

2016

From Nursery to Nature: Evaluating Native Herbaceous Flowering Plants Versus Native Cultivars for Pollinator Habitat Restoration

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FROM NURSERY TO NATURE:
EVALUATING NATIVE HERBACEOUS FLOWERING PLANTS
VERSUS NATIVE CULTIVARS FOR POLLINATOR HABITAT RESTORATION

A Dissertation Presented

by

Annie S. White

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
Specializing in Plant and Soil Science

October, 2016

Defense Date: May 26, 2016
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ABSTRACT

There is growing awareness about the value of preserving and restoring floral-rich habitats for the benefit of pollinators, especially native bees. The increasing demand for native plants in pollinator habitat restoration and other ecological landscaping applications, combined with the desire for more robust and predictable plant habits, have led to the selection and breeding of native cultivars. Yet, little is known about how these cultivated varieties differ from the native species in their ability to attract and support pollinators. I compared flower visitation by all insect pollinators to 12 native herbaceous plant species and 14 native cultivars in a replicated field experiment at two sites over two years. I classified insect pollinators during visual field observations into seven taxonomic and functional groups. I found seven native species to be visited significantly more frequently by all insect pollinators (combined) than their cultivars, four were visited equally, and one native cultivar was visited more frequently than the native species. Bees (both native and non-native) and moths/butterflies exhibited similar preferences, whereas flies showed no preference between the native species and the native cultivar. Our study shows that many insect pollinators prefer to forage on native species over cultivated varieties of the native species, but not always, and not exclusively. Some native cultivars may be comparable substitutions for native species in pollinator habitat restoration projects, but all cultivars should be evaluated on an individual basis.

Plant selection is integral to the value and success of pollinator habitat restorations, yet there is little consistency and overlap in pollinator planting recommendations and very little empirical data to support plant choice. Non peer-reviewed pollinator plant lists are widely available and are often region-specific, but they are typically based on anecdotal rather than empirical data and lack in specificity. To help close the gap between anecdotal and empirical data, and between practice and research, I reviewed the published literature on plant selection for pollinator habitat restoration. I explicitly reviewed and compared the value of native plant species, near-natives, non-natives and native cultivars. From there, I identified gaps in the literature that are most needed in practice and recommended basic strategies for practitioners to navigate plant lists and choose the best plants for a site's success.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my advisor, Dr. Leonard Perry, for his continuous support throughout my PhD studies and research endeavors. His knowledge and experience were instrumental in helping me turn my research ideas into actualized funded projects. I am enormously grateful to Dr. Stephanie Hurley for her mentorship throughout my graduate work at UVM. She continually inspired and encouraged me to be a better teacher, researcher, and writer. I also owe thanks to Dr. Hurley's Lab Group for their friendship, support, and for providing valuable feedback on my work—particularly on the figures in this dissertation. I am thankful to Dr. Cathy Paris and Dr. Sid Bosworth for their interest in this research, for pushing me intellectually, and for their contributions to improving this dissertation. The knowledge and patience of Alan Howard was instrumental in helping me statistically analyze this challenging dataset. I am grateful for the editing prowess of Jennifer Duffield White, which has helped me polish many publications throughout my degree, including this dissertation.

I have the deepest appreciation for the Plant & Soil Science Department and all the faculty, staff, and students that have made this degree such a growing and worthwhile experience. I owe special thanks to Dr. Deb Neher, Jon Turmel, Colleen Armstrong, and Jane Sorensen for inspiring me with their enthusiasm and excellence in teaching.

Furthermore, I thank Jane Sorensen and David Marchant at River Berry Farm, Tim White at Maidstone Plant Farm, and Sarah Salatino at Full Circle Gardens for graciously letting me carry out research on their properties and for all their help and support along the way. I am greatly indebted to interns Larissa DiMarco and Hannah Brill for all their sweat and toil out in the field. This research would not be possible without funding from Northeast SARE and the New Hampshire Horticulture Endowment. Additional support came from Green Works, the Vermont Nursery and Landscape Association.

I am most grateful for the support of my whole family, all of whom have been instrumental in my success throughout this journey. I am particularly lucky to have had the unrelenting love and encouragement of my partner, Paul Schmidt, whose support was especially important during the final few months of writing this dissertation. Above all, I'm grateful for our daughter, who brought new and interesting challenges to my PhD pursuit, but also brought a renewed sense of purpose and clarity—along with an endless supply of smiles and laughter to each and every day. Isla, you make everything worthwhile.

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GENERAL INTRODUCTION

Pollinating insects—bees in particular—play a critical role in ensuring the pollination of food crops, the production of seed in flowering plants, and the maintenance of natural plant communities and ecosystems. Bee communities, both wild and managed, have declined dramatically in recent years, and habitat loss is one of the factors identified as contributing to their decline.

The loss of pollinator diversity threatens global agricultural productivity, and for this reason, the prospect of a pollination crisis is garnering the interest of scientists, policy-makers, and the general public. Special initiatives to address pollinator decline are widespread and growing in the United States. Numerous efforts are underway to encourage the restoration of pollinator habitat into agricultural lands, natural areas, and landscape gardens, but little research exists to quantitatively justify plant selection decisions.

The use of native flowering plants is encouraged for pollinator habitat restoration projects, and the nursery and landscape industry is responding to the increase in demand by making native plant material commercially available and marketing their ecological benefits. Ornamental cultivars of native perennials are commonly propagated and sold in the nursery and landscape industry, but there is a lack of quantitative research evaluating how native cultivars compare to the native species from which they originate.

In the horticulture and landscape industries, native species are sometimes referred to as the “species,” “straight species” or “true species” and native cultivars are sometimes called “nativars.” In my work, I refer to native cultivars as native cultivars or simply “cultivars” and native species as native species or simply “species.”

There is an emerging debate over whether cultivars of native plant species provide the same ecosystem services as the native species themselves. There is a tremendous amount of variation in the origin of native cultivars, how they are propagated, and the desirable traits for which they are maintained. Because cultivars have been selected primarily based on ornamental and cultural traits, it is not clear whether or not they perform the same ecological roles as the species, which evolved naturally in the landscape.

The primary objective of my field research was to evaluate the ecological differences between open-pollinated native wildflower species and cultivars of the same species in terms of their ability to attract and support beneficial pollinator populations. I evaluated the attractiveness of floral resources to beneficial insect pollinators and quantified floral abundance and bloom duration for 12 native species and 14 native cultivars. Improved cultivars of native plants are sometimes well suited for landscape applications in terms of plant size, form, uniformity, and other characteristics, but it is important that we fully understand the ecological trade-offs of using native cultivars as substitutions for native species. To my knowledge, this is the first study to compare the ecological value of native species and native cultivars for pollinators in a replicated field experiment.

Furthermore, this dissertation includes an in-depth review paper comparing the value of native plant species, near-natives, non-natives, and native cultivars for pollinator habitat restoration. Plant selection is integral to the value and success of pollinator habitat restorations, yet there is little consistency and overlap in pollinator planting recommendations and very little empirical data to support plant choice. To help close the gap between anecdotal and empirical data, and between practice and research, this review paper identifies gaps in the literature and recommends basic strategies for practitioners to navigate plant lists and choose the best plants for a project's success.

CHAPTER 1

COMPREHENSIVE LITERATURE REVIEW

POLLINATORS AS AN ECOSYSTEM SERVICE PROVIDER

Pollinators are currently receiving more attention by conservationists, scientists, farmers, and the general public than at any other time in history. Efforts are ongoing to better understand the numerous drivers of pollinator decline and the most effective strategies for preserving, restoring, and creating flower-rich landscapes that support healthy populations of beneficial pollinators.

In an era of increasing landscape fragmentation and climate change, it is important to understand how anthropogenic land-use decisions affect species that provide vital ecosystem services and how we can develop conservation strategies to mitigate for habitat loss. The pollination services provided by insect pollinators are a key ecosystem service in most terrestrial ecosystems. The functional role of pollinators is integral to the sustainability of wild plant communities and the productivity of agricultural crops worldwide. Almost 90% of flowering plant species on earth rely on animals for pollination. Seventy-five percent of the leading global food crops are dependent on animal-mediated pollination for fruit, vegetable, and seed production, accounting for 35% of the volume of global food crops (Klein et al. 2007; Ollerton et al. 2011).

As the human population continues to grow worldwide, patterns of land use will intensify. How pollinators respond to land-use change and how we preserve and restore

pollinator habitat in anthropogenic and agricultural landscapes has important implications for much of the world's wild flora and agricultural crops.

The proficiency of pollinators

Bees are by far the most important and prolific pollinators worldwide, visiting and pollinating flowers more frequently than other pollinators (Neff & Simpson 1993).

About 18,000 bee species have been described worldwide, with the actual number of species likely around 20,000 (Michener 2007). The effectiveness of bees as pollinators is largely due to the fact that all bee species are obligate florivores. Both larval and adult life stages feed on floral products, mainly pollen and nectar. In other pollinator taxa, florivory is often limited to the adult life stage. Furthermore, bees are covered in a dense coat of feathery hairs that effectively catch pollen grains. Most female adult bees have specialized pollen-collecting structures and spend much of their time collecting pollen to provision their young (Michener 2007).

One species, the globally ubiquitous and well-studied honey bee (*Apis mellifera*) is managed commercially by humans to enhance agricultural crop pollination worldwide. According to USDA statistics, there were an estimated 2.74 million managed honey bee colonies in the U.S. in 2014 (Steinhauer et al. 2015).

Among wild bees, bumble bees (*Bombus* spp.) are especially proficient pollinators and are integral in the pollination of native plant communities. Of the roughly 4,000 species of native bees in North America, 45 of these species are *Bombus*. Bumble bees also improve the yields of many agricultural crops, making them the second most valuable pollinator in agriculture behind honey bees. The recent domestication of bumble bees has further boosted their economic importance in crop production (Delaplane &

Mayer 2000). Although other taxa including wasps, flies, beetles, butterflies, birds, lizards, and mammals are important pollinators for particular plants species in some ecosystems, none provide the same widespread pollination services as bees (Anderson 2003; Kearns 2001).

Flies (order Diptera) are the second most frequent visitors to flowers, with the most frequent flower visitors being syrphid flies (family Syrphidae) (Larson et al. 2001). Nearly all of the 6,000 species of syrphid fly adults consume nectar and some species also consume pollen. Butterflies and moths (order Lepidoptera) form a diverse group of 300,000 species worldwide. With few exceptions, Lepidopterans are nectarivorous and do not consume pollen. The collection and transference of pollen by Lepidopterans is an involuntary outcome of their nectar feeding. The research is limited, but it is thought that Lepidopterans visit flowers less frequently than bees and may also deposit less pollen per flower (Sahli & Conner 2007). However, Lepidopterans may be important for maintaining genetic diversity in plant populations because they carry pollen longer distances than other insect pollinators (Herrera 1987).

Less frequent pollinators can be observed from a variety of taxonomic groups including beetles (order Coleoptera) and wasps and ants (order Hymenoptera). Birds and bats provide pollinator services to morphologically distinct flowers, most of which are found in tropical regions. In the Northeastern U.S., one species of hummingbird—the ruby-throated hummingbird (*Archilochus colubris*)—visits a diversity of flowers for nectar.

The importance of pollinators in agroecosystems

More than one-third of the land area in the lower 48 states is managed as cropland, pasture, or rangeland, making agriculture the largest land-use activity in the United States (Heard et al. 2000). Understanding plant-pollinator interactions in agroecosystems is important for both maximizing crop productivity and for conserving beneficial pollinator populations.

Bees are the primary pollinators of most insect-pollinated agricultural crops. Agricultural landscapes frequently consist of large monocultures, which provide an abundance of floral resources for pollinators for a few weeks per year and then the landscape is relatively devoid of food sources. Such landscapes lack sufficient habitat for native bees so commercial honey bees are often employed to pollinate the crop during bloom time. The introduction of managed honey bee hives to agroecosystems can impact native pollinators inhabiting the same area through competition for resources. In the United States, Thomson (2006) found that niche overlap between *Apis* and *Bombus* varied but increased to levels as high as 80-90% during periods of resource scarcity.

Honey bees pollinate approximately 75% of the fruits, nuts, and vegetables grown in the U.S.; however, in agroecosystems that include preserved natural or semi-natural habitat, native bees can meet all of the crop's pollination requirements without the need for managed honey bees (Kremen et al. 2004; Morandin & Winston 2006; Winfree et al. 2007).

POLLINATOR DECLINE AND POTENTIAL DRIVERS

Documented losses in domestic and wild bee populations

There is clear evidence for significant declines in managed honey bee stocks in the United States and Europe. Between 1947 and 2005, 59% of hives were lost in the United States (National Research Council 2007; vanEngelsdorp et al. 2010). An estimated 23.1% of the colonies managed in the United States were lost over the 2014/2015 winter, slightly down from 23.7% in 2013/2014. The nine-year average total loss is 28.7% (Steinhauer et al. 2015). In central Europe, 25% of colonies were lost between 1985 and 2005 (Potts et al. 2010 a). These losses raise concern over the future sustainability and availability of managed honey bee stocks for pollinator-dependent agricultural crops.

Although more bee colonies were lost over the last decade than ever before, the abundance of managed honey bee colonies increased, largely due to compensatory apiculture techniques such as hive splitting. However, the global stock of domesticated honey bees is growing slower than agricultural demand for pollination. The global abundance of managed honey-bee hives has increased about 45% over the last 50 years, but the land area of pollinator-dependent crops has grown more than 300% (Aizen & Harder 2009).

Wild bee populations have also declined in recent decades (Colla & Packer 2008; Cameron et al. 2011; Biesmeijer et al. 2006). Bumble bees (*Bombus*) are the most-studied wild bee taxon and are particularly well studied in Europe. The widespread agricultural intensification of 20th century Europe is considered the primary cause of *Bombus* decline in the UK and western Europe (Goulson et al. 2003).

Bombus declines are less well studied in North America. Colla & Packer (2008) provided the first quantitative evidence that bumble bees have declined in Eastern North America. They resurveyed sites in Ontario, Canada, which were previously surveyed in 1974, finding that bumble bee species richness, evenness, diversity, and relative abundance have declined in recent decades. Of the 14 bumble bee species identified in the historic survey, seven were either absent or decreasing. *Bombus affinis*, a historically widespread and abundant species, was found to have significantly declined and is believed to be extirpated throughout much of its historic range.

An investigation of wild bumble bee populations in the United States also found significant population declines (Cameron et al. 2011). In North America, the relative abundances of four *Bombus* species have declined up to 96% and their geographic ranges have reduced by 23-87% (Cameron et al. 2011).

Fewer research efforts have evaluated potential population declines of other non-*Apis* and non-*Bombus* bee species, but some studies suggest there is little difference among bee genera in terms of their sensitivity to human disturbance and, subsequently, their potential population declines (Winfrey et al. 2009). Of further concern, widespread declines in both wild and domesticated pollinators parallel declines in plant communities that rely on them for reproduction (Potts et al. 2010b).

Questioning the pollinator crisis

Some have suggested that a global crisis may not be imminent, and therefore, widespread pollinator habitat restoration efforts are unjustified (Ghazoul 2005). This argument is based on a perceived lack of evidence of a global pollinator population decline. Ghazoul (2005) acknowledged the reports of honey bee decline in North

America and bumble bee and butterfly decline in Europe but did not believe these documented regional declines indicated a more widespread and global crisis.

Additionally, Ghazoul (2005) argued that pollinator services are not required for several globally significant staple crops (maize, wheat, and rice), which are wind pollinated. Therefore a “global crisis” linked to pollinator declines may be exaggerated. Even if some pollinators species do decline or go extinct, Ghazoul (2005) argued that other generalist pollinator species and domesticated honey bees can fill in the gaps in pollination. Newer research refutes this latter point (Garibaldi et al. 2013).

From strictly a food production perspective, some have questioned whether the decline of wild pollinators is of great concern if domesticated honey bee hives can provide all crop pollination services. A study of 41 crop systems from 600 field sites worldwide found that wild insects pollinated crops more effectively, and managed honey bees supplemented, rather than substituted for, pollination by wild insects (Garibaldi et al. 2013). They found that honey bees are less effective than wild insects at depositing pollen. Fruit production after visitation from wild insects was twice that of flowers visited by honey bees. Furthermore, wild pollinators were more consistent. The increase of pollination services associated with wild pollinators did not depend on whether or not honey bees were present, suggesting that the conservation of wild bee abundance and diversity is beneficial even in cropping systems typically pollinated by managed honey bees.

Potential drivers of pollinator decline

Plant-pollinator interaction networks are influenced by phenology, behavior, physiology, and relative abundances of multiple species (Tylianakis 2013), making them

particularly susceptible to anthropogenic disturbances. Rare and specialized species, species occupying higher trophic levels, and cavity-nesting species are more vulnerable to habitat loss and fragmentation and climate change (Burkle et al. 2013).

Several recent reviews of diverse sets of studies sought to identify the drivers of pollinator decline, the potential consequences, and the most vital research topics for the scientific community moving forward (Potts et al. 2010b; Vanbergen 2013; Tylianakis 2013; Spivak et al. 2011). Most studies evaluate specific drivers in isolation, likely underestimating the significance of multiple drivers occurring in concert.

Among the most significant drivers of pollinator declines are habitat loss and fragmentation due to land-use change; increased prevalence of non-native plant species; climate change; the spread of pathogens; increasing pesticide application and environmental pollution; and decreased resource diversity (Potts et al. 2010).

Habitat loss and fragmentation

A meta-analysis of bees' responses to anthropogenic disturbance shows that habitat loss and fragmentation negatively affect the abundance and species richness of wild bees (Winfree et al. 2009). Wild bees, unlike honey bees, rely on natural habitat for all their life stages. Honey bees appear to be less affected by habitat fragmentation (Garibaldi et al. 2011).

Some bee species persist well in human-disturbed landscapes, including less-intensively managed agricultural lands (Winfree et al. 2007; Brosi et al. 2007; Brosi et al. 2008; Tylianakis et al. 2005; Winfree et al. 2008) and suburban gardens (Winfree et al. 2007; McFrederick & LeBuhn 2006; Cane et al. 2006).

To assess the extent to which environmental changes affect plant-pollinator networks, sites in Illinois that were sampled in the late 1800s and in the 1970s were resampled in 2010-2011 (Burkle & Alarcón 2011). This study identified significant degradation of the plant-pollinator interaction network in terms of structure and function. Shifts in forb and bee phenology resulted in temporal mismatches, nonrandom species extinctions, and loss of spatial co-occurrences between extant species in modified landscapes. Less than 25% of the historical plant-pollinator interactions were still observed in 2010-2011. Fifty percent of the bee species that were present historically were extirpated. The quality and quantity of pollen also declined over time as environmental changes heightened. The historic plant-pollinator network showed flexibility in response to phenological change and bee species extirpation; however, the data also suggested that networks will be less resilient to future changes. With reduced redundancy in the network structure and reduced strength of interactions, vulnerability of the overall network increases.

Invasive/non-native species

The presence of invasive and non-native plant species can affect the surrounding plant community and plant-pollinator relationships within the community. Several studies suggest that wild bees prefer to forage—but not necessarily exclusively—on the nectar and pollen from native plants (Harmon-Threatt & Kremen 2015; Morandin & Kremen 2013a; Morales & Traveset 2009; Tuell et al. 2008). The effect of non-native plants in plant-pollinator interaction webs varies between ecosystems and the species studied. Non-native plants that are known to attract pollinators typically compete with native

plants for pollinator visits but don't necessarily decrease reproductive output (Bjerknes et al. 2007).

Climate change

Climate change carries the potential of widespread pollinator extinctions, as it does for many other organisms. If pollinator species can't migrate and adapt in concert with climatic changes, mismatches in the temporal and spatial co-occurrence of plant and pollinator species could lead to population declines and eventual extinctions. Habitat specialists and less mobile species will likely be more challenged by climate change.

The impacts of climate change are identified at all organizational levels, ranging from the individual species level to community levels (Potts et al. 2010). Warm-up rates and body temperatures in bees suggest climate change may affect temporal activity of individual bee species (Stone & Willmer 1989). Climate change can also influence the population genetics of a species, as was identified by Thomas et al. (2001) in evolutionary changes in butterfly populations. Species level shifts were identified from changes in phenology (Hegland et al. 2009), declines due to narrower climatic niches (Williams et al. 2007), and local and regional extinction of butterfly species (Parmesan et al. 1999; Thomas et al. 2001). At the community level, Memmott et al. (2007) simulated data to determine that climate change affects the composition and functioning of pollinator communities.

Diseases

As far back as records go, both domesticated and wild bee populations have suffered from diseases; however, in recent decades, new parasites and pathogens are particularly devastating to pollinator populations in the United States. The tracheal mite (*Acarapis*

woodi) and the varroa mite (*Varroa destructor*) were both inadvertently introduced to United States honey bee hives in the 1980s. The varroa mite has been especially destructive and difficult to combat. It can facilitate the transmission of at least five viruses between adult bees and larvae (Chen & Siede 2007) and some of these viruses have the potential to invade multiple hosts and infect non-*Apis* wild bees. Without varroa treatment, 80-90% of hives in the United States would likely die within two to three years (Spivak et al. 2011).

Bumble bee declines in North America are attributed in part to the inadvertent introduction of the microsporidian pathogen *Nosema bombi* from Europe, which is linked to the global trade of domesticated bumble bee colonies for the pollination of greenhouse crops (Goulson et al. 2008). Cameron et al. (2011) confirmed that declining populations of bumble bees in their study had significantly higher infection levels of the parasite.

The first reports of massive bee die-offs in the winter of 2006/2007 became what is now known as Colony Collapse Disorder (CCD). Nearly a decade later, scientists still struggle to pinpoint a primary cause of CCD. Most likely, CCD is the result of multiple, interactive factors, including habitat loss, nutritional stress, pesticide use, and disease (vanEngelsdorp et al. 2009; Johnson et al. 2009; Mullin et al. 2010).

Fertilizers/pesticides

In the last half-century, many of the small farms in the United States, along with their diverse landscape mosaics of woods, wetlands, meadows, and small crop fields have been replaced by larger-scale homogeneous cropping landscapes (Dimitri et al. 2005). The predominate crops in the United States are now corn, soybeans, and wheat—all of which are wind-pollinated.

The increase in the scale of farms in the United States coincided with the widespread availability of low-cost synthetic fertilizers. These fertilizers replaced crop rotation practices that utilized nitrogen-fixing flowering species like clover and alfalfa. These flowering cover crops were also excellent food sources for pollinators. Chemical pesticides also became more affordable and readily available, many of which are directly toxic to insect pollinators (Spivak et al. 2011). The widespread effect of insecticides—especially systemic insecticides such as neonicotinoids—is a hotly debated topic. The topic is garnering much attention from both industries and the popular media, but the science remains inconclusive on the exact role of insecticides in widespread pollinator population declines.

RESTORING HABITAT FOR POLLINATOR CONSERVATION

The ability of bees to persist in disturbed landscapes, including agricultural borders and domestic gardens, allows unique opportunities for the conservation of pollinators. Traditional conservation planning strategies for threatened or endangered species often entail establishing nature reserves, but pollinators can benefit from small habitat patches integrated into otherwise disturbed agroecosystems or residential landscapes. Localized pollinator habitat efforts can be effective in the biological conservation of pollinators, in the preservation of local pollination services, and are economically more feasible than large-scale regional preserves (Winfree 2010).

Initiatives for pollinator conservation and habitat restoration

The loss of pollinator diversity threatens global agricultural productivity, and for this reason, the prospect of a pollination crisis is garnering the interest of scientists,

policy-makers, and the general public. Special initiatives to address pollinator decline are widespread and growing in the United States. Working under the United States Farm Bill, USDA's Farm Service Agency (FSA) and the Natural Resources Conservation Service (NRCS) have worked with farmers in recent years to improve pollinator habitat conservation on agricultural lands. One such program is the Conservation Reserve Program (CRP), which provides cash incentives to farmers to establish permanent, non-crop vegetation on highly erodible lands. Other programs include the Wildlife Habitat Incentives Program (WHIP) and the Environmental Quality Incentives Program (EQIP). The 2008 (and subsequently, the 2013) Farm Bill recognized the enhancement of bee habitat on private farms as a priority of all conservation programs.

The Xerces Society (xerces.org), a nonprofit organization for invertebrate conservation, is at the forefront of pollinator conservation in the United States. Other nonprofits, including The Pollinator Partnership (pollinator.org) and The National Wildlife Federation (nwf.org/Pollinators) are actively promoting the use of native plants in garden design to provide the most beneficial habitat for pollinators and other wildlife.

President Obama's 2014 Presidential Memorandum on Pollinator Health (Obama 2014) and subsequent National Strategy to Promote the Health of Honey Bees and Other Pollinators (Pollinator Health Task Force 2015) say that federal action combined with private-sector partnerships and citizen engagement can help restore pollinator populations. One goal detailed by the Task Force is to restore or enhance 7 million acres of land for pollinators over the next five years.

In 2015, an unprecedented collaboration of dozens of conservation and gardening organizations formed the National Pollinator Garden Network and launched the Million

Pollinator Garden Challenge (millionpollinatorgardens.org). The goal of the program is to register one million pollinator gardens in the United States by 2017.

Pollinator habitat restoration practices

The recent buzz supporting pollinator conservation and habitat restoration efforts is well supported by published literature. Pollinator-friendly land management practices, which value natural or restored habitat, can improve bee abundance, richness, and productivity, even in landscapes with little natural habitat (Williams and Kremen 2007; Ricketts et al. 2008; Garibaldi et al. 2013; Nicholls and Altieri 2013).

The natural history of our world's pollinator species is widely divergent, but one commonality of these species is their reliance on flowers as a food source. Floral resources can be a limiting factor for populations of bees (Roulston & Goodell 2011) and Lepidoptera (Öckinger & Smith 2006; Summerville & Crist 2001). When floral resources decrease in response to land-use change, pollinators decrease; when floral resources increase with land-use change, so do pollinators (Winfrey et al. 2011).

Pollinator habitat restoration in agroecosystems

Numerous studies, which have been reviewed by Nicholls and Altieri (2013), provide mounting evidence that the preservation and restoration of plant biodiversity within and around agricultural landscapes can improve habitat for both domestic and wild bees, as well as for other beneficial insects; thus, enhancing pollination services for crops. Additionally, pollinator habitat provides multifunctional benefits to the landscape, including biodiversity conservation, conservation biological control, soil and water quality protection, weed suppression, and aesthetics (Wratten et al. 2012).

In intensively farmed agricultural landscapes, the limited bloom time of the crop monoculture, combined with potentially suboptimal nectar and pollen resources, can be detrimental to both wild and managed pollinator populations. Additional floral resources available in non-cropped areas of agricultural landscapes can sustain pollinators before and after the crop bloom (Decourtye et al. 2010). A crop's proximity to natural or semi-natural habitat affects pollinator richness, visitation rate, and fruit set (Williams & Kremen 2007; Ricketts et al. 2008; Garibaldi et al. 2011; Kremen et al. 2004; Morandin & Winston 2006).

Synthesizing data across 23 studies on five continents representing 16 crops, Ricketts et al. (2008) found strong declines in both pollinator richness and native visitation rate as distance from natural or semi-natural habitat increased. Similarly, Garibaldi et al. (2011) synthesized data from 29 studies with various pollinator communities, crop species, and biomes and found that stability of flower-visitor richness, visitation rate (for all insect pollinators except honey bees), and fruit set all decreased with distance from natural areas. Honey bee visitation did not change with isolation.

More specifically, Kremen et al. (2004) found that pollination services provided by native bees on watermelon farms in California strongly depend on the proportion of natural upland habitat within 1-2.5 km of the farm site. This spatial scale correlates with the maximum foraging distances of the predominant native bees. Similarly, Morandin and Winston (2006) found that bee abundance was greatest in Canadian canola fields that had more uncultivated land within 750 m of field edges and that seed set was greater in fields with higher bee abundance.

