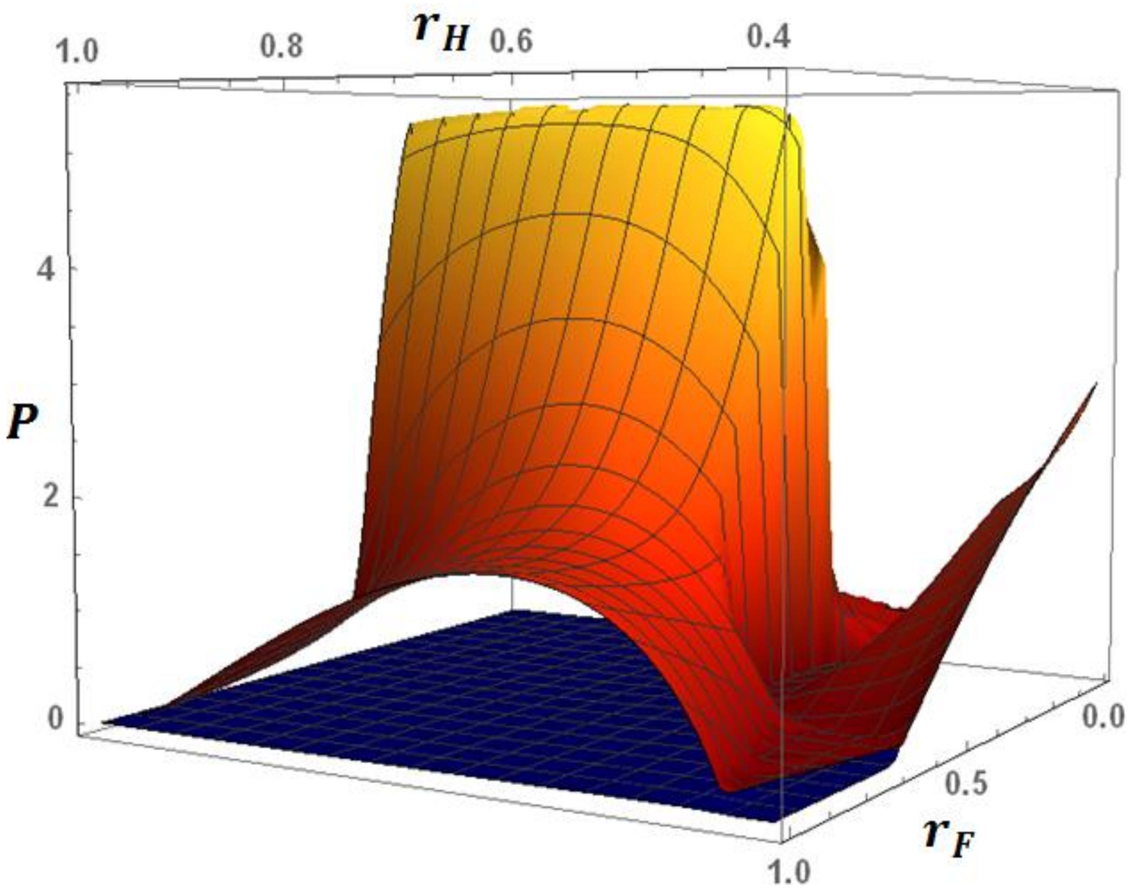


Figure D.10 - 2-D bifurcation for P. A two dimensional bifurcation plot for P (pollinator population) across different parameter values of r_F and r_H (intrinsic growth rate of flowering plant population and herbivore attack rate respectively). Combinations which create stable equilibria have just one P value plotted whereas combinations which create limit cycles are plotted with both a P minimum and P maximum. Values are plotted with fitted curves to show contours. Maximum limit cycle values and equilibria values are shown in sunset colors. Minimum limit cycle values are shown in dark blue. Areas with no minimum value shown (right side of figure) are equilibria. At both low and high values of $r_H$an increased intrinsic growth rate of the flowering plant (higher r_F) can actually lead to reductions in pollinator abundance. $b_F = 1.04$; $b_P = 0.85$; $c = 1.2$; $d_F = 0.2$; $d_H = 0.302$; $d_P = 0.2$; $a = 0.1$; $h_F = 1$; $h_P = 1$; $c_{FH} = 1$. See Table 1 in the main text for parameter and variable definitions.

This surprising benefit to the pollinator of higher herbivore growth can be hindered in two ways. First, and most intuitively, if r_H is too high, the troughs in H abundance are short and P is not afforded as much time to grow. This results in a decline in peak P abundance (Figure D.10). Second, increased intrinsic growth of F (i.e. higher r_F) can speed the growth of H populations in troughs and limit time available for P population growth. All of these various conditions and tradeoffs for pollinator growth create a complicated condition for pollinator persistence that depends on visitation reduction, growth rate of the herbivore, and the intrinsic growth rate of the flowering plant (values of c, r_H, r_F respectively).

In order to investigate the effect of each of these key parameters of the pollinator population, we compiled a large numerical analysis of P abundance in asymptotic model behavior (Figure D.11). Equation 5.1 was simulated 76880 times across values of c, r_H, and r_F and the depending on the dynamic of the model (stable equilibrium or limit cycles) the equilibrium value or peak limit cycle value of P was recorded. These values of P are presented as a color gradient. The data shown in Figure D.11 only represents situations where the flowering plant has a high enough r_F that it can survive without pollination.

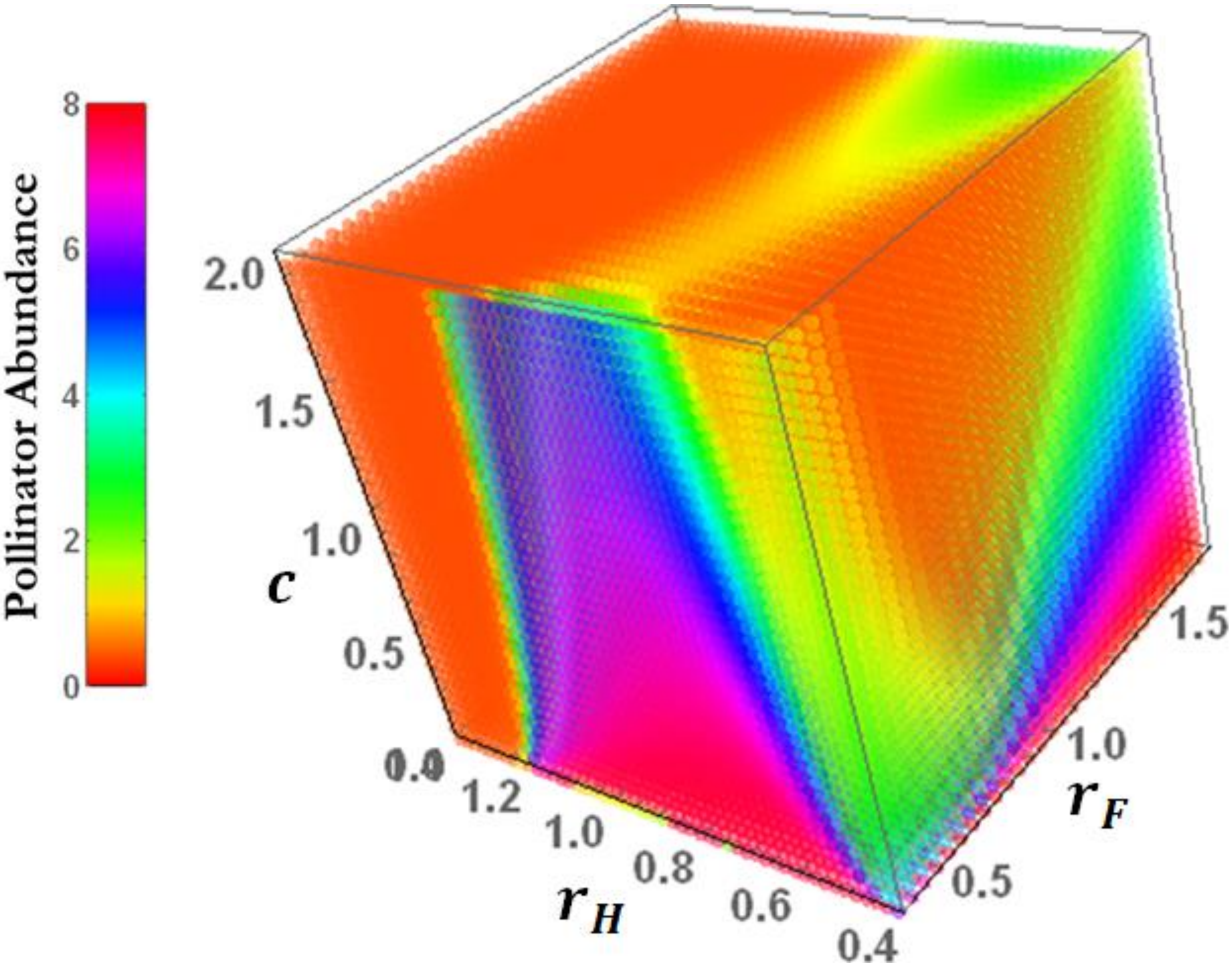


Figure D.11 - Pollinator abundance across parameter space. The equilibrium value or peak limit cycle value of P (pollinator population) at separate values of c, r_H, r_F. Parameter c represents the degree of herbivore-induced pollinator limitation. Parameter r_H represents the attack rate of the herbivore population. Parameter r_F represents the intrinsic reproductive rate of the flowering plant population. Colors represent either the equilibrium value of P or the value it takes at the maximum of oscillations in limit cycles. $b_F = 1.04, b_P = 0.85, a = 0.1, d_F = 0.2, d_H = 0.302, d_P = 0.2$; $h_F = 1$; $h_P = 1$; $c_{FH} = 1$. See Table 1 in the main text for parameter and variable definitions.

Appendix D.8 – HIPL driven rescue effect with Type I Functional Response

While we argue that the Type II functional response has the most support in the available data, it is possible that other pollination systems may support a different functional form. Therefore, there is merit in investigating the consistency of the rescue effect provided through

HIPL when using other functional responses in the model. In other words, here we will test the potential for the rescue effect with the Type I, Type III, Mixed Saturating, and Concave functional responses. Analysis shows that the rescue effect can be readily replicated across all functional response forms, with only the Concave response showing a noticeable reduction in the range of parameter space supporting community persistence. The Type I functional response for HIPL is the linear equation, $v(c,H) = 1 - c * H$. We can incorporate this form of $v(c,H)$ into the model using the Piecewise function:

$$v(c,H) = \begin{cases} 1 - c * H & when\ 1 > c * H \\ 0 & when\ 1 \leq c * H \end{cases} \tag{D.10}$$

The Piecewise formulation stops $v(c,H)$ from becoming negative at any time in simulations. This formulation means that $v(c,H)$ decreases linearly with increased herbivore abundance (H) until it reaches 0. The value of $v(c,H)$ then remains at 0 when $H \geq 1/c$. As in the main paper, the interaction rate of pollinators and flowering plants is assumed to be 1 when herbivore abundance and damage is zero. With this instantiation of the model, the linear Type I HIPL functional response can still produce the rescue effect. It is possible to create similar bifurcation heatmaps as shown in Figure D.4 in the main paper to illustrate this result (Figure D.12).

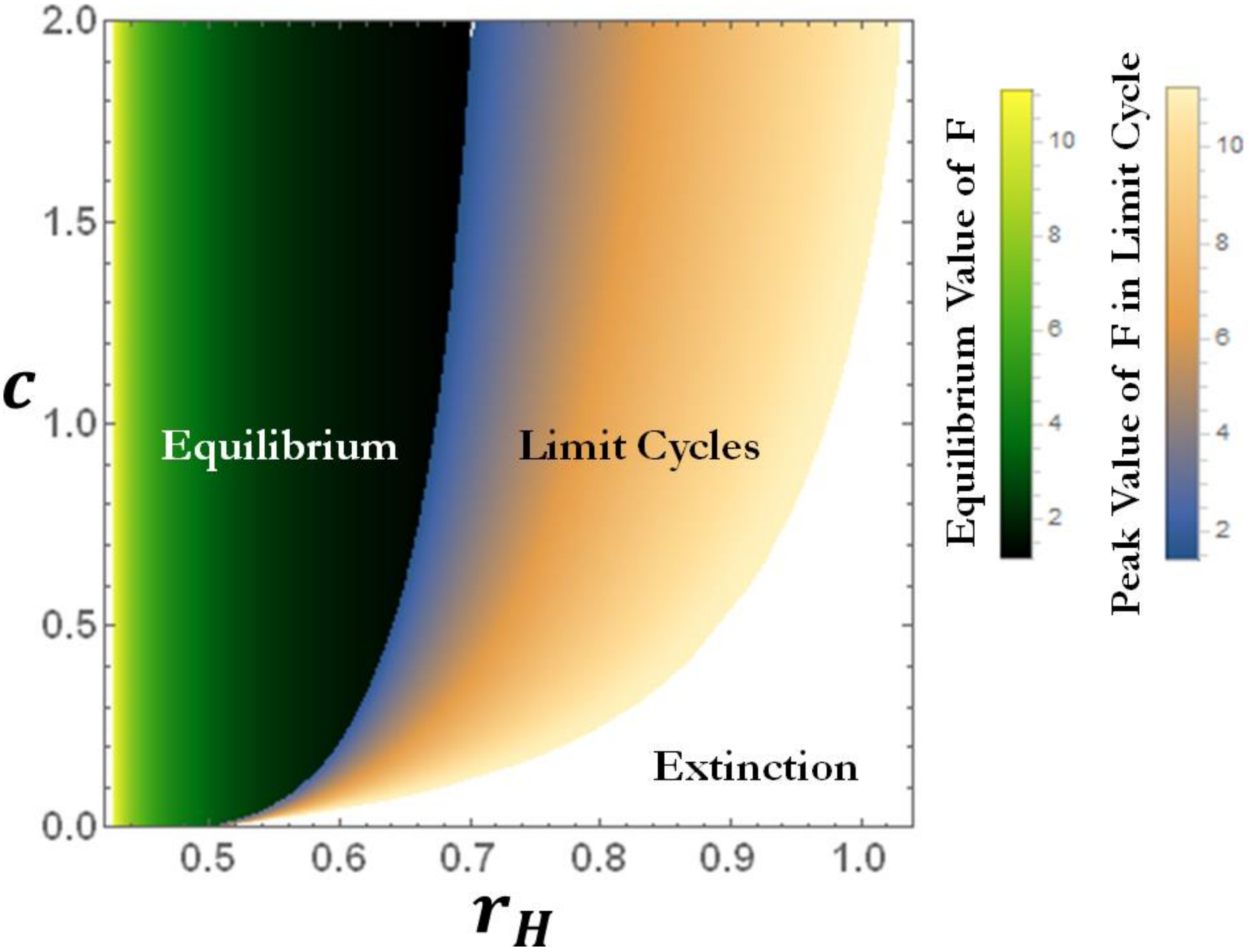


Figure D.12 - 2-D bifurcation heatmaps with TYPE I HIPL. A two-dimensional bifurcation heatmap showing the abundance of F (flowering plant) in the asymptotic behavior of the model using a TYPE I functional response for HIPL. Different asymptotic behaviors of the model are shown as different colors across the $\{r_H, c\}$ parameter space. Where parameter combinations create stable equilibria, F abundance is shown in the green color scale. Where values create stable limit cycles, F abundance is shown in the sunset color scale. Areas in white represent herbivore driven local extinction. $r_F = 0$; $b_F = 1.265$; $b_P = 1.4$; $c_{FH} = 0.7$; $d_F = 0.2$; $d_H = 0.25$; $d_P = 0.2$; $h_F = h_P = 1.1$; $\alpha = 0.1$.