Isolation from natural habitat can also affect bee reproduction and survival. Williams & Kremen (2007) found that increasing isolation from natural habitat significantly decreased offspring production and survival of solitary bees nesting in conventionally farmed agroecosystems. Isolation from natural habitat had less affect on bees in patches of semi-natural habitat and had little impact on those at organic farm sites. Beneficial natural habitats are not limited to undisturbed ecological communities. Significant biodiversity can be maintained in agricultural areas that include mosaics of natural and managed habitat and where on-site farming practices are less intensive.

A model by Carvell et al. (2011) suggests that targeted pollinator habitat restoration efforts in agroecosystems can deliver the greatest net benefits in more intensively farmed areas rather than in heterogeneous landscapes where other foraging habitats already exist. The most common and well-studied strategies for enhancing floral resources in agroecosystems include the creation and protection of non-cropped areas interspersed in the landscape. Large strips of flowering herbaceous plants (often non-native annuals) are implemented within crop rows and on field margins and herbaceous and woody native plants are restored in natural areas adjacent to cropping systems to permanently enhance pollinator habitat (Decourtye et al. 2010; Wratten et al. 2012).

Replicated field research to validate the creation of pollinator habitat in agroecosystems is limited; however, several case studies support the value of pollinator habitat restoration for specific crops (Carvalho et al. 2012; Blaauw & Isaacs 2012)

Using highbush blueberries in Michigan (*Caccinium corymbosum*) as a model system, Blaauw and Isaacs (2014) found that wild bee and syrphid populations increased annually following the establishment of wildflower plantings adjacent to the blueberry

crop. Percentage fruit set, berry weight and mature seeds per berry were also significantly greater in fields adjacent to wildflower plantings. In addition to providing pollinator habitat, large plantings of wildflowers also increase the density and diversity of other beneficial insects (Blaauw & Isaacs 2012).

Similarly, Carvalheiro et al. (2012) found Mango (*Mangifera indica*) trees in closer proximity to small patches of perennial native wildflowers had significantly higher diversity and abundance of pollinators, as well as increased production, according to the South African study (Carvalheiro et al. 2012). However, the largest pollinator populations and the highest yields were adjacent to natural areas, suggesting that preserving natural habitat is more important than creating new habitat.

PLANT SELECTION FOR POLLINATOR HABITAT RESTORATION

Many plants and pollinators have mutualistic relationships; insects help move pollen to facilitate plant reproduction, and in return, plants offer the insect a food “reward” of pollen and nectar. Pollen is an important protein-rich food source for bees. Female bees also collect pollen and combine it with nectar to form a food product for bee larvae. Nectar is a source of sugar (carbohydrates) and water and provides energy to foraging insects.

Floral attractiveness & resource access

Flowers have evolved flower phenologies, morphologies, color schemes, and fragrances that pollinators find attractive; these traits lure pollinators to the flowers and furthermore to the reproductive parts of the flower. Many pollinators can rapidly associate several flower characteristics with food rewards, including floral color schemes

(Wilbert et al. 1997; Wesselingh & Arnold 2000), floral fragrance (Knudsen et al. 2001; Raguso 2008), and size and shape of flowers or inflorescences (Møller & Sorci 1998; Wignall et al. 2006; Whitney & Glover 2007; Davis et al. 2008; Spaethe et al. 2001).

Among visual cues for pollinators, color is considered one of the most significant signals, enabling pollinators to discriminate between flowers at a distance. Bumble bees and honey bees prefer colors of higher spectral purity and prefer colors that they have learned are associated with high floral rewards (Rohde et al. 2013). Bees have a broad range of color vision that extends into the ultraviolet (UV) part of the light spectrum (Schoonhoven et al. 2005). Most bees have three color receptor types that are most sensitive in the UV, blue, and green parts of the spectrum (Chittka 1996) and least sensitive in the red part of the spectrum. Butterflies and hummingbirds are able to see UV, blue, green, and red, while humans can see blue, green, and red, but not UV.

Flower morphology can dictate what types of pollinating insects visit the flower and can access the flower's resources. Influential flower features include size, shape and habit of the flower; corolla width and depth; location of the nectaries; and presentation of the pollen (Holm 2014). For example, different species of *Bombus* have different tongue lengths; species with short tongues are adapted to forage on short open flowers while species with long tongues can feed on flowers with long corolla tubes (Goulson 2003). Olfactory discrimination is also highly developed in plant-pollinator relationships (Knudsen et al. 2001; Raguso 2008). Most floral scents are complex bouquets of numerous volatiles. Nectar may also contain odorous compounds that serve as a signal to potential pollinator visitors.

To boost their foraging efficiency, some bees leave volatile pheromones or “footprints,” on visited flowers to cue themselves and other pollinators that the flower was recently visited and has low nectar availability (Schoonhoven et al. 2005). Flying by a flower, they are able to assess the reward available and if it is worth stopping and expending the energy to access the flower’s nectaries.

The duration that a bee knows to avoid a flower appears to be inversely correlated with nectar secretion rates. For example, *Bombus terrestris* avoided revisiting *Symphytum officinale* flowers, which have a high nectar secretion rate, for three to ten minutes. They avoided revisiting *Melilotus officinalis* and *Lotus corniculatus*, which both have low rates of nectar production, for at least two to 24 hours (Stout & Goulson 2002). Some bees, including bumble bees, can also leave a pheromone message on flowers indicating that the food source is worthwhile to visit. By using these signals, bees improve the efficiency of foraging by reducing the time they spend visiting unrewarding flowers.

Nectar Dynamics

To interpret the nectar foraging behavior of pollinating insects, it is important to understand the dynamics of nectar production. Measurements of the quantity and dynamics of nectar secretion are useful tools in understanding the ecological and evolutionary interactions of plants and pollinators (Zimmerman 1988; Kearns and Inouye 1993). Better understanding nectar dynamics in flowering plants used in pollinator habitat enhancement efforts can help improve plant selection, ultimately providing a greater concentration of desirable flower resources to target pollinators.

Flower nectar consists mainly of sugar (sucrose, glucose and fructose) and water. A range of other compounds are found in minute quantities, including free amino acids,

lipids, minerals, and secondary compounds (Schoonhoven et al. 2005). Nectar is secreted from the flower's nectaries, which are typically located near the base of the ovary, making access difficult or even impossible for some insects. Insects have to insert their mouthparts, heads and sometimes abdomens into the corolla of the flower. This action often puts the pollinator in contact with the anthers and stigma of the flower, facilitating the movement of pollen and the fertilization of the plant.

The timing of nectar production varies by plant species. Some plants secrete nectar throughout the day (or night) while others secrete most of their nectar at a certain time of day (Comba et al. 1999). Some plants, such as Spiderwort (*Tradescantia* spp.) do not offer nectar as a reward but instead offer a large quantity of pollen. To understand nectar dynamics, it is important to measure both standing crop and secretion rate of nectar (Kearns & Inouye 1993; Corbet 2003). The standing crop is the quantity of nectar in a flower at a given time and secretion rate is a measure of the rate at which nectar is replenished by the flower following extraction.

In the field, the sugar content of nectar can be estimated from measurements of nectar volume and solute concentration, measured with a sucrose refractometer (Kearns & Inouye 1993; Corbet 2003; Marrant et al. 2009). The quantity of nectar in a flower and the nectar's sugar concentration fluctuates through time as nectar is secreted by the plant and depleted by foraging pollinators or reabsorption (Comba et al. 1999). The amount of water in nectar can also fluctuate with secretion, condensation from humid air, and precipitation, and it can decrease with evaporation (Corbet 2003).

Planting lists for pollinators

Our understanding of the importance of individual flower species, flower continuity, and pollinator nutrition is growing, yet we still have much to learn about region-specific planting lists for pollinator habitat. Several studies demonstrate the attractiveness of perennial wildflowers to pollinators and their positive effects at boosting pollinator abundance and diversity (Meek et al. 2002; Carvell et al. 2004; Pywell et al. 2005; Tuell et al. 2008).

In the United States, Fabaceae (e.g. *Dalea* spp. and *Lupinus* spp.), Asteraceae (e.g. *Silphium* spp., *Solidago* spp., *Symphyotricum* spp.), and Lamiaceae (e.g. *Agastache* spp., *Monarda* spp., *Pycnanthemum* spp.) are considered particularly valuable pollen and nectar sources for both honey bees and wild bees (Mader et al. 2011). However, this is largely based on anecdotal observations, not replicated field science.

Several studies report that Fabaceae plants (legumes) are among the most visited flowering plants by both honey bees and some wild bee taxa, including megachilids, eucerines and antophorines, in Sweden (Lagerlöf & Wallin 1993) and England (Carvell et al. 2007). However, other wild bees such as andrenids, colletids and halictids, and many pollen-specialist megachilids may not benefit from legume-rich plants (Rasmont & Mersch 1988). With some wild bee taxa preferring more specific sources of nectar and pollen, it is generally recommended to use a diversity of wildflowers in pollinator habitat restoration efforts in the United States (Decourtye et al. 2010).

Tuell et al. (2008) examined the relative attractiveness of 43 eastern United States native perennial plants to wild and managed bees. The plants most attractive to wild bees in their peak bloom order were as follows: *Fragaria virginiana*, *Zizia aurea*, *Penstemon*

hirsutus L., *Coreopsis lanceolata*, *Potentilla fruticosa*, *Apocynum cannabinum* L., *Rosa setigera* Michx., *Scrophularia marilandica*, *Verbena stricta* Vent., *Asclepias incarnata*, *Veronicastrum virginicum*, *Ratibida pinnata*, *Amorpha canescens* Pursh, *Allium cernuum*, *Spiraea alba*, *Agastache nepetoides*, *Monarda punctata* L., *Vernonia missurica* Raf., *Silphium perfoliatum*, *Cacalia atriplicifolia* L., *Eupatorium perfoliatum*, *Lobelia siphilitica*, *Helianthus strumosus* L., *Lespedeza hirta* L., *Liatris aspera* Michx., *Solidago riddellii*, *Solidago speciosa*, *Aster novae-angliae* L., and *Aster laevis* L.

Pollinator preference for native versus non-native plants

Several studies suggest that wild bees prefer to forage—but not necessarily exclusively—on the nectar and pollen from native plants (Memmott & Waser 2002; Fiedler & Landis 2007a; Fiedler & Landis 2007b; Harmon-Threatt & Kremen 2015; Morandin & Kremen 2013; Morales & Traveset 2009). Another study suggests no preference between native and non-native plants (Williams et al. 2011). In some specific cases, non-native plants may be more attractive than co-flowering native plants (Bartomeus et al. 2008; Tepedino et al. 2008; Brown et al. 2002).

Plants that are native to a particular region are well adapted to the local climate and soil conditions and frequently have lower water, nutrient, and pest-control requirements than introduced species. Native plants also have evolutionary associations with other local plants and herbivores that are beneficial to the whole ecosystem (Tallamy 2004). Properties landscaped with native plants support significantly more caterpillars and birds than properties dominated by non-native vegetation (Burghardt et al. 2010). An analysis of historic records from a diverse landscape in southwestern

Illinois found that the web of interactions between plants and pollinators was less richly connected for non-native plants than for natives (Memmott & Waser 2002).

Evaluating a data set of 40 previous studies, Morales and Traveset (2009) found that non-native plants compete with native plant species for pollination. Overall, they found a significantly negative effect of non-native plant species on visitation to and the reproduction of co-flowering native species. The negative effect was most detrimental when non-native and native co-flowering species had phenotypic similarity, particularly color or flower symmetry. In a replicated field trial in Michigan, 43 species of native perennial plants and five non-native flowering annuals frequently recommended for habitat restoration were evaluated for attractiveness to arthropod enemies and herbivores. The study found that native plants were generally associated with a greater abundance of beneficial arthropods, including native bees, than non-native plant species (Fiedler & Landis 2007a; Fiedler & Landis 2007b).

At both mature and newly established agricultural hedgerow sites in California, wild bees prefer to forage from native plants over non-native plants (Morandin & Kremen 2013). Likewise, in California grasslands, bumble bees collect significantly more pollen from native plants than from non-native plants (Harmon-Threatt & Kremen 2015). Interestingly, this study found no differences in the nutrient availability (essential amino acid content and protein), suggesting that exotic species could meet the nutritional needs of bumble bees, if they were selected.

In contrast to the aforementioned studies, an investigation of the interactions between bees and non-native plants in disturbed habitats in central California and southern New Jersey found no effect of non-native plant abundance or richness on bee

abundance or richness. This suggests that in disturbed landscapes bees may use, but do not prefer, non-native plants (Williams et al. 2011). However, species richness of plant and insect species may decline as the levels of non-native plant invasion increases (Heleno et al. 2009).

In other specific scenarios, non-native plants may attract more pollinators than co-flowering native plants. This is the case with *Carpobrotus affine acinaciformis*, a succulent perennial, and *Opuntia stricta*, a cactus. Both of these species have large and showy flowers and received more pollinator visitors than co-flowering native plant species in Mediterranean Spain (Bartomeus et al. 2008). Tepedino et al. (2008) also found that three non-native plant species, salt cedar (*Tamarix* spp.) and white and yellow sweet clover (*Melilotus albus*, *M. officinalis*) had as many or more associated bee species individuals as did native plant species in Capitol Reef National Park, Utah. Both Memmott & Waser (2002) and Tepedino et al. (2008) found that nonnative plants likely benefit generalist bee species more than they benefit specialist bee species.

A limitation of studies that compare plant-pollinator interactions among plant species is that the list of species selected for study is often biased by *a priori* observations. In the cases of Bartomeus et al. (2008) and Tepedino et al. (2008), the non-native plant species were chosen for the research because they had already been observed to be attractive to pollinators; they were not randomly selected from all non-native flowering species in their ecological communities.

Despite numerous studies demonstrating pollinator preference for native flowering plant species, the use of native wildflowers in pollinator habitat restorations is sometimes limited by the lack of availability of native plants or seed mixes in commercial

quantities, high plant/seed cost, and comparatively long establishment period. However, once habitat plantings of native perennial plants are established, they generally persist with minimal maintenance. (Maintenance may be needed to control for invasive species and to prevent the establishment of woody species in the herbaceous plant community). Additionally, the restoration of native plant communities in agricultural landscapes can help mitigate for native plant community losses during past periods of agricultural intensification.

In domestic garden settings, where non-native flower options are bountiful and come in colors, sizes, and morphologies known to be attractive to bees, the differences in attractiveness between native and non-native plants appear less pronounced. Although pollinators may still prefer native plants over non-natives in domestic gardens (Corbet et al. 2001; Salisbury et al. 2015), numerous non-native species are also frequently visited by bees (Hanley et al. 2014; Salisbury et al. 2015). Approximately 80% of plant species in conventionally landscaped suburban yards in the United States are non-native (Burghardt et al. 2009) and approximately 70% of plant species in domestic gardens in the United Kingdom are non-native (Loram et al. 2008). Many landscape designers and home gardeners wish to attract pollinators and other wildlife to their gardens to help support biodiversity, but the values of particular plant species and plant assemblages aren't well studied, and the studies that do exist, are sometimes conflicting.

Comparing insect visits and nectar production in four British native plants and four non-native plants, Corbet et al. (2001) found all native species to be nectar-rich and frequently visited by pollinators. Conversely, the non-native species had fewer pollinator visits, and in cases where nectar was readily available, it was inaccessible. They also

found that double flowering varieties of the non-native flowers secreted little or no nectar (Corbet et al. 2001).

In another British study, Salisbury et al. (2015) performed a replicated field experiment, establishing garden plots planted with an assemblage of plants based on origin. The three treatments included assemblages of native, near-native and exotic flowering plant species. There was a greater abundance of total pollinators recorded on native and near-native plots compared to the exotic plots; however, some exotic flowers were also frequently visited. The authors suggest that pollinator gardens in the UK should include a variety of flowering plants, biased towards native and near-native species, but also incorporating a selection of non-native species that potentially provide resources for specialist groups or help extend the flowering season.

A recent study of bumble bee preferences in urban gardens in the United Kingdom (Hanley et al. 2014) did not offer much more clarity on the debate over native versus non-native plant preference by bees in garden landscapes. Their analysis of flower use by bumble bees produced conflicting results depending on which plant species and which bumble bee species were included. This suggests that floral attractiveness varies among both native and non-native flowers, as do floral preferences among pollinator species.

CULTIVARS OF NATIVE PLANTS AND POTENTIAL IMPLICATIONS FOR POLLINATOR ECOSYSTEMS

The propagation of native plant species, both herbaceous and woody, is a specialized field, requiring access to local seed sources and knowledge about seed collection, pre-treatment, and germination techniques. The growing demand for native

plants, combined with these propagation challenges and a desire for more robust or predictable plant habits in domestic gardens, have led to the selection and breeding of native cultivars.

If using native plants in pollinator habitat restorations and gardens is important for maximizing the availability of preferred floral resources for pollinators, then can cultivars of native plants fill this role? Many plants marketed as “natives” in garden centers and plant catalogs have never grown naturally in the wild. They are cultivars and hybrids of native plants that have been selected, cross-bred or hybridized by botanists and breeders for desirable characteristics that can be maintained through propagation. These characteristics include flower size and color, foliage color, extended bloom periods, more predictable and manageable plant forms and sizes, sterility, and disease resistance.

Shifts in floral displays and resources

Although cultivars of native perennials are commonly propagated and sold in the nursery and landscape industry, there is a lack of quantitative research evaluating how native cultivars compare to native species. Observationally, we know that compared to the straight species, the flowers of native cultivars may vary in size, abundance, color, morphology, and phenology—all attributes we know influence floral visitation. Stems may be sturdier and leaves may be variegated or vary in color. The plants may be taller or more compact; more or less vigorous; more or less hardy; prefer leaner or richer soils; prefer more or less soil moisture; and be more or less tolerant of pests and diseases. It is also possible that cultivars produce more or less nectar and pollen with varying levels of nutrition. All of these variables have the potential to impact the attractiveness of the plant variety to pollinators and the availability and accessibility of the floral reward; however,

to my knowledge, none of these variables has been studied in a replicated field experiment.

Loss of genetic variation in native cultivars

A major consideration when using human-bred and hybridized native cultivars in the landscape is the loss of genetic variation naturally found in open-pollinated plant populations and the potential for cultivars to hybridize with surrounding populations of native species. In a large-scale planting of native cultivars, the cultivars provide a significant source of foreign genes and the small remnant population of native species act as a sink (Byrne et al. 2011). This is the case in Estonia, where extensive introgressive hybridization is seen between wild and cultivated varieties of alfalfa (Kaljund & Leht 2013).

When hybridization occurs between native species and maladapted cultivars in the landscape, the population may experience a reduction in fecundity, germination rates, competitiveness, and survivorship (Byrne et al. 2011). In the face of environmental change, native plant populations may need the naturally occurring genetic variation within their open-pollinated species to adapt to stochastic environmental events, such as drought, floods, and temperature extremes. In a comparison of 9 native, 9 weedy, and 14 improved cultivars of sunflowers (*Helianthus spp.*) in Indiana, researchers found that although improved cultivars increased their allocations to flowers, they were significantly less drought tolerant (Koziol et al. 2012).

For specific applications, such as erosion control and biofuel crops, native cultivars are being selected for high biomass production. These are also characteristics associated with invasiveness. The potential negative consequences of introducing the

genes of vigorous cultivars into native plant populations are concerning and are not well studied (Kwit & Stewart 2012).

Researchers in Illinois found enhanced physiological performance (higher net photosynthesis, stomatal conductance, and water use efficiency) in three dominant prairie grass cultivars compared to native species (Lambert et al. 2011). These characteristics, also associated with invasiveness, may have implications for competitive interactions that affect community structure and ecosystem function in native prairie ecosystems. Similarly, Schröder & Prasse (2013) found cultivated varieties of *Plantago lanceolata* and *Lotus corniculatus* (two species frequently used in restoration projects in Germany) offered enhanced biomass production but were less resilient to environmental fluctuations.

For the reasons discussed above, the use of strongly selected cultivars is generally discouraged in ecological restoration projects (e.g. prairie or wetland restorations) (Lesica & Allendorf 1999; Schröder & Prasse 2013), but the availability and use of native cultivars in the horticultural industry is high. Potential differences between native species and native cultivars is not discussed in pollinator habitat guides and actual differences have not been previously studied.

To maximize the floral resources available to pollinators in habitat restoration projects, including agricultural land and landscape gardens, it is important that we better understand the advantages and disadvantages of using cultivars of native plants as substitutions for native species. These plant choices can affect the abundance, quality, and accessibility of the floral resources for pollinators.

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CHAPTER 2

POLLINATOR PREFERENCE FOR NATIVE SPECIES VERSUS NATIVE CULTIVARS IN POLLINATOR HABITAT RESTORATION

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ABSTRACT

There is growing awareness about the value of preserving and restoring floral-rich habitats for the benefit of pollinators, especially native bees. The increasing demand for native plants in pollinator habitat restoration and other ecological landscaping applications, combined with the desire for more robust and predictable plant habits, have led to the selection and breeding of native cultivars. Yet, little is known about how these cultivated varieties differ from the native species in their ability to attract and support pollinators. We compared flower visitation by all insect pollinators to 11 flowering herbaceous plant pairs in a replicated field experiment at 2 sites over 2 years. Each plant pair was composed of the native species and a cultivated variety of the native species. We classified insect pollinators during visual field observations into 7 taxonomic and functional groups. Across the 11 plant pairs, we found 6 native species to be preferable to their cultivars to all insect pollinators, 4 were equally preferred, and one native cultivar was preferred over the native species. Bees (both native and non-native) and moths/butterflies exhibited similar preferences, whereas flies showed no preference between the native species and the native cultivar. Our study shows that many insect pollinators prefer to forage on native species over cultivated varieties of the native species, but not always, and not exclusively. Some native cultivars may be comparable substitutions for native species in pollinator habitat restoration projects, but all cultivars should be evaluated on an individual basis.

INTRODUCTION

The functional role of pollinators is integral to the sustainability of wild plant communities and the productivity of agricultural crops worldwide. Almost 90% of flowering plant species on earth rely on animal-mediated pollination (Ollerton, Winfree, & Tarrant, 2011). Seventy-five percent of global food crops are dependent upon animal pollinators for fruit, vegetable, and seed production, accounting for 35% of the volume of global food crops (Klein et al., 2007).

The estimated annual value of agricultural crops directly dependent on pollination from honey bees (*Apis mellifera*) and other (non-*Apis*) pollinators reached \$11.68 billion and \$3.44 billion respectively in 2009 (Calderone 2012). Although honey bees are responsible for about 70% of the total crop pollination value in the U.S., relying exclusively on honey bees for pollination is risky. As the global cultivation of pollinator-dependent crops rapidly increases (Aizen & Harder 2009), so have concerns about the health of honey bee colonies (Carreck & Neumann 2010) and the overall sustainability of this pollination model. Awareness is growing about the value of non-*Apis* pollinator species and how to restore habitat in and around agricultural lands for their benefit.

Habitat loss and fragmentation

Among the most significant drivers of pollinator population declines are habitat loss and fragmentation due to land-use change (Potts et al. 2010). Habitat loss and fragmentation over the past century have caused plant-pollinator networks to become significantly degraded in terms of structure and function (Burkle & Alarcón 2011). A meta-analysis of bee response to anthropogenic disturbance shows that habitat loss and fragmentation negatively affect the abundance and species richness of wild bees (Winfree et al. 2009). In agricultural landscapes that include preserved natural or semi-natural habitat, native bees can meet all of the crop's pollination requirements without utilizing managed honeybee colonies (Kremen et al. 2004; Morandin & Winston 2006; Winfree et al. 2007). However, 39% of the pollinator-dependent crop area in the U.S. suffers from a mismatch between supply of wild bees and the need for their pollination services (Koh et al., 2016).

Special initiatives to address pollinator decline are widespread and growing in the U.S. Pollinator-friendly land management practices, which value natural or restored habitat, can improve bee abundance, richness, and productivity, even in landscapes with little natural habitat (Williams & Kremen 2007; Ricketts et al. 2008; Garibaldi et al. 2013; Nicholls & Altieri 2013). This provides mounting evidence that the preservation and restoration of plant biodiversity within and around agricultural landscapes can improve habitat for both domestic and wild bees, as well as for other beneficial insects, thus enhancing pollination services for crops.

In intensively farmed agricultural landscapes, the limited bloom time of a crop monoculture, combined with potentially suboptimal nectar and pollen resources, can be detrimental to both wild and managed pollinator populations. Restoring or enhancing floral resources in non-cropped areas of agricultural landscapes can sustain pollinators before and after the crop bloom (Decourtye et al. 2010).

Plant lists for pollinator habitat restoration frequently recommend native species. A native plant is an endemic species that occurs naturally in a plant community, ecosystem, ecoregion, or biome without direct or indirect human involvement (U.S. Forest Service 2012). Several studies suggest that wild bees prefer to forage—but not necessarily exclusively—on the nectar and pollen from native plants (Harmon-Threatt & Kremen 2015; Memmott & Waser 2002; Morales & Traveset 2009; Morandin & Kremen 2013; Tuell et al. 2008). The growing demand for native plants in ecological landscaping, combined with the desire for more robust and predictable plant habits, have led to the selection and breeding of native cultivars. Native cultivars are cultivated lineages of

native species; they are selected by humans for desirable characteristics that can be maintained through propagation.

There is a tremendous amount of variation in the origin of native cultivars, how they are propagated, and the desirable traits for which they are maintained. Native cultivars can be derived from a unique selection from a natural population of the native species, a selection from nursery-grown stock of the native species, selections from repeated interspecific crosses in a breeding program, selection of a naturally occurring hybrid of two native species in the same genus, or intentional hybrid crosses of two or more native species in a breeding program. The flowers of native cultivars may differ from the species in size, abundance, color, morphology, and phenology—all attributes known to influence pollinator visitation (Wilbert et al. 1997; Møller & Sorci 1998; Wesselingh & Arnold 2000; Knudsen et al. 2001; Spaethe et al. 2001; Wignall et al. 2006; Whitney & Glover 2007; Davis et al. 2008). Other characteristics for which selections are often made include more predictable and manageable plant forms and sizes, sterility, and disease resistance. Native cultivars may differ from the native species in the food rewards they make available to visiting pollinators (A. White & L. Perry, unpublished data).

Because cultivars have been selected primarily based on ornamental traits, it is not clear whether they perform the same ecological roles as the species, which evolved naturally in the landscape. All of these variables have the potential to impact the attractiveness of the plant selection to pollinators and the availability and accessibility of the floral reward; however, to our knowledge, none of these variables has been studied in a replicated field experiment. Furthermore, the potential differences between native

species and native cultivars are not discussed in pollinator habitat restoration guides. The use of native cultivars, especially those that have undergone repeated selections, is generally discouraged in ecological restoration projects (Lesica & Allendorf 1999; Schröder & Prasse 2013), but native cultivars are dominant in terms of availability and use in the nursery and landscape industries.

The National Pollinator Garden Network aims to register 1 million pollinator gardens by 2017. President Obama's 2015 Pollinator Health Task Force aims to enhance 7 million ac (2.8 million ha) of land for pollinators. Bee habitat on private farms remains a priority of all conservation programs under the U.S. Farm Bill. Accordingly, it is important that we ask the question: Are native cultivars equivalent substitutions for native species in pollinator habitat restorations?

METHODS

Study sites

We established pollinator habitat research gardens in 2012 at two farms in northern Vermont, U.S.A. (Fig. 2.1&2.2). Site A (44°39'9.75"N, 72°58'32.68"W) was established on farmland previously in sunflower production on a diversified organic farm in Franklin county. The farm grows approximately 28 ha (70 ac) of vegetables in USDA hardiness zone 4b and on soils classified as excessively drained Windsor loamy fine sand. Approximately 30-50% of the cropped areas on the farm are insect-pollinated fruits and vegetables, including strawberries, raspberries, cucurbits, and cover crop seed production. Organic and Integrated Pest Management (IPM) practices are used throughout the farm. Seven to ten hives of honeybees are maintained on the farm and located approximately 200 m southeast of the research site.