Appendix D.9 – HIPL driven rescue effect with Type III Functional Response

Similar to the Type I and Type II functional response, the Type III form of HIPL was also found to produce the rescue effect. In this case, $v(c, H) = \frac{1}{1+cH^2}$. Again we present the results in the bifurcation heatmap figure (similar to Fig 5.3 in the main paper). The Type III functional response can allow for the rescue effect over similarly large subset of the parameter space (Figure D.13).

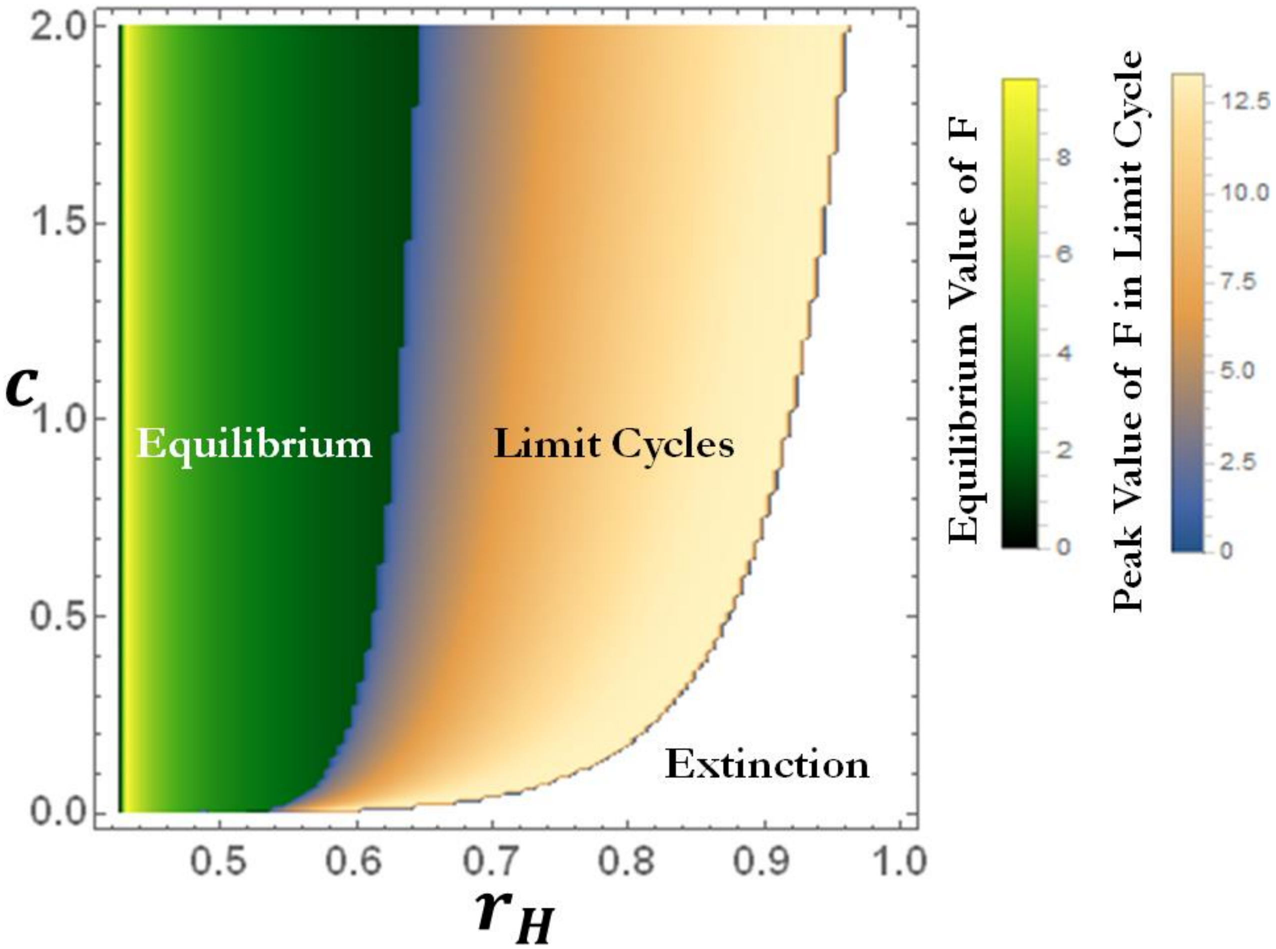


Figure D.13 - 2-D bifurcation heatmaps with TYPE III HIPL. A two-dimensional bifurcation heatmap showing the abundance of F (flowering plant) in the asymptotic behavior of the model using a TYPE III functional response for HIPL. Different asymptotic behaviors of the model are shown as different colors across the $\{r_H, c\}$ parameter space. Where parameter combinations create stable equilibria, F abundance is shown in the green color scale. Where values create stable limit cycles, F abundance is shown in the sunset color scale. Areas in white represent herbivore driven local extinction. $r_F = 0$; $b_F = 1.465$; $b_P = 1.615$; $c_{FH} = 0.7$; $d_F = 0.2$; $d_H = 0.25$; $d_P = 0.2$; $h_F = h_P = 1.1$; $\alpha = 0.1$.

Appendix D.10 – HIPL driven rescue effect with Mixed Saturating Functional Response

The Type III functional response is actually a subset/subcase of the Mixed Saturating form. From a modeling standpoint (both statistical and dynamic), the Mixed Saturating Case is a more complicated case because there are three parameters to test ($\{r_H, c, b\}$). Regardless, the Mixed Saturating form can produce the rescue effect result described in the main paper, but the details are more involved. The Type I, II, III functional responses only had one parameter per function (c), so it was possible to make the 2-D bifurcation heatmaps. In this case, there is more than one parameter for the mixed saturating functional response (parameter c and parameter b):

$$v(c, b, H) = \frac{1}{1+cH^b} \qquad \text{(D.11)}$$

Therefore, the previous 2-D $\{r_H, c\}$ bifurcation heatmaps do not show all the details and we will need to show multiple figures to describe the full dynamics. In this model we are actively changing the values of b for the first time, so we initially parse through values of b to test their comparative effects. The values of b will vary from 1 to 3 allowing us to compare dynamics of a Type II response ($b = 1$) with a Type III ($b = 2$) and the Mixed Saturating case (b generally greater than 1). First, testing the effect of b on a lower interacting system reveals that higher values of b do not restrict the range of community persistence (Figure D.14a). In fact, on the lower values of c, it appears higher b values allow for community persistence. Testing a more interactive system (Figure D.14b) offers clearer support for this idea.

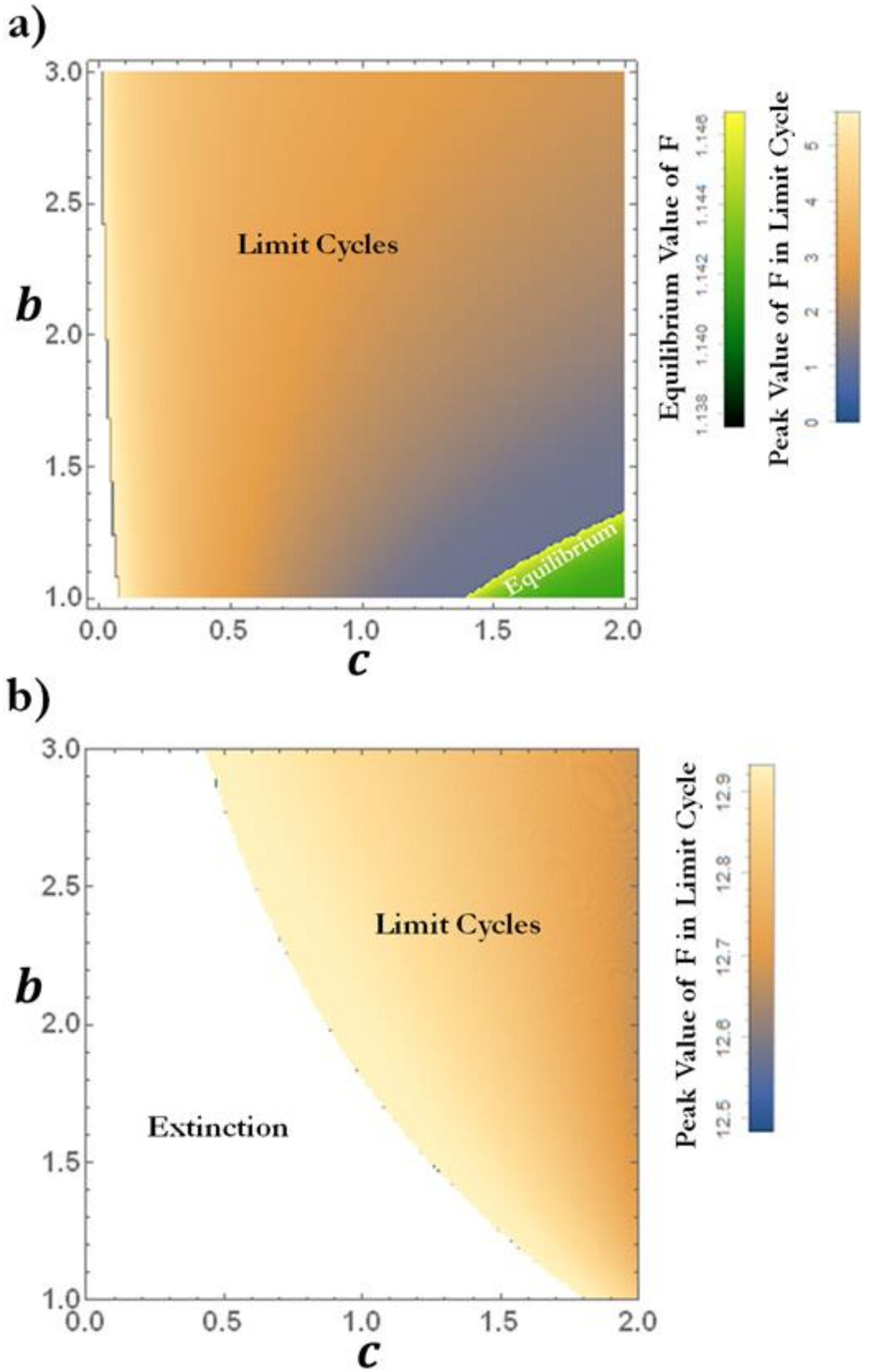


Figure D.14 - 2-D bifurcation heatmaps with Mixed Saturating HIPL. a) Two-dimensional bifurcation heatmaps showing the abundance of F (flowering plant) in the asymptotic behavior of the model using a Mixed Saturating functional response for

HIPL. Different asymptotic behaviors of the model are shown as different colors across the $\{b, c\}$ parameter space. Where parameter combinations create stable equilibria, F abundance is shown in the green color scale. Where values create stable limit cycles, F abundance is shown in the sunset color scale. Areas in white represent herbivore driven local extinction. a) $b_F = b_P = 0.78$, $r_H = 0.67$, $c_{FH} = 0.7$; $d_F = 0.2$; $d_H = 0.25$; $d_P = 0.2$; $h_F = h_P = 1.1$; $\alpha = 0.1$. b) $b_F = 1.45$, $b_P = 1.55$, $r_H = 0.91$, $c_{FH} = 0.7$; $d_F = 0.2$; $d_H = 0.25$; $d_P = 0.2$; $h_F = h_P = 1.1$; $\alpha = 0.1$.

To more fully understand the role of parameter b in model dynamics and the rescue effect, we expanded the parameter sweep to include r_H so that persistence could be measured across over 453,000 parameter combinations in $\{c, b, r_H\}$ parameter space. The parameter sweep done to construct this graph was done with r_H values from 0.45 to 1.0 with 0.01 steps, c values from 0.0 to 2.0 with 0.02 steps, and b values from 1 to 3 with 0.02 steps. Upon completion of the analysis, we found that increased values of b expand the range of the HIPL derived rescue effect in $\{r_H, c\}$ parameter space (Figure D.15). As indicated in Figure D.14b, this expansion largely results from the reduction in the value of c required to sufficiently control the herbivore population prompting the rescue effect.

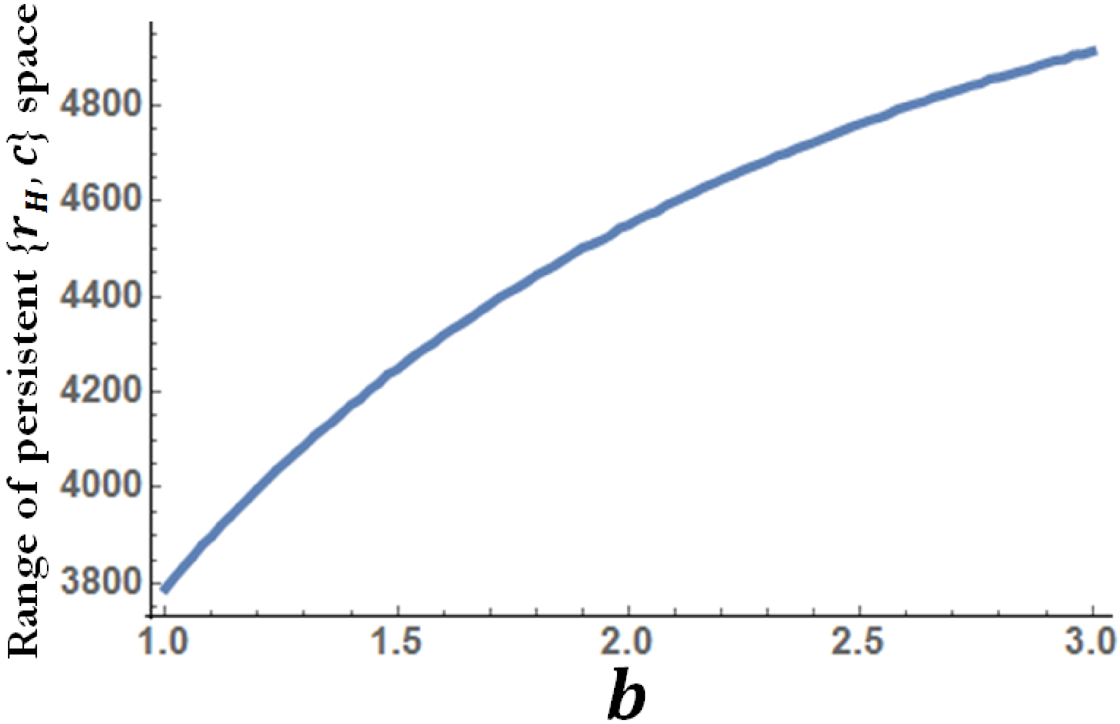


Figure D.15 - Change in persistent parameter space across values of b. Measurements of the number of $\{r_H, c\}$ parameter combinations across a range of b values where the HIPL rescue effect enables persistent communities. The y-axis in the case is the actual count of distinct parameter combinations which HIPL supports persistent communities. This shows the range of the rescue effect increases with higher values of b. Parameter values are $b_F = 1.45, b_P = 1.55, c_{FH} = 0.7,\ d_F = 0.1, d_P = 0.1, d_H = 0.1, h = 1.1,\ \alpha = 0.1$.

Higher values of b not only reduce the level of c required for persistence, they also slightly increase the level of herbivore attack rate (i.e. higher r_H) that the system can withstand before local extinction (Figure D.16). The heatmap in Figure D.16 does not show asymptotic value of the flowering plant population as it does in other heatmaps. Instead it shows the lowest value of c (lowest level of HIPL) that the system could withstand and still persist. Intuitively, lower values of r_H require lower values of c for the rescue effect. Higher values of b also can also decrease the minimum value of c needed to support community persistence. This is shown in two color schemes in Figure D.16 to make the point clearer.

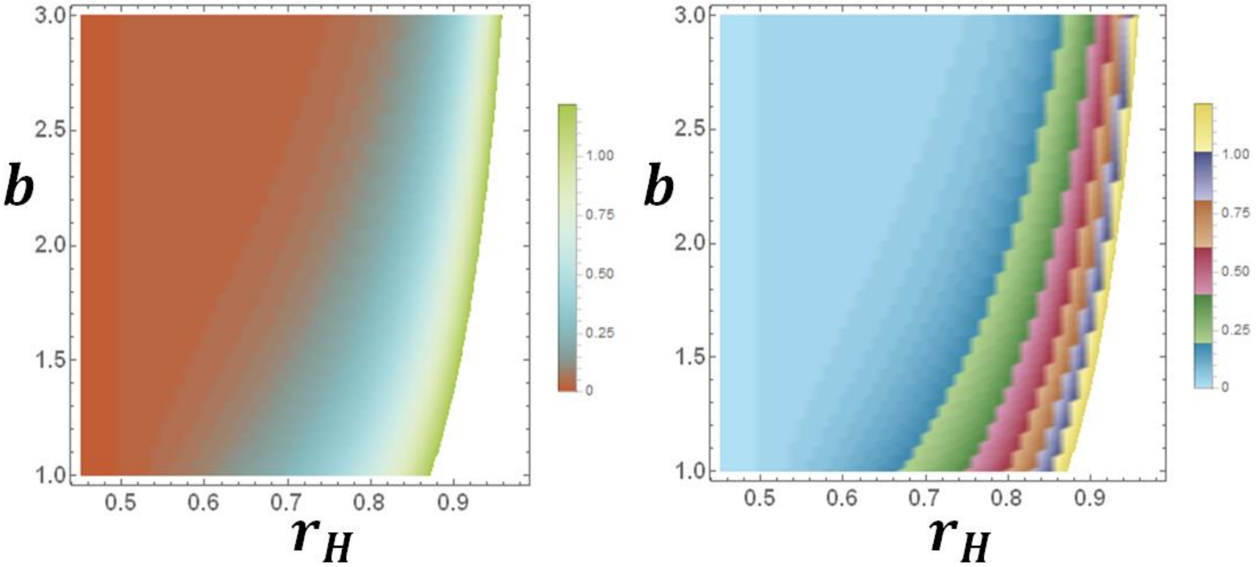


Figure D.16 - Minimum value of c required for community persistence. Heatmap showing the minimum value of c required to support system persistence through the rescue effect of HIPL across the range of all tested values of r_H and b. This minimum value of c is shown in the colors of each graph explained by the color legend to the right of each figure. The same figure is shown with two different color schemes to represent the minimum required c value in an easily visible manner. Parameter values are $b_F = 1.45, b_P = 1.55, c_{FH} = 0.7,\ d_F = 0.1, d_P = 0.1, d_H = 0.1, h = 1.1, \alpha = 0.1$.

The cause of this increase in the range of community persistence across parameter space results from the fact that higher b values (i.e. $b > 1$) do two things to the shape of the $v(c, H)$ function. First, it creates a delay in the immediate effect of HIPL, such that higher herbivore abundance is required to see a decrease in pollinator visitation ($v(c, b, H)$). Second, once the herbivores are abundant, higher b values make the resulting decrease in pollinator visitation progressively steeper, such that the decline in pollinator visitation is quite rapid. While the first effect would seem detrimental, when coupled with the second effect, it can actually be beneficial. A less immediate decline in $v(c, b, H)$ at low herbivore abundance can actually help the pollinator and plant populations rebound during troughs in the population trajectory because low herbivore abundance won't impede pollination. This effect by itself would then fail to control herbivore populations as the populations rebounded, but the concurrent steep decline in pollination once herbivore abundance become sufficiently high (the second effect above), helps regain the indirect control of the herbivore population growth through greater reductions in v (Figure D.17).

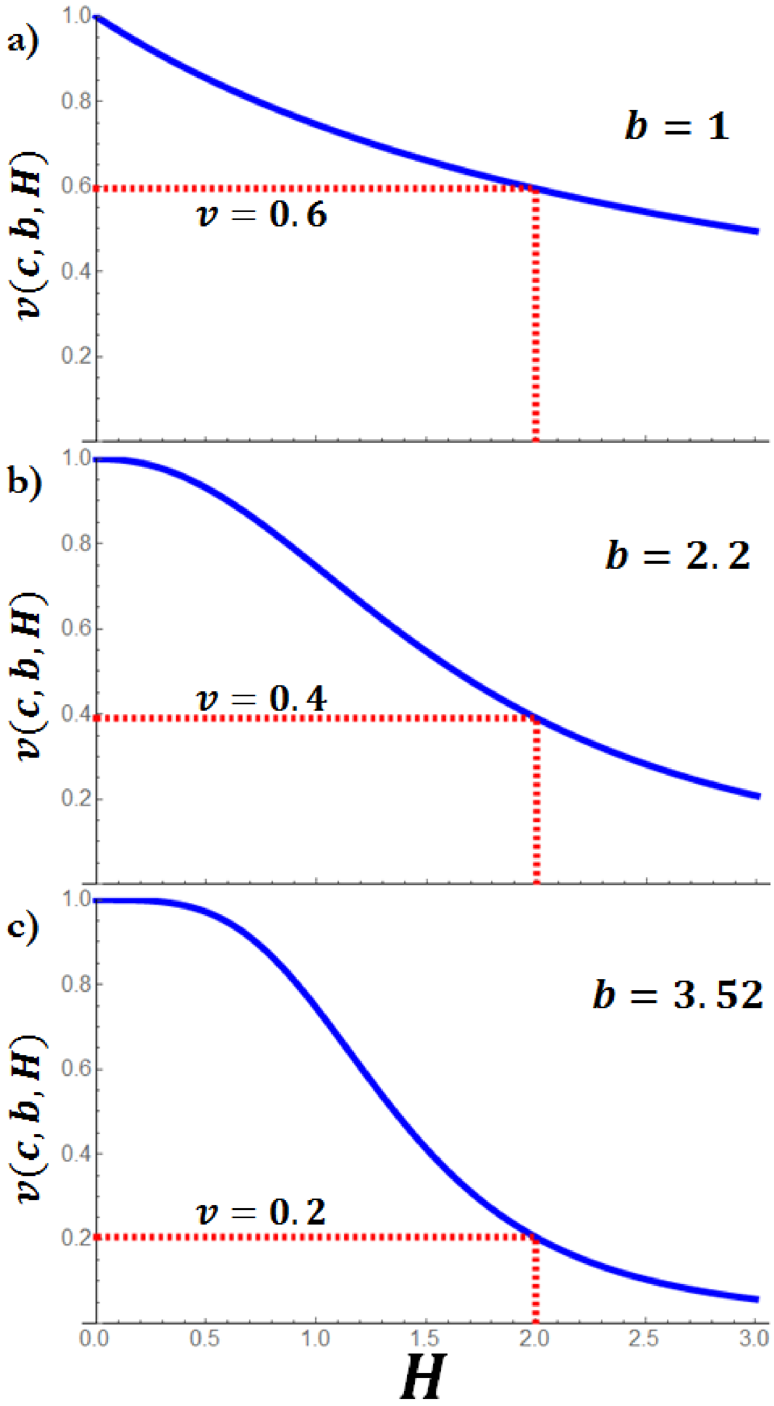


Figure D.17 - Changes in the shape v for different values of b. The resultant value of the pollination visitation parameter $v(c, b, H)$ (shown in blue) across herbivore abundance (H) at different levels of the parameter b when using the Mixed Saturating functional response form: a) $b = 1$, b) $b = 2.2$, c) $b = 3.52$. The red dashed line shows the value of $v(c, b, H)$ when the herbivore abundance (H) equals 2.0. Here, $c = 0.34$. As the value of b increases, the shape of the function changes such that the eventual decrease in $v(c, b, H)$ becomes very steep. Therefore, $v(0.34, b, 2)$ decreases resulting in more HIPL and lower pollination rates.

Appendix D.11 – HIPL driven rescue effect with Concave functional response

Various numerical simulations show that it is possible to recreate the rescue effect with the Concave Functional Response (Figure D.18). However, the Concave functional response generally created the smallest parameter space in which the rescue effect could be found. By creating the longest delays in declining the pollinator visitation rate (v), the Concave functional response can significantly hinder any possible direct control of the herbivore population through HIPL. The concave model is the least supported direct curve fit we attempted, so we claim that the only functional response type that noticeable reduces the range of the rescue effect in the model does not seem well supported. With this we can claim that the main results presented in the paper are robust to most functional responses types.

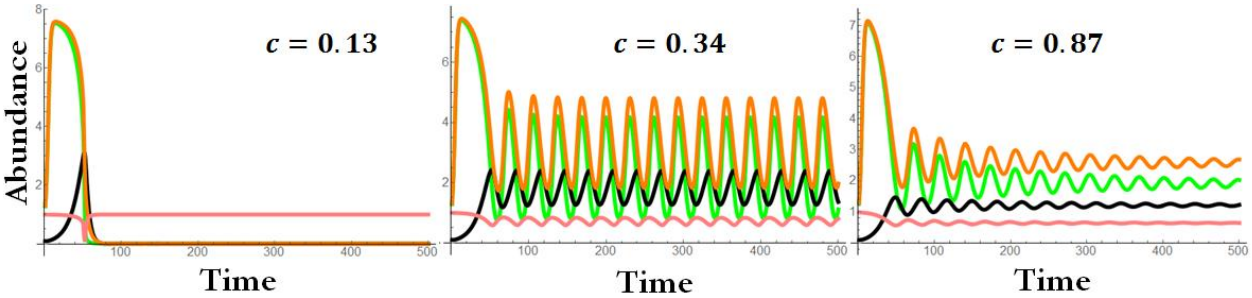


Figure D.18 - Rescue effect of HIPL with Concave functional response. Three time series showing the rescue effect using a Concave functional form of HIPL. Parameter values: $r_H = 0.58,\ b_F = 1.095,\ b_P = 1.095,\ c_{FH} = 0.7, h = 1.1,\ c = 0.13,$ $0.338,\ 0.868, \alpha = 0.1, d_F = 0.1, d_P = 0.1, d_H = 0.1$,. The green line, orange line, and black line represent the flowering plant, pollinator, and herbivore respectively. The pink line is the value of the $v(c, H)$ function as a response to the herbivore abundance.

Appendix D.12 - References:

Adler LS & Irwin RE. 2005. Ecological costs and benefits of defenses in nectar Ecology. 86(11): 2968–2978.

Barber N, et al. Herbivory reduces plant interactions with above- and belowground antagonists and mutualists. Ecology 93(7): 1560-1570 (2012).

Kessler A & Halitschke R. .2009. Testing the potential for conflicting selection on floral chemical traits by pollinators and herbivores: predictions and case study. Functional Ecology 23: 901–912

Kessler A, Halitschke R, Poveda K.2011. Herbivory-mediated pollinator limitation: negative impacts of induced volatiles on plant–pollinator interactions. Ecology 92(9): 1769–1780.

Krupnick GA, Weis AE, Campbell DR. 1999. The consequences of floral herbivory for pollinator service to Isomeris arborea. Ecology 80:125–134.

Strogatz SH. Nonlinear Dynamics and Chaos: with Applications to Physics, Biology, Chemistry and Engineering. 1994. Westview Press, 11 Cambridge Center, Cambridge, MA 02142.

Appendix E– Appendices to Chapter 6

Appendix E.1 - Plant Reproduction Obligate on Syrphid Pollination ($\boldsymbol{r_F = 0, b_F > 0}$)

E.1.1 - Non-zero, positive-real-valued 4-variable equilibria for obligate-specialist pollination model:

Below are printed the two real-valued non-zero positive 4-variable equilibria of the obligate pollination model in their parametric expressions. The parametric expressions of the equilibria are too large to show any biological relevance themselves. Numeric and graphical investigations are required and presented in the main paper.

Equilibrium 6.1:

$$F^* \to \frac{\alpha a_S d_S + b_F c_{FH} d_S a_H - \dfrac{\sqrt{d_S}\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}}{\sqrt{c_{HS}}}}{2\alpha a_S b_s}$$

$$H^* \to \frac{-\left(2\alpha d_S^{\frac{3}{2}}\right)}{\alpha a_S c_{HS}\sqrt{d_S} - b_F c_{FH} c_{HS}\sqrt{d_S} a_H + \sqrt{c_{HS}}\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}}$$

$$S_L^* \to -\frac{1}{2\alpha a_S^2 b_S}\left(\begin{array}{c} -b_F c_{FH}^2 d_S a_H^2 + \alpha a_S(-2b_s d_H - c_{FH} d_S a_H) + \\ \dfrac{c_{FH}\sqrt{d_S} a_H}{\sqrt{c_{HS}}}\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2} \end{array}\right)$$

$$S_A^* \to \frac{\left(\begin{array}{c} \dfrac{\alpha a_S c_{HS} d_S (b_S d_H - c_{FH} d_S a_H) - b_S\sqrt{c_{HS}} d_H \sqrt{d_S}}{\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}} \\ \dfrac{+c_{FH}\sqrt{c_{HS}} d_S^{\frac{3}{2}} a_H}{\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}} \\ c_{FH} d_S a_H\big(2b_S d_S a_H + b_F c_{HS}(b_S d_H - c_{FH} d_S a_H)\big) \end{array}\right)}{2a_S b_S(b_F b_S c_{HS} d_H + (b_S - b_F c_{FH} c_{HS}) d_S a_H)}$$

Equilibrium 6.2:

$$F^* \to \frac{\begin{array}{c}\alpha a_S d_S + b_F c_{FH} d_S a_H + \\ \dfrac{\sqrt{d_S}\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}}{\sqrt{c_{HS}}}\end{array}}{2\alpha a_S b_s}$$

$$H^* \to \frac{\left(2\alpha d_S^{\frac{3}{2}}\right)}{\begin{array}{c}\alpha a_S c_{HS}\sqrt{d_S} - b_F c_{FH} c_{HS}\sqrt{d_S}\, a_H + \\ \sqrt{c_{HS}}\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}\end{array}}$$

$$S_L^* \to -\frac{1}{2\alpha a_S^2 b_S}\left(\begin{array}{c}-b_F c_{FH}^2 d_S r_H^2 + \alpha a_S(-2b_s d_H - c_{FH} d_S r_H) - \\ \dfrac{c_{FH}\sqrt{d_S}\, a_H}{\sqrt{c_{HS}}}\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}\end{array}\right)$$

$$S_A^* \to \frac{\left(\begin{array}{c}\dfrac{\alpha a_S c_{HS} d_S (b_S d_H - c_{FH} d_S a_H) + b_S\sqrt{c_{HS}}\, d_H\sqrt{d_S}}{\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}} \\ \dfrac{-c_{FH}\sqrt{c_{HS}}\, d_S^{\frac{3}{2}}\, a_H}{\sqrt{\alpha a_s c_{HS}(-4b_F b_S d_H + \alpha a_S d_S) + 2\alpha a_S(-2b_S + b_F c_{FH} c_{HS}) d_S a_H + b_F^2 c_{FH}^2 c_{HS} d_s a_H^2}} \\ c_{FH} d_S a_H\big(2b_S d_S a_H + b_F c_{HS}(b_S d_H - c_{FH} d_S a_H)\big)\end{array}\right)}{2a_S b_S(b_F b_S c_{HS} d_H + (b_S - b_F c_{FH} c_{HS}) d_S a_H)}$$

E.1.2 - Graphical representation of parameter space which creates positive-real valued Eqm 6.1 and Eqm 6.2:

Figure E.1 gives an example of the parameter space where Eqm 6.1 and Eqm 6.2 are real-valued and positive in the obligate model. There is no parameter space which created stable versions of Eqm 6.1 or Eqm 6.2.