Approximately 114 miles to the east, on the opposite side of the Green Mountains, we established Site B (44°35'19.04"N, 71°32'54.29"W) on farmland previously in pumpkin production at a small 4 ha (10 ac) conventional horticultural operation in Essex County. The farm grows approximately 1000 m² of potted chrysanthemums, 300 m² of pumpkins, and maintains perennial flower gardens in USDA hardiness zone 4a and on soils classified as well-drained Adams loamy fine sand. No honeybees were kept on the farm or, to our knowledge, within 1 km of the research site. No honeybees were observed on flowers at Site B from May to August, but they were observed visiting late-blooming flowers in September and October of 2013, 2014 and 2015.

Plant selection

We selected 11 species of native herbaceous flowering plants for the study (Fig. 2.3). We aimed to include early-, mid-, and late-blooming species and to have a diversity of floral morphologies represented in the plant list (Table 1). Each native species was paired with a native cultivar of the same species; cultivars chosen are commonly available and used in the nursery and landscape industries. We included cultivars with varied origins from selections to intentional hybrid crosses, and that represent a variety of phenotypic changes from the native species, including changes in flower color, floral abundance, plant stature, and leaf color. Plant availability of both the species and cultivars also affected plant selection.

All species are considered present and native in Franklin and Essex counties by The Biota of North America Program (BONAP) (Kartesz 2016), with two exceptions. *Agastache foeniculum* is listed by BONAP as present and native in northern NY and NH

counties, but not in VT. *Rudbeckia fulgida* is identified as present and native in northern NY counties. We chose to include *Agastache* because of its observed attractiveness to pollinators and *Rudbeckia* because of its popularity in the landscape industry.

Local genotype native plants are not commercially available in our study region; thus, both native species and cultivars were purchased as landscape plugs (12.7 cm deep x 5.1 cm wide) from North Creek Nursery in Landenberg, PA, in June of 2012. *Achillea millefolium* was collected from an indigenous population in Essex County, VT. All plugs were transplanted into 2-liter plastic pots (Dillen 5.5 Sq Jumbo, Griffin Greenhouse Supply, Tewksbury, MA) using an organic compost-based potting soil (Fort Vee Potting Soil, Vermont Compost Company, Montpelier, VT). The pots were placed in trays on a black lumite ground cover (Lumite GCB, Griffin Greenhouse Supply, Tewksbury, MA) and irrigated as needed with overhead sprinklers through summer 2012.

Plant establishment and maintenance

Site A and Site B were tilled in preparation for fall planting. The sites were planted on 2 September 2012 and 4 September 2012. We applied approximately 1 liter per 90 sq m of an organic custom blend 5-1-9 fertilizer (North Country Organics, Bradford, VT) and installed T-tape drip irrigation (T-Systems Irrigation, San Diego, CA). Irrigation was applied only as needed during the fall of 2012 and spring of 2013. To encourage the presence of ground-nesting solitary bees, mulch and other weed barriers were not used; weeds were controlled manually for the duration of the study.

Individual plants that did not overwinter were replaced in the spring of 2013 and 2014 with plants of the same size and age that were maintained in reserve. Reserve plants were heeled into the ground in pots during the winter of 2012 and then planted in a

garden area adjacent to the study area at Site B in the spring of 2013. *Agastache foeniculum* ‘Golden Jubilee,’ *Asclepias tuberosa*, *Asclepias tuberosa* ‘Hello Yellow,’ *Rudbeckia fulgida* var *fulgida*, and *Rudbeckia fulgida* ‘Goldsturm’ experienced high winter mortality rates. Without sufficient replacement plants, we only replaced *Agastache* spp. at Site A and *Asclepias* and *Rudbeckia* spp. at Site B.

Experimental design

Both pollinator habitat research areas were approximately 9 m wide and 30 m long or 270 m² (Fig. 2.4). The long rectangular shape of the sites best fit the landscape constraints at both farms. We designed the research area at each farm as randomized complete blocks with three replicates. Within each replicate, we randomly assigned plant types to 1 x 1.5 m planting units. Each unit contained a group of 6 plants of the same type, planted approximately 45 cm on center. We did not locate a native species and its cultivar within 3 m of each other. Massed plantings are often recommended in pollinator habitat restoration to allow foraging bees to more easily practice flower constancy (Heinrich et al. 1977; Waser 1986). Planting units had a 30-cm space between them and replicates had a 1-m wide row between them. A total of 18 plants of each native species and 18 of each cultivar were planted at each site. Together the research gardens contained a total of 1,224 plants and 34 plant types; 792 plants and 22 plant types are analyzed in this paper.

Data collection

We visited Site A and Site B a minimum of four times per month between late May and early October of 2013 and 2014. The *Baptisias* and *Veronicastrums* were monitored again in 2015 because of their slow maturation rate. To maximize potential

for pollinator presence, we collected data on days with no precipitation, temperatures greater than 15°C, cloud cover less than 50%, average wind speeds less than 15 kph, and between 9:00 am and 4:00 pm.

Bloom Duration & Floral Abundance: At each site visit, we evaluated flowers for bloom status and categorized each plant type as non-flowering, budding, pre-peak, peak bloom, or post-peak. Each year during the peak bloom period (>75% of buds in flower) for each species and cultivar, we counted the number of individual flowers for all plants. We measured floral abundance instead of floral cover because flower size did not differ significantly between each species-cultivar pair in our study and floral abundance was deemed a more accurate measure for plants with equal flower sizes, but different forms.

Pollinator Visitation: At each site visit, we visually monitored planting units in peak bloom for pollinator visits. One experienced human observer (A. White) collected data to minimize human error and variability. All plant species in all replicates were observed in random order. We observed plant pairs (i.e., a native species and its cultivar) in each replicate sequentially to minimize the effects of weather changes throughout the day on pollinator visitation rates. We visually observed and recorded pollinator visits to the reproductive parts of flowers during five-minute scans of each unit (i.e., 6 plants of the same type planted in a unit). At the beginning of each scan period, pollinators present on the flowers within the unit were recorded and then new pollinators entering the unit were recorded over the subsequent five minutes. Pollinators moving from flower to flower within the unit were counted once. A pollinator leaving and reentering the unit during the scan period could be counted more than once.

All pollinators were classified into seven visually identifiable taxonomic and/or functional insect groups: Honey Bees (*Apis mellifera*), Bumble Bees (*Bombus spp.*), Other Native Bees (order: Hymenoptera), Butterflies/Moths (order: Lepidoptera), Wasps/Ants (order: Hymenoptera), Bugs/Beetles (orders: Hemiptera/Coleoptera), and Flies (order: Diptera). We chose to employ direct observation methods instead of capturing and exterminating pollinators visiting flowers so as not to remove any pollinator visitors from the site's population. Direct observation may also be a better method for recording bees at flowers than collection methods, such as vacuum sampling (Tuell et al., 2008). A limitation of direct observation is the inability to identify most pollinators down to the species level.

Visitation data analysis

We designed this study to compare the mean number of visits by 7 pollinator groups to 11 native species of flowering plants and 11 cultivars of the same species. We did not randomly select the plant species in this study from all possible native plants recommended for pollinator habitat restoration, nor did we randomly select the native cultivars from all possible cultivars for each species. Therefore, our plant list is not necessarily representative of all native plants and native cultivars. For this reason, our models are for comparing mean pollinator visits between each species-cultivar pair, not for comparing and ranking all species to each other.

Challenges to our analysis of pollinator visits included: the data not fitting a normal distribution and not being well-suited for transformation, some pollinator groups visiting some plant species and cultivars at very low rates, significant differences

between the sites and between years, and having imbalance in the data between sites and years.

We compared mean pollinator visits by 7 pollinator groups and 3 composite groups (All Pollinators, All Bees, and All Native Bees) for each species/cultivar pair using generalized linear mixed models (GLIMMIX) with a log-link function and Poisson or negative binomial distribution. (A negative binomial distribution was used if Poisson did not correct for over-dispersion.) Generalized linear models are an extension, or generalization, of the linear modeling process, which allow for non-normal distributions. The values of the parameters in the generalized linear models were obtained by maximum likelihood (ML) estimation, which requires iterative computational procedures. All statistics were run at 0.05 level of significance and generated using SAS software Version 9.4 (SAS 2014).

In each model, we included plant type (two levels), site (two levels), and year (two levels) as fixed effects; the two-way interactions between the fixed effects; replicate as a random factor; and weeks nested within years as a repeated factor. Multiple observations on the same replicate were averaged for each week. For some pollinator groups with sparse data, our models needed to be simplified (e.g. removing two-way interactions between fixed effects) to converge. For very sparse data, models could not converge and no results are presented; however, the data are compiled in the composite group All Pollinators.

Resource selection by animals often involves comparing the usage of food to the availability of food resources (Johnson, 1980). Our methods aimed to standardize the availability of food resources by making the same number of each plant type available to

pollinators within the research site. Unlike Morandin and Kremen (2013), we did not standardize for floral abundance when determining pollinator preference and the estimated mean pollinator visits from our model (Table 2) do not include floral abundance as a covariate. In practical applications, where restoration ecologists, designers, and landscapers are faced with making a choice between planting a native species or planting a cultivar, knowing the pollinator preference per *plant* is more relevant than per *flower*.

However, standardizing for floral abundance can sometimes explain why pollinators exhibit preferences for some plants, i.e. there are simply more flowers per plant to forage on. Therefore, we ran the models with floral abundance as a covariate for species-cultivar pairs that differed significantly in floral abundance. These outcomes are discussed in the results section for each species-cultivar pair.

RESULTS & DISCUSSION

We recorded a total of 14,824 pollinators during 1,146 five-minute observation periods during this study. At site A, we recorded 8,143 pollinators during 572 observation periods, and at Site B, we recorded 6,681 pollinators during 573 observation periods (Fig. 2.5). The predominant pollinator groups at Site A were Bumble Bees (43%) and Honey Bees (30%), followed by Other Native Bees (13%), Flies (6%), Beetles/Bugs (4%), Butterflies/Moths (2%), and Wasps/Ants (2%). The predominant pollinator groups at Site B were Bumble Bees (68%), Flies (14%), and Other Native Bees (11%), followed by Honey Bees (5% - only observed in September and October of each year), Beetles/Bugs (1%), Butterflies/Moths (1%), and Wasps/Ants (1%). Across the 11 plant pairs, we found

6 native species to be more preferable than their cultivars to All Insect Pollinators, 4 were equally preferred, and one native cultivar was preferred over the native species.

Site and year were also significant in most models. In all models with a significant site effect, Site A had more pollinator visits than Site B, which corresponds with the higher relative abundance of total pollinators at Site A (Fig. 2.5). In only one model (*Monarda*) did plant type preferences differ between the two sites. In all models with a significant year effect, pollinator visits increased significantly between year 1 and year 2. This is likely the result of an increase in floral abundance as the plants matured as well as more pollinators using the research gardens as habitat in year 2. In no cases did plant type preferences differ between years. Results are given for the sites and years combined unless otherwise noted.

***Achillea millefolium* and *A. millefolium* ‘Strawberry Seduction’**

We observed 1,414 pollinator visits to *Achillea millefolium* and 119 visits to *A. millefolium* ‘Strawberry Selection.’ The species was most visited by Other Native Bees (54.9%) and Flies (34.2%); the cultivar was most visited by Flies (60.3%) and Other Native Bees (28.5%) (Fig. 2.6). All Pollinators exhibited a strong preference for the species ($F_{[1,44]} = 119.04$, $p < 0.001$), as did Other Native Bees ($F_{[1,45]} = 137.50$, $p < 0.001$). Flies, however, showed no significant preference between the species and cultivar ($F_{[1,44]} = 0.85$, $p = 0.3616$) (Figs. 2.6 & 2.7, Table 2.2). Both the species and the cultivar were hardy at both sites with 100% winter survival. The species had significantly more flowers per plant than the cultivar ($t_{[135]} = 7.52$, $p < 0.001$), but standardizing for floral abundance did not change the preference outcome of the model.

A. millefolium ‘Strawberry Seduction’ was selected as a whole plant mutation that arose from repeated selections from seed originally sown of the strain *Achillea* ‘Summer Pastels.’ It was derived from a breeding program that focused on obtaining *Achillea* cultivars with long bloom durations and unique flower colors resistant to fading. Bee vision is less sensitive in the red wavelengths, making red flowers less attractive to bees (Proctor et al. 1996). Although the species was more attractive to bees, it can become highly aggressive in some habitats and should be planted cautiously. Less aggressive cultivars with more pollinator-friendly colors should be evaluated.

***Agastache foeniculum* and *Agastache* ‘Golden Jubilee’**

We observed a total of 973 pollinator visits to *Agastache foeniculum* and 566 visits to *Agastache* ‘Golden Jubilee.’ Bumble Bees (40.2%), Honey Bees (32.6%), and Beetles/Bugs (21.6%) were the predominant pollinators observed on the species. Bumble Bees (60.6%) and Honey Bees (25.6%) were observed most frequently on the cultivar (Fig 2.6). All Bee Pollinators showed no significant preference for the species or cultivar ($F_{[1,7]} = 1.21$, $p = 0.308$), but Beetles/Bugs exhibited a preference for the species ($F_{[1,4]} = 20.3$, $p = 0.013$) (Figs. 2.6 & 2.7, Table 2.2).

This cultivar is marketed interchangeably as *A. foeniculum* ‘Golden Jubilee,’ *A. rugosa* ‘Golden Jubilee,’ and *Agastache* x ‘Golden Jubilee.’ It varies little in morphology and phenology from the species except for its chartreuse-colored foliage, which may be a deterrent to Beetles/Bugs. Both the species and cultivar had high winter mortality, but reseeded readily. ‘Golden Jubilee’ may be an appropriate substitution for the species for bee habitat enhancement but not for restorations aiming to maximize biodiversity.

***Asclepias tuberosa* and *A. tuberosa* ‘Hello Yellow’**

Asclepias tuberosa received 230 pollinator visits during our observations and *A. tuberosa* ‘Hello Yellow’ received 331 visits. Bumble Bees were the predominant pollinator for both the species (92.2%) and the cultivar (97.3%) (Fig. 2.6). This plant pair was located at Site B only where honey bees were not present in the landscape during its bloom period. Bumble Bees showed no significant preference for the species or cultivar during their foraging ($F_{[1,9]} = 4.72$, $p = 0.054$). Likewise, All Pollinators showed no preference ($F_{[1,9]} = 4.43$, $p = 0.066$) (Figs. 2.6 & 2.7, Table 2.2).

A. tuberosa ‘Hello Yellow’ is a bright-yellow selection from the typically orange-colored species. Otherwise, the morphology and phenology of the plants are nearly identical. The cultivar was hardier (78% winter survival) at our research site than the species (35% winter survival) ($t_{[70]} = -3.14$, $p < 0.002$). Our data suggest *A. tuberosa* ‘Hello Yellow’ is a reasonable substitute for the species in pollinator habitat restorations.

***Baptisia australis* and *B. x varicolor* ‘Twilite’**

We observed a total of 182 pollinators foraging on *Baptisia australis* and 78 pollinators foraging on *B. x varicolor* ‘Twilite’ Prairieblues. Bumble Bees comprised 72.2% of the visits to the species and 88.9% of the visits to the cultivar. Other Native Bees comprised 26.4% of the visits to the species and 6.7% of the visits to the cultivar (Fig. 2.6). All Pollinators showed a significant preference for the species ($F_{[1,25]} = 42.36$, $p < 0.001$), including Bumble Bees ($F_{[1,8]} = 23.59$, $p < 0.001$) and Other Native Bees ($F_{[1,23]} = 15.78$, $p < 0.001$) (Figs. 2.6 & 2.7, Table 2.2).

B. x varicolor ‘Twilite’ is a patented bicolor *Baptisia*, selected from a controlled cross of *B. australis* and *B. sphaerocarpa*. The flowers are maroon colored with yellow

keels, unlike *B. australis*, which displays bright-purple flowers. Once fully established, ‘Twilite’ offers taller spikes and significantly more flowers than *B. australis* ($t_{[74]} = -6.37$, $p < 0.001$). Both the species and the cultivar had winter survival rates of about 90%. For pollinator habitat restorations *B. x varicolor* ‘Twilite’ is not an equivalent substitution. The decreased visitation to the cultivar may be a result of the color change or possibly a reduction in the floral rewards (nectar and pollen) produced by this hybrid cultivar.

***Helenium autumnale* and *Helenium* ‘Moerheim Beauty’**

Helenium autumnale received 1,887 pollinator visits and *Helenium* ‘Moerheim Beauty’ received 222 visits during our observations. The predominant pollinators on the species were Honey Bees (70.1%) and Bumble Bees (23.9%). The predominant pollinators on the cultivar were Other Native Bees (34.7%), Bumble Bees (21.3%), and Honey Bees (18.7%) (Fig. 2.6). All Pollinators exhibited a preference for the species ($F_{[1,35]} = 238.01$, $p < 0.001$). The species was also preferred by foraging Honey Bees ($F_{[1,20]} = 92.9$, $p < 0.001$) and Bumble Bees ($F_{[1,32]} = 137.79$, $p < 0.001$). No significant preference was exhibited by Other Native Bees ($F_{[1,29]} = 0.17$, $p = 0.679$) and Flies ($F_{[126]} = 0.17$, $p < 0.683$) (Figs. 2.6 & 2.7, Table 2.2).

Helenium ‘Moerheim Beauty’ (often inaccurately marketed as *Helenium autumnale* ‘Moerheim Beauty’) is a reddish bronze hybrid of *H. autumnale* and *H. bigelovii*. The cultivar is shorter statured than the species and blooms mid-summer, about a month earlier than the species (Table 1). There was no overlap in bloom time between the species and the cultivar; therefore, varying competing floral resources in the landscape and changes in pollinator abundance may have affected visitation rates differently for this plant pair.

Unlike the all-yellow flowers of the species, ‘Moerheim Beauty’ features coppery-red rays and dark center disks that gradually fade to burnt orange. This color selection may make the flowers less attractive to bee pollinators. *H. autumnale* had 5.2 times more flowers per plant than the cultivar ($t_{[174]} = 29.39$, $p < 0.001$) In general, ‘Moerheim Beauty’ was a weak plant that struggled at our research sites and likely was not well suited for the site conditions. Increased moisture and fertility may have supported more vigorous and floriferous specimens of this cultivar. The species was also significantly hardier than the cultivar at our research sites with a winter survival rate of 93% compared to 74% ($z_{[142]} = 3.13$, $p = 0.002$). Based on the pollinator foraging preference we observed, ‘Moerheim Beauty’ is not an equivalent substitution for *H. autumnale* for pollinator habitat restoration efforts.

***Monarda fistulosa* and *M. fistulosa* 'Claire Grace'**

We observed a total of 877 pollinators foraging on *Monarda fistulosa* and 660 pollinators foraging on *M. fistulosa* ‘Claire Grace.’ Bumble Bees were the predominant pollinators for both the species (81.2%) and the cultivar (89.1%) (Fig. 2.6). No significant preference for the species or cultivar was exhibited by Bumble Bees ($F_{[1,41]} = 3.92$, $p = 0.0544$) or by All Pollinators ($F_{[1,46]} = 2.87$, $p = 0.097$) (Figs. 2.6 & 2.7, Table 2.2) at Site A and Site B combined. However, at Site A alone, All Pollinators did show a significant preference for the species ($F_{[1,28]} = -3.56$, $p < 0.001$) as did Bumble bees ($F_{[1,19]} = -4.93$, $p < 0.001$).

‘Claire Grace’ is a selection of *M. fistulosa* from the southern U.S. that is marketed for its increased drought tolerance and resistance to powdery mildew. The flowers are slightly darker and pinker than the species. Plant height, bloom time, and

bloom duration are similar to the species, but ‘Claire Grace’ was less hardy in zone 4 (84% winter survival) than the species (100% winter survival) ($z_{[142]} = 3.62, p < 0.001$). ‘Claire Grace’ may be an equivalent substitution for the species in pollinator habitat restoration if consideration is given to weighing the benefits of mildew resistance and drought tolerance against the decreased hardiness in northern climates.

***Penstemon digitalis* and *P. digitalis* ‘Husker Red’**

We observed a total of 229 pollinators on *Penstemon digitalis* and 147 pollinators on *P. digitalis* ‘Husker Red.’ Other Native Bees (54.9%) and Honey Bees (27%) were the predominant pollinators on the species. Other Native Bees (73.3%) and Bumble Bees (16.3%) were the predominant pollinators on the cultivar (Fig. 2.6). All Pollinators exhibited no significant preference between the species and cultivar ($F_{[1,32]} = 4.00, p = 0.054$). Bumble Bees ($F_{[1,19]} = 0.48, p = 0.498$) and Other Native Bees ($F_{[1,23]} = 1.78, p = 0.199$) also showed no preference. Honey Bees, however, showed a preference for the native species ($F_{[1,10]} = 9.31, p = 0.013$) (Figs. 2.6 & 2.7, Table 2).

‘Husker Red’ is a red-foliaged selection of *P. digitalis* with a stronger upright form. The cultivar’s flowers are similar in shape and size to the species but sometimes exhibit a pink blush in the otherwise white blooms. Floral abundance for *P. digitalis* is about 1.3 times greater per plant than the cultivar ($t_{[149]} = 5.96, p < 0.001$). Both the species and the cultivar were equally hardy in zone 4 ($z_{[142]} = 1.00, p < 0.316$). ‘Husker Red’ may be an equivalent substitute for the native species to support most pollinators, including all native bees, but honey bees may find it less attractive than the species.

***Rudbeckia fulgida* var. *fulgida* and *R. fulgida* var. *sullivantii* ‘Goldsturm’**

We observed a total of 119 pollinators visiting the flowers of *Rudbeckia fulgida* var. *fulgida* and 120 pollinators visiting *R. fulgida* var. *sullivantii* ‘Goldsturm.’ Flies and Other Native Bees were the predominant pollinators for both the species and the cultivar. Flies composed 49.6% of the visits to the species and 51.7% of the visits to the cultivar. Other Native Bees composed 44.5% of the visits to the species and 36.6 % of the visits to the cultivar (Fig. 2.6). All Pollinators showed no significant preference for the species or cultivar ($F_{[1,6]} = 0.22$, $p = 0.657$), nor did any pollinator subgroups (Figs. 2.6 & 2.7, Table 2.2).

‘Goldsturm’ is a selection of *Rudbeckia fulgida* var. *sullivantii* discovered in a nursery in the 1930s. ‘Goldsturm’ is more compact and coarse than the species and has a shorter bloom duration (Table 2.1). The species and cultivar had similar winter survival rates at 41% and 55% respectively ($z_{[106]} = -1.54$, $p < 0.123$). ‘Goldsturm’ may be an appropriate substitution for the species *R. fulgida* var. *fulgida* in a pollinator habitat restoration, with consideration given to its shorter bloom duration.

***Symphotrichum novae-angliae* and *S. novae-angliae* ‘Alma Pötschke’**

We observed a total of 2,100 pollinators visiting *Symphotrichum novae-angliae* and 234 pollinators visiting *S. novae-angliae* ‘Alma Pötschke.’ Bumble Bees composed 54.1% and Honey Bees composed 42.6% of all pollinator visits to the species, whereas Bumble Bees composed 56.2% and Honey Bees composed 38.2% of all pollinator visits to the cultivar (Fig. 2.6). All Pollinators showed a significant preference for the native species ($F_{[1,16]} = 687.49$, $p < 0.001$), as did all other subgroups of pollinators (Figs. 2.6 & 2.7, Table 2.2).

‘Alma Pötschke,’ also known as ‘Andenken an Alma Pötschke’ is a selection of *S. novae-angliae* bred in Germany. ‘Alma Pötschke’ is marketed as a cultivar of *S. novae-angliae*, but it may be hybrid cultivar. This cultivar has a more compact form than the species and the flowers have magenta pink rays instead of the purple rays seen in the species. The species features about 2.1 times more flowers per plant than the cultivar ($p < 0.001$); however, standardizing for floral abundance did not change the preference outcome of the model. Both the species and cultivar were very hardy in our field sites. With all pollinators groups showing a highly significant preference for foraging on the flowers of the native species versus the cultivar ‘Alma Pötschke,’ we do not recommend this cultivar as an equivalent substitute for the species in the context of pollinator habitat restoration.

***Tradescantia ohiensis* and *Tradescantia* ‘Red Grape’**

Tradescantia ohiensis received 552 pollinator visits and *Tradescantia* ‘Red Grape’ received 279 visits during our observations. Honey Bees and Other Native Bees were the predominant pollinator groups for both the species and the cultivar. The species was visited 68.5% of the time by Honey Bees and 16.4% of the time by Other Native Bees. The cultivar was visited 41.1% of the time by Honey Bees and 31.5% of the time by Other Native Bees (Fig. 2.6). All Pollinators exhibited a significant preference for the species ($F_{[1,33]} = 19.50$, $p < 0.001$), as did Honey Bees ($F_{[1,23]} = 19.52$, $p < 0.001$) and Other Native Bees ($F_{[1,44]} = 119.04$, $p < 0.001$) (Figs. 2.6 & 2.7, Table 2.2).

Tradescantia ohiensis had a mean floral abundance per plant of 38.18 ± 11.94 , which was significantly greater ($t_{[171]} = 14.17$, $p < 0.001$) than *Tradescantia* ‘Red Grape’ at 14.09 ± 7.19 . All Pollinators showed a significant preference for the species ($F_{[1,33]} =$

19.50, $p < 0.001$) but did not show a preference per flower ($F_{[1,33]} = 0.11$, $p = 0.737$) when floral abundance was included as a covariate in the model.

‘Red Grape’ is of complex hybrid origin, derived from multiple crosses between native species *T. virginiana*, *T. ohiensis*, and *T. subaspera*. ‘Red Grape’ has a more compact form than *T. ohiensis* and features magenta-colored flowers. The species was significantly hardier at our research sites with a winter survival rate of 93% compared to the cultivar’s 43% ($z_{[171]} = 14.17$, $p < 0.001$). ‘Red Grape’ had a substantially longer bloom period (Table 2.1), but floral abundance was 2.7 times greater ($t_{[171]} = 14.17$, $p < 0.001$) for the species than the cultivar. Including floral abundance as a covariate in the model did not show a preference ($F_{[1,33]} = 0.11$, $p = 0.737$), suggesting that the difference in floral abundance explains the difference in visitation. Based on our plant-to-plant comparison during overlapping peak bloom periods, the cultivar was not an equivalent substitute for the *species*. However, the longer bloom period of the cultivar should be weighed against greater floral abundance and increased hardiness of the species.

***Veronicastrum virginicum* and *V. virginicum* ‘Lavendelturm’**

We observed a total of 616 pollinators foraging on *Veronicastrum virginicum* and 1,347 pollinators foraging on *V. virginicum* ‘Lavendelturm.’ Bumble Bees (42.0%) and Honey Bees (39.8%) were the predominant pollinator groups visiting the species. Honey Bees (50.3%) and Other Native Bees (31.5%) were the predominant pollinator groups visiting the cultivar (Fig. 2.6). All Pollinators exhibited a significant preference for the cultivar over the species ($F_{[1,20]} = 6.65$, $p = 0.018$). Honey Bees did not exhibit a significant preference ($F_{[1,23]} = 3.58$, $p = 0.071$), nor did Bumble Bees ($F_{[1,18]} = 0.23$, $p = 0.064$) (Figs. 2.6 & 2.7, Table 2.2).

‘Lavendelturm’ (sometimes marketed as ‘Lavender Towers’) is an earlier and longer-blooming selection of *V. virginicum* with pale purple flowers (Table 2.1). Floral abundance was not significantly different between the species and cultivar ($t_{[170]} = -1.00$, $p = 0.319$). The species had a significantly higher winter survival rate (99%) than the cultivar (86%) at our research sites ($z_{[142]} = 4.78$, $p < 0.001$). ‘Lavendelturm’ is an excellent substitution for the species in terms of pollinator attractiveness in a pollinator habitat restoration.