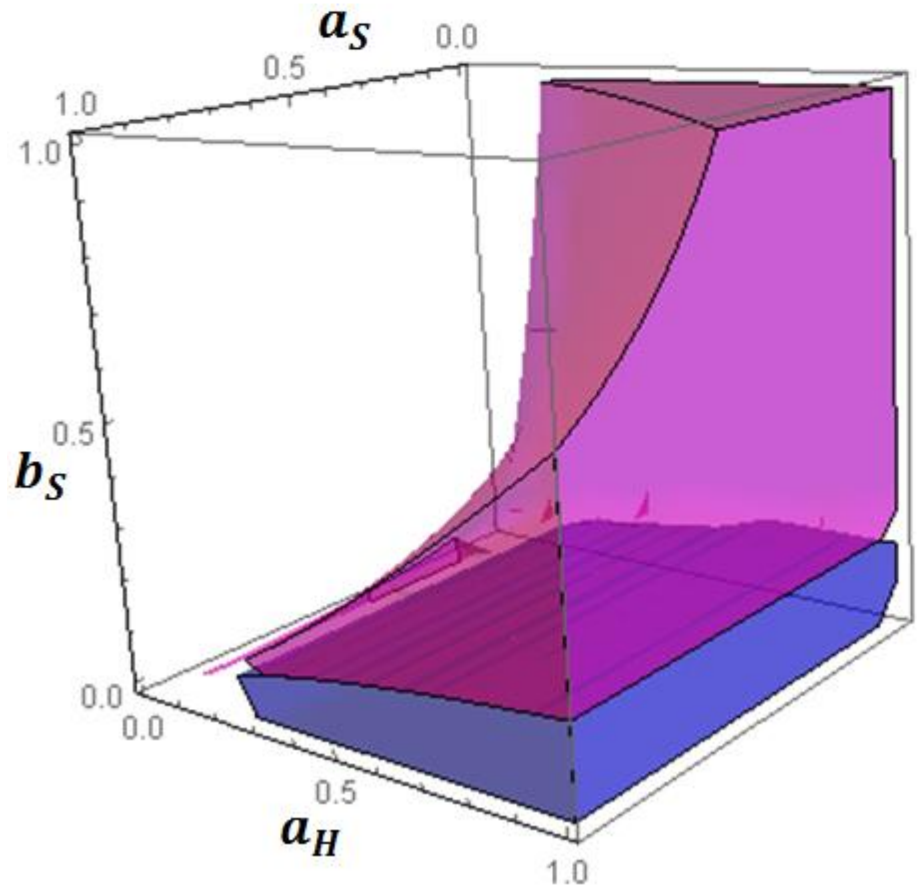


Figure E.1 - A graphical representation of the some of the parameter space which creates positive-real valued Eqm 6.1 and Eqm 6.2 in the obligate-specialist model. The blue shaded region represents parameter space where only Eqm 6.1 is positive-real valued. The magenta shaded region represents parameter space where both Eqm 6.1 and Eqm 6.2 are positive-real valued. Non-shaded regions support no positive-real valued equilibrium. $b_F = 0.3$.

Appendix E.2 - Nominal Syrphid Pollination, Non-Syrphid Dependent Growth ($\boldsymbol{r_F > 0, b_F = 0}$)

E.2.1 - Non-zero, positive-real-valued equilibria for nominal pollination model:

Below are printed the two real-valued non-zero positive 4-variable equilibria of the nominal pollination model in their parametric expressions. The parametric expressions of the equilibria are too large to show any biological relevance themselves. Numeric and graphical investigations are required and presented in the main paper.

Equilibrium 6.1:

$$F^* \to \frac{\alpha d_S + b_S r_F - \frac{\sqrt{a_S c_{HS}(\alpha d_S - b_S r_F)^2 - 4\alpha b_S d_S^2 a_H}}{\sqrt{a_S}\sqrt{c_{HS}}}}{2\alpha b_S}$$

$$\frac{H^* \to \sqrt{a_S c_{HS}}(-\alpha d_S + b_S r_F) + \sqrt{a_S c_{HS}(\alpha d_S - b_S r_F)^2 - 4\alpha b_S d_S^2 a_H}}{2\sqrt{a_S}\, b_S \sqrt{c_{HS}}\, a_H}$$

$$S_L^* \to \frac{\begin{pmatrix} -c_{FH} a_H \sqrt{a_S c_{HS}(\alpha d_S - b_S r_F)^2 - 4\alpha b_S d_S^2 a_H} \\ +\sqrt{a_S c_{HS}}(-2\alpha b_S d_H + \alpha c_{FH} d_S a_H + b_S c_{FH} r_F a_H) \end{pmatrix}}{2\alpha a_S^{\frac{3}{2}} b_S \sqrt{c_{HS}}}$$

$$S_A^* \to \frac{\begin{pmatrix} 2 b_S c_{FH} d_S^2 a_H^2 + \alpha a_S c_{HS} d_S (b_S d_H - c_{FH} d_S a_H) + a_S b_S c_{HS} r_F (-b_S d_H + c_{FH} d_S a_H) + \\ \sqrt{a_S c_{HS}}(-b_S d_H + c_{FH} d_S a_H)\sqrt{a_S c_{HS}(\alpha d_S - b_S r_F)^2 - 4\alpha b_S d_S^2 a_H} \end{pmatrix}}{2 a_S b_S^2 d_S a_H}$$

Equilibrium 6.2:

$$F^* \to \frac{\alpha d_S + b_S r_F + \frac{\sqrt{a_S c_{HS}(\alpha d_S - b_S r_F)^2 - 4\alpha b_S d_S^2 a_H}}{\sqrt{a_S}\sqrt{c_{HS}}}}{2\alpha b_S}$$

$$\frac{H^* \to \sqrt{a_S c_{HS}}(-\alpha d_S + b_S r_F) - \sqrt{a_S c_{HS}(\alpha d_S - b_S r_F)^2 - 4\alpha b_S d_S^2 a_H}}{2\sqrt{a_S}\, b_S \sqrt{c_{HS}}\, a_H}$$

$$S_L^* \to \frac{\begin{pmatrix} c_{FH} a_H \sqrt{a_S c_{HS}(\alpha d_S - b_S r_F)^2 - 4\alpha b_S d_S^2 a_H} \\ +\sqrt{a_S c_{HS}}(-2\alpha b_S d_H + \alpha c_{FH} d_S a_H + b_S c_{FH} r_F a_H) \end{pmatrix}}{2\alpha a_S^{\frac{3}{2}} b_S \sqrt{c_{HS}}}$$

$$S_A^* \to \frac{\begin{pmatrix} 2 b_S c_{FH} d_S^2 a_H^2 + \alpha a_S c_{HS} d_S (b_S d_H - c_{FH} d_S a_H) + a_S b_S c_{HS} r_F (-b_S d_H + c_{FH} d_S a_H) + \\ \sqrt{a_S c_{HS}}(b_S d_H + c_{FH} d_S a_H)\sqrt{a_S c_{HS}(\alpha d_S - b_S r_F)^2 - 4\alpha b_S d_S^2 a_H} \end{pmatrix}}{2 a_S b_S^2 d_S a_H}$$

E.2.2 - Finding 3-dimensional volumes in $\{a_H, b_S, a_S\}$ parameter space

In the nominal pollination model, dynamics are investigated across values of four parameters: $\{r_H,\ a_H, b_S, a_S\}$. In order to complete a linear stability analysis in a 4-dimensional parameter space, the volume of local stability inducing 3-dimensional parameter space $\{a_H, b_S, a_S\}$ is measured across different values of r_F. This is a way to indirectly see the effects of r_F on the amount of $\{a_H, b_S, a_S\}$ parameter combinations that cause Equilibrium 6.1 to be locally stable.

In order to calculate these volumes, stable regions of $\{a_H, b_S, a_S\}$ parameter space were first found at specific values of r_F using the RegionPlot3D function in Mathematica 10. This was able to produce the 3-dimensional regions like that shown in Fig 6.4a. Once these regions were found, they were split into sub-regions where only Eqm 6.1 exists (Figure E.2a) and where Eqm 6.1 and 6.2 exist (Figure E.2b). Discretized-mesh versions of each of these regions were then created using the DiscretizeGraphics function. These discretized regions of stable $\{a_H, b_S, a_S\}$ parameter space were created where only Equilibrium 6.1 exists (see Figure E.2a&E.2c) and regions where both Equilibrium 6.1 and Equilibrium 6.2 exist (see Figure E.2b&E.2d) across different values of r_F. Depending on the thinness of the stable regions, this would occasionally produce some tearing in the approximate regions. Given that these are approximations and used to show relative effect of r_F on stable $\{a_H, b_S, a_S\}$ volume (not the absolute volume), this is acceptable. An example of these discretized regions of parameter space is available in Figure E.1 where it shows the discretized versions of the stable parameter space shown in Fig 6.4a.

Volumes of discretized regions can be calculated by utilizing tetrahedrons constructed from the mesh triangles and some fixed fourth point. The volume of each tetrahedron is calculated and either added or subtracted from the total region volume depending on the direction of the normal of the surface. For an in-depth description of this process please see Zhang & Chen (2001). Volumes of stable $\{a_H, b_S, a_S\}$ parameter space were calculated across $0 \leq r_F \leq 1$. They are displayed in Figure 6.4e.

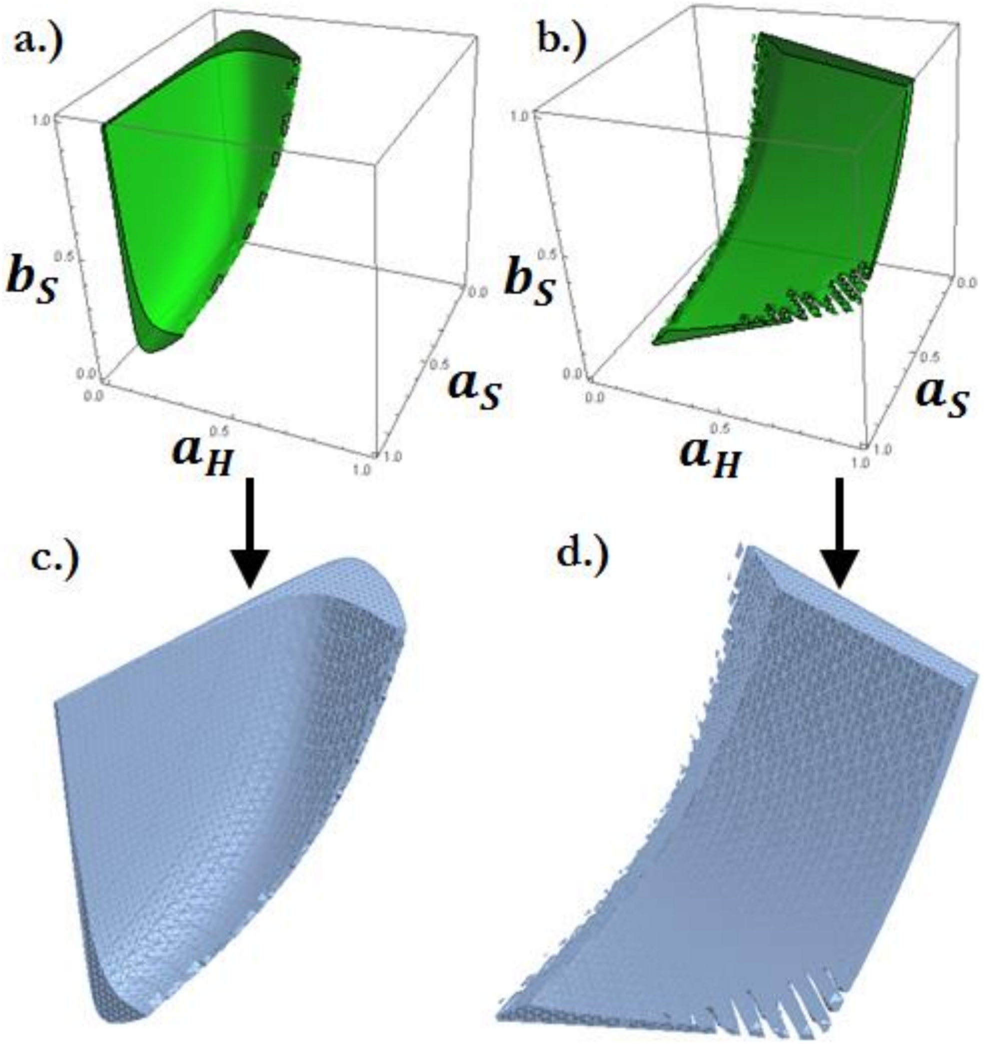
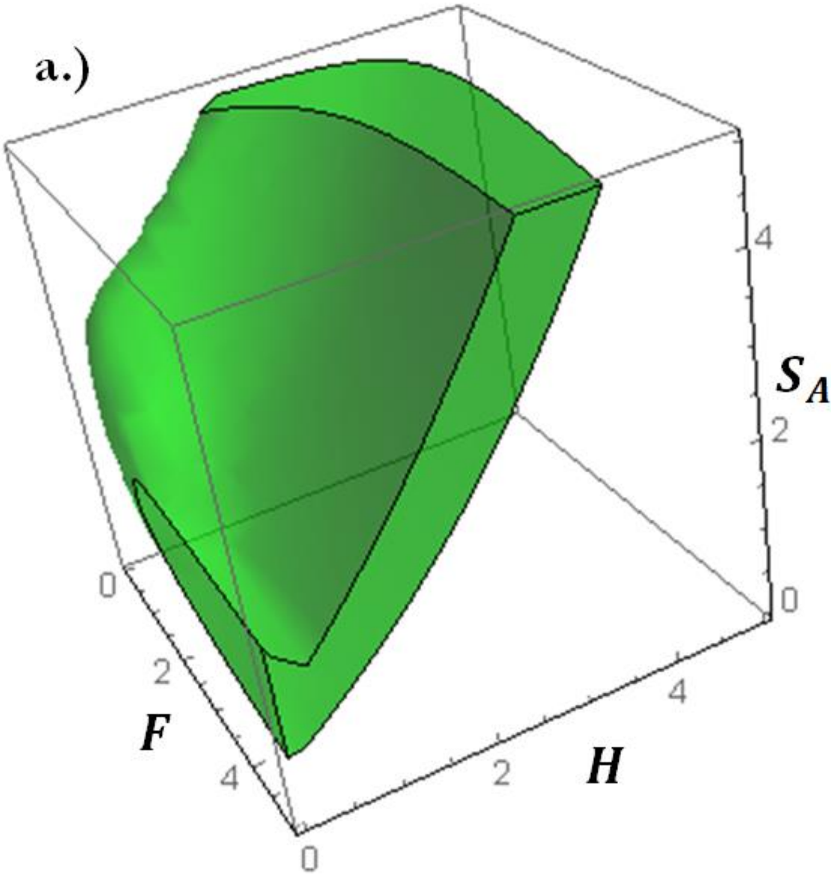


Figure E.2 - Discretized versions of the stable $\{a_H, b_S, a_S\}$ parameter space shown in Fig 6.4a where $r_F = 0.1$. a) Region of stable $\{a_H, b_S, a_S\}$ parameter space where only Eqm 6.1 exists. b) Region of stable $\{a_H, b_S, a_S\}$ parameter space where both Eqm 6.1 and Eqm 6.2 exist. c) The discretized stable region where only Eqm 6.1 exists. d) discretized stable region when both Eqm 6.1 and Eqm 6.2 exist. The areas of each were calculated separately and added to together across values of r_F to make Fig 6.4b.