Overall discussion

Our data show that insect pollinators prefer to forage on native species over cultivated varieties of the native species, but not in all cases, and not exclusively. Rarely do pollinators prefer to forage on a native cultivar over a native species. This suggests that some native cultivars may be comparable substitutions for native species in pollinator habitat restoration projects and others may not be. The mixed results among native cultivars highlights the need for cultivars to be evaluated on an individual basis and for more research efforts to quantify the attractiveness of more species and cultivars, and furthermore, to assess the floral rewards available and accessible to pollinators.

Our data suggest that using native species is the best planting strategy for pollinator habitat restorations given that native cultivars are either equally attractive or less attractive to pollinators. Similarly, we found that *Echinacea* cultivars and hybrids were not equivalent substitutions for the native species in terms of maximizing attractiveness to pollinators (A. White & L. Perry, unpublished data). However, cultivars might be good alternatives, independent of pollinator preference, on a plant-by-plant and site-by-site basis. Cultivars often are selected for attractive aesthetic traits, longer bloom

times, disease resistance, and more predictable, uniform, and manageable forms—all attributes that are highly valued in the landscape industry and may be valued for pollinator habitat gardens that have specific aesthetic or performance expectations. Cultivars are often easier to propagate, keeping costs lower and availability higher in the market. Conversely, native cultivars may have characteristics that decrease their longevity and resiliency in the landscape. For example, almost half of all the cultivars in our study were significantly less hardy in USDA hardiness zone 4 than the native species. Nine of 11 cultivars in our study are propagated vegetatively, meaning that if they are able to set seed, the offspring won't necessarily exhibit the same traits the parents were selected for.

All cultivars in our study, albeit sometimes less attractive to pollinators than the native species, were still visited by pollinators, suggesting that cultivars can still provide valuable floral resources in the landscape. For example, all pollinators combined exhibited a significant preference for *Agastache foeniculum* over the cultivar *Agastache* 'Golden Jubilee'. However, 'Golden Jubilee' had a higher mean pollinator visitation rate than all but two other native species in the study. This is similar to Williams et al. (2011) and Morandin & Kremen (2013) studies, which both found that bees preferred native plants, but still used non-native plants.

All pollinators combined preferred the native species over the native cultivar in all cases where the cultivar had either undergone repeated selections in a breeding program or was a known hybrid of two or more species. This suggests that cultivars that are selections from wild or nursery plant populations and are most similar to the species in color, morphology, and phenology are more likely to be equivalent substitutions for the

species in pollinator habitat restorations. Lesica and Allendorf (1999) and Schröder and Prasse (2013a) also cautioned against using highly modified cultivars in ecological restorations; however, their reasons pertained to preserving the ecological genetics of native plant communities.

Bee pollinators were the most abundant pollinators for all plants in our study and showed more and stronger preferences for native species. Non-native honey bees (*Apis mellifera*) exhibited the same preferences for native plant species as native bees (*Bombus* sp., etc.), and in two cases (*Penstemon* and *Agastache*), honey bees showed a preference for the native plant species when native bees did not. This disfavors the hypothesis that native bees may show a closer relationship to native plants than do non-native bees because native plants and native bees share an evolutionary history. Honey bees are likely identifying the most floriferous and rewarding floral patches and communicating the location and floral odor to other foragers in the hive (Arenas et al. 2007).

In only one case (*Tradescantia*) did standardizing for floral abundance change the preference outcome. This suggests that differences in floral abundance do not fully explain most of the differences in pollinator visits per plant. This leads us to hypothesize that in addition to floral abundance/cover, the differences in flower color, flower odor, and the availability, accessibility, quantity and quality of nectar and pollen rewards are influencing pollinator preferences.

Our study provides the first evidence that not all cultivars are ecologically equivalent substitutions for the native species. However, some cultivars are equally attractive to pollinators, and in rare cases, may even be more attractive. Additional research is needed to quantify the attractiveness, and furthermore the nectar and pollen

rewards, of more native species and more cultivars. Our data indicate that cultivars that have undergone repeated crosses and selections as well as interspecific hybrid cultivars should be scrutinized most carefully.

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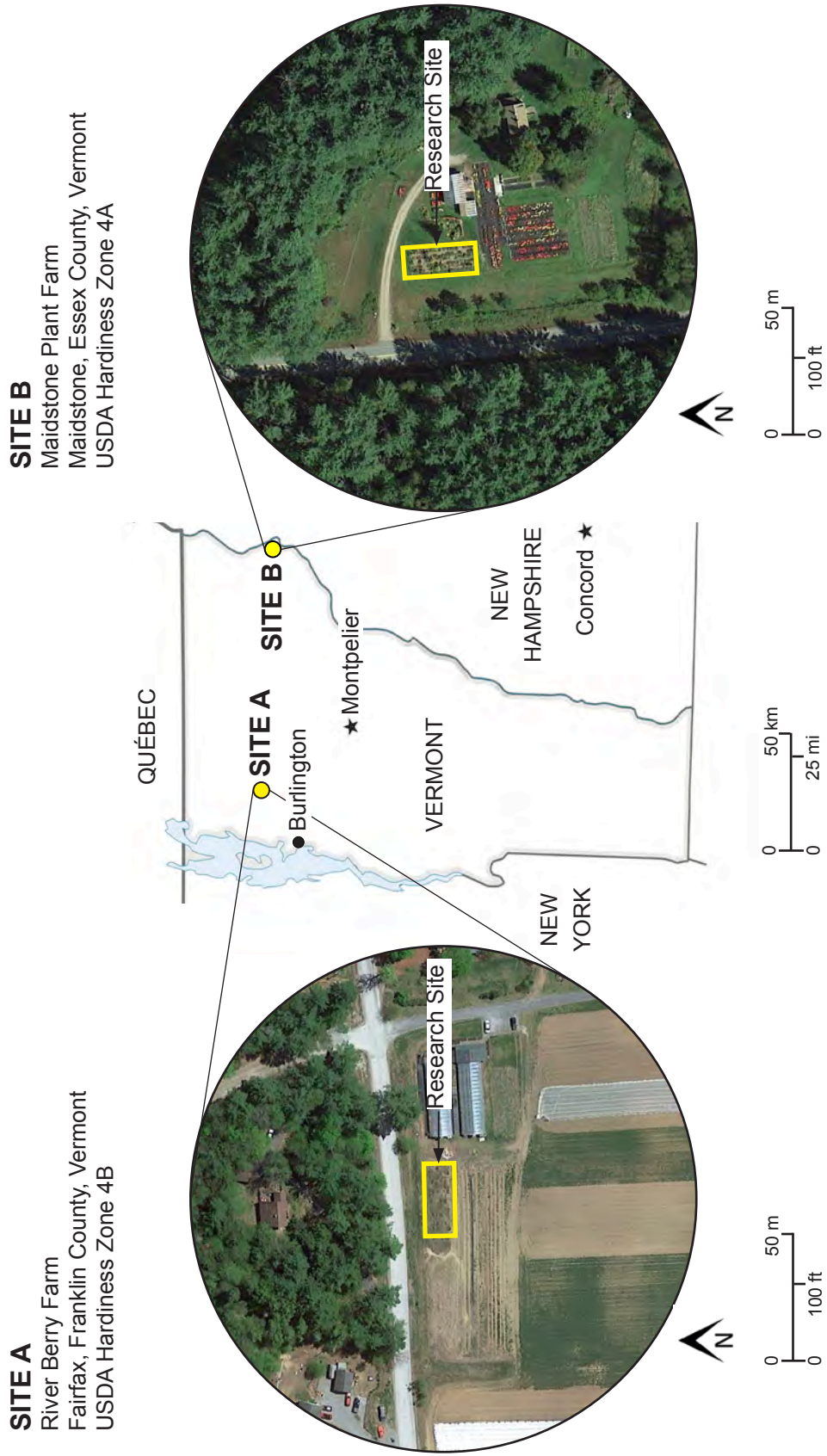
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Table 2.2. Mean pollinator visits reported as least squares means. Pollinator preferences between the native species and native cultivar of each plant pair was determined using a generalized linear mixed model. A preference is considered significant if $P < 0.05$. Plant types with (+) in honey bee visits indicates that the species was only at Site B and no honey bees were present in the landscape during bloom. Cells with (-) had data that was too sparse to analyze with the model, but the counts were incorporated into the composite groups for analysis.

	All Insect Pollinators	All Bee Pollinators	All Native Bees	Honey Bees	Bumble Bees	Other Native Bees	Flies	Butterflies/Moths	Beetles/Bugs	Wasps/Ants
Selections	<i>Asclepias tuberosa</i>	14.87 ± 1.73	14.53 ± 1.80	14.53 ± 1.80	+	14.40 ± 1.71	-	0.13 ± 0.08	-	-
	<i>A. tuberosa</i> 'Hello Yellow'	10.89 ± 1.40	10.46 ± 1.39	10.46 ± 1.39	+	10.30 ± 1.32	-	0.27 ± 0.15	-	-
	Significance	$P = 0.066$	$P = 0.057$	$P = 0.057$		$P = 0.0540$		$P = 0.2914$		
	<i>Monarda fistulosa</i>	10.28 ± 0.78	9.21 ± 0.78	9.14 ± 0.70	-	12.73 ± 0.712	-	-	-	-
	<i>M. fistulosa</i> 'Claire Grace'	8.88 ± 0.67	7.90 ± 0.67	7.81 ± 0.92	-	9.68 ± 0.58	-	-	-	-
	Significance	$P = 0.097$	$P = 0.139$	$P = 0.152$		$P = 0.0544$				
	<i>Penstemon digitalis</i>	4.85 ± 0.69	4.31 ± 0.62	3.71 ± 0.50	1.35 ± 0.31	0.93 ± 0.23	2.22 ± 0.43	-	-	-
	<i>P. digitalis</i> 'Husker Red'	3.40 ± 0.51	3.10 ± 0.46	2.98 ± 0.41	0.23 ± 0.12	0.79 ± 0.20	1.56 ± 0.33	-	-	-
	Significance	$P = 0.054$	$P = 0.068$	$P = 0.197$	$P = 0.0129$	$P = 0.4976$	$P = 0.1989$			
	<i>Rudbeckia fulgida</i> var. <i>fulgida</i>	4.80 ± 0.59	2.28 ± 0.25	2.28 ± 0.25	+	0.26 ± 0.11	2.15 ± 0.22	2.34 ± 0.44	-	-
<i>R. fulgida</i> var. <i>sullivantii</i> 'Goldsturm'	5.12 ± 0.62	2.34 ± 0.25	2.32 ± 0.25	+	0.32 ± 0.12	1.81 ± 0.23	2.54 ± 0.47	-	-	
Significance	$P = 0.657$	$P = 0.910$	$P = 0.910$		$P = 0.6814$	$P = 0.3029$	$P = 0.6882$			
<i>Veronicastrum virginicum</i>	14.36 ± 1.10	12.24 ± 0.93	6.95 ± 0.79	3.80 ± 0.76	5.94 ± 1.55	-	-	-	-	
<i>V. virginicum</i> 'Lavendelturm'	27.35 ± 1.76	26.30 ± 1.45	19.04 ± 1.48	5.60 ± 1.37	16.22 ± 4.45	-	-	-	-	
Significance	$P = 0.018$	$P = 0.011$	$P = 0.011$	$P = 0.071$	$P = 0.640$					
<i>Achillea millefolium</i>	22.33 ± 2.74	8.81 ± 1.54	8.70 ± 1.48	-	-	8.59 ± 1.09	8.39 ± 3.33	0.45 ± 3.93	-	
<i>Achillea</i> 'Strawberry Seduction'	3.17 ± 0.62	0.37 ± 0.21	0.38 ± 0.21	-	-	0.39 ± 0.11	4.57 ± 2.75	0.04 ± 0.37	-	
Significance	$P < 0.001$	$P < 0.001$	$P < 0.001$			$P < 0.0001$	$P = 0.3616$	$P = 0.0019$		
<i>Agastache foeniculum</i>	31.07 ± 6.06	23.11 ± 4.76	13.35 ± 2.67	9.03 ± 2.32	12.31 ± 2.29	-	-	4.63 ± 1.55	-	
<i>Agastache</i> 'Golden Jubilee'	20.03 ± 4.14	18.63 ± 3.88	13.30 ± 2.66	4.96 ± 1.30	11.39 ± 2.15	-	-	0.33 ± 0.19	-	
Significance	$P = 0.041$	$P = 0.308$	$P = 0.980$	$P = 0.0112$	$P = 0.4531$			$P = 0.0128$		
<i>Baptisia australis</i>	7.01 ± 0.49	6.88 ± 0.52	6.88 ± 0.52	-	5.51 ± 0.52	1.30 ± 0.23	-	-	-	
<i>B. x varicolor</i> 'Twilite Prairieblues'	3.12 ± 0.32	3.07 ± 0.34	3.07 ± 0.34	-	2.89 ± 0.29	0.15 ± 0.08	-	-	-	
Significance	$P < 0.001$	$P < 0.001$	$P < 0.001$		$P < 0.0001$	$P = 0.0006$				
<i>Helenium autumnale</i>	35.99 ± 5.07	31.17 ± 5.43	15.89 ± 4.49	12.85 ± 3.69	14.30 ± 3.21	0.20 ± 14.47	0.57 ± 0.33	-	-	
<i>Helenium</i> 'Moerheim Beauty'	3.53 ± 0.40	2.52 ± 0.37	2.31 ± 0.30	0.46 ± 0.12	1.21 ± 0.22	0.17 ± 12.66	0.76 ± 0.29	-	-	
Significance	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.0001$	$P < 0.0001$	$P = 0.6788$	$P = 0.6835$			
<i>Symphoricarpon novae-angliae</i>	46.04 ± 1.42	43.89 ± 1.27	30.59 ± 1.04	9.02 ± 0.56	29.89 ± 1.08	0.40 ± 0.14	1.23 ± 0.27	-	-	
<i>S. novae-angliae</i> 'Alma Potschke'	4.98 ± 0.41	4.93 ± 0.40	2.92 ± 0.31	1.83 ± 0.22	2.84 ± 0.32	0.09 ± 0.05	0.09 ± 0.06	-	-	
Significance	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.0001$	$P < 0.0001$	$P = 0.0267$	$P = 0.0021$			
<i>Tradescantia ohioensis</i>	5.35 ± 0.70	3.44 ± 0.61	1.71 ± 0.38	3.65 ± 0.80	-	-	0.83 ± 0.14	-	-	
<i>Tradescantia</i> 'Red Grape'	3.17 ± 0.40	1.43 ± 0.29	0.82 ± 0.19	1.39 ± 0.29	-	-	0.42 ± 0.60	-	-	
Significance	$P < 0.001$	$P = 0.001$	$P = 0.006$	$P = 0.0002$			$P = 0.8856$			

KEY: Preference for species Preference for cultivar No significant preference Preference for cultivar

Figure 2.1. Site location map of research plots at Site A in Franklin County and Site B in Essex County, Vermont, U.S.A.
 Imagery: Google Earth, 2015.



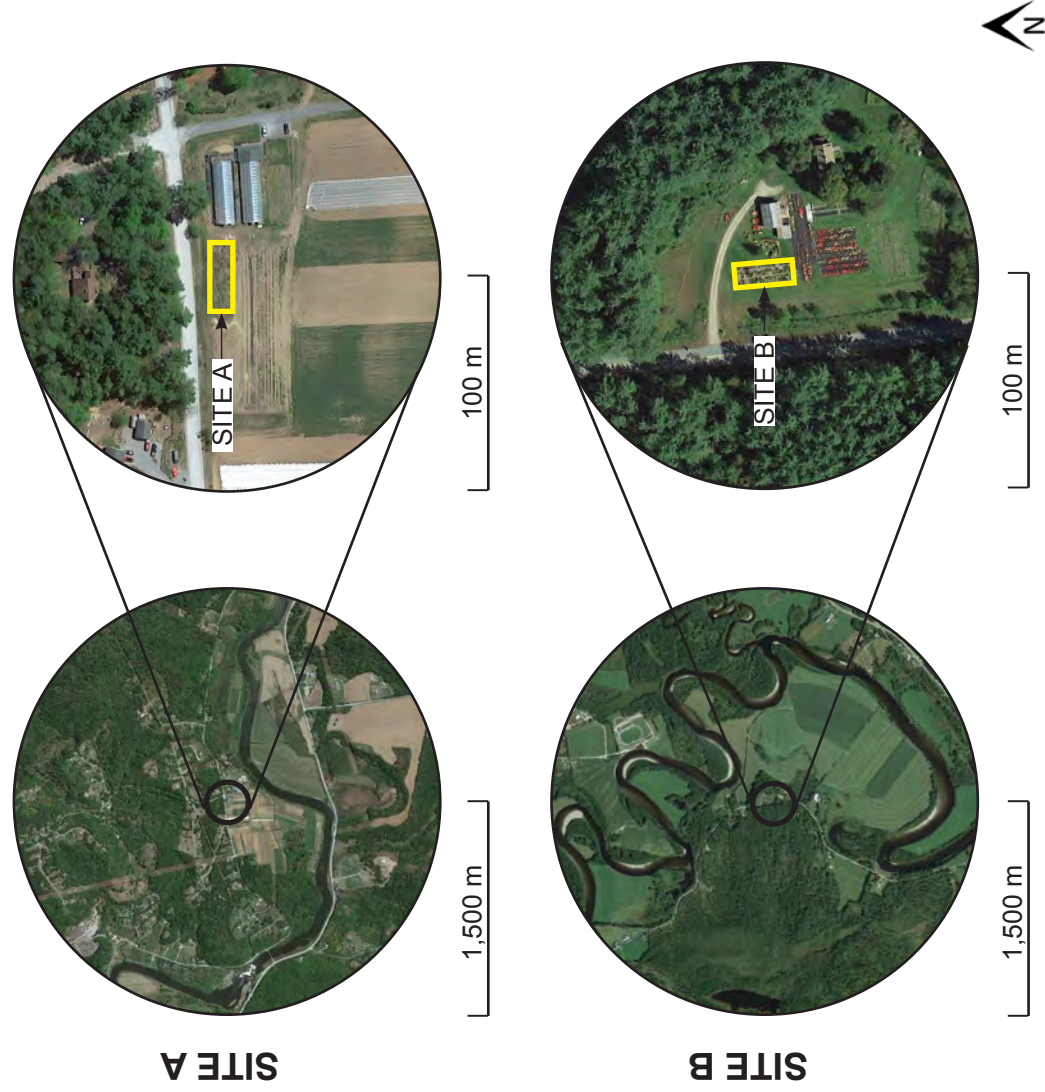


Figure 2.2. Landscape context of Site A in Franklin County and Site B in Essex County, Vermont, U.S.A. Maps indicate landscape at 1,500 m radius from the research site and 100 m radius. Imagery: Google Earth, 2015.



Figure 2.3. Flower images of all native species and native cultivar pairs analyzed in this study. The species is shown on the left and the cultivar on the right in each pair.

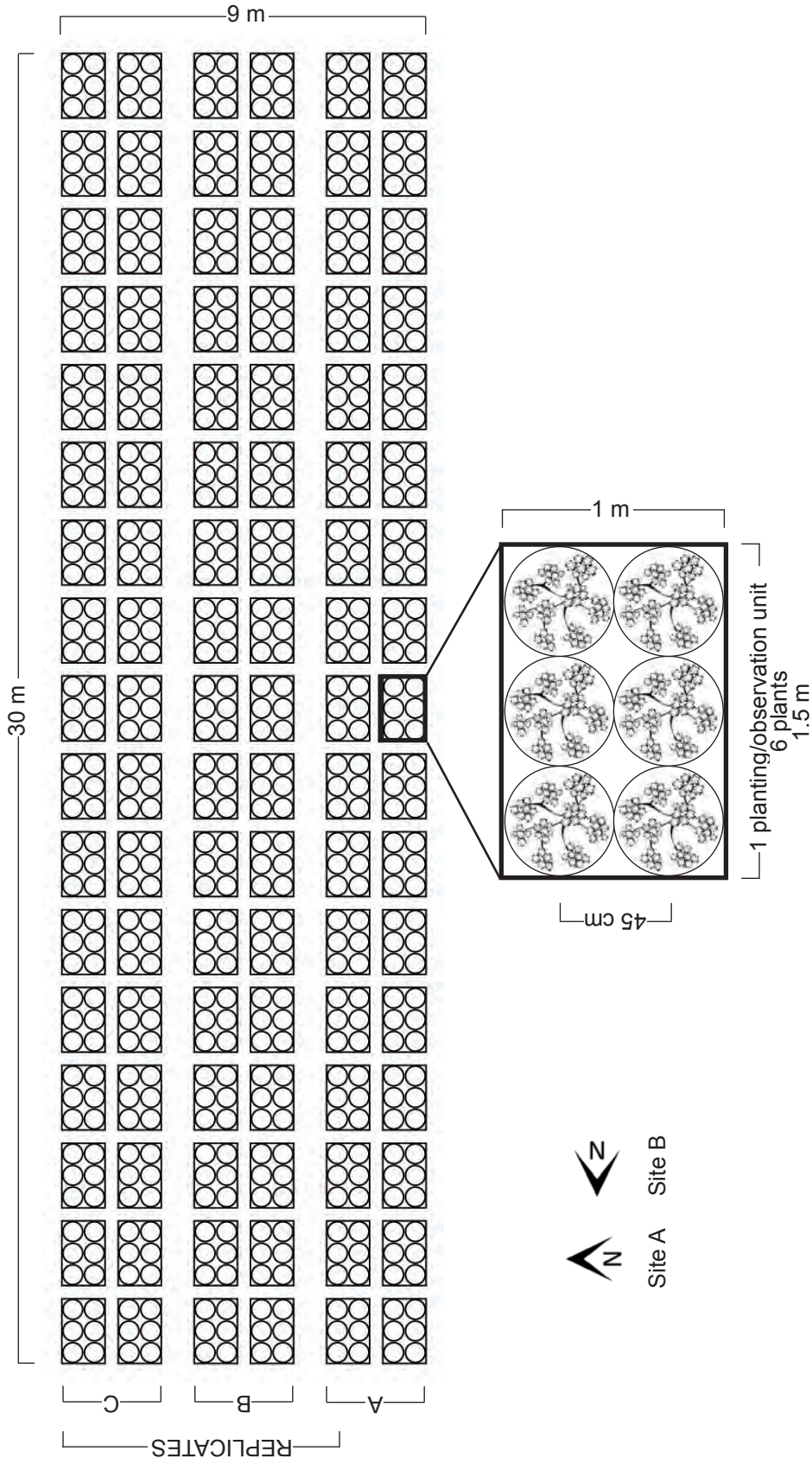
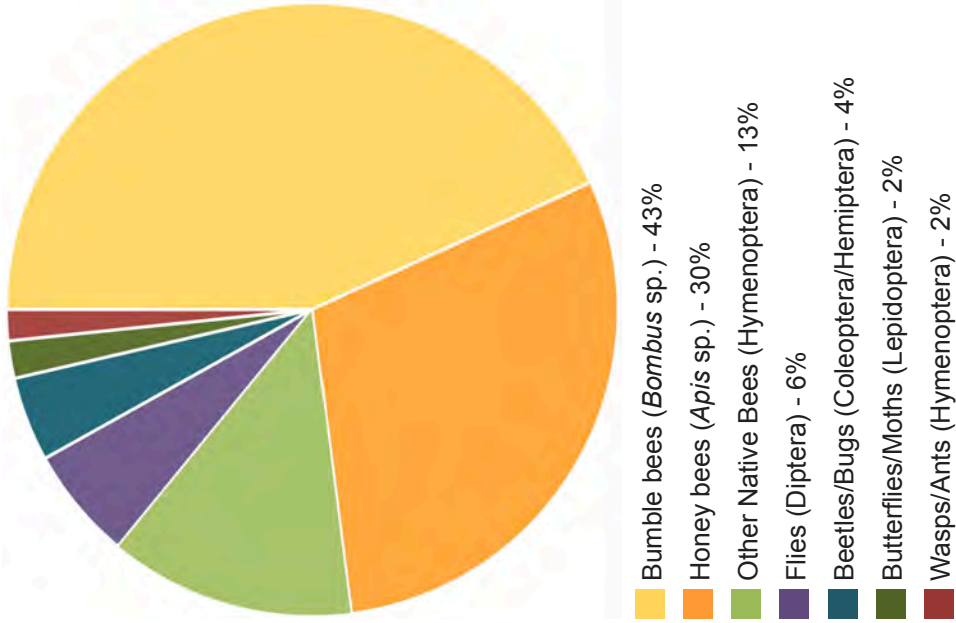


Figure 2.4. Experimental design layouts at Site A and Site B were randomized complete block designs with three replicates per field site. Planting units composed of six plants of a single type were randomized within the replicates; however, each cultivar was not located within 3 m of the species, both within and across replicates. At each site, 18 individual specimens of 34 plant types were represented, totaling 612 plants per site. This paper analyzes 22 of these plant types.

Site A: 8,143 total pollinators observed during 572 five-minute scans



Site B: 6,681 total pollinators observed during 573 five-minute scans

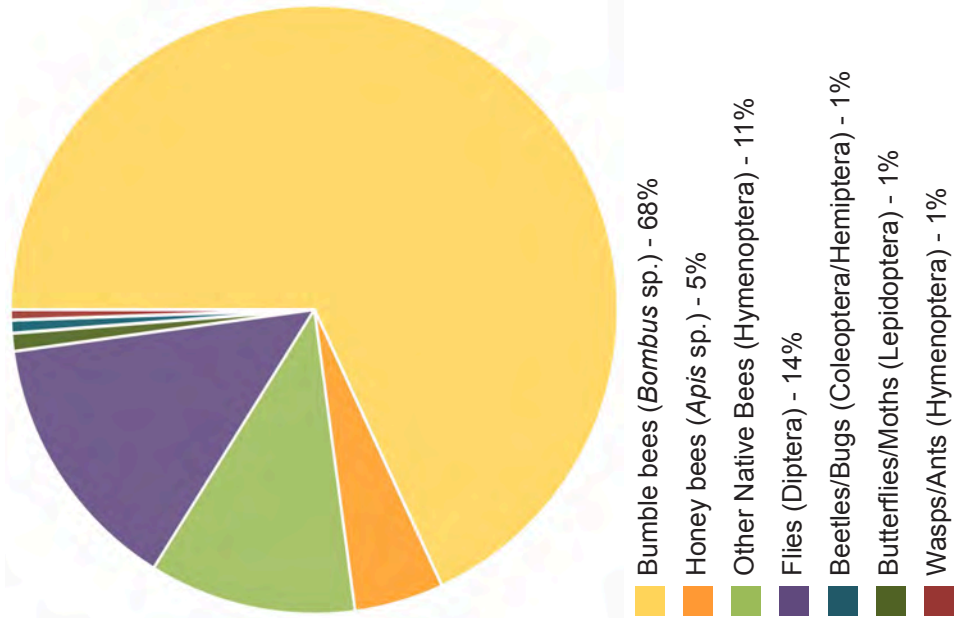


Figure 2.5. Proportions of pollinator groups observed during all observations on all plants from 2013-2015 at Site A and Site B. Honey bees were only observed during September and October of each year at Site B.

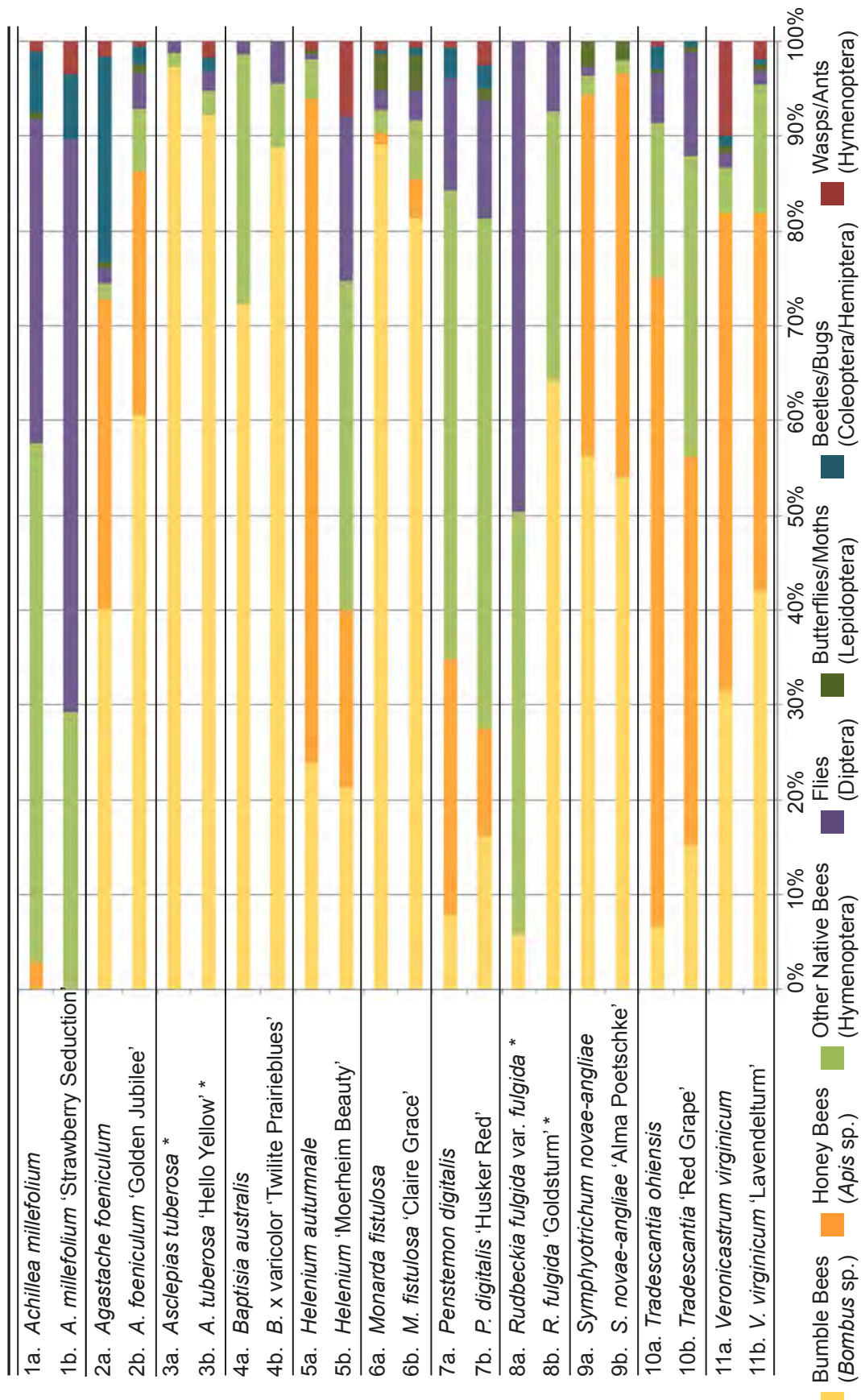


Figure 2.6. Proportions of pollinator groups observed visiting each native species and native cultivar at Site A from 2013-2015.

* Plants studied only at Site B where no honey bees were present in the landscape at bloom time.

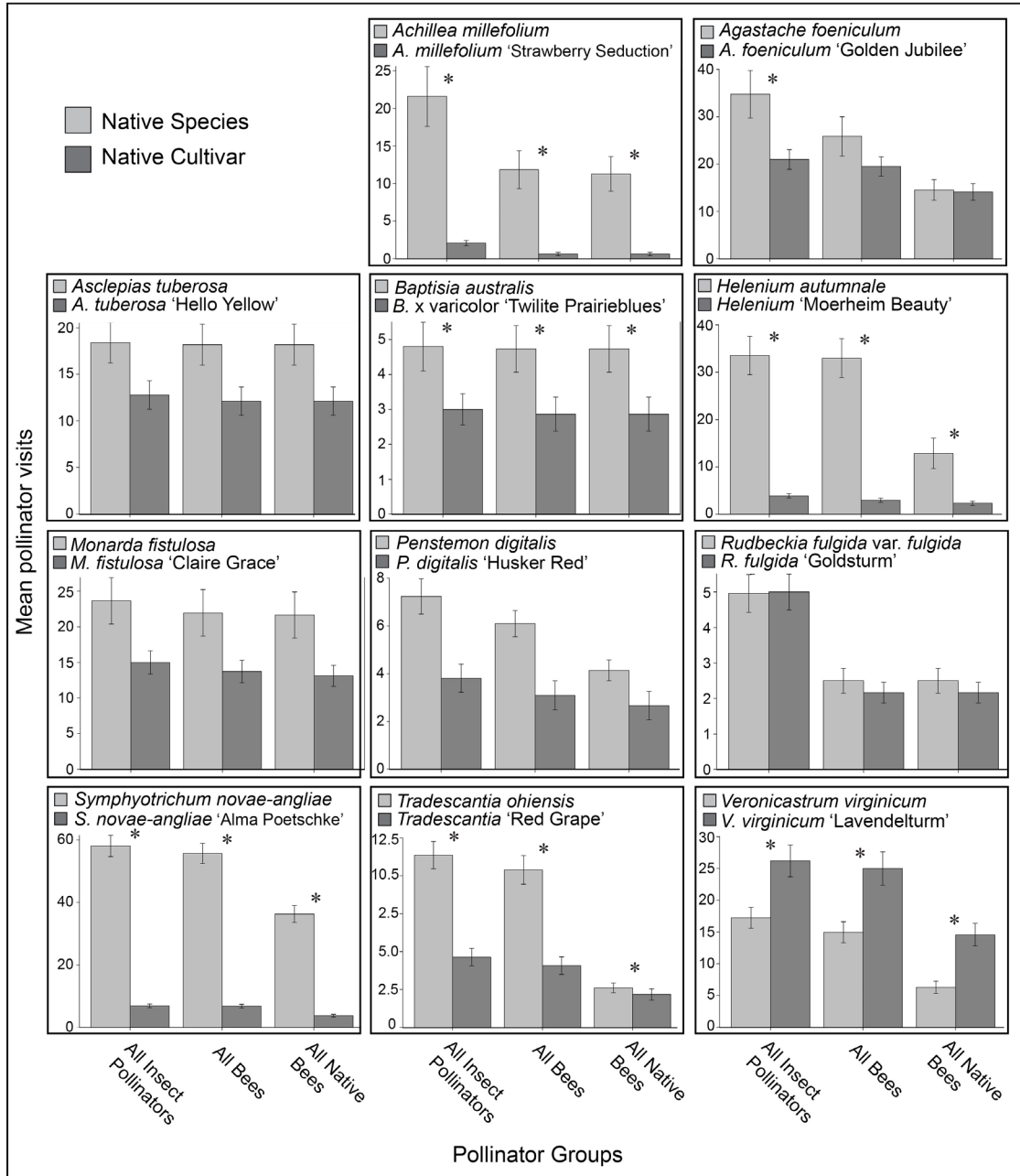


Figure 2.7 Mean pollinator visits \pm SEM for species-cultivar pairs for all years and sites combined. Significant pollinator preferences were determined using a generalized linear mixed model. *Above bars indicates mean pollinator visits are significantly different between the native species and native cultivar at $p < 0.05$.

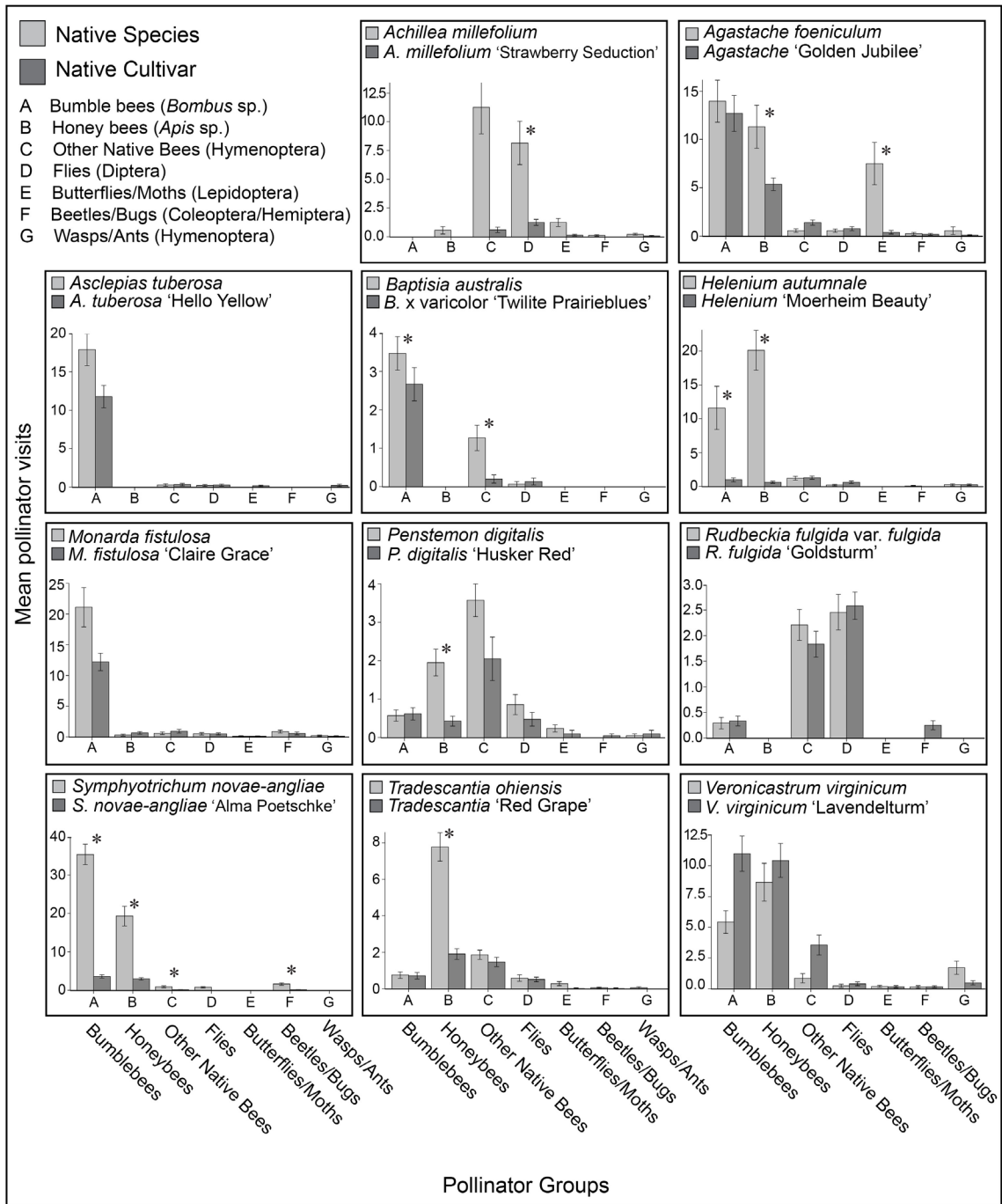


Figure 2.8. Mean pollinator visits \pm SEM by pollinators to species-cultivar pairs for all years and sites combined. Significant pollinator preferences were determined using a generalized linear mixed model. *Above bars indicates mean pollinator visits are significantly different between the native species and native cultivar at $p < 0.05$.

CHAPTER 3

BREEDING CULTIVARS FOR ORNAMENTAL AND CULTURAL TRAITS CAN DECREASE POLLINATOR ATTRACTION IN *ECHINACEA*

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ABSTRACT

Initiatives to restore and enhance pollinator habitat to support healthy pollinator populations are widespread and growing. This has led to an increasing trend in the nursery and landscape industries to promote plants that provide optimal floral resources for pollinators. Native perennial plants are frequently recommended for pollinator gardens and *Echinacea purpurea* is one of the most widely promoted species. In the last decade, modern ornamental breeders have turned the *Echinacea* genus into one of the most highly bred and hybridized garden plants. Cultivars feature unique forms and traits that are valuable to gardeners; however, it is unknown whether *Echinacea* cultivars provide the same benefit to pollinators as the native species. With the push for pollinator habitat restoration and pollinator-friendly gardens, it is important that we evaluate how selection and hybridization of native flowering plants affect their attractiveness to pollinators. In this study, we quantitatively assessed pollinator visitation to *Echinacea purpurea* in its native form and three *Echinacea* cultivars with varying degrees of trait selection. We conducted the study in replicated research gardens at two distinct sites in northern Vermont. Our study provides the first evidence that selected and hybridized *Echinacea* varieties may not be equivalent substitutions for the native species in terms of maximizing attractiveness to pollinators. In pollinator gardens, where the goal is to maximize floral resources for foraging pollinators, selected and hybridized varieties should be scrutinized carefully. The benefits of using cultivars should be weighed against the potential reduction in floral resources available and accessible to pollinators.

INTRODUCTION

Pollinating insects—bees in particular—play a critical role in ensuring the pollination of food crops (Klein et al. 2007), the production of seed in flowering plants (Ollerton et al. 2011), and the maintenance of natural plant communities and ecosystems. Bee communities, both wild and managed, have declined in recent years (Carreck & Neumann 2010), and habitat loss is one of the factors identified as contributing to their decline (Potts et al. 2010).

The weakening of healthy pollinator populations threatens agricultural productivity in many regions (Koh et al. 2016) and, for this reason, the prospect of a pollination crisis is garnering the interest of scientists, policy-makers, and even the public. Special initiatives to address pollinator decline are widespread and growing in the United States. Efforts are underway to encourage the restoration of pollinator habitat in agricultural lands, natural areas, and landscape gardens. This has led to an increasing trend in the nursery and landscape industries to identify, propagate, and market plants that maximize floral resources for pollinators.

Echinaceas for pollinators

Native perennial plants are frequently recommended for pollinator gardens and *Echinacea purpurea* is one of the most widely promoted species. *Echinacea purpurea*, commonly known as purple coneflower, is an herbaceous flowering perennial in the Asteraceae family. *Echinacea purpurea* has a very broad native and naturalized range that includes much of the central and eastern United States (Kartesz 2015), making it well-adapted for garden cultivation in much of the country. It is just one of nine *Echinacea* species native to the United States (McGregor 1968), but is the most prevalent in the horticultural and landscape industries and is the subject of intensive breeding efforts. *Echinacea angustifolia*, *E. pallida*, *E. paradoxa*, and *E. tennesseensis* also are cultivated for ornamental purposes but have not undergone the same degree of breeding and selection as *E. purpurea*. In the last decade, modern ornamental breeders have turned the genus *Echinacea* into one the most selected and hybridized garden plants. Echinaceas (all types) are one of the top-five perennial garden flowers in the United States (USDA

2015); however, it is unknown whether cultivated and hybridized varieties of *Echinaceas* provide the same benefit to pollinators as the native species.

Wild *Echinaceas* rely on insect pollinators for cross-pollination and, likewise, many pollinators rely on the nectar and pollen produced by the plant for food and energy. Common visitors include bumble bees; sweat bees; bees in the genera *Diadasia*, *Melissodes*, and *Svastra*; the sunflower leafcutter bee (*Megachile pugnata*); one specialist bee (*Andrena helianthiformis*); and many butterflies such as monarchs, swallowtails, sulfurs, and more (Mader et al. 2011). *Echinacea*'s long bloom duration (Armitage 2006) provides pollinators with valuable nectar and pollen resources in mid to late summer.

***Echinacea* cultivation and hybridization**

In the early 2000s, numerous ornamental breeders established successful breeding programs, bringing dozens of *Echinaceas* with new colors, flower forms, and scents to the horticulture and landscape industries each year—a trend that continues today. The number of *Echinacea* varieties now available is upwards of 200, over 120 of which have been trialed by Leonard Perry, this paper's coauthor. Most, if not all, *Echinacea* species can be intercrossed (McGregor 1968; Ault 2007) providing even more opportunities for ornamental breeders. A formal classification for modern *Echinacea* hybrids has not been defined. *Echinacea* hybrids are sometimes marketed as *Echinacea hybrida*, *Echinacea x hybrida*, or simply with the genus and cultivar name, e.g. *Echinacea* 'Sunrise.'

Given the efforts to maximize floral resources to support pollinator populations, there is concern that highly bred and hybrid *Echinaceas* may have decreased fertility (Carey & Avent 2012), or even sterility, and may be less beneficial for pollinators. Early hybridization studies found that interspecific crosses of *Echinacea* could form fertile F₁

hybrids (McGregor 1968). This was further explored by Jim Ault at the Chicago Botanic Garden, who found many interspecific *Echinacea* hybrids to be highly fertile, while other crosses yielded low percentages of fertile seeds or progeny with low fertility (Ault 2007). Several patented *Echinacea* cultivars, including *E. purpurea* ‘Little Giant’ (USPP16183P2), *Echinacea* ‘Paranoia’ (USPP16587P2), and *E. purpurea* ‘Hope’ (USPP17194P2) are described in their patents as being male sterile and non-pollen producing. The fertility of many more patented *Echinacea* selections and hybrids are listed as unknown. This suggests that both non-hybrid selections and interspecific hybrids can yield sterile plants. Male-sterile plants may be attractive ornamental selections because of their long bloom durations and low- or non-pollen producing cut flowers but, in the context of gardening for pollinators, they may have less ecological value than the native species or fertile cultivars.

Echinacea can be propagated from seed, basal shoot cuttings, root cuttings, division of the crown, and through tissue culture (Ault 2007). Most of the original ornamental cultivars such as ‘White Swan’ and ‘Magnus’ are propagated from seed. Maintaining reasonably uniform seed lines is a challenge of *Echinacea* breeding programs because *Echinacea* inflorescences are mostly self-infertile and must be cross-pollinated by insects (McKeown 1999; Ault 2007). Thus, seed cultivars can still be quite variable in the characteristics they present. Today, many of the new *Echinacea* cultivars are propagated asexually via tissue culture. Asexual propagation ensures that the progeny exhibit desirable characteristics identical to the parent plant.

Wild populations of *Echinacea* are threatened by habitat degradation, habitat loss, unsustainable harvesting practices driven by the plant’s medicinal value, and potential

genetic pollution from cultivated stands of ornamental and/or medicinal *Echinacea* varieties. Van Gaal et al. (1998) examined gene flow between a wild type of *E. purpurea* and the cultivar *E. purpurea* ‘White Swan’ and found that F₁ hybrid plants could successfully survive and reproduce under field conditions, thus continuing the gene flow and genetic pollution of the wild population.

Selected forms and traits

Breeding programs focused on selecting unique and improved cultivars of *Echinacea* have traditionally focused on selecting forms and traits that are valuable to ornamental gardeners. These characteristics include blooming in the first year from seed; fragrant flowers; compact, sturdy stems; ray flowers in white, yellow, pink, magenta, orange, or red; ray flowers with different orientation (i.e. horizontal or erect), extended bloom duration; double flower forms; resistance to leaf hoppers, aster yellows, and Fusarium and Sclerotinia rots; greater tolerance of wet soils; and greater heat and/or cold tolerance (Ault 2007).

Because *Echinacea* cultivars and hybrids are selected primarily based on ornamental and cultural traits, it is not clear whether they perform the same ecological roles as the native species, which evolved naturally in the landscape. Cultivated and hybridized varieties of *Echinacea* may differ from the species in flower size, color, odor, abundance, morphology, and phenology—all attributes known to influence pollinator visitation (Wilbert et al. 1997; Møller & Sorci 1998; Wesselingh & Arnold 2000; Knudsen et al. 2001; Spaethe et al. 2001; Wignall et al. 2006; Whitney & Glover 2007; Davis et al. 2008).

To support President Obama’s executive strategy to “Promote the Health of Honey Bees and Other Pollinators,” the National Pollinator Garden Network (NPGN) aims to register one million pollinator gardens by 2017. With the push for pollinator habitat restoration and pollinator-friendly gardens, it is important that we evaluate how cultivation and hybridization of native flowering plants affect their attractiveness to pollinators. In this study, we quantitatively assessed pollinator visitation to *Echinacea purpurea* (also referred to as the “species”) and three *Echinacea* cultivars with varying degrees of trait selection. We conducted the study in replicated research gardens at two distinct sites northern Vermont. We asked the questions: (1) Do insect pollinators forage on cultivated and hybridized varieties of *Echinacea* as frequently as they forage on the native species, when all are available simultaneously and at the same plant abundance? (2) Do floral preferences within the *Echinacea* taxa differ among different taxonomic and functional groups of insect pollinators? (3) Are cultivated and hybridized varieties of *Echinacea* equivalent substitutions for the native species when aiming to maximize floral resources in pollinator gardens?

METHODS

Study sites

We established research gardens at two farms in northern Vermont, U.S.A. in 2012. Site A (44°39'9.75"N, 72°58'32.68"W) was established on a diversified organic farm in Franklin County in USDA hardiness zone 4b and on soils classified as excessively drained Windsor loamy fine sand. Seven to ten hives of honeybees were maintained at Site A and located approximately 200 m southeast of the research garden.

Approximately 114 miles to the east, on the opposite side of the Green Mountains, we established Site B (44°35'19.04"N, 71°32'54.29"W) at a small conventional horticultural operation in Essex County in USDA hardiness zone 4a and on soils classified as well-drained Adams loamy fine sand. No honeybees were kept on the farm or, to our knowledge, within 1 km of the research site. No honeybees were observed in the landscape at Site B during the mid-summer *Echinacea* bloom periods.

Plant selection

We chose three popular cultivars/hybrids of *Echinacea* to compare to the native species, *Echinacea purpurea*, in our replicated field experiment (Table 3.1). Each of these plant types represents one of four major *Echinacea* groups that are available commercially and may be considered for planting in pollinator gardens. These include:

- (a) Native species, open-pollinated, not selected for ornamental traits (*Echinacea purpurea*)
- (b) Seed cultivar, open-pollinated, selected for color/form (*E. purpurea* ‘White Swan’)
- (c) Double-flowered cultivar (*E. purpurea* ‘Pink Double Delight’)
- (d) Interspecific hybrid cultivar (*Echinacea* ‘Sunrise’)

Plant descriptions

Echinacea purpurea features numerous erect stalks bearing showy daisy-like flowers in mid to late summer. The composite inflorescences have numerous fertile disc florets atop a flattened or raised receptacle surrounded by a single outer whorl of pinkish-purple, sterile, ray florets (McGregor 1968).

Echinacea purpurea ‘White Swan’ is an old and popular white-flowered seed cultivar of *E. purpurea*. Like most *Echinacea* cultivars ‘White Swan’ is not as cold hardy

or vigorous as the species, but it remains one of the sturdier and more reliable *Echinacea* cultivars, particularly in colder climates (Armitage 2006).

Echinacea purpurea 'Pink Double Delight' is a double-flowered *E. purpurea* selection bred by Arie Blom of AB Cultivars in The Netherlands and introduced by Plants Nouveau. Patented in 2006 (US PP18803), 'Pink Double Delight' has flowers that are similar to the first patented double-flowered *Echinacea* cultivar 'Razzmatazz' (from Witteman & Co.), but has a shorter, more compact habit. The flowers are long lasting, fading to a lavender pink as they age. 'Pink Double Delight' is propagated via tissue culture.

ItSaul Plants of Atlanta, Georgia, introduced *Echinacea* 'Sunrise' in 2005 (US PP16235 P2) as part of their Big Sky series. It originated from a cross of *E. purpurea* 'White Swan' as the female parent and an unnamed selection of *E. purpurea* x *E. paradoxa*, as the male parent. 'Sunrise' is one of the first yellow-flowered *Echinacea* hybrids and is highly fragrant. This is a clonal *Echinacea* that will not come true from seed and is commercially propagated via tissue culture.

Plant establishment and maintenance

All plants in the study were purchased as landscape plugs (12.7 cm deep x 5.1 cm wide) from North Creek Nurseries Inc. in Landenberg, PA, in June of 2012. All plugs were transplanted into 2-L plastic pots (Dillen 5.5 Sq Jumbo, Griffin Greenhouse Supply, Tewksbury, MA) using an organic compost-based potting soil (Fort Vee Potting Soil, Vermont Compost Company, Montpelier, VT). The pots were placed in trays on a black lumite ground cover (Lumite GCB, Griffin Greenhouse Supply, Tewksbury, MA) and irrigated as needed with overhead sprinklers through summer 2012.

We tilled the sites in preparation for fall planting. The sites were planted on 2 Sept. 2012 and 4 Sept. 2012. We applied approximately 1 L per 90 sq m of an organic custom blend 5-1-9 fertilizer (North Country Organics, Bradford, VT) and installed T-tape drip irrigation (T-Systems Irrigation, San Diego, CA). No mulch or weed barriers were employed in an effort to encourage the presence of ground-nesting solitary bees (Splawski et al. 2014). Weeds were controlled manually for the duration of the study. Individual plants that did not overwinter in the planting units were replaced in the spring of 2013 and 2014 with plants of the same size and age. Reserve plants were heeled into the ground in pots during the winter of 2012 and then planted in a garden area adjacent to the study area at Site B in the spring of 2013.

Experimental design

This study was part of a larger effort to evaluate pollinator preference for native species versus native cultivars (A. White & L. Perry, unpublished data.) The four *Echinaceas* were part of the research gardens containing a total of 1,224 plants and 34 plant types. The research gardens were approximately 9 m wide and 30 m long or 270 m². We designed the research area at each farm as randomized complete blocks with three replicates. Within each replicate, we randomly assigned plant types to 1 x 1.5 m planting units. Each unit contained a group of six plants of the same type, planted approximately 45 cm on center (Fig. 3.1). We planted in masses to allow foraging bees to exhibit flower constancy (Heinrich et al. 1977; Waser 1986; Chittka et al. 1999). Planting units were separated by 30 cm of bare soil and replicates were separated by a 1-m wide row of bare soil. A total of 36 plants of each *Echinacea* type were planted and evaluated for this study among both sites.

Data collection

We visited Site A and Site B a minimum of once per week in July and August of 2013 and 2014 to evaluate pollinators foraging on *Echinacea*. To maximize potential for pollinator presence, we collected data on days with no precipitation, temperatures greater than 15°C, cloud cover less than 50%, average wind speeds less than 15 kph, and between 9:00 am and 4:00 pm. During the peak bloom period for each *Echinacea* type, we counted the number of inflorescences for all plants.

Pollinator visitation: At each site visit, we visually monitored planting units in peak bloom for pollinator visits. We observed all plant units in random order. We visually observed and recorded pollinator visits to the disk florets on *Echinacea* inflorescences during five-minute scans of each unit (i.e., six plants of the same type planted in a unit). At the beginning of each scan period, pollinators present on the flowers within the unit were recorded and then new pollinators entering the unit were recorded over the subsequent five minutes. Pollinators moving from flower to flower within the unit were counted once. A pollinator leaving and reentering the unit during the scan period could be counted more than once. All pollinators were classified into seven visually identifiable taxonomic and/or functional insect groups: Honey Bees (*Apis mellifera*), Bumble Bees (*Bombus spp.*), Other Native Bees (order: Hymenoptera), Butterflies/Moths (order: Lepidoptera), Wasps/Ants (order: Hymenoptera), Bugs/Beetles (orders: Hemiptera/Coleoptera), and Flies (order: Diptera).

We chose to employ direct observation methods instead of capturing and exterminating pollinators visiting flowers based on Tuell et al. (2008) finding that direct observation was a comparable, and possibly better, method for recording bees at

flowers than collection methods. Direct observation also kept the pollinator community intact. A drawback of direct observation is the inability to identify many pollinators down to the species level.

Our observation methods were best suited for bee pollinators, so non-bee pollinators may be underrepresented in the data. One experienced human observer (A. White) collected data to minimize human error and variability. The observer situated 1 m from the planting units did not appear to affect the foraging action of any pollinator groups, except for butterflies and moths, which were noticeably affected by human movement. Furthermore, small beetles, bugs, and ants were sometimes hidden when foraging inside flowers.