E.2.3 - Basin of Attraction: Evidence for a lack of global stability

Both the stable equilibria and stable oscillatory dynamics were found to have limited basins of attraction such that the 4-variable attractors are not globally stable. Phase space is split between the basin of attraction for attractors which support persistence of all four variables and the basin of attraction for the two-variable solution where only F and H remain. This two-variable solution is the result of large peaks in syrphid oscillations which cause crashes in both S_L and S_A. Recall that because $r_F > 0$ the consumer resource F, H system is a viable solution in this system.

While Eqm 6.1 was found to be locally stable at numerous parameter combinations, these locally stable parameter combinations were found to create equilibria which are not globally stable in simulations. In these cases, phase space is split into two basins of attraction: a basin for the stable Eqm 6.1 and a basin for the two population solution where the syrphid population goes extinct leaving only F and H (consumer-resource) community (Figure E.3a). Note, Figure E.3 is not meant to be an accurate representation of the basins of attraction in phase space for either attractor. I have fixed the initial condition of S_L. This figure only illustrates the point that the stable 4-variable is not globally stable for certain parameter combinations. Figure E.3b gives an example of two different initial conditions leading to two different outcomes. The green trajectory lies in the basin of attraction for 4-variable-full community equilibrium. The orange trajectory lies in the basin of attraction for the F, H consumer-resource community. Note, in Figure E.3a, S_A represents just the syrphid adults. In Figure E.3b, S_R represents $S_A + S_L$.



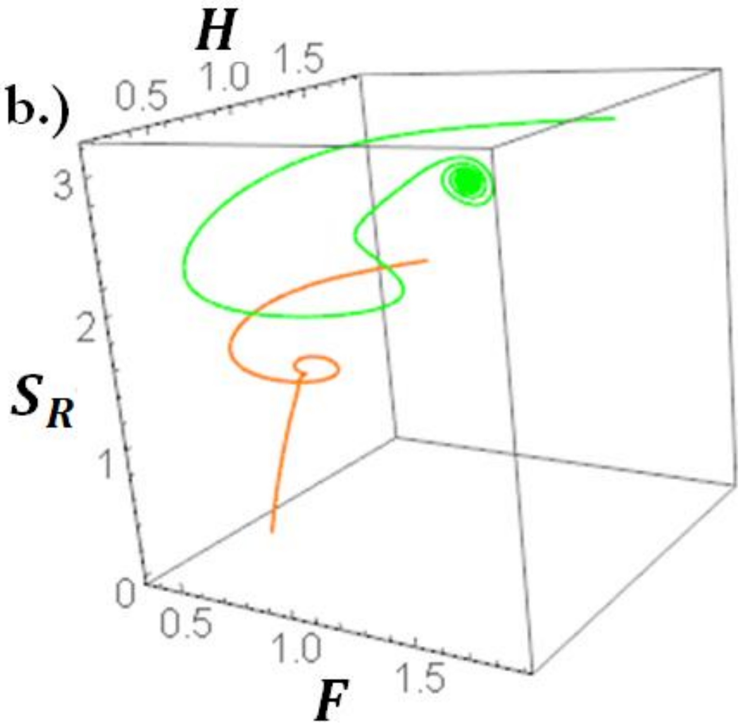


Figure E.3 - An example of parameter space splitting phase space into two different basins of attraction in the nominal pollination model. a) Phase space is split between the basin of attraction for a stable Eqm 6.1 (green) and the basin for the $\{F, H\}$ system after S_F extinction (all other non-green regions). Only 3 dimensions are shown here, $F, H,$ and S_A. S_L is constant at.68. b) Two time series in either basin of attraction. The green trajectory lies in the basin of attraction for 4-variable-full community equilibrium. The orange trajectory lies in the basin of attraction for the F, H consumer-resource community. Parameter values: $r_F = 0.235;\ a_H = 0.262;\ b_S = 0.15;\ a_S = 0.215;\ b_S = 0; a = 0.1; c_{FH} = c_{HS} = 1; dh = 0.13; d_{SL} = 0.2; d_{SA} = 0.05.$

Appendix E.3 - Facultative Pollination ($r_F > 0, b_F > 0$)

E.3.1 - Non-zero, positive-real-valued equilibria for facultative pollination model:

The parametric expressions of Equilibrium 6.1 and Equilibrium 6.2 in the facultative model are large enough that they will not cleanly fit onto a manuscript page. Therefore, they will not be produced here as they do not add any further biological inference into the model's behavior. However, below I reproduce simple Mathematica code that will allow the interested reader to print each equilibrium in Mathematica:

$$\begin{aligned}
\text{Solve}[F * (\text{rf} + (\text{bf} * \text{Sa}) - a * F) - (\text{ah} * F * H) = \\
= 0\&\&(\text{ah} * \text{cfh} * F * H) - (\text{as} * \text{Sl} * H) - \text{dh} * H = \\
= 0\&\&\text{Sa} * (\text{bs} * F) - (\text{as} * \text{chs} * \text{Sl} * H) - \text{ds} * \text{Sl} = \\
= 0\&\&(\text{as} * \text{chs} * \text{Sl} * H) - \text{ds} * \text{Sa} == 0, \{F, H, \text{Sl}, \text{Sa}\}]//\text{FullSimplify}
\end{aligned}$$

The parameters are the same those described in Table 1. The four populations are: F the flowering plant, H the herbivore, Sl the syrphid larvae, Sa the syrphid adult.

E.3.2 - Effects of b_F and r_F on facultative model stability

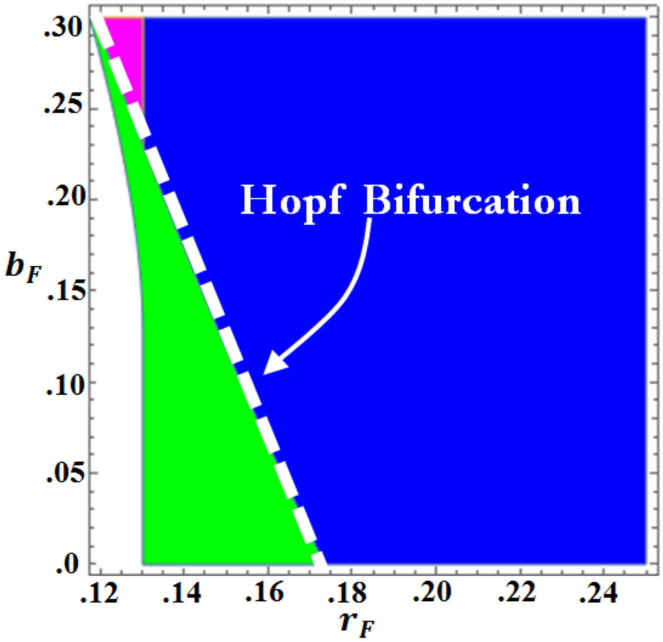


Figure E.4 - Diagram showing stable and unstable parameter space for Equilibrium 6.1 in the facultative pollination model. The dark blue region depicts where Equilibrium 6.1 exists in positive-real-valued phase space but is unstable. The small magenta region depicts where both Equilibrium 6.1 and 6.2 exist as unstable equilibria in positive-real-valued phase space. The green region depicts where Equilibrium 6.1 exists and is stable. The dashed white line shows the super critical Hopf bifurcation. $a_H = 0.126, b_S = 0.216, a_S = 0.27, c_{FH} = c_{HS} = 1, d_h = 0.13; d_{SL} = 0.2; d_{SA} = 0.05$.

E.3.3 - Oscillatory dynamics in facultative model:

Regardless of whether FHS system oscillations are stable or chaotic, sufficiently high values of b_F cause the maxima of S_L to rise high enough that predation pressure lowers H to the point that the syrphid population cannot be sustained. This causes S_R to tend toward zero. This leaves only F which is able to persist due to positive r_F values. With a persistent F population, H is able to increase and there is a temporary 2-variable solution as the F, H community tends toward equilibrium. This is the case given a Lotka-Volterra consumer resource model with density dependence and no functional response. Eventually, the S_L and S_A populations experience positive growth as syrphid larvae feed on H and syrphids recover from the population crash. This then causes another large spike in overall community growth and subsequent crash in syrphid abundance (Figure E.5).

These population trajectories function somewhat similarly to what is known as a homoclinic cycle. In homoclinic cycles the system nearly reaches a stable equilibrium before being moved away from the equilibrium, only to nearly return to the equilibrium again repeating the cycle. The FHS model does exhibit this behavior in this case. However, in homoclinic cycles, trajectories stay near the equilibrium for increasingly longer periods of time in each consecutive cycle as time evolves. The FHS model does not exhibit this behavior. Each period between cycles is consistent across time.

The periods between these peaks and the positive growth spikes in syrphid populations does increase with higher b_F values and is generally part of the expanding period between maxima detailed in Fig 6.7. However, once b_F values are sufficiently high enough to cause the long periods of F, H communities (Figure E.5c&E.5d), the recovery of the syrphid populations is mainly a product of the ODE structure of the model allowing for infinitesimally small abundances to exist without extinction. One could argue that even though, increasing b_F does generally lead to longer periods in oscillations (Fig 6.7), once b_F reaches some undefined value, the model essentially results in extinction of the syrphid population. Given the mutualistic relationship between the syrphid and flowering plant, this is a somewhat unintuitive result.

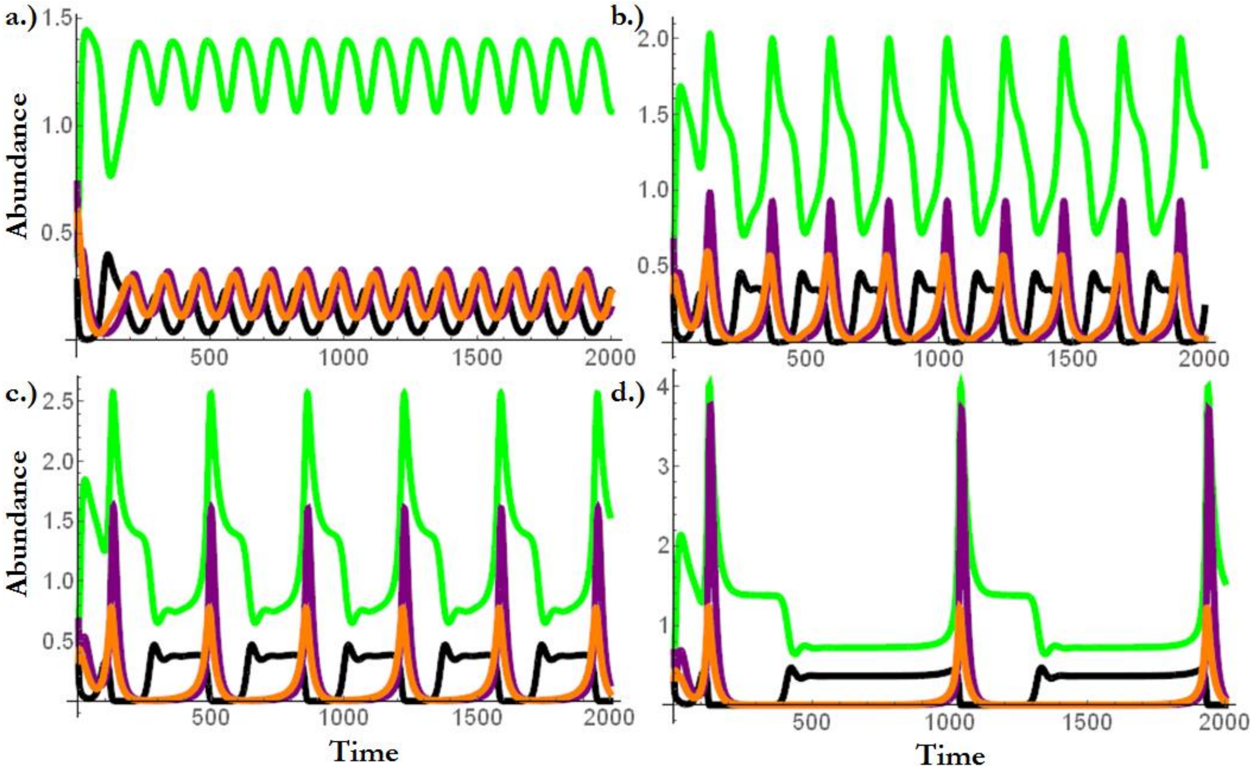


Figure E.5 - Example time series across different values of b_F in the facultative model showing that while periods of oscillations do increase, there are long stretches with the syrphid population approaching zero. Time dependent variables F, H, S_L, and S_A are shown in green, black, purple, and orange respectively. a.) $b_F = 0.045$. b) $b_F = 0.138$. c) $b_F = 0.18$. d) $b_F = 0.24$. Other parameters: $r_F = 0.138, r_H = 0.18, b_S = 0.204, a_S = 0.475, c_{FH} = c_{HS} = 1$.

Appendix E.4 - Non-linear Interactions/Functional Responses:

Certain results warrant an initial investigation into the effects of non-linear interactions. With some alterations, the model can also take into account non-linear interactions (e.g. functional responses) for pollination, herbivory, and predation (Equation E.1). Handling time of pollination, herbivory of flowering plants, and syrphid predation of herbivores is given by h_F, h_H, and h_{SR} respectively. The shape of the functional responses for pollination, herbivory, and predation are controlled by the exponents t_F, t_H, and t_{SR} respectively. With handling times greater than zero, when $t_F, t_H, t_{SR} \leq 1$, interactions are moderated by a Type II functional response. If t_F, t_H, or $t_{SR} > 1$, then the interaction is moderated by a sigmoidal Type III functional response. All time independent parameter definitions for Equation E.1 are given in Table E.1. With some simple algebra, the non-linear model with functional response is:

Equation E.1 (non-linear functional responses):

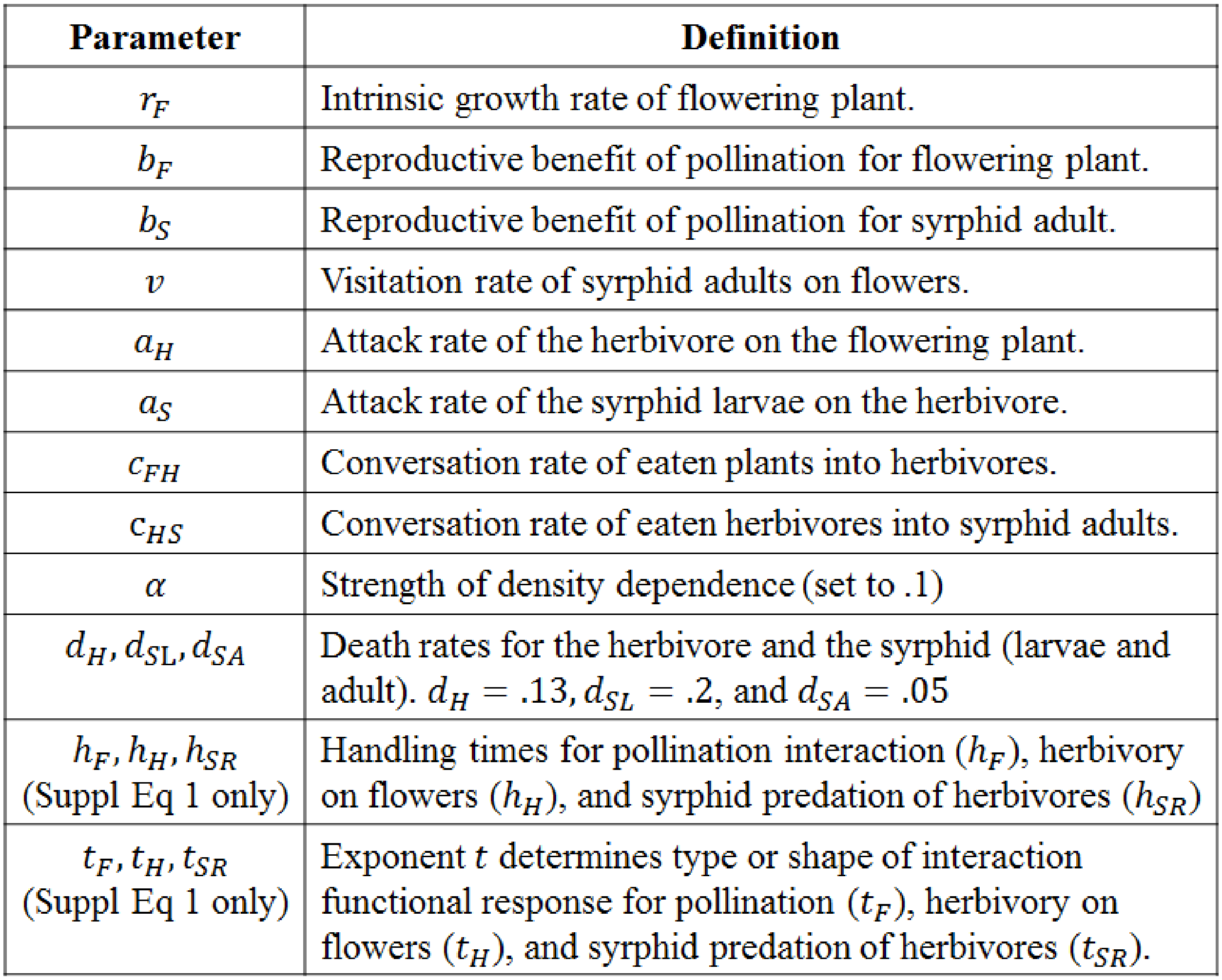
$$\frac{dF}{dt} = Fr_F + \frac{b_F v F^{t_F} S_A}{1 + v h_F F^{t_F}} - \alpha F^2 - \frac{a_H F^{t_H} H}{1 + a_H h_H F^{t_H}}$$

$$\frac{dH}{dt} = \frac{a_H c_{FH} F^{t_H} H}{1 + a_H h_H F^{t_H}} - \frac{a_S H^{t_{SR}} S_L}{1 + a_S h_{SR} H^{t_{SR}}} - d_H H$$

$$\frac{dS_L}{dt} = \frac{b_S v F^{t_F} S_A}{1 + v h_F F^{t_F}} - \frac{a_S c_{HS} H^{t_{SR}} S_L}{1 + a_S h_{SR} H^{t_{SR}}} - d_{SL} S_L$$

$$\frac{dS_A}{dt} = \frac{a_S c_{HS} H^{t_{SR}} S_L}{1 + a_S h_{SR} H^{t_{SR}}} - d_{SA} S_A$$

Table E.1 - Time independent parameters of Equation E.1 and their definitions.



Parameter	Definition
r_F	Intrinsic growth rate of flowering plant.
b_F	Reproductive benefit of pollination for flowering plant.
b_S	Reproductive benefit of pollination for syrphid adult.
v	Visitation rate of syrphid adults on flowers.
a_H	Attack rate of the herbivore on the flowering plant.
a_S	Attack rate of the syrphid larvae on the herbivore.
c_{FH}	Conversation rate of eaten plants into herbivores.
c_{HS}	Conversation rate of eaten herbivores into syrphid adults.
α	Strength of density dependence (set to .1)
d_H, d_{SL}, d_{SA}	Death rates for the herbivore and the syrphid (larvae and adult). $d_H = .13, d_{SL} = .2$, and $d_{SA} = .05$
h_F, h_H, h_{SR} (Suppl Eq 1 only)	Handling times for pollination interaction (h_F), herbivory on flowers (h_H), and syrphid predation of herbivores (h_{SR})
t_F, t_H, t_{SR} (Suppl Eq 1 only)	Exponent t determines type or shape of interaction functional response for pollination (t_F), herbivory on flowers (t_H), and syrphid predation of herbivores (t_{SR}).

E.4.1 - Plant Reproduction Obligate on Syrphid Pollination ($r_F = 0, b_F > 0$) *w/ Functional Response*

Analysis of the obligate pollination system started with Type II functional responses with $t_F = t_H = t_{SR} = 1$ and $0 < h_F = h_H = h_{SR} > 2$. With all of the other model parameters, this creates a 10-dimensional parameter space in which to analyze dynamics. As was done in the investigation of Eq 6.1, all parameters will be tested for values 0 to 1, except for the handling times, which will be studied from 0 to 2. Even taking only 10 intervals per parameter, across 10 parameters, this would still require 10,000,000,000 parameter combinations to check for local stability or oscillatory dynamics. To avoid such a large parameter sweep, Latin Hyper Spacing was used to create a comparatively sparse but well dispersed sweep of parameter space with 10,000 parameter combinations taken from uniform distributions across the range of each parameter. These combinations were then tested for linear stability.

As with the linear interactions analyzed in Eq 6.1, the obligate version of Eq E.1 with Type II functional responses seems to be prone to extinction. None of the tested parameter combinations were found to create locally stable equilibrium in either Equilibrium E.1 or Equilibrium E.2. Furthermore, numerical simulations did not find any persistent oscillatory dynamics. The negative feedback process described in the analysis of Eq 1 appears to be consistent in this case as well (Figure E.6a). Though, given the saturating effect of a Type II functional response, the negative feedback effect can take comparatively longer to play out as interactions are regulated at higher densities of resources (Figure E.6b).

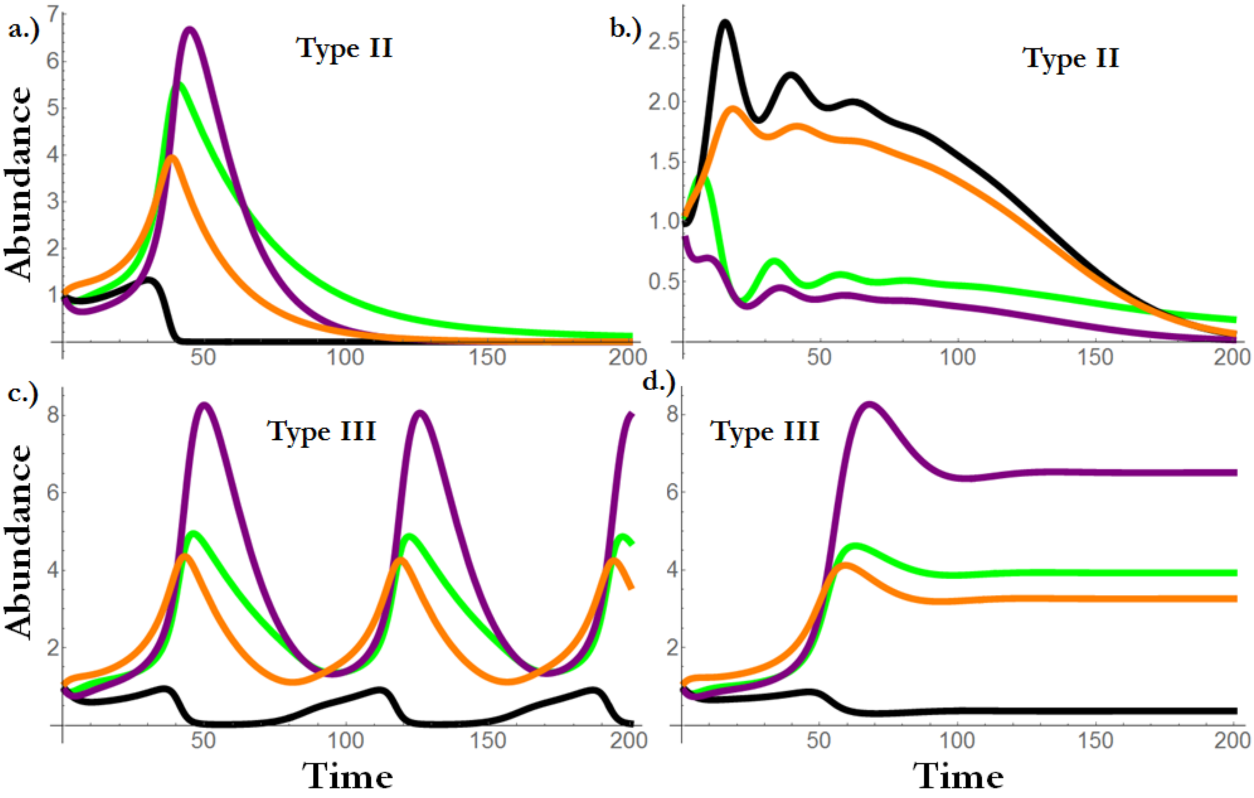


Figure E.6 - Time series of the obligate pollination FHS model with Type II (a and b) or Type III (c and d) functional responses (Eq E.1). Time dependent variables F, H, S_L, and S_A are shown in green, black, purple, and orange respectively. a) Example of extinction in Type II functional response: $b_F = 0.7, a_H = 0.522,\ b_S = 0.38,\ v = 0.636,\ a_S = 0.262,\ c_{FH} = 0.836,\ c_{HS} = 0.694,\ h_F = 0.57,\ h_H = 1.095,\ h_{SR} = 1.27,\ t_F = t_H = t_{SR} = 1$. b) Example of extinction in Type II functional response: $b_F = 0.872, a_H = 0.522,\ b_S = 0.286,\ v = 0.694,\ a_S = 0.262,\ c_{FH} = 0.835,\ c_{HS} = 0.694,\ h_F = 0.405,\ h_H = 1.055,\ h_{SR} = 1.32,\ t_F = t_H = t_{SR} = 1$. c) Example of stable limit cycle in Type III functional response: $b_F = 0.482,\ a_H = 0.522,\ b_S = 0.38,\ v = 0796,\ a_S = 0.262,\ c_{FH} = 0.8,\ c_{HS} = 0.79,\ h_F = 0.57,\ h_H = 1.095,\ h_{SR} = 1.27,\ t_F = 1.11,\ t_H = 2.85,\ t_{SR} = 1.29$. d) Example of stable equilibrium in Type III functional response: $b_F = 0.482,\ a_H = 0.522,\ b_S = 0.38,\ v = 0796,\ a_S = 0.262,\ c_{FH} = 0.8,\ c_{HS} = 0.79,\ h_F = 0.57,\ h_H = 1.02,\ h_{SR} = 0.985,\ t_F = 1.11,\ t_H = 1.985,\ t_{SR} = 2.055$. In all panels $r_F = 0,\ d_H = 0.13,\ d_{SL} = 0.2,\ d_{SA} = 0.05$.

However, when implementing a Type III functional response, the obligate version of Eq E.1 is able to persist under certain conditions. In order to implement a Type III response, I use handling times greater zero and the exponents of the Type II response are allowed to be greater than 1, i.e. $t_F,\ t_H,\ t_{SR} > 1$. Sigmoidal functional responses can be strongly stabilizing and this preliminary analysis shows that is possible in the FHS system as well. Both stable limit cycles and equilibria are possible (Figure E.6c&E.6d).

In general system persistence through either oscillations or equilibrium was contingent upon a strong initial sigmoidal response in the functional response terms. In other words, one or multiple functional response exponents ($t_F,\ t_H,\ t_{SR}$) needed to be set to approximately 2 or 3. This sigmoidal functional response creates a delayed reaction in pollination, herbivory, and/or predation when resources have low abundance. This disrupts the negative feedback process in pollination and herbivory when flower plants have low abundance, and in predation when herbivores have low abundance. This allows for the system to recover from low abundances creating steady oscillations (Figure E.6c) or dampened oscillations when the sigmoidal response creates sufficient delays in interactions at low abundances (Figure E.6d).

E.4.2 - Nominal Syrphid Pollination, Non-Syrphid Dependent Growth ($r_F > 0, b_F = 0$) w/ Functional Response

The nominal syrphid pollination version of Eq 6.1 was chaotic across much of the parameter space tested (Figure 6.5). Results from numerical simulations of Eq E.1 with a Type II functional response ($t_F = t_H = t_{SR} = 1$ and $0 < h_F = h_H = h_{SR} > 2$) showed no mitigation of chaotic dynamics. Non-zero handling times in any of the pollination, herbivory, or predation interactions (or all three) generally produced chaotic dynamics with only intermittent breaks into limit cycles. An example is shown in the bifurcation diagram in Figure E.7a across different handling times for syrphid predation on herbivores (h_{SR}). On the other hand, Type III functional responses are potentially stabilizing, similar to obligate pollination case. In particular, a strong sigmoidal response in syrphid predation of herbivores can stabilize oscillations and even lead to dampened oscillations when t_{SR} is only moderately greater than 1 (Fig E.7b). Type III functional responses in pollination or herbivory were not found to exhibit such a strong stabilizing ability.

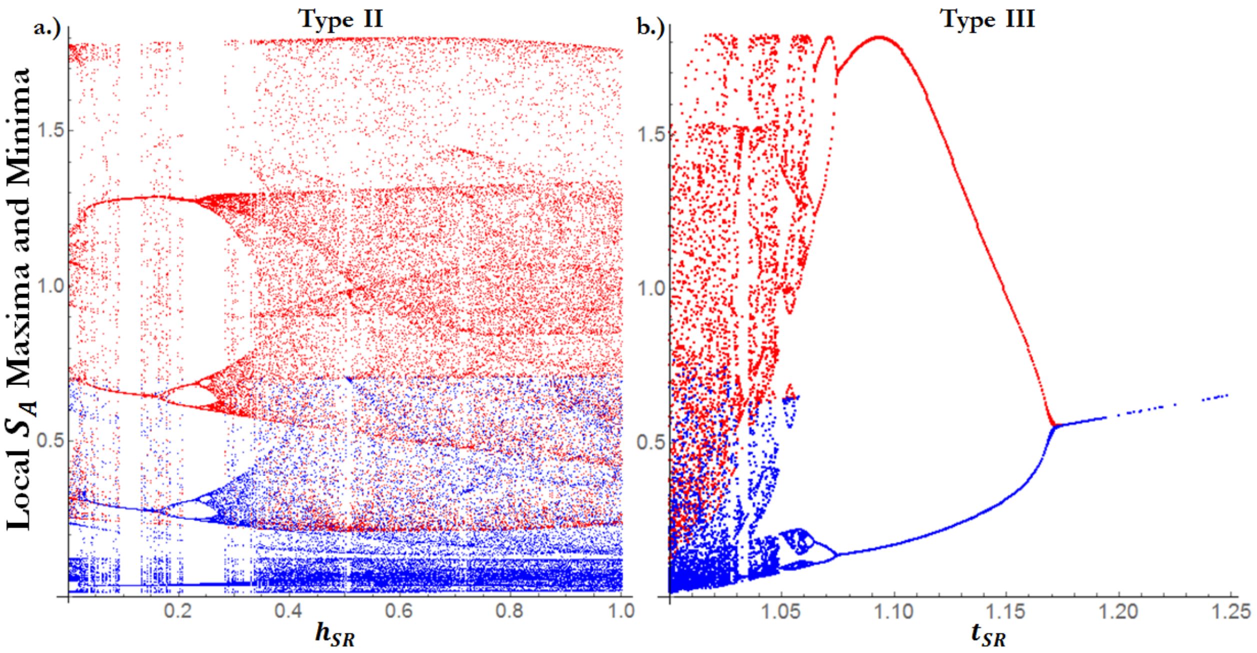


Figure E.7 - Bifurcation diagrams of Equation E.1 showing local maxima and minima of S_A for a Type II and Type III functional response in the case of nominal pollination. Dynamics were recorded after 6000 time steps worth of transient behavior. Red dots represent local maxima and blue dots represent local minima. a) Dynamics of a Type II functional response across values of h_{SR}. $r_F = 0.302,\ b_f = 0, a_H = 0.504,\ b_S = 0.57,\ v = 1,\ a_S = 0.416,\ c_{FH} = 0.914,\ c_{HS} = 0.8,\ h_F = 0.3,\ h_H = 0.605,\ t_F = t_H = t_{SR} = 1$. b) Dynamics of Type III functional response across values of t_{SR}. $r_F = 0.302,\ b_f = 0, a_H = 0.504,\ b_S = 0.57,\ v = 1,\ a_S = 0.416,\ c_{FH} = 0.914,\ c_{HS} = 0.8,\ h_F = 0.3,\ h_H = 0.605,\ h_{SR} = 1.0,\ t_F = t_H = 1$.