Data analysis

We compared mean pollinator visits by seven pollinator groups and two composite groups (All Bee Pollinators and All Non-Bee Pollinators) to four *Echinacea* types using generalized linear mixed models (GLIMMIX) with log-link functions and Poisson distributions. All statistics were run at 0.05 level of significance and generated using SAS software Version 9.4 (SAS 2014). In each model, we included plant type (four levels), site (two levels), and year (two levels) as fixed effects; the two-way interactions between the fixed effects; replicate as a random factor; and weeks nested within years as a repeated factor. Multiple observations on the same replicate were averaged for each week. For the pollinator groups Beetles/Bugs and Wasps/Ants, the floral visitation data were too sparse to be analyzed with our model, but the visits were included in the composite group All Pollinators. Floral abundance was compared using a two-sample t-

test. Differences in winter survival are reported as the significance of the difference between two independent proportions.

RESULTS

Echinacea purpurea

We recorded a total of 1,339 pollinator visits to all *Echinacea* planting units during 184 five-minute observations. The native species, *Echinacea purpurea* received the most pollinator visits, totaling 729 visits recorded during 48 five-minute observations at both sites. The predominant pollinators visiting *E. purpurea* at Site A were Bumble Bees (64.5%) and Honey Bees (12.5%). At Site B, where no Honey Bees were present in the landscape, the predominant pollinators were Bumble Bees (84.4%) and Other Native Bees (7.1%).

Echinacea purpurea 'White Swan'

We recorded a total of 404 pollinator visits to *E. purpurea* 'White Swan' during 48 five-minute observations at both sites. The predominant pollinators visiting *E. purpurea* 'White Swan' at Site A were Bumble Bees (48.8%) and Honey Bees (15.5%); at Site B the predominant pollinators were Bumble Bees (73.7%), Flies (14.3%), and Other Native Bees (7.9%). All Bee Pollinators visited *E. purpurea* 'White Swan' significantly less frequently than the native species, *E. purpurea* ($F_{[1,70]} = -3.11$, $p = 0.003$) (Fig. 3.2), while all Non-Bee Pollinators exhibited no preference between the species and the cultivar ($F_{[1,79]} = -0.23$, $p = 0.818$). Bumble Bees exhibited a significant preference for the species ($F_{[1,69]} = 4.81$, $p < 0.001$), but Honey Bees (Site A only) did not exhibit a preference ($F_{[1,24]} = 0.61$, $p = 0.551$). Other Native Bees ($F_{[1,100]} = 1.41$, $p = 0.163$), Flies

($F_{[1,90]} = -1.22$, $p = 0.227$), and Butterflies/Moths ($F_{[1,78]} = 1.55$, $p = 0.125$) also found the species and the cultivar ‘White Swan’ equally attractive. *Echinacea purpurea* ‘White Swan’ had significantly fewer flowers per plant than *E. purpurea* ($t_{[142]} = 29.39$, $p < 0.001$). However, when standardizing the visits for floral abundance, there was still a significant overall preference for the species, suggesting that floral abundance alone does not explain pollinator preference for the species over this cultivar. The species and the cultivar had identical winter survival rates at 82% ($z_{[142]} = 0.00$, $p = 1.00$).

***Echinacea purpurea* 'Pink Double Delight'**

We recorded a total of 94 pollinator visits to *E. purpurea* ‘Pink Double Delight’ during 48 five-minute observations at both sites. The predominant pollinators visiting *E. purpurea* ‘Pink Double Delight’ at Site A were Other Native Bees (28.5%), Beetles/Bugs (14.5%), and Flies (13%); at Site B the predominant pollinators were Flies (32.0%), Wasps/Ants (28.0%), and Other Native Bees (20%). All Bee Pollinators visited *E. purpurea* ‘Pink Double Delight’ significantly less frequently than the native species, *E. purpurea* ($F_{[1,81]} = -5.97$, $p < 0.001$) (Fig. 3.2), while All Non-Bee Pollinators exhibited no preference between the species and the cultivar ($F_{[1,45]} = -2.11$, $p < 0.145$). Other Native Bees exhibited a significant preference for the species ($F_{[1,100]} = -2.38$, $p = 0.019$), as did Honey Bees ($F_{[1,26]} = -2.8$, $p = 0.010$), Bumble bees ($F_{[1,84]} = -4.06$, $p = 0.001$), and Butterflies/Moths ($F_{[1,89]} = -2.14$, $p = 0.035$), but Flies did not exhibit a preference ($F_{[1,93]} = -0.93$, $p = 0.352$). *Echinacea purpurea* ‘Pink Double Delight’ had significantly more flowers per plant (1.6 times more) than the species ($t_{[142]} = -10.95$, $p < 0.001$). The species and the cultivar had no significant difference in winter survival rates at 75% and 82%, respectively ($z_{[142]} = 1.01$, $p = 0.311$).

***Echinacea* 'Sunrise' Big Sky**

We recorded a total of 112 pollinator visits to *Echinacea* 'Sunrise' during 40 five-minute observations at both sites. The predominant pollinators visiting *Echinacea* 'Sunrise' at Site A were Bumble Bees (44.7%) and Other Native Bees (12.9%); at site B the predominant pollinators were Bumble Bees (53.6%) and Beetles/Bugs (14.3%).

All Bee Pollinators visited *Echinacea* 'Sunrise' significantly less frequently than the native species, *E. purpurea* ($F_{[1,69]} = 7.08$, $p < 0.001$) (Fig. 3.2), while all Non-Bee Pollinators exhibited no preference between the species and the cultivar ($F_{[1,77]} = 1.52$, $p = 0.134$). Bumble Bees exhibited a significant preference for the species ($F_{[1,69]} = 6.03$, $p < 0.001$), as did Honey Bees ($F_{[1,19]} = 2.48$, $p = 0.023$), Other Native Bees ($F_{[1,92]} = 2.82$, $p = 0.006$), and Butterflies/Moths ($F_{[1,76]} = 2.11$, $p = 0.038$). Flies found the species and the hybrid cultivar 'Sunrise' equally attractive. *Echinacea* 'Sunrise' had significantly fewer flowers per plant than *E. purpurea* ($t_{[142]} = 29.39$, $p < 0.001$), but when standardizing the visits for floral abundance, there was still a significant preference for the species, suggesting that floral abundance alone does not explain pollinator preference for the species over this cultivar. *Echinacea* 'Sunrise' was significantly less hardy than the species with a winter survival rate of 32% compared to 82% ($z_{[142]} = 6.06$, $p < 0.001$). The cultivar is listed as hardy in USDA hardiness zones 4-9, but did not perform well in our zone 4 gardens.

DISCUSSION

Preference differences between bee pollinators and non-bee pollinators

Our data indicate that the breeding and selection of cultivars and hybrids can decrease the attractiveness of *Echinacea* to bee pollinators. Foraging bee pollinators visited *Echinacea purpurea* significantly more frequently than *E. purpurea* ‘White Swan,’ *E. purpurea* ‘Pink Double Delight,’ and *Echinacea* ‘Sunrise.’ The selection *E. purpurea* ‘White Swan’ was visited significantly more frequently than double-flowered selection *E. purpurea* ‘Pink Double Delight,’ and interspecific hybrid *Echinacea* ‘Sunrise.’ Non-bee pollinators, including flies, bugs, beetles, wasps and ants did not exhibit any significant preferences between the *Echinacea* types but in all cases were minor pollinators compared to bees. Butterflies and moths preferred the species and the selection ‘White Swan’ to ‘Pink Double Delight’ and ‘Sunrise.’

Bumble bees and honey bees are frequently used as models to test foraging hypotheses (Waddington & Holden 1979; Pyke 1981). All bee species are obligate florivores (Michener 2007). Both larval and adult life stages feed on pollen and nectar from flowers. In other pollinator taxa, such as butterflies, florivory is often limited to the adult life stage of the insect, and they are only seeking nectar from the flowers, not pollen. Furthermore, bumble bees and honey bees, which are eusocial, use complex systems of learning, memory, and communication to improve their foraging efficiency (Hammer & Menzel 1995; Chittka et al. 1999; Arenas et al. 2007). Based on foraging efficiency theories, we can make the assumption that the foraging preferences of bumble bees and honey bees are representative of the quality of the floral rewards, whereas the foraging patterns of non-bee pollinators (or even solitary bees) may be less indicative of the quality of the floral resources. In this study, we hypothesize that the cultivars ‘White Swan’ and ‘Sunrise’ are still attracting pollinators with their floral displays and producing

nectar in large enough quantities for non-bee pollinators to forage on the flowers; however, honey bees and bumble bees are identifying *Echinacea purpurea* as the best floral resource and communicating this information with other foragers, thus increasing total bee pollinator visits to the species.

Forms and traits and their effects on pollinators

Flowers have evolved morphologies, color schemes, and fragrances that pollinators find attractive; these traits lure pollinators to the flowers, and furthermore, to the reproductive parts of the flower. Many pollinators can rapidly associate several flower characteristics with food rewards, including floral color schemes (Wilbert et al. 1997; Wesselingh & Arnold 2000), floral fragrance (Knudsen et al. 2001; Raguso 2008), and size and shape of flowers or inflorescences (Møller & Sorci 1998; Spaethe et al. 2001; Wignall et al. 2006; Whitney & Glover 2007; Davis et al. 2008). Breeding and selecting cultivars of native flowers can make the native plants more attractive for ornamental applications, but it may come at a cost for pollinators. Our data suggest that the higher the level of selection, the more the native flower traits have been altered and the more likely it is that the *Echinacea* cultivar is less attractive to pollinators than the species.

Color: Among visual cues for pollinators, color is considered one of the most significant signals, enabling pollinators to discriminate between flowers at a distance. Bumble bees and honey bees prefer colors of higher spectral purity and prefer colors that they have learned are associated with high floral rewards (Rohde et al. 2013). Each of the *Echinaceas* we studied exhibited a significant color change from the species, but

additional research is needed to explore how color alone may be influencing pollinator attraction in these examples.

Compactness: Breeding for more compact and predictable forms is common with *Echinacea* as well as other native plant taxa. Compactness, however, often equates with fewer flowers per plant and fewer floral resources. In pollinator gardens, where area might be limited, less compact and more floriferous plants would make better use of vertical space and, ultimately, provide a greater abundance of floral resources to pollinators. Choosing compact varieties such as *E. purpurea* ‘White Swan’ and *Echinacea* ‘Sunrise,’ provides fewer floral resources per unit area.

Double-flowers: Selecting for a double flower also comes at a cost for pollinators. The reproductive organs (stamens and carpels) in double-flowered varieties have been modified into additional petals, thus rendering the plant sterile or near sterile, and reducing the quantity and/or accessibility of floral rewards (Comba et al. 1999; Corbet et al. 2001). The small number of pollinators we recorded visiting doubled-flowered *Echinacea* ‘Pink Double Delight’ suggests that it may also have decreased floral rewards and/or limited accessibility.

Hybridization: The hybrid *Echinacea* in our study was significantly less attractive to pollinators than both the species and the selection ‘White Swan.’ Hybridization may uncouple trait combinations (e.g. color and nectar availability) that are present in parental species and influence pollinator foraging. Melendez-Ackerman (1997) found individuals from hybrid populations of *Ipomopsis aggregata* and *I. tenuituba* showed considerable variation in color. Furthermore, nectar quality in the hybrids resembled the parent with the weaker nectar production. Similarly, A. White and L. Perry (unpublished data) found

commercial hybrid cultivars of *Lobelia cardinalis* and *Lobelia siphilitica* to be intermediate in corolla depth and length, exhibit the color of either parent, but have nectar dynamics comparable to *L. siphilitica*, which only produces 20% of the nectar of *L. cardinalis*.

Conversely, other studies indicate that some interspecific plant hybrids do not yield inferior floral resources. In a study of *Iris brevicaulis* and *Iris fulva*, Wesselingh and Arnold (2000) found F₁ hybrids were not intermediate, but they had the high nectar concentration of *I. brevicaulis* combined with the long life span of *I. fulva* flowers, meaning the F₁ hybrids produced the highest amounts of nectar and nectar sugar over their life spans. Garbuzov and Ratnieks (2014) found several hybrid *Lavandula* varieties to be equally attractive to pollinators as non-hybrid varieties.

Our data, in combination with previous studies, suggest that in general, hybridization does not intrinsically yield plants with inferior floral resources for pollinators. However, hybrids may, to varying degrees, uncouple trait combinations that are present in the parents and that influence pollinator foraging. Intentionally hybridizing native plant species to create unique garden plants may yield trait combinations that are less attractive to pollinators than one or both parents. However, modern breeding programs also have the knowledge and the technology to develop cultivars that are pollinator-friendly and do not have diminished floral rewards. For example, Schemske and Bradshaw (1999) found an allele that increased nectar production and doubled hummingbird visitation in a hybrid of *Mimulus lewisii* and *Mimulus cardinalis*.

Sterility: Echinacea purpurea ‘Pink Double Delight’ and *Echinacea* ‘Sunrise’ are sterile or near sterile and these were significantly less attractive to bee pollinators than

both the fertile selection ‘White Swan’ and the species. Breeding for sterility can inhibit flowers from setting seed, hence resulting in longer bloom durations. This could be a benefit to pollinators if the flowers continue producing ample nectar and pollen, but this is often not the case. Degrees of sterility can vary among cultivars, along with quality of nectar and pollen production, making it important that floral resources for pollinators are evaluated on a plant-by-plant basis. To our knowledge, nectar and pollen production has not been studied in *Echinacea* cultivars, but in other species, male-sterile cultivars have significantly decreased nectar and pollen flow. For example, male-sterile rapeseed offers only 35% of the pollen flow and 60% of the nectar flow in comparison to non-male-sterile cultivar selections (Koltowski 2003).

Conclusions

Our study provides the first evidence that selected and hybridized *Echinacea* varieties may not be equivalent substitutions for the native species in terms of maximizing attractiveness to pollinators. In pollinator gardens, where the goal is to maximize floral resources for foraging pollinators, selected and hybridized varieties should be scrutinized carefully. The benefits of using cultivars should be weighed against the potential reduction in floral resources available and accessible to pollinators.

Traditionally, plant breeders have focused their programs on selecting for traits that humans find desirable, e.g. unique colors, compact/predictable forms, extended bloom durations, disease resistance, hardiness, etc. However, as we take on the challenge of restoring and creating floral-rich landscapes to support pollinator populations, there is a tremendous opportunity for plant breeders to introduce selections to the market that

have desirable traits for the benefit of gardeners, but that also maximize nectar and pollen production for the benefit of pollinators.





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Table 3.1. Summary information for four *Echinacea* types analyzed in this study, including their origin, forms and traits selected for in the breeding process, general fertility, floral abundance, and hardiness. Sample size for floral abundance and winter survival is 36 plants of each type over two seasons. Winter survival rate is for field-grown plants in Zone 4a and 4b in northern Vermont and may be significantly higher in warmer climates.

Botanical Name	Description	Breeder	Selected traits	Fertility	Bloom duration	floral abundance	Winter Survival
 <i>Echinacea purpurea</i>	Native Species	N/A	None	high	30-45 days	20.8 ± 8.81	82%
 <i>E. purpurea</i> 'White Swan'	Open-pollinated selection	N/A	White ray flowers, compactness	high	30-45 days	12.63 ± 5.70	82%
 <i>E. purpurea</i> 'Pink Double Delight'	Double-flowered selection	AB Cultivars	Pink, double-flowers, many blooms, disease resistance	low	45-60 days	34.22 ± 10.02	75%
 <i>Echinacea</i> 'Sunrise'	Interspecific hybrid	ItSaul Plants	Yellow ray flowers, disease resistance, compactness	low	30-45 days	8.62 ± 3.65	32%

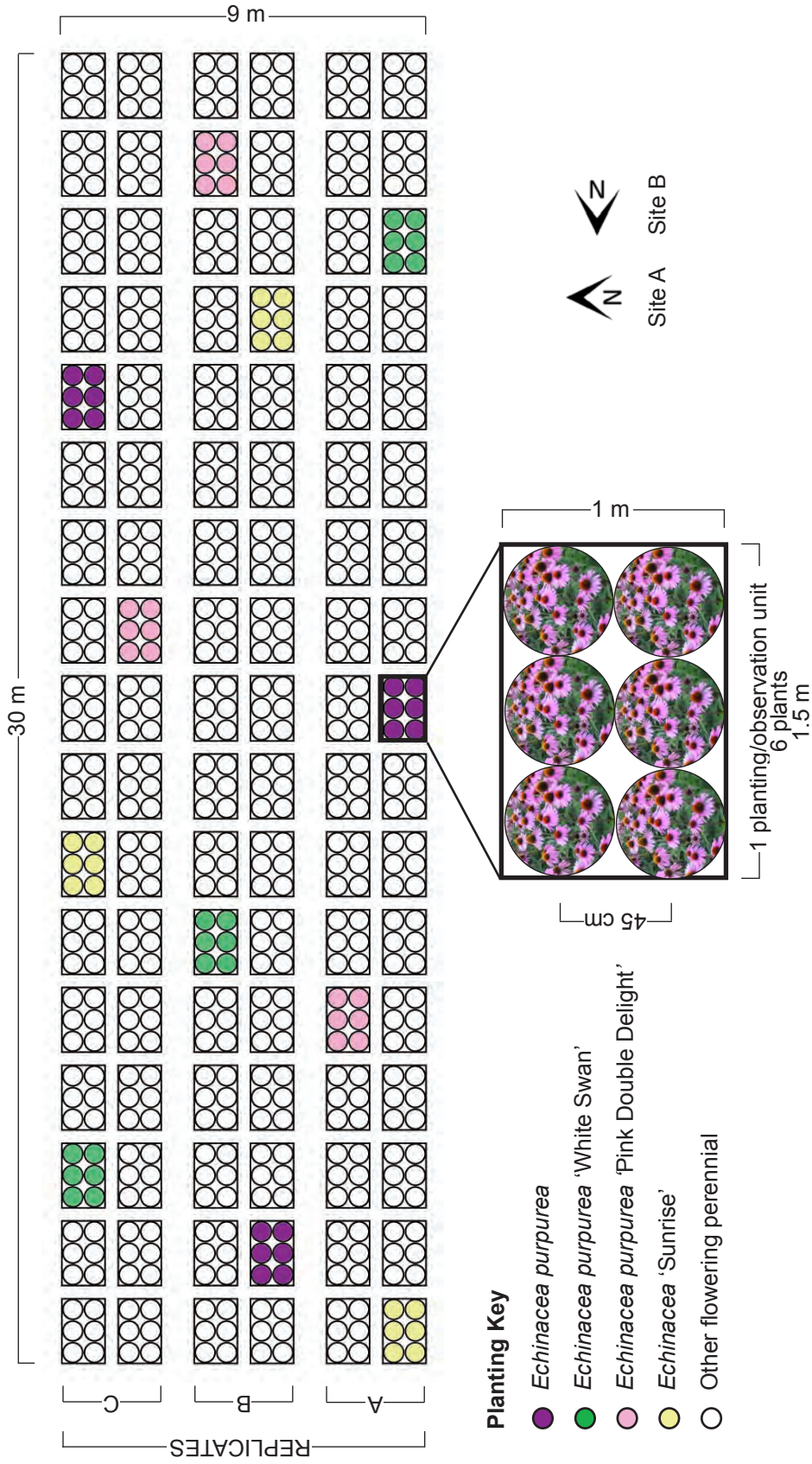


Figure 3.1. Experimental design layouts at Site A and Site B were randomized complete block designs with three replicates per field site. Typical planting layout is illustrated. Planting units composed of six plants of a single type were randomized within the replicates; however, each *Echinacea* was not located within 2 m of another *Echinacea*, both within and across replicates. At each site, 18 individual specimens of 34 plant types were represented, totaling 612 plants per site. This paper analyzes four of these plant types, *Echinacea purpurea*, *E. purpurea* 'White Swan', *E. purpurea* 'Pink Double Delight', and *Echinacea* 'Sunrise'.

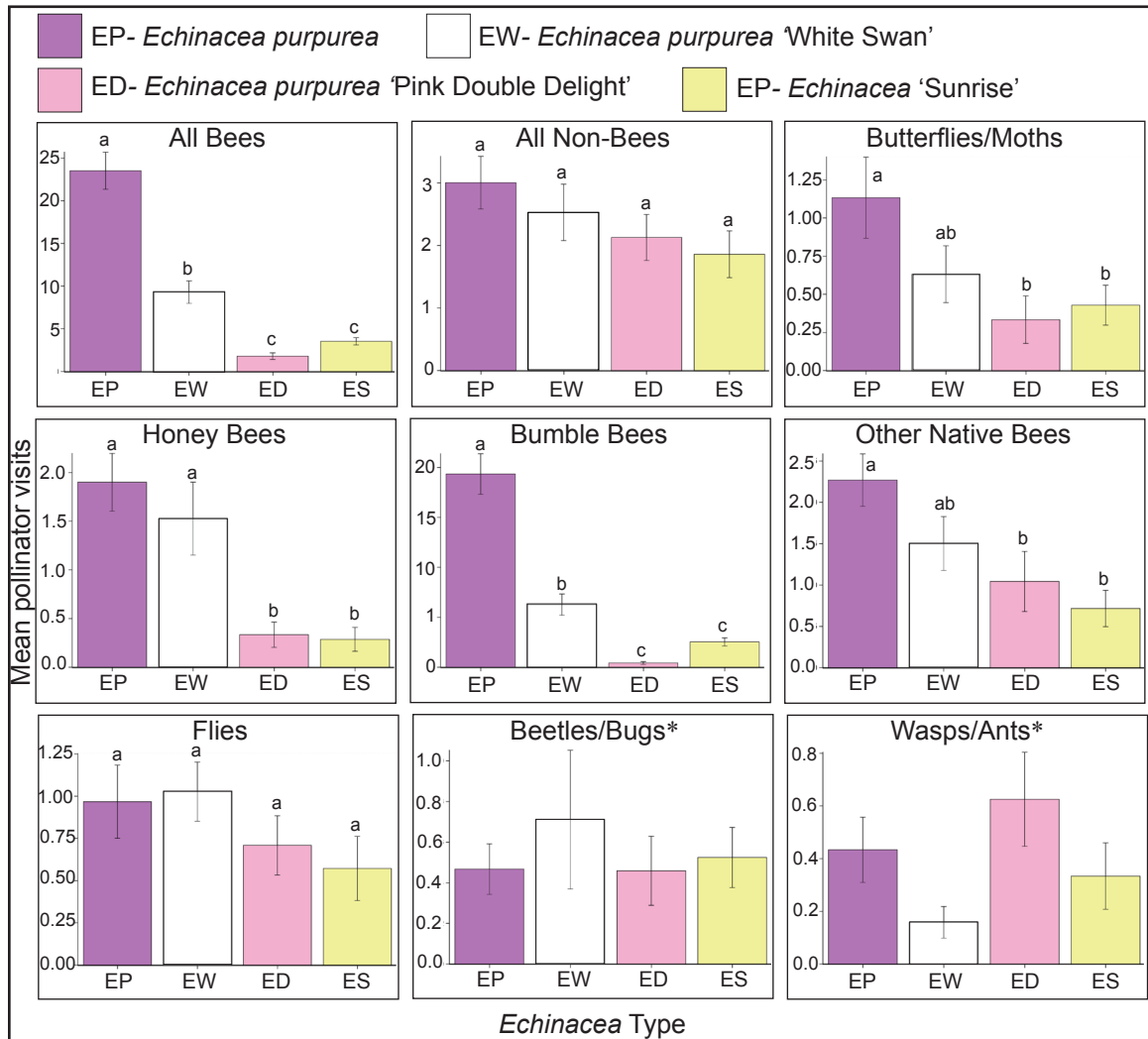


Figure 3.2. Mean pollinator visits \pm SEM per planting unit (1 x 1.5 m, 6-plant mass) per 5 minutes recorded on 4 *Echinacea* types at 2 sites in 2013 and 2014. Significant differences based on a generalized linear mixed model (GLIMMIX) analysis. Types sharing a common letter above the bar are not significantly different from each other at, $p < 0.05$. *Visitation data for Beetles/Bugs and Wasps/Ants were too sparse to be modeled.

CHAPTER 4

A REVIEW OF PLANTING STRATEGIES FOR POLLINATOR HABITAT: THE VALUE OF NATIVES, NEAR-NATIVES, NON-NATIVES, AND NATIVE CULTIVARS

Formatted for publication in *Ecological Applications*

ABSTRACT

Pollinators are currently receiving more attention by conservationists, scientists, farmers, and gardeners than at any other time in history. Efforts are ongoing to better understand the numerous drivers of pollinator decline as well as the most effective strategies for preserving, restoring, and creating floral-rich landscapes that support healthy populations of beneficial pollinators. As the human population continues to grow worldwide, patterns of land use will intensify. How pollinators respond to land-use change and how we preserve and restore pollinator habitat in anthropogenic and agricultural landscapes has important implications for much of the world's wild flora and agricultural crops. The natural history of our world's pollinator species is widely divergent, but one commonality of these species is their reliance on flowers as food sources. Floral resources can be a limiting factor for pollinator populations. When floral resources decrease, pollinators decrease; when floral resources increase, so do pollinators. Consequently, plant selection is integral to the value and success of pollinator habitat restorations, yet there is little consistency and overlap in pollinator planting recommendations and very little empirical data to support plant choice. Non peer-reviewed pollinator plant lists are widely available and are often region-specific, but they are typically based on anecdotal rather than empirical data and lack in specificity. To help close the gap between anecdotal and empirical data, and between practice and research, we reviewed the published literature on plant selection for pollinator habitat restoration. We explicitly reviewed and compared the value of native plant species, near-natives, non-natives and nativars (cultivars of native species). From there, we identified gaps in the literature that are most needed in practice and recommended basic strategies for practitioners to navigate plant lists and choose the best plants for the site's success.

INTRODUCTION

The functional role of pollinators and their troubling decline

Pollination provided by insects is a key ecosystem service in most terrestrial ecosystems. The functional role of pollinators is integral to the sustainability of wild plant communities and the productivity of agricultural crops worldwide. Almost 90% of flowering plant species on earth rely on animals for pollination (Ollerton et al. 2011).

Seventy-five percent of the leading global food crops are dependent on animal-mediated pollination for fruit, vegetable, and seed production, accounting for 35% of the volume of global food crops (Klein et al. 2007). The estimated annual value of agricultural crops directly dependent on pollination from honey bees (*Apis mellifera*) and non-*Apis* pollinators reached \$11.68 billion and \$3.44 billion respectively in 2009 (Calderone 2012).

There is clear evidence for significant declines in managed honey bee stocks in the United States and Europe. Between 1947 and 2005, 59% of hives were lost in the United States (National Research Council 2007; vanEngelsdorp et al. 2010). Wild bee populations also have declined in recent decades (Colla & Packer 2008; Cameron et al. 2011; Biesmeijer et al. 2006; Burkle et al. 2013). Of further concern, widespread declines in both wild and domesticated pollinators parallel declines in plant populations that rely on them for reproduction (Potts et al. 2010; Burkle et al. 2013).

Several recent reviews of diverse sets of studies sought to identify the drivers of pollinator decline, the potential consequences, and the most vital research topics for the scientific community moving forward (Potts et al. 2010; Spivak et al. 2011; Tylianakis 2013; Vanbergen 2013). Among the most significant drivers of pollinator declines are habitat degradation, fragmentation, and loss due to land-use change; increased prevalence of non-native plant species; climate change; the spread of pathogens; increasing pesticide application and environmental pollution; and decreased resource diversity (Potts et al. 2010).

Restoring patches of floral resources can help mitigate for habitat loss and help alleviate one the more significant drivers of pollinator decline. Habitat fragmentation and

habitat loss negatively affect the abundance and species richness of wild bees (Winfree et al. 2009). Non-native honey bees (*Apis* spp.) appear to be less affected by habitat fragmentation (Garibaldi et al. 2011). While honey bees nest in managed hives, wild native bees rely on natural habitat for all their life stages. Some bee species thrive in human-disturbed landscapes, including less-intensively managed agricultural lands (Tylianakis et al. 2005; Brosi et al. 2007; Winfree et al. 2007; Brosi et al. 2008; Winfree et al. 2008), urban parks (McFrederick & LeBuhn 2006), and suburban gardens (Winfree et al. 2007); however, rare and specialized species, species occupying higher trophic levels, and cavity-nesting species are more vulnerable to habitat loss and fragmentation and climate change (Burkle et al. 2013).