Literature Cited:

Zhang, C. and Chen T. 2001. Efficient feature extraction for 2d/3d objects in mesh representation. 2001 International Conference on Image Processing: 935-938(3). DOI: 10.1109/ICIP.2001.958278.

Appendix F– Appendices to Chapter 7

Appendix F.1 – Dynamics of a Persistent Plant Population (Models 1, 2, 3)

Through the addition of stage structure across the ontogeny of a growing autotroph population, the logistically growing population oscillates to equilibrium in a continuous model framework, unlike the non-stage structured counterpart. The emergence of oscillations is apparent through an isocline analysis of Model 1 and Model 2 (Fig F.1).

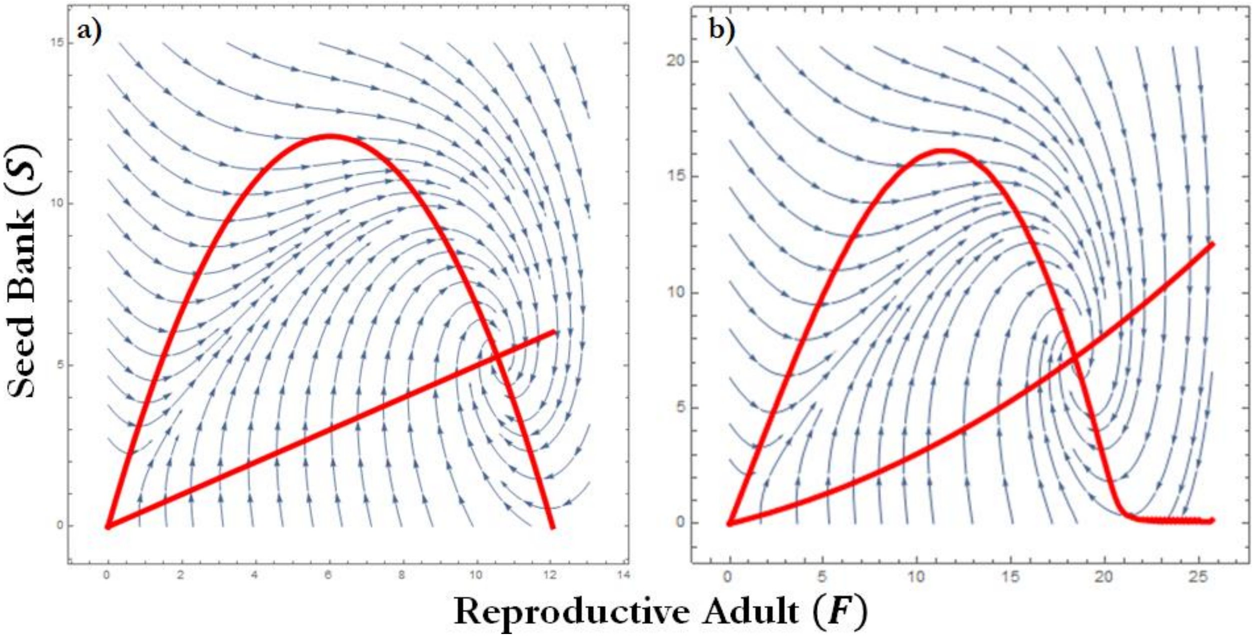


Figure F.1: Phase plane of 2-stage plant populations. Phase plane (blue vectors) and isoclines (shown in red) of the 2-stage-structured plant population (seed bank (S_1) and the fecund adults (F), no consumers). a) Model 1 with logistic reproduction ($\alpha_F = 0.1$) but no density dependent seed germination ($\alpha_g = 0$). Unlike non-stage structured logistic growth population models, logistic reproduction rates induce damped oscillations to equilibrium with two stages. Isoclines are calculated with $x(S) \approx 1$ for tractability such that the two isoclines are $S = \frac{d_F}{g_1}F$ and $S = \frac{-\alpha_F F^2 + r_F F}{g_1 + d_S}$. Parameter values are $r_F = 1.2$; $g_1 = 0.2$; $d_F = d_S = 0.1$. b) Similar phase plane and isocline pattern using the full 2-stage plant population Model 2. Parametric expressions of isoclines are too large reproduce here. Parameter values are $r_F = 1.24$; $g_1 = 0.495$; $\alpha_F = 0.06$; $\alpha_g = 0.048$; $d_F = d_S = 0.1$. Dampened oscillations are preserved with the addition an additional stage. Other parameters are $\epsilon = 0.2$; $\omega = 0.001$.

Given its role in forming the basis of further models and analysis, we can find parametric conditions for persistence of the population in the 2-variable Model 2 were we have the reproductive plant (F) and seed bank (S_1):

Model 2

$$\frac{dF}{dt} = \frac{g_1 S_1}{1 + \alpha_g (F + \epsilon S_1)} - d_F F$$
$$\frac{dS_1}{dt} = F(r_F - x(S_1)\alpha_F F) - \frac{g_1 S_1}{1 + \alpha_g (F + \epsilon S_1)} - d_S S_1$$
$$x(S_1) = \frac{S_1}{\omega + S_1}$$

This system has one positive equilibrium and the 0-equilbirum {0,0} representing local extinction. The non-linearities of the system make parametric analysis of its dynamics difficult, but it is possible to find a parametric expression for general system persistence. Using the Jacobian and classic linear stability analysis, we find conditions required for the origin to be unstable. The Jacobian for Model 2 is:

$$Jac = \begin{bmatrix} -d_F - \frac{a_g g_1 S_1}{\left(1 + a_g (F + S_1 \epsilon)\right)^2} & \frac{g_1}{1 + a_g (F + S_1 \epsilon)} - \frac{a_g g_1 S_1 \epsilon}{\left(1 + a_g (F + S_1 \epsilon)\right)^2} \\ r_F - \frac{2 a_F F S_1}{S_1 + w} + \frac{a_g g_1 S_1}{\left(1 + a_g (F + S_1 \epsilon)\right)^2} & -d_S + F\left(\frac{a_F F S_1}{(S_1 + w)^2} - \frac{a_F F}{S_1 + w}\right) + \frac{a_g g_1 S_1 \epsilon}{\left(1 + a_g (F + S_1 \epsilon)\right)^2} - \frac{g_1}{1 + a_g (F + S_1 \epsilon)} \end{bmatrix}$$

Inputting the 0-equilbrium ($F^* \to 0, S_1^* \to 0$) gives:

$$Jac_{F^*, S_1^* \to 0} = \begin{vmatrix} -d_S & g_1 \\ r_F & -d_S - g_1 \end{vmatrix}$$

The eigenvalues for $Jac_{F^*, S_1^* \to 0}$ are:

$$\lambda_1 = \frac{1}{2}\left(-d_F - d_S - g_1 - \sqrt{(d_F + d_S + g_1)^2 - 4(d_F d_S + d_F g_1 - g_1 r_F)}\right)$$
$$\lambda_2 = \frac{1}{2}\left(-d_F - d_S - g_1 + \sqrt{(d_F + d_S + g_1)^2 - 4(d_F d_S + d_F g_1 - g_1 r_F)}\right)$$

The first eigenvalue, λ_1, is always negative. However, $\lambda_2 > 0$, thus rendering the origin unstable and the system persistent, when the following conditions are met:

$$\lambda_2 = \frac{1}{2}\left(-d_F - d_S - g_1 + \sqrt{(d_F + d_S + g_1)^2 - 4(d_F d_S + d_F g_1 - g_1 r_F)}\right) > 0$$
$$\left(-d_F - d_S - g_1 + \sqrt{(d_F + d_S + g_1)^2 - 4(d_F d_S + d_F g_1 - g_1 r_F)}\right) > 0$$
$$\left(\sqrt{(d_F + d_S + g_1)^2 - 4(d_F d_S + d_F g_1 - g_1 r_F)}\right)^2 > (d_F + d_S + g_1)^2$$
$$(d_F + d_S + g_1)^2 - 4(d_F d_S + d_F g_1 - g_1 r_F) > d_F^2 + 2 d_F d_S + d_S^2 + 2 d_F g_1 + 2 d_S g_1 + g_1^2$$
$$d_F^2 - 2 d_F d_S + d_S^2 - 2 d_F g_1 + 2 d_S g_1 + g_1^2 + 4 g_1 r_F$$
$$> d_F^2 + 2 d_F d_S + d_S^2 + 2 d_F g_1 + 2 d_S g_1 + g_1^2$$
$$-2 d_F d_S - 2 d_F g_1 + 4 g_1 r_F > 2 d_F d_S + 2 d_F g_1$$
$$4 g_1 r_F > 4 d_F d_S + 4 d_F g_1$$
$$g_1 r_F > d_F d_S + d_F g_1$$
$$g_1 r_F - d_F g_1 > d_F d_S$$

Equation F.2

$\boldsymbol{g_1 > \frac{d_F d_S}{r_F - d_F}}$ ***Conditions for persistent sole plant species**

$$\boldsymbol{r_F > \frac{d_F d_S}{g_1} + d_F}$$

As is visible in Figure 7.1, plotting the function $g_1 = \frac{d_F d_S}{r_F - d_F}$ overlaid on the heatmap of persistent populations tested through numerical simulations, the function $g_1 = \frac{d_F d_S}{r_F - d_F}$ fits the divide between persistence and extinction. It is noteworthy that the conditions for persistence do not include the effects density dependence stemming from mature plants or seeds. The rate of germination (g_1) required for persistence is inversely proportional to the required seed production rate (r_F).

If the above conditions for persistence are met, the system exhibits dampened oscillations to a stable non-0 equilibrium. Due to multiple non-linearities in the resource equations, parametric expression of the positive equilibrium are quite large. However, since $x(S_1) \approx 1$ for all $S_1 > 0$, we can allow $x(S_1) = \frac{S_1}{\omega + S_1} = 1$. Doing so allows for more reasonable approximated expressions of the equilibria (see Model 2 Equilibrium - Equation F.3, F^* and S_1^*). Changes in F^* and S_1^* based on demographic rates r_F (seed production) and g_1 (seed germination) are shown in Figure F.2.

Model 2 Equilibrium - Equation F.3:

$$F^* = \frac{a d_F d_S + a g_1 - a d_F^2 \epsilon + a d_F r_F \epsilon \sqrt{a^2 \left(4 d_F (d_F (d_S + g_1) - g_1 r_F) \epsilon + \left(g_1 + d_F (d_S + (r_F - d_F) \epsilon)\right)^2\right)}}{2 a^2 d_F \epsilon}$$

$$S_1^* = \frac{\begin{gathered} -a (d_F d_S + g_1)^2 + a d_F \left(d_F^2 d_S + g_1 r_F - d_F \big(g_1 + d_S (2 + r_F)\big)\right) \epsilon \\ + (d_F d_S + g_1) \sqrt{a^2 \left((d_F d_S + g_1)^2 + 2 d_F \left(-d_F^2 d_S - g_1 r_F + d_F \big(g_1 + d_S (2 + r_F)\big)\right) \epsilon + d_F^2 (d_F - r_F)^2 \epsilon^2\right)} \end{gathered}}{2 a^2 d_F^2 d_S \epsilon^2}$$

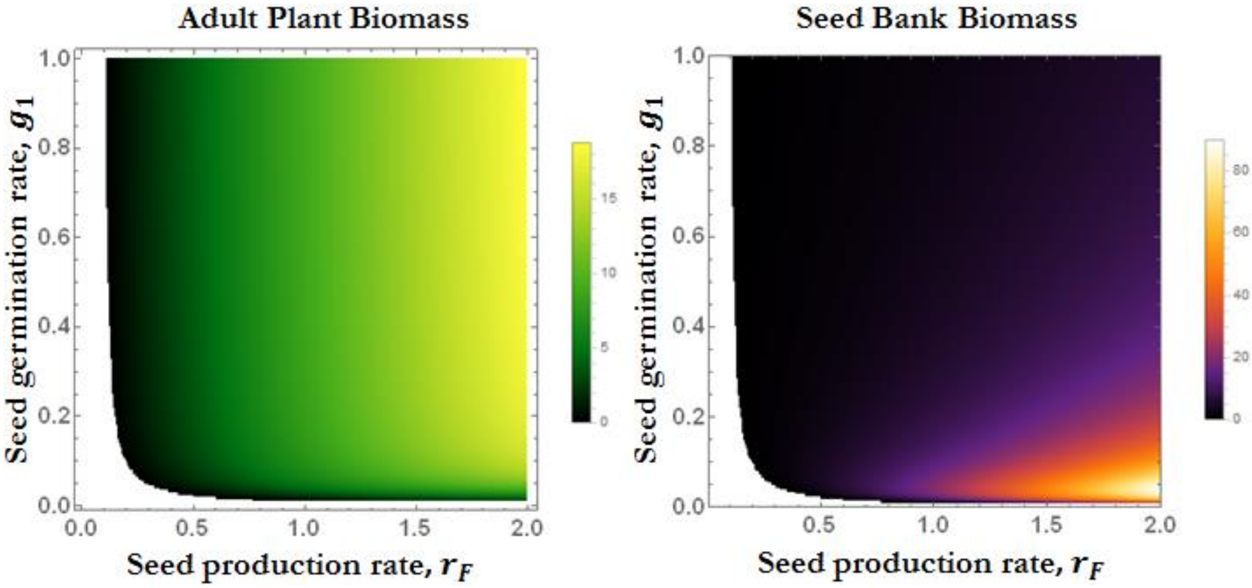


Figure F.2 - Absolute changes in biomass of Model 2 at equilibrium from relative change seen in Fig 6.1. Abundances of adult plants (F, left) and the seed bank (S_1, right) are shown across base demographic rates seed germination rate (g_1) and seed production rate (r_F). No consumers are present in these simulations. All values represent biomass at stable equilibrium. No persistent oscillations were found. Other parameters: $d_F = d_S = 0.1, a_F = a_g = 0.1, \omega = 0.001$.

While all tested parameter space in Model 2 eventually led to stable state dynamics, the demographic parameters do affect the transient behavior of the model. Namely, the time taken to equilibria does changes non-monotonically with seed germination and/or seed production values (Figure F.3). These changes underpin the non-additive effects seen in the span of single parameters of Models 3,4, and 5. Particularly, with the inclusion of a third stage in Model 3, the expanding and contrasting time to equilibrium becomes the de- stabilization and re-stabilization seen in Fig 6.2a. Similar dynamics as those shown in Fig 6.2a are available across a range of parameter space (Fig F.4). Note that the exact shape of stable parameter space is not of direct importance at this stage, but is instead provided to show the consistency of leaving stable parameter by monotonically changing one parameter value, only to return to it.

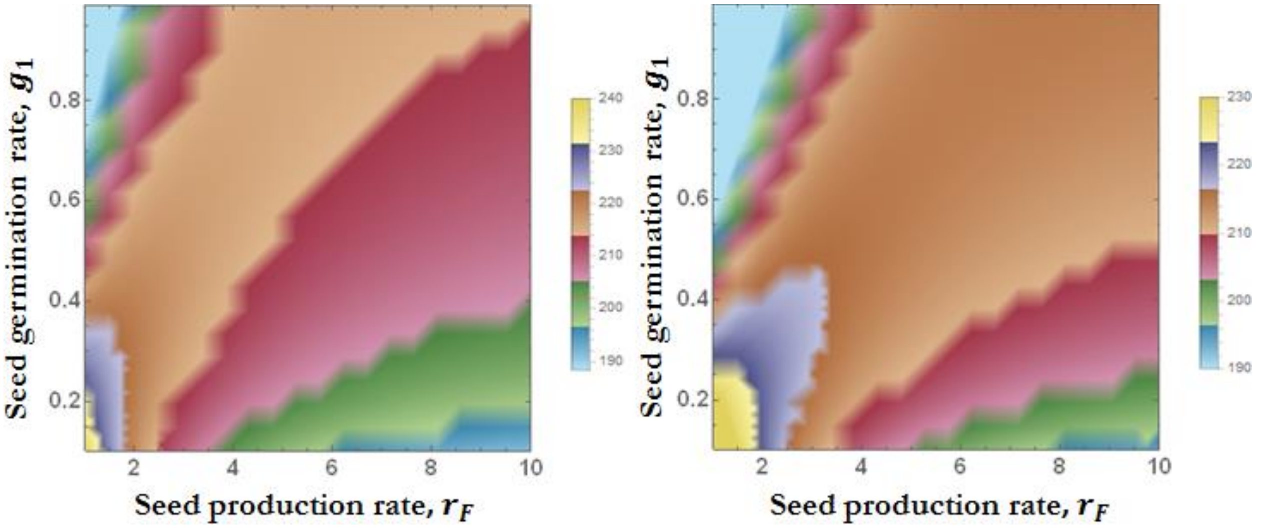


Figure F.3 - Time to equilibrium for Model 2. Colors (delineated in figure legends) represent the number of time steps required for transience to dampen and for all variables to reach equilibria. Two examples are shown. Left Panel - $a_F = .0015; a_g = .09$; $\omega = 0.1; \epsilon = 0.15$; $d_F = d_S = 0.1$. Right Panel - $a_F = .0015$; $a_g = .07$; $\omega = 0.1$; $\epsilon = 0.15$; $d_F = d_S = 0.1$.

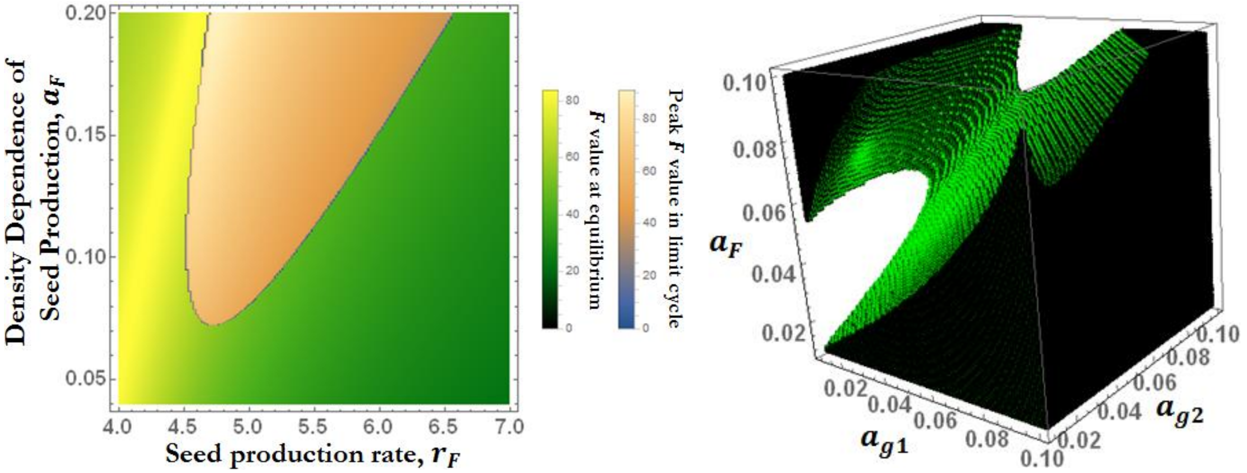


Figure F.4 - Simulations showing the non-additive effects on dynamic stability across multiple parameters. a) Two-dimensional heatmap bifurcation diagrams showing the dynamics of the plant population Model 3 across $\{r_F, a_F\}$ parameter space. Colors represent the values of F from the time series. The avocado color scale shows F^* values when the system is at stable equilibrium. The sunset color scale shows F at peak values in oscillations when the system supports stable oscillations. b) List of parameter combinations in $\{\alpha_F, \alpha_{g1}, \alpha_{g2}\}$ parameter space which create dampened oscillations to stable equilibrium. Empty space represents parameter combinations that created unstable equilibria and persistent oscillations. The coloration in the figure is there only to show contour and shape in the stable parameter space.
$d_F = d_S = 0.1$.

Appendix F.2 – Dynamics of Herbivore Consumer-Resource System (Model 4 w/ $H_F > 0$, $H_S = 0$)

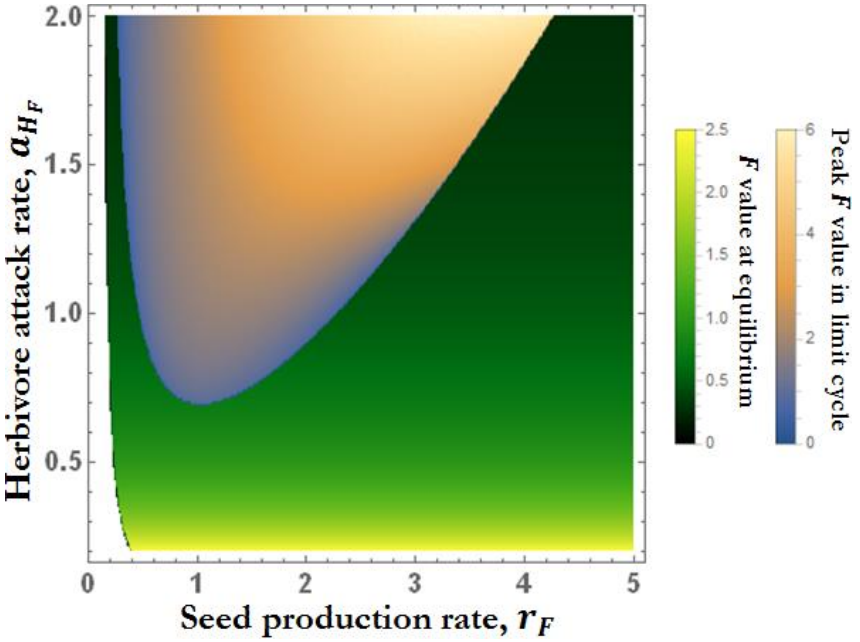


Figure F.5 - Two-dimensional heatmap bifurcation diagrams showing the dynamics of the herbivore consumer-resource system of Model 4 ($H_F > 0$, $H_S = 0$) across $\{r_F, a_{H_F}\}$ parameter space. Colors represent the values of F from the time series. The avocado color scale shows F^* values when the system is at stable equilibrium. The sunset color scale shows F at peak values in oscillations when the system supports stable oscillations. Higher seed production rates can stabilize system dynamics in presence of herbivory on fecund adults (F). Other parameters: $g_1 = 0.308, k_r = 0.7, c_{F_H} = 0.6, h_{H_F} = 1.0, a_g = a_F = 0.1, d_F = d_S = 0.1, d_{H_F} = 0.2, \epsilon = 0.2, \omega = 0.001$.

Appendix F.3 – Dynamics of Seed Predator Consumer-Resource System (Model 4 w/ $H_F = 0$, $H_S > 0$)

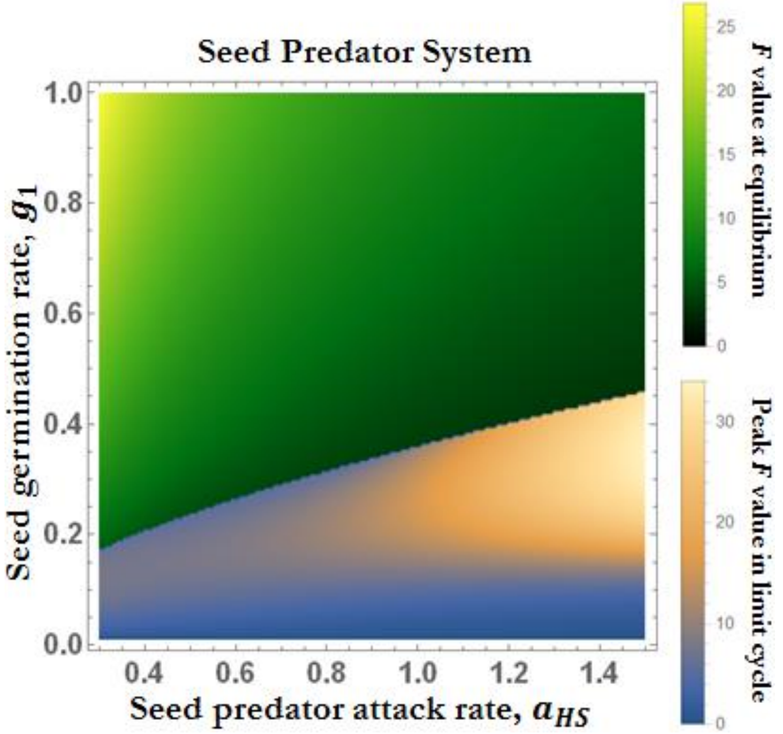


Figure F.6 - Two-dimensional heatmap bifurcation diagrams showing the dynamics of the seed predator-consumer system of Model 4 ($H_F = 0$, $H_S > 0$) across $\{a_{HS}, g_1\}$ parameter space. Colors represent the values of F from the time series. The avocado color scale shows values F^* when the system is at stable equilibrium. The sunset color scale shows F at peak values in oscillations when the system supports stable oscillations. Under specific conditions, i.e. weak density dependence and large handling times, the seed predator-consumer system can support stable oscillations. We can see that higher seed germination rates (g_1) can stabilize the system. This stabilization comes through limiting the amount of available seed biomass for seed predators when seeds germinate at a quicker rate (see Fig 6.1). Higher attack rates (a_{HS}) require higher rates of germination to allow for stabilization. Other parameters: $r_F = 0.9, k_r = 0.7, c_{S_H} = 0.6, h_{H_S} = 2, a_g = a_F = 0.01, d_F = d_S = 0.1, d_{H_S} = 0.2, \epsilon = 0.2, \omega = 0.001$.

Appendix F.4 – Emergent Facilitation in Model 4 w/ $H_F > 0$ *and* $H_S > 0$

Emergent facilitation of one stage specific consumer due to the presence of another stage-specific consumer is possible over a range of parameter space tested here.

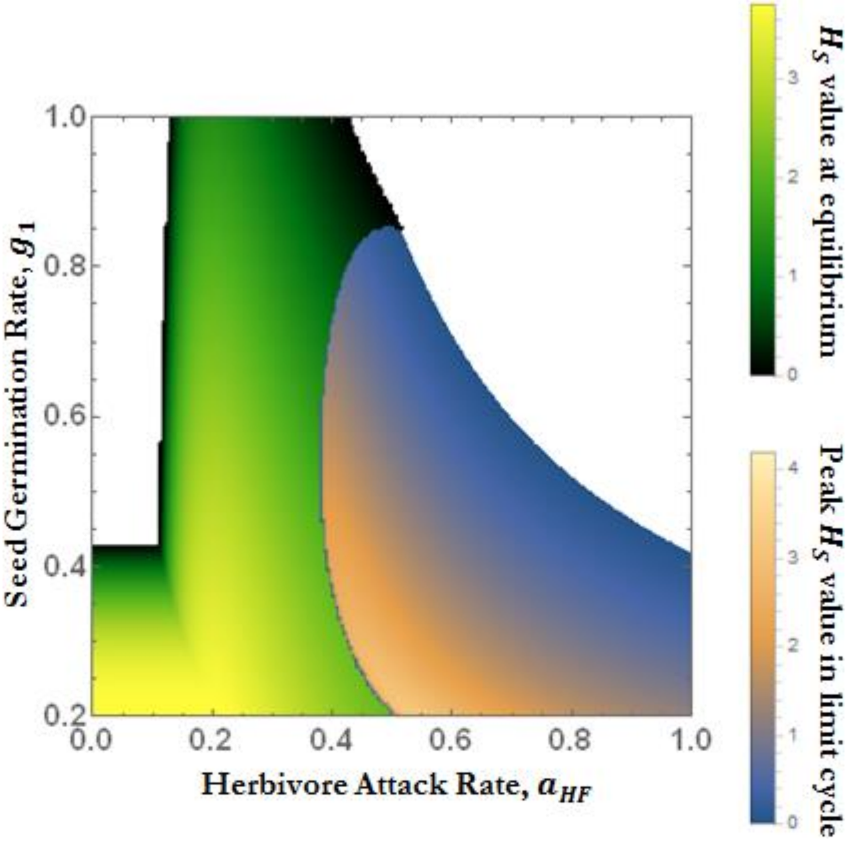


Figure F.7 - Two-dimensional heatmap bifurcation diagrams showing the emergent facilitation of the seed predator in the presence of the herbivore in Model 4 ($H_F > 0$, $H_S > 0$) across $\{a_{H_F}, g_1\}$ parameter space. Colors represent the values of H_S from the time series. The avocado color scale shows values H_S^* when the system is at stable equilibrium. The sunset color scale shows H_S at peak values in oscillations when the system supports stable oscillations. The white areas indicate parameter values which cause extinction of the seed predator ($H_S \to 0$), while other variables continue to persist. Given high density dependent effects on seed production (α_F), the seed predator can only persist in the presence of its herbivore competitor at germination rates (g_1) above ~0.42. Other parameters: $r_F = 1.38$; $a_{H_S} = 0.47$; $\alpha_F = 0.3$; $a_{g1} = .0245$; $d_F = d_S = 0.1$; $d_{H_F} = d_{H_S} = 0.2$; $k_r = 0.7$; $h_{H_F} = h_{H_S} = 1$; $c_{FH} = c_{SH} = 0.6$; $\omega = 0.001$; $\epsilon = 0.2$.