The restoration of floral resources for pollinators

Numerous studies, which have been reviewed by Nicholls and Altieri (2013), provide mounting evidence that the preservation and restoration of plant biodiversity within and around agricultural landscapes can improve habitat for both domestic and wild bees, as well as for other beneficial insects, thus enhancing pollination services for crops. In intensively farmed agricultural landscapes, the limited bloom time of the crop monoculture, combined with potentially suboptimal nectar and pollen resources, can be detrimental to both wild and managed pollinator populations. Additional floral resources available in non-cropped areas of agricultural landscapes can sustain pollinators before and after the crop bloom (Decourtye et al. 2010). A crop's proximity to natural or semi-natural habitat affects pollinator richness, visitation rate, and fruit set (Kremen et al. 2004; Morandin & Winston 2006; Williams & Kremen 2007; Ricketts et al. 2008; Garibaldi et al. 2011). Additionally, pollinator habitat provides multifunctional benefits

to the landscape, including biodiversity conservation, conservation biological control, soil and water quality protection, weed suppression, and aesthetic benefits (Wratten et al. 2012).

Replicated field research to guide the creation of pollinator habitat in agroecosystems is limited; however, several case studies support the value of pollinator habitat restoration for specific crops (Carvalho et al. 2012; Blaauw & Isaacs 2012). For example, Blaauw and Isaacs (2014) found that wild bee and syrphid populations increased annually following the establishment of wildflower plantings adjacent to highbush blueberry crops in Michigan. Percentage fruit set, berry weight and mature seeds per berry were also significantly greater in fields adjacent to wildflower plantings. In addition to providing pollinator habitat, large plantings of wildflowers also increase the density and diversity of other beneficial insects (Blaauw & Isaacs 2012). Similarly, Carvalho et al. (2012) found Mango (*Mangifera indica*) trees in closer proximity to small patches of perennial native wildflowers had significantly higher diversity and abundance of pollinators, as well as increased production, according to the South African study.

Habitat also is important for bees in urbanized landscapes. In a study about how the bumble bee community in San Francisco, California, has responded to urbanization, McFrederick and LeBuhn (2006) found that bumble bee abundance was positively associated with resource availability within city parks. This suggests that even in highly urbanized and fragmented landscapes, maximizing floral resources and nesting habitat for bees can boost their populations. The ability of bees to persist in disturbed landscapes, including agricultural borders, city parks, and residential gardens, allows unique

opportunities for the conservation of pollinators. Traditional conservation planning strategies for threatened or endangered species often entail establishing nature reserves, but pollinators can benefit from small habitat patches integrated into otherwise disturbed agroecosystems or residential landscapes. Furthermore, localized pollinator habitat efforts can be effective in the biological conservation of pollinators and the preservation of local pollination services, and they are economically more feasible than large-scale regional preserves (Winfrey 2010).

Initiatives for pollinator conservation and habitat restoration

The loss of pollinator diversity threatens global agricultural productivity, and for this reason, the prospect of a pollination crisis is garnering the interest of scientists, policy-makers, and the general public. With numerous studies highlighting the importance of preserving and restoring pollinator habitat in both agricultural and urbanized landscapes, special initiatives to address pollinator decline are widespread and growing in the United States.

The Presidential Memorandum on Pollinator Health (Obama 2014) and subsequent National Strategy to Promote the Health of Honey Bees and Other Pollinators (Pollinator Health Task Force 2015) say that federal action combined with private-sector partnerships and citizen engagement can help restore pollinator populations. One goal detailed by the Task Force is to restore or enhance 7 million acres of land for pollinators over the next five years. On the heels of this federal action plan, a collaboration of dozens of conservation and gardening organizations created the National Pollinator Garden Network in 2015. They quickly launched the Million Pollinator Garden Challenge

(millionpollinatorgardens.org) with the goal of registering one million pollinator gardens in the United States by 2017.

These new initiatives build upon some long-established efforts, particularly in the agricultural sector, to promote pollinator conservation. Working under the United States Farm Bill, USDA's Farm Service Agency (FSA) and the Natural Resources Conservation Service (NRCS) have worked with farmers in recent years to improve pollinator habitat conservation on agricultural lands. The 2008 (and subsequently, the 2013) U.S. Farm Bill recognized and continues to recognize the enhancement of bee habitat on private farms as a priority of all conservation programs.

PLANT LIST REVIEW

Floral resources are a fundamental component of any pollinator habitat restoration or pollinator garden. Flowers have evolved morphologies, color schemes, and fragrances that pollinators find attractive: these traits lure pollinators to the flowers, and furthermore, to the reproductive parts of the flower. Many pollinators can rapidly associate several flower characteristics with food rewards, including floral color schemes (Wilbert et al. 1997; Wesselingh & Arnold 2000), floral fragrance (Knudsen et al. 2001; Raguso 2008), and size and shape of flowers or inflorescences (Møller & Sorci 1998; Wignall et al. 2006; Whitney & Glover 2007; Davis et al. 2008; Spaethe et al. 2001).

Restoring floral resources boosts pollinator abundance and diversity (Meek et al. 2002; Carvell et al. 2004; Pywell et al. 2005; Tuell et al. 2008), yet we still have very little empirical data to support region-specific planting lists for pollinator habitat. Garbuzov and Ratnieks (2014a) reviewed the strengths and weaknesses of commonly available lists of garden plants to help pollinators. They concluded that lists often

included poor recommendations, omitted many good plants, lacked details, and were consistently based on the authors' general expertise rather than on empirical data.

Furthermore, they found very little overlaps in the lists, even within the same geographic regions. This leads us to consider what planting recommendations might look like if they were based solely on peer-reviewed empirical data.

The purpose of the remainder of this paper is to (a) review the empirical data that is available to support plant selection decisions for pollinator plantings, (b) identify gaps in published literature relating to choosing the best plant species for pollinator habitat restoration and pollinator-friendly gardens, and (c) recommend basic strategies for practitioners of all types to navigate plant lists and choose the best plants for a site's success. We discuss the reviewed literature in three distinct sections, helping to elucidate three commonly asked questions: 1) Are native or non-native flowering plants better for pollinators? 2) Are cultivated varieties of native plants as beneficial to pollinators as the native species? 3) What are the best overall plant species for pollinators?

Are native or non-native plants better for pollinators?

A native plant is an endemic plant species that occurs naturally in a plant community, ecosystem, ecoregion, or biome without direct or indirect human involvement (U.S. Forest Service 2012). With thousands of flowering plants to consider, eliminating all non-native plants is often the first and easiest way to narrow a planting palette. Native plants are routinely recommended for pollinator plantings, but it is frequently questioned whether published literature supports the exclusion of non-native plants from pollinator habitat restorations.

Several studies suggest that wild bees prefer to forage—but not necessarily exclusively—on the nectar and pollen from native plants (Harmon-Threatt & Kremen 2015; Morandin & Kremen 2013b; Morales & Traveset 2009). However, all these studies also identify specific non-native species that also are valuable foraging resources for pollinators. An analysis of historic records from a diverse landscape in southwestern Illinois found that the web of interactions between plants and pollinators was less richly connected for non-native plants than for natives (Memmott & Waser 2002). Both Memmott & Waser (2002) and Tepedino et al. (2008) found that non-native plants likely benefit generalist bee species more than they benefit specialist bee species.

Pollinator preference for native plant species is documented the strongest in agricultural landscapes. At both mature and newly established agricultural hedgerow sites in California, wild bees prefer to forage from native plants over non-native plants (Morandin & Kremen 2013a). Likewise, in California grasslands, bumble bees collect significantly more pollen from native plants than from non-native plants (Harmon-Threatt & Kremen 2015). Interestingly, this study found no differences in the nutrient availability (essential amino acid content and protein), suggesting that if they were selected, exotic species could meet the nutritional needs of bumble bees. In contrast to these agriculturally based studies, an investigation of the interactions between bees and non-native plants in disturbed habitats in central California and southern New Jersey found no effect of non-native plant abundance or richness on bee abundance or richness. This suggests that in disturbed landscapes bees may use, but do not prefer, non-native plants (Williams et al. 2011).

There are, however, exceptions to these generalizations. In other specific scenarios, non-native plants attract more pollinators than co-flowering native plants. This is the case with *Carpobrotus affine acinaciformis*, a succulent perennial, and *Opuntia stricta*, a cactus. Both of these species have large and showy flowers and received more pollinator visitors than co-flowering native plant species in Mediterranean Spain (Bartomeus et al. 2008). Tepedino et al. (2008) also found that three non-native plant species, salt cedar (*Tamarix* spp.) and white and yellow sweet clover (*Melilotus albus*, *M. officinalis*) had as many or more associated bee species individuals as did native plant species in Capitol Reef National Park, Utah.

In domestic garden settings, where non-native flower options are bountiful and come in colors, sizes, and morphologies known to be attractive to bees, the differences in attractiveness between native and non-native plants appear less pronounced. Although pollinators may still prefer native plants over non-natives in domestic gardens (Corbet et al. 2001; Salisbury et al. 2015), numerous non-native species also are frequently visited by bees, some even being preferred over natives (Hanley et al. 2014; Salisbury et al. 2015; Garbuzov & Ratnieks 2014b). In some landscapes there are very few to no pollinator preferences between native and non-native plant species (Hanley et al. 2014).

Comparing insect visits and nectar production in four British native plants and four non-native plants, Corbet et al. (2001) found all native species to be nectar-rich and frequently visited by pollinators. Conversely, the non-native species had fewer pollinator visits, and in cases where nectar was readily available, it was inaccessible. They also found that double-flowering varieties of the non-native flowers secreted little or no nectar (Corbet et al. 2001).

Recognizing that the classification of all plants as native or exotic may be too coarse in the context of pollinator use, another British researcher (Salisbury et al. 2015) performed a replicated field experiment, establishing garden plots planted with an assemblage of plants based on origin. The three treatments included assemblages of native, near native, and exotic flowering plant species. There was a greater abundance of total pollinators recorded on native and near-native plots compared to the exotic plots; however, some exotic species were also frequently visited.

A recent study of bumble bee preferences in urban gardens in the UK (Hanley et al. 2014) did not offer much more clarity on the debate over native versus non-native plant preference by bees in garden landscapes. Their analysis of flower use by bumble bees produced conflicting results depending on which plant species and which bumble bee species were included. This suggests that floral attractiveness varies among both native and non-native flowers, as do floral preferences among pollinator species.

Based on all available empirical data, we agree with the general suggestion of Salisbury (2015): Pollinator gardens should include a variety of flowering plants, biased towards native and near-native species but also incorporating a selection of non-native species that potentially provide resources for specialist pollinator groups or help extend the flowering season.

Are cultivated varieties of native plants as beneficial to pollinators as the native species?

Biasing plant selection for pollinators towards native plants is supported by the literature and is exemplified in numerous plant lists; however, many plants marketed as “natives” in garden centers and plant catalogs have never grown naturally in the wild.

They are cultivars and hybrids of native plants that have been selected, cross-bred or hybridized by botanists and breeders for desirable characteristics that can be maintained through propagation. These characteristics include flower size and color, foliage color, extended bloom periods, more predictable and manageable plant forms and sizes, sterility, and disease resistance.

The propagation of native plant species, both herbaceous and woody, is a specialized field, requiring access to local seed sources and knowledge about seed collection, pre-treatment, and germination techniques. The growing demand for native plants, combined with these propagation challenges and a desire for more robust or predictable plant habits in domestic gardens, have led to the selection and breeding of native cultivars.

There is a tremendous amount of variation in the origin of native cultivars, how they are propagated, and the desirable traits for which they are maintained. Because cultivars have been selected primarily based on ornamental traits, it is not always clear whether or not they perform the same ecological roles as the native species, which evolved naturally in the landscape.

The flowers of native cultivars may vary from the species in size, abundance, color, morphology, and phenology—all attributes we know influence floral visitation. Stems may be sturdier and leaves may be variegated or vary in color. The plants may be taller or more compact, more or less vigorous, more or less hardy, prefer poorer or richer soils, prefer more or less soil moisture, and be more or less tolerant of pests and diseases. Some cultivars also produce more or less nectar and pollen with varying levels of

nutrition. All of these variables have the potential to impact the attractiveness of the plant variety to pollinators and the availability and accessibility of the floral reward.

Comba et al. (1999b) published the first study suggesting that horticulturally modifying ancestral plants for ornamental traits may negatively affect pollinators. The study examined six garden annuals and cultivars that differed from their ancestral species in the loss of a functional spur; in the number of floral parts; or in the size, form or color of the corolla. The study found that in most cases, the modifications reduced the value of the floral reward to insects and/or made the reward inaccessible. This ultimately affected the abundance and species composition of insect visitors to the flowers. More specifically, the study found that the loss of a functional spur (the site of nectar secretion) could yield nectarless flowers. Furthermore, the doubling of flowers increases the number of petals at the expense of other floral parts such as anthers or carpels, decreasing the flower's pollen and/or nectar production, and making it inaccessible to foraging pollinators. Alterations to the flower color and the form and size of a flower's corolla can disrupt a coevolved morphological match between flower and insect. This study was limited in that it only evaluated six highly modified cultivars, but it exemplified how horticultural modifications in ornamental garden flowers can render the flowers less attractive and less valuable to foraging insects.

White and Perry (unpublished data 2016) aimed to evaluate whether commonly available native cultivars were equivalent substitutes for the native species in the context of pollinator habitat restoration. Across the 14 plant pairs studied, 9 native species were preferred by most insect pollinators, 4 were equally preferred, and 1 native cultivar was preferred over the native species. In general, bees (both native and non-native) and

moths/butterflies exhibited similar preferences, whereas flies showed no preference between the native species and the native cultivar. This study shows that many insect pollinators prefer to forage on native species over cultivated varieties of the native species, but not always, and not exclusively. The more the cultivars were modified from their native form, the less attractive they became. Some native cultivars may be comparable substitutions for native species in pollinator habitat restoration projects, but all cultivars should be evaluated on an individual basis.

The little research that is available on the topic of native cultivars suggests that cultivated and hybridized varieties of native plants may have horticultural modifications that render the flowers less attractive or less rewarding. Much more research is needed to evaluate more plant species and more cultivars of each species.

Other challenges with native cultivars

The implications of using native cultivars as equivalent substitutes for native species go beyond pollinator attraction. A major consideration when using human-bred and hybridized native cultivars in the landscape is the loss of genetic variation naturally found in open-pollinated plant populations and the potential for cultivars to hybridize with surrounding populations of native species. In a large-scale planting of native cultivars, the cultivars provide a significant source of altered genes and the small remnant population of native species act as a sink (Byrne et al. 2011). When hybridization occurs between native species and maladapted cultivars in the landscape, the population may experience a reduction in fecundity, germination rates, competitiveness, and survivorship (Byrne et al. 2011). In the face of environmental change, native plant populations may need the naturally occurring genetic variation within their open-pollinated species to

adapt to stochastic environmental events, such as drought, floods, and temperature extremes. The use of strongly selected cultivars is generally discouraged in ecological restoration projects (e.g. prairie or wetland restorations) (Lesica & Allendorf 1999; Schröder & Prasse 2013), but the availability and use of native cultivars in the horticultural industry is high. Potential differences between native species and native cultivars is not discussed in pollinator habitat guides and actual differences have not been previously studied.

In a comparison of 9 native, 9 weedy, and 14 improved cultivars of sunflowers (*Helianthus spp.*) in Indiana, researchers found that although improved cultivars increased their allocations to flowers, they were significantly less drought tolerant (Koziol et al. 2012). In USDA hardiness zone 4, White and Perry (2016a,b) found about half of the 14 cultivars they studied were significantly less hardy than the native species in their northern climate. For specific applications, such as erosion control and biofuel crops, native cultivars are being selected for high biomass production. These are also characteristics associated with invasiveness. The potential negative consequences of introducing the genes of vigorous cultivars into native plant populations are concerning and are not well studied (Kwit & Stewart 2012).

To maximize the floral resources available to pollinators in habitat restoration projects, including agricultural land and landscape gardens, it is important that we better understand the advantages and disadvantages of using cultivars of native plants as substitutions for native species. These plant choices can affect the abundance, quality, and accessibility of the floral resources for pollinators.

A significant weakness of most pollinator plant lists is their lack of specificity. Plant recommendations are often given at the genus level, leaving people to assume that all species within that genus are equally attractive to pollinators and well suited for their site. Furthermore, recommendations are almost never more specific than the species levels, implying that all horticulturally modified cultivars of a species are of equal value. The literature is limited, but in general, native cultivars vary in their value to pollinators. Some cultivars are equivalent substitutes for the native species and others are not (White & Perry, 2016).

What are the best overall plant species for pollinators?

The ultimate goal of any author compiling a list of plant species for pollinators is to recommend the top plant choices. However, doing so is complicated, if not impossible. Empirical data are extremely limited, and even when data are available, it is unknown whether it is applicable beyond the region, ecosystem, and pollinator species studied. Efforts are ongoing to evaluate plants for pollinators in different ecosystems, but the task is enormous, given the thousands of plant choices available.

Comba et al. (1999a) evaluated 24 native and/or naturalized species in the UK for pollinator visitation. Nectar production in ten of these species also was studied. The study revealed differences between plant species in insect visitors, and in the magnitude and temporal distribution of the nectar reward. In general, all of the flowers studied by Comba et al. (1999) were attractive to pollinators and produced nectar, so the value in the data is its exploration of which plant species are most valuable to which pollinator species. They suggested that plant species that received numerous insect visits were good choices for general pollinator gardens, but the study also highlighted that opportunities

exist to create resource refuges for specific pollinators. This level of detail is largely absent from pollinator lists but is much needed to maximize the benefits of pollinator plantings.

Tuell et al. (2008) examined the relative attractiveness of 43 eastern U.S. native perennial plants to wild and managed bees. This work remains the most comprehensive evaluation of native plant species for pollinator conservation programs to date. The list is most applicable for pollinator habitat restorations in agricultural landscapes. Nine of the species were deemed highly attractive, including *Dasiphora fruticosa*, *Scrophularia marilandica*, *Veronicastrum virginicum*, *Ratibida pinnata*, *Agastache nepetoides*, *Silphium perfoliatum*, *Lobelia siphilitica*, *Solidago riddellii*, and *Solidago speciosa*. An additional 20 plant species were moderately attractive. More studies of this type are needed to evaluate more species, including non-natives and annuals, using replicated research methods.

Garbuzov and Ratnieks (2014) conducted the most comprehensive peer-reviewed studies of garden plant varieties to date. They evaluated 32 plant varieties, including 19 species and hybrids, both native and exotic to Britain, with particular focus on varieties of lavender (*Lavandula* spp.). Similar to Comba et al. (1999a) and Tuell et al. (2008), they found garden flowers varied enormously (about 100 fold) in their attractiveness to foraging insects. Certain plants were particularly attractive to some pollinator groups and less so to others. Interestingly, they found hybrid *Lavandula x intermedia* cultivars were more attractive than both *L. angustifolia* and *L. stoechas* varieties. Within the Dahlia genus, two open-flowered varieties were consistently more attractive when compared with the two varieties with highly modified flower forms. The study did not explicitly

compare all native plant species to exotic plant species, but their results indicated some native plants were of higher value than exotic plants; likewise, some exotic varieties were of higher value to pollinators than native plants.

The existing literature is valuable in specific regions and for specific applications, but there remains a great need for more research that quantifies the attractiveness of individual plant species/varieties to insect pollinators and the quality and accessibility of the floral rewards in different regions and ecosystems.

CONCLUSIONS

The value and limitations of planting lists

Pollinator plant lists from both peer-reviewed and common sources have their benefits and their limitations. An abundance of pollinator plant lists can be found in books, on websites, and within reports/bulletins from government and non-profit agencies devoted to pollinator conservation. Many of these sources lack specificity and may be biased based on the author's personal experiences; however, such lists are widely available and often region-specific. Empirical data published in peer-reviewed scientific journals has been collected using replicated research methods and analyzed using rigorous statistical analyses, limiting bias; however, at this time, the body of literature is small and not wide enough in scope to support plant selection decisions at the species level (or furthermore, the variety level) in most regions. In regions/ecosystems/applications where empirical data is not applicable or is sparse, relying on anecdotal data conveyed in unreferenced pollinator plant lists is the best alternative.

Gaps in research

Optimizing pollinator habitat restoration for the conservation of pollinator species relies on making the best plant selection decisions possible. The existing body of literature is valuable in specific regions and for specific applications, but there remains a significant need for more research that quantifies the attractiveness of individual plant species/varieties to insect pollinators and the quality and accessibility of the floral rewards in different regions and ecosystems. Furthermore, there are almost no empirical data specifically evaluating annual flowering plant species for pollinators. Annual plant species are relevant—and sometimes the only—options for certain applications. These include agricultural landscapes where crops are rotated and perennial flowers are not well suited, in annual landscape beds, and in raised beds and container gardens in urban environments.

Moving forward, pollinator conservation would benefit from better bridging the gap between practice and research by using the breadth and depth of anecdotal knowledge about pollinator foraging trends to inform the development of new research efforts to evaluate plants using rigorous and replicated methods.

Basic strategies for evaluating and selecting plants for pollinators

Based on all available empirical data, we offer the following simple generalizations pertaining to plant selection for pollinator habitat:

1. Plants vary significantly in their value to different taxonomic and/or functional groups of pollinators; thus, plant a diversity of flowering plant species in varying colors and flower forms to support a diversity of pollinators.

2. Conversely, planting palettes can be designed to create foraging refuges for the conservation of particular pollinator species, e.g. butterflies or long-tongued bumble bees.
3. Bias plant selections towards native or near-native species, but keep in mind that many non-native plants, including annuals, may be valuable (Fig. 4.1).
4. In landscape gardens, non-native plants may be incorporated to meet the aesthetic goals of the application and to fill in gaps in the floral continuity.
5. Cultivated and hybridized varieties of native plants should be evaluated on a case-by-case basis. Typically, the higher the degree of horticultural modifications, the less likely it is to be as valuable to pollinators as the unmodified native species. Avoid double-flowered varieties.

Other considerations in the evaluation of plants for pollinators

It is important to recognize that both the values and the drawbacks of each plant selection go beyond their direct relationship to pollinators. Other aspects of the plant's relationship to the site and the surrounding ecosystems need to be considered. In Table 2, we outline the most significant benefits and challenges of using native, non-native, near-native, and native cultivar plants in a pollinator habitat restoration or pollinator garden. We consider topics such as availability, genetic preservation, and aesthetic diversity, which may not directly affect pollinators but influence the perceived and ecological success of a project. There are always exceptions, so this table should be used only as a general framework for evaluating plant choices. Ultimately, the suitability of a particular plant should be evaluated on a species-by-species basis with knowledge of the site conditions and the goals of the project.

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Table 4.1. Summary of published peer-reviewed literature evaluating the value of native, near-native, non-native and native cultivar plant species for pollinators

		Reference	Total No. of Species Studied	Region	Limitations	Key Findings
Native vs. Non-native	Natural Areas	Memmott & Waser 2002	456 plant species	US - IL	Analyzed historic data published in 1929. Lacked data on flower and pollinator abundance and interaction frequencies	Non-native flowering plants were visited by significantly fewer pollinators than native plants
	Agricultural Applications	Morandin & Kremin 2013	15 native and non-native flowering plants	US - CA	Relatively low diversity of plant species in agricultural hedgerows	Wild bees, and in some cases honey bees, prefer to forage on native plants over co-occurring weedy, non-native plant species in agricultural hedgerows. A diversity of plants is needed to enhance native bee diversity.
Ranking All Native	Agricultural Applications	Tuell et al. 2008	43 native perennials	US - MI	1 site, 1 year, and low bee diversity	Identified the most attractive early-, mid-, and late-blooming native perennials for wild bees, bumble bees, and honey bees in agroecosystems
Native vs. Non-native & Variants	Agricultural Applications	Corbet et al. 2001	5 native, 3 exotic, 1 naturalized; double variants of 4 species	UK	Small sample of species; may not be representative of all species	All native species nectar rich and accessible to pollinators. Non-natives, especially double variants, had fewer pollinator visits and decreased access to floral rewards
Native vs. Near-native vs. Non-native	Garden/Landscape Applications	Salisbury et al. 2015	24 species comprising native, near-native, and exotic treatments plots	UK	Results not species specific	Greater abundance of total pollinators recorded on native and near-native treatments plots compared to exotic plots
		Hanley et al. 2014	119 garden plants along residential transect, 36 of which were visited by bumble bees	UK	Recorded bumble bees only, minimal replication	Native and near-native garden plants received more bumble bee visits than non-native plants, but only if native “weed species” were included in the analysis

Non-native & Variants	Garden/Landscape Applications	Comba et al. 1999(a)	6 garden annuals and 2-4 modified cultivars of each	UK	Small sample of annuals and may not be representative of all annuals	Less-modified cultivars of garden annuals received more pollinator visits and yielded more abundant and more accessible rewards.
Native Species vs. Native Cultivars		White & Perry 2016 a	11 native species and 11 native cultivars	US - VT	Evaluated only one cultivar for each native species. In the instances of hybrid cultivars, only one parent was evaluated	Native perennial species and less-modified cultivars of native species received more pollinator visits than more modified cultivars (e.g. multiple selections from breeding programs and hybrids). Foraging preferences vary between pollinators groups.
		White & Perry 2016 b	4 <i>Echinacea</i> including 1 species, 1 open-flowered selection, 1 double-flowered selection, and 1 hybrid	US - VT	Small sample of dozens of <i>Echinacea</i> cultivars commercially available	The unmodified species and less-modified varieties of <i>Echinacea purpurea</i> were more attractive to bee pollinators. A double-flowered variety and interspecific hybrid were the least attractive. Foraging preferences vary between pollinators groups.
All Native		Comba et al. 1999(b)	24 native or naturalized species	UK	One study site at a botanic garden (high alternative availability) in an urban area (low pollinator population)	Most native and naturalized flowers are nectar rich but floral attributes and patterns of nectar production limit usage to some pollinator groups.
Non-native & cultivars		Garbuzov et al. 2014	32 garden plant varieties, mostly non-native cultivars	UK	Focus on <i>Lavandula</i> cultivars. Made no comparison between native and non-native groups.	Garden flowers vary enormously (about 100 fold) in their attractiveness to pollinators. Foraging preferences vary between pollinators groups. Hybrid lavenders more attractive than either parent. Doubled-flowered varieties less attractive.

Table 4.2. Summary of the general benefits and challenges to planting native, non-native, near-native, and native cultivar plants in a pollinator habitat restoration or garden.

Native Plant Species		Non-Native Plant Species	
a plant species that has evolved over thousands of years in a defined region, ecosystem and/or habitat		an introduced, alien, exotic, or non-indigenous plant species that is planted outside its native distributional range	
Benefits	Challenges	Benefits	Challenges
<ul style="list-style-type: none"> - Often the preferred foraging resources for pollinators, bees in particular - Preferred host plants for native insects and birds - Adapted to local soil & climate conditions - Maintain genetic diversity and resiliency in plant population - Promote conservation and stewardship of natural plant populations 	<ul style="list-style-type: none"> -Less uniform and predictable in size/shape than many cultivated perennial plants -Aesthetic perception that native plants are too “wild” and “weedy” -Less diversity in colors and textures for design than cultivated perennials -May be difficult to find local plant sources for native species 	<ul style="list-style-type: none"> - Cultivated varieties are more uniform and predictable in size/shape - More design options in terms of colors, textures, and plant heights -Widely available in local garden centers -Can fill in gaps in bloom times -Annuals can fill crop areas or landscape beds that are in a seasonal rotation and not well suited for perennial species 	<ul style="list-style-type: none"> -Sometimes have less value to foraging pollinators compared to native species -Higher risk of aggressiveness/invasiveness in the landscape -Less adapted to local soils & climate -May conflict with the conservation and stewardship of natural plant populations
Near-Native Plant Species		Native Cultivar	
a species that is not native to the immediate region but is native to a broader region (e.g. not native to VT but native to the northeastern U.S.)		a cultivated variety of a native species that has been selected, cross-bred or hybridized for ornamental traits, a.k.a. “nativar”	
Benefits	Challenges	Benefits	Challenges
<ul style="list-style-type: none"> -Intermediate compromise between many of the benefits/challenges of native versus non-natives - Expands planting options beyond strictly native species but without using exotics -The native distributional range of near-native plant species may more closely align with the distributional range of native pollinators 	<ul style="list-style-type: none"> -Less uniform and predictable in size/shape than many cultivated perennial plants -Aesthetic perception that native plants are too “wild” and “weedy” -Less diversity in colors and textures for design than cultivated perennials -May be difficult to find local plant sources for native species 	<ul style="list-style-type: none"> - Offer aesthetically improved versions of native species for garden landscapes -Have unique aesthetic traits (e.g. new flower or foliage color) -May be selected for more flowers and longer bloom times -Easier to propagate than wild genotype native species; thus, they are more widely available commercially 	<ul style="list-style-type: none"> -May have less value to pollinators compared to native species -May have reduced fertility, be sterile, or may not come true to type from seed -Loss of genetic diversity found in native plant populations -Risk of genetically polluting wild native plant populations -May be less hardy and resilient to environmental fluctuations

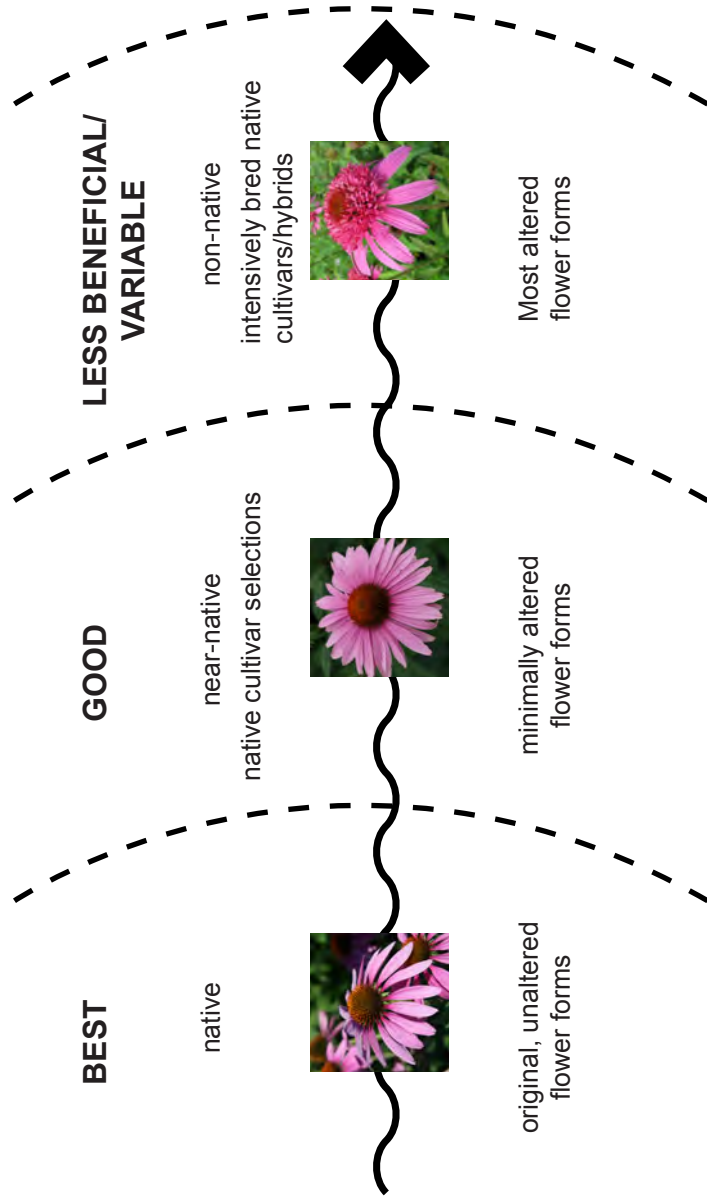


Figure 4.1. Key for evaluating plants for pollinator habitat restoration. The best plants for pollinators are original, unaltered flower forms typically found in native species. Near-native flowering plants or those that have been minimally altered are typically equally or nearly as attractive. Flowers that have been highly altered from their original forms are more likely to have a mismatch between the quantity/quality and accessibility of floral rewards and the foraging requirements of local pollinators.

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APPENDIX A.1 - INDIVIDUAL PLANT DESCRIPTIONS

Achillea millefolium

Achillea millefolium, also known as common yarrow, is a spreading, mat-forming perennial herb in the Asteracea (sunflower) family. Plants produce one to several stems from a fibrous, rhizomatous, root system. Inflorescences have a flattened dome-shaped corymbiform with approximately 10-20 ray flowers. The long-lasting flowers are white to yellowish white. The plant typically flowers from early to mid summer. This species is widely distributed throughout the United States and is considered both native and introduced by the USDA Plant Database. The plant grows best in lean, well-drained soil with dry to medium moisture and in full sun. *A. millefolium* is frequently found in mildly disturbed soil of roadsides, grasslands, and forest openings. The plant may become weedy or aggressive in some habitats. The native species is not commonly sold in the landscape industry; however, cultivars and hybrids are popular. Cultivars come in a variety of colors and tend to have larger flowers and stronger stems that support more upright habitats.

Achillea millefolium 'Strawberry Seduction'

Cultivar type: Breeding program/repeated selections

Propagation: Vegetative

The cultivar 'Strawberry Seduction' was patented in 2008 (US PP18401 P3) by Michiel Zwaan in The Netherlands. It was derived from a breeding program that focused on obtaining *Achillea* cultivars with long bloom durations and flower colors resistant to fading. 'Strawberry Seduction' is characterized by its long blooming habit; vigorous

growth habit; dense, dark-green foliage held on sturdy stems; and red flowers that are consistent in color and resistant to fading. The flowers have no fragrance. ‘Strawberry Seduction’ was selected as a whole plant mutation that arose from repeated selections from seed originally sown of the strain *Achillea* ‘Summer Pastels’ (not patented) in Boskoop, The Netherlands. Propagation is achieved through basal stem cuttings.

Agastache foeniculum

Agastache foeniculum, commonly known as anise hyssop, is a clump-forming upright perennial in the Lamiaceae (mint) family. In mid summer, lavender to purple flowers appear in many-flowered false whorls, which are densely packed on terminal flower spikes. The small individual flowers are two-lipped. The flowers have no fragrance, but the plant’s foliage is distinctly anise scented. Typically found in prairies, dry upland forests, and fields, the plant prefers well-drained, average, dry to medium moisture soils in full sun to part shade. Plants spread by rhizomes and readily self-seed in good conditions. The native range of *A. foeniculum* includes much of the northern United States and southern Canada.

***Agastache foeniculum* 'Golden Jubilee'**

Cultivar type: Breeding program selection, possible hybrid

Propagation: Seed cultivar

The cultivar ‘Golden Jubilee’ was released by Sahin Seed Co. of The Netherlands. It is a 2002 Fleuroselect award-winning perennial and a 2003 All-America Selection. It forms a dense 2-ft-tall clump of chartreuse-colored and anise-scented foliage. This cultivar

flowers similarly to the species. 'Golden Jubilee' requires especially good winter drainage. The exact parentage of this cultivar is not clear. It is marketed interchangeably as *A. foeniculum* 'Golden Jubilee,' *A. rugosa* 'Golden Jubilee,' and *Agastache* x 'Golden Jubilee.' Numerous cultivars of *Agastache* are available in the nursery industry, most of which are hybrids of American native *Agastache foeniculum* and Asian native *Agastache rugosa*.

Asclepias tuberosa

Asclepias tuberosa is a milkweed in the Asclepiadaceae family. Commonly called butterfly weed, the erect hairy stems are branched near the top and feature cymes of small and showy flowers. The flowers are typically a vibrant orange color but can vary in color from more red to more yellow. Following a long mid- to late-summer bloom, the plant develops prominent seed follicles, typical of milkweeds. The plant prefers sandy, moderately fertile, slightly acidic, and well-drained soils in full sun. The native range of *A. tuberosa* includes most of the United States, excluding the Northwest. The plant grows naturally in open prairies, meadows, and woodland edges. Popular cultivars include 'Gay Butterflies' and 'Hello Yellow.'

Asclepias tuberosa ‘Hello Yellow’

Cultivar type: Selection

Propagation: Seed cultivar

This well-established and widely used cultivar is a bright-yellow selection from the orange-colored native species. Plant height, floral abundance, and bloom period are identical to the species.

Baptisia australis

Family: Fabaceae

This slow-to-mature and clump-forming perennial in the Fabaceae family features upright terminal racemes with indigo-blue, pea-like, bisexual flowers. Commonly known as wild blue indigo or wild blue redneck lupine, the tall blue spikes of *Baptisia australis* bloom for about four weeks in late spring and are followed by inflated seedpods. *B. australis* is best-adapted to average, dry to medium, well-drained soil in full sun to part shade. It grows naturally in open woods, on riverbanks, and on sandy floodplains but is also well adapted to landscape uses. The plant’s native range includes most of the eastern half of the United States, stretching from Vermont southward to Georgia. Most cultivars of *B. australis* are hybrids with *B. sphaerocarpa* or *B. alba*.

***Baptisia x varicolor* ‘Twilite’**

Cultivar type: Breeding program/hybrid

Propagation: Vegetative

Baptisia x varicolor ‘Twilite’ Prairieblues is a patented (US PP19011 P2) bicolor *Baptisia*, selected from a controlled cross of *B. australis* and *B. sphaerocarpa*. The breeding was conducted by Dr. Jim Ault at the Chicago Botanic Garden in Glencoe, Illinois. This was the first cultivar introduced from the program. ‘Twilite’ is robust and vigorous, and once fully established, it offers taller spikes and more flowers than its parents. The flowers are uniquely maroon colored with yellow keels.

Echinacea purpurea

Echinacea purpurea, commonly known as purple coneflower, is an herbaceous perennial in the Asteraceae family with numerous erect stalks bearing showy daisy-like flowers in mid to late summer. The inflorescences are composite with a spiny orange center surrounded by showy, drooping ray petals. Typically, *E. purpurea* plants are 2-4 ft tall and the flowers are purplish pink in color. *E. purpurea* is considered a highly adaptable plant that is tolerant of drought, heat, humidity, and poor soil, but it is happiest grown in average, dry to medium, well-drained soils. Plants perform best in full sun, but will tolerate filtered shade with fewer flowers. *E. purpurea* is native to moist prairies, meadows and open woods of the central to eastern United States. There are numerous cultivars of *E. purpurea* available in a range of colors and heights. New cultivars of *E. purpurea* are introduced every year. Cultivars include both naturally occurring selections, repeated selections from breeding programs, and hybrids.

***Echinacea* 'Sunrise Big Sky'**

Cultivar type: Hybrid

Propagation: Tissue culture

Plantsman Richard Saul of Georgia introduced 'Sunrise Big Sky' in 2005. It is a patented (US PP16235 P2) cross of *Echinacea purpurea* and *Echinacea paradoxa*. 'Sunrise Big Sky' is one of the first yellow-flowered *Echinacea* hybrids. Plants form a 2-tall by 2-ft - wide clump with buttery-yellow flowers that age to creamy white. This cultivar is recognized as being a very sturdy *Echinacea* and a good re-bloomer.

***Echinacea purpurea* 'Pink Double Delight'**

Cultivar type: Breeding program selection

Propagation: Tissue culture

'Pink Double Delight' is a hybrid selection introduced by Plants Nouveau and bred by Arie Blom of AB Cultivars in The Netherlands. Patented (PP18803) in 2006, 'Pink Double Delight' has flowers that are similar to patented cultivar 'Razzmatazz' (from Witteman & Co.), but has a shorter, more compact habit. Stems are strong and well branched. An abundance of 3-in diameter, bright-pink, double flowers are produced in mid through late summer on strong and well-branched stems. The flowers are long lasting, fading to a lavender pink as they age.

***Echinacea purpurea* 'White Swan'**

Cultivar type: Selection

Propagation: Seed cultivar

'White Swan' is an old and popular white-flowered form of *E. purpurea*. Like most *Echinacea* cultivars, 'White Swan' is not as cold hardy or vigorous as the species, but it remains one of the sturdier and more reliable *Echinacea* cultivars, particularly in colder climates. Plants form medium to tall clumps and bloom midsummer with 3-in diameter white flowers with slightly drooping petals.

Helenium autumnale

Commonly known as sneezeweed or Helen's flower, *Helenium autumnale* is an erect, clump-forming, native perennial in the Asteracea family. The plant typically grows 3 to 5 ft tall and has winged stems that branch near the top. Clusters of 2-in-diameter, daisy-like, composite flowers bloom from late summer to autumn. The bright-yellow rays are distinctively wedge shaped and surround a dull yellow center disk. *H. autumnale* grows easily in moderately fertile, medium to wet soils in full sun. Its native range includes most of the continental United States where it grows naturally in moist soils along streams, ponds, and ditches.

***Helenium autumnale* 'Moerheim Beauty'**

Cultivar type: Hybrid

Propagation: Vegetative

'Moerheim Beauty' is a reddish bronze hybrid of *H. autumnale* and *H. bigelovii*. Created by Dutch Plant Breeder Bonne Ruys at Moerheim Nursery in The Netherlands, it received an Award of Garden Merit from the Royal Horticultural Society in 2001. The erect, clump-forming perennial is shorter statured than the species, typically growing 2 to 3 ft tall. 'Moerheim Beauty' blooms mid-summer, about a month earlier than the species, but it will reflower later in the season if meticulously deadheaded. The flowers feature coppery-red rays and dark center disks. Ray flowers gradually fade to burnt orange. Like the species, 'Moerheim Beauty' grows best in medium to wet, well-drained soil in full sun, but it prefers richer soils than the species and is less tolerant of dry soils.

Monarda fistulosa

Family: Lamiaceae

Commonly known as wild bergamot or bee balm, *Monarda fistulosa* is a clump-forming native perennial in the Lamiaceae family with distinctively aromatic foliage. Atop 3 to 4-ft-tall square stems, lavender-colored, two-lipped, tubular flowers blossom in solitary terminal heads. The flowers have a long bloom period in mid summer. *M. fistulosa* prefers rich, dry to moist soils and full sun to part sun. Its native range includes most of the United States, but it is most prevalent in prairie and savanna ecosystems in the Midwest.

***Monarda fistulosa* 'Claire Grace'**

Cultivar type: Selection

Propagation: Vegetative

‘Claire Grace’ is a selection of *M. Fistulosa* that is more tolerant of drought and powdery mildew than the species. Barbara and Michael Bridges discovered ‘Claire Grace’ at their nursery in southern Mississippi and named it after their daughter. The flowers are slightly darker and pinker than the species. Plant height, bloom time, and bloom duration are similar to the species, but ‘Claire Grace’ is less hardy in northern climates.

Penstemon digitalis

Family: Scrophulariaceae

Penstemon digitalis, commonly known as beardtongue or smooth white Penstemon, is a clump-forming, native perennial in the Scrophulariaceae family. The common name beardtongue comes from the tuft of small hairs on the flower’s staminoid. Atop erect, 3-ft-tall, rigid stems, *P. digitalis* features white, two-lipped, and tubular flowers in panicles. Flowers bloom mid spring to early summer. It prefers medium to medium-dry soils in full sun to part shade. The native range of *P. digitalis* includes most of the eastern half of the United States. It is found naturally in prairies, fields, woodland edges, and open woods.

***Penstemon digitalis* ‘Husker Red’**

Cultivar type: Selection

Propagation Type: Vegetative

‘Husker Red’ is a red-foliaged form of *P. digitalis* selected and introduced in 1983 by Dr. Dale Lindgren of The University of Nebraska. It was selected for its deep bronze-red foliage and upright form. The Perennial Plant Association named ‘Husker Red’ the 1996 Perennial Plant of the Year. Flowers are similar in shape and size to the species but

sometimes exhibit a pink blush in the otherwise white blooms. The plants bloom mid-spring to early summer, similar to the species, and are slightly more compact at 2-3 ft tall. 'Husker Red' grows best in full sun and well-drained soil.

Symphotrichum novae-angliae

Symphotrichum novae-angliae, commonly called New England aster, is a native perennial in the Asteraceae family. From late summer through the fall, *S. novae-angliae* plants feature profuse blooms of composite flowers with purple rays and yellow center disks. The plants typically grow 3 to 6 ft tall, with stiff, hairy stems maintaining a robust, upright habit. The plants prefer moist and rich soils in full sun, but they also grow in moderately fertile, medium to well-drained soil. The native range of *S. novae-angliae* includes most of the central and eastern United States. It grows naturally in moist meadows, thickets, and on stream banks.

***Symphotrichum novae-angliae* 'Alma Pötschke'**

Cultivar type: Unknown/possible hybrid

Propagation: vegetative

'Andenken an Alma Pötschke' or simply 'Alma Pötschke,' is an American native cultivar of *S. novae-angliae*, bred by German Plantsman Werner Pötschke. It was named in memory of his grandmother, Alma Pötschke. 'Andenken an' translates as 'in memory of.' The parentage of 'Alma Pötschke' is not documented, but it is believed to be a hybrid cultivar. This cultivar has a more compact form than the species and the flowers have rose-pink rays and yellow center disks.

Rudbeckia fulgida* var. *fulgida

Family: Asteraceae

Rudbeckia fulgida, commonly known as black-eyed Susan or orange coneflower, is an upright, rhizomatous, clump-forming native perennial in the Asteraceae family. The 3-ft-tall plants feature daisy-like composite flowers with yellow rays and brownish-purple center disks. They have a long bloom period from mid-summer to early fall. *R. fulgida* prefers dry to medium, well-drained soil with average fertility in full sun but will tolerate light shade. The native range of *R. fulgida* includes most of the eastern United States, excluding northern New England. It occurs naturally in both dry and moist soils in open woods, meadows, and thickets. The species is infrequently sold by nurseries because of the popularity of improved cultivars like ‘Goldsturm.’

***Rudbeckia fulgida* ‘Goldsturm’**

Cultivar type: Selection

Propagation: Seed cultivar

‘Goldsturm’ is a selection of the American native *Rudbeckia fulgida* var. *sullivantii* discovered by *Heinrich Hagemann* at *Gebrueder Schuetz’s* nursery in the *Czech Republic*. Hagemann’s employer, *Karl Foerster* of *Potsdam Germany*, introduced the selection in 1949. Since its introduction ‘Goldsturm’ has remained one of the most popular landscape perennials. The Perennial Plant Association selected ‘Goldsturm’ as the 1999 Perennial Plant of the Year. ‘Goldsturm’ is slightly more compact and coarse than the species.

Tradescantia ohiensis

Family: Commelinaceae

Commonly known as spiderwort, *Tradescantia ohiensis* is a multi-stemmed grass-like perennial in the Commelinaceae family. Its upright arching habit forms dense clumps that reach 2- 3 ft tall. The plant features attractive bluish-grey foliage, and in early summer, clusters of violet-blue flowers with three petals. Each flower blooms for only one day, is bisexual, and produces no nectar. Bee pollinators still visit the flowers to collect the abundant pollen. Unlike others in the genus, *T. ohiensis* tolerates hot sunny locations. It grows best in full sun to filtered shade and in moist to dry, well-drained soils. *T. ohiensis* is found naturally in meadows, prairies, wood margins, and roadsides in the eastern United States.

Tradescantia 'Red Grape'

Cultivar type: Hybrid

Propagation: Vegetative

This native cultivar hybrid is similar to the species with narrow grassy foliage and triangular flowers. It forms a more compact mound than the species and feature magenta-colored flowers. It also has a longer bloom duration than the species, starting in early summer, and continuing throughout the season, especially if old blooms are removed. Like most commercially available garden spiderworts, 'Red Grape' is of complex hybrid origin, derived from multiple crosses between *T. virginiana*, *T. ohiensis*, and *T. subaspera*. All of these spiderwort species are native to the eastern United States and can

be found naturally in overlapping regions. Their hybrids closely resemble each other in form but offer a variety of flower colors, plant sizes, and foliage colors. Garden selections of these hybrids are often mislabeled as *T. x andersoniana*, but are better described as Andersoniana Group.

Veronicastrum virginicum

Family: Plantaginaceae

Culver's root is a large, erect, native perennial in the Plantaginaceae family, reaching up to 7 ft tall when in full bloom. In early to mid summer, long and slender spikes (racemes) of tiny, tubular, densely packed white flowers bloom atop strong, upright stems. *V. virginicum* prefers moist, well-drained soils in full to partial sun but will tolerate a variety of soil conditions. Plants can be found growing naturally in meadows, thickets, and prairies in much of the eastern half of the United States.

***Veronicastrum virginicum* ‘Lavendelturm’**

Cultivar type: Selection

Propagation: Vegetative

Introduced by German Nurseryman and Breeder Ernst Pagel, ‘Lavendelturm’ (sometimes marketed as ‘Lavender Towers’) is an early and long-blooming selection with pale purple flowers.

APPENDIX B.1 - RESEARCH PHOTOGRAPHS



Transplanting of plugs into larger pots, spring 2012.



Field planting at Site A, Sept. 2012.



Landscape Plugs from North Creek Nurseries, Inc., spring 2012.



Growing out plants at Site B, summer 2012.



Site A at River Berry Farm, Fairfax, Vermont, summer 2014.



Looking southwest from field border, across research Site A and agricultural fields at River Berry Farm.



Looking east from the middle of Site A.



View looking west across Site A.



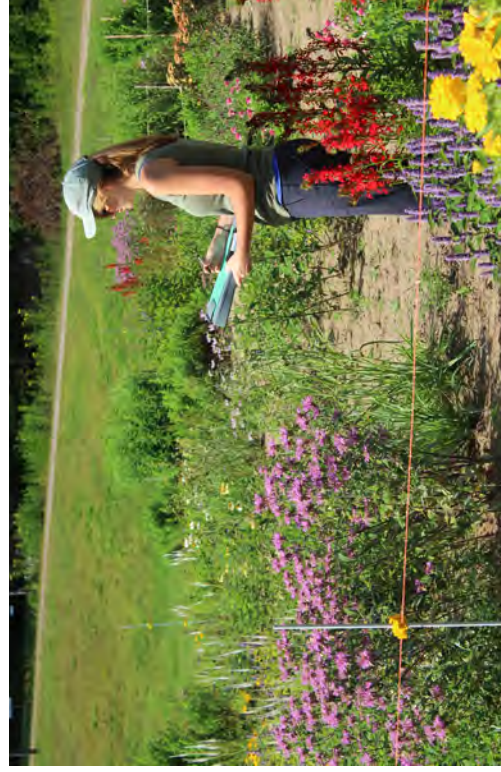
Site B, Maidstone Plant Farm, Maidstone, Vermont, summer 2013.



Informative research signs, Site B, summer 2013.



Site B, summer 2014.



Conducting field observations on pollinator visitation, summer 2014.



Laying out educational pollinator garden at Full Circle Gardens, Essex, Vermont, summer 2012. Educational outreach was part of the SARE grant.



Pollinator-friendly display garden at Maidstone Plant Farm, summer 2013.



Renovating an existing garden at Maidstone Plant Farm (adjacent to Site B) to become an educational pollinator garden, summer 2012.



Pollinator-friendly display garden at Maidstone Plant Farm, summer 2013.

APPENDIX B.2

Table of mean floral abundance for Site A and Site B in 2013 and 2014. Means were compared with a two-sample t-test with independent samples. ACH MIL = *Achillea millefolium*, ACH STR = *A. millefolium* 'Strawberry Seduction,' AGA FOE = *Agastache foeniculum*, AGA GOL = *A. foeniculum* 'Golden Jubilee,' ASC TUB = *Asclepias tuberosa*, ASC HEL = *A. tuberosa* 'Hello Yellow,' BAP AUS = *Baptisia australis*, BAP TWI = *Baptisia* 'Twilite,' HEL AUT = *Helenium autumnale*, HEL MOE = *Helenium* 'Moerheim Beauty,' MON FIS = *Monarda fistulosa*, MON CLA = *M. fistulosa* 'Claire Grace,' PEN DIG = *Penstemon digitalis*, PEN HUS = *P. digitalis* 'Husker Red,' RUD FUL = *Rudbeckia fulgida*, RUD GOL = *R. fulgida* 'Goldsturm,' SYM NOV = *Symphytotrichum novae-angliae*, SYM ALM = *S. novae-angliae* 'Alma Potschke,' TRA OHI = *Tradescantia ohiensis*, TRA RED = *Tradescantia* 'Red Grape,' VER VIR = *Veronicastrum virginicum*, VER LAV = *V. virginicum* 'Lavendelturm'

Botanical Name	Site B Mean FA 2013	Site A Mean FA 2013	Site B Mean FA 2014	Site A Mean FA 2014	Overall Mean FA	t-value	df	p-value
ACH MIL	20.4	19.25	15.62	14.88	15.24	7.52	135	< 0.001
ACH STR	8.77	9.13	10.82	10.41	10.59			
AGA FOE	n/a	63.75	n/a	87.96	75.31	-2.95	75	0.004
AGA GOL	n/a	58.31	n/a	61.87	60.21			
ASC TUB	10.38	n/a	13	n/a	11.76	0.47	67	0.64
ASC HEL	9.33	n/a	13.41	n/a	11.31			
BAP AUS	n/a	n/a	8.89	7.21	8.05	-6.37	74	< 0.001
BAP TWI	n/a	n/a	13.00	12.05	12.53			
HEL AUT	269.27	267.09	385.64	348.82	367.23	29.39	174	< 0.001
HEL MOE	30.59	24.05	36.36	25.64	31.00			
MON FIS	86.71	105.32	107.05	113.55	110.22	0.06	153	0.952
MON CLA	80.10	95.95	107.63	121.14	114.73			
PEN DIG	9.12	10.71	11.53	13.56	12.52	5.96	149	< 0.001
PEN HUS	6.24	6.65	9.50	10.05	9.77			
RUD FUL	16.82	15.59	26.68	23.77	25.23	-3.63	174	< 0.001
RUD GOL	20.05	21.55	30.50	28.73	29.61			
SYM NOV	295.50	287.16	332.23	363.55	347.89	29.03	171	< 0.001
SYM ALM	104.91	111.55	168.36	161.14	164.75			
TRA OHI	29.90	28.00	36.50	39.86	38.18	14.17	171	< 0.001
TRA RED	13.23	12.91	14.91	13.24	14.09			
VER VIR	5.59	5.45	13.41	14.29	13.84	-1.00	170	0.319
VER LAV	6.24	5.86	14.90	14.86	14.88			

APPENDIX B.3

Winter survival results for plants in research areas at Site A and Site B. ACH MIL = *Achillea millefolium*, ACH STR = *A. millefolium* 'Strawberry Seduction,' AGA FOE = *Agastache foeniculum*, AGA GOL = *A. foeniculum* 'Golden Jubilee,' ASC TUB = *Asclepias tuberosa*, ASC HEL = *A. tuberosa* 'Hello Yellow,' BAP AUS = *Baptisia australis*, BAP TWI = *Baptisia* 'Twilite,' HEL AUT = *Helenium autumnale*, HEL MOE = *Helenium* 'Moerheim Beauty,' MON FIS = *Monarda fistulosa*, MON CLA = *M. fistulosa* 'Claire Grace,' PEN DIG = *Penstemon digitalis*, PEN HUS = *P. digitalis* 'Husker Red,' RUD FUL = *Rudbeckia fulgida*, RUD GOL = *R. fulgida* 'Goldsturm,' SYM NOV = *Symphotrichum novae-angliae*, SYM ALM = *S. novae-angliae* 'Alma Potschke,' TRA OHI = *Tradescantia ohiensis*, TRA RED = *Tradescantia* 'Red Grape,' VER VIR = *Veronicastrum virginicum*, VER LAV = *V. virginicum* 'Lavendelturm'

Plant	Site A Winter Survival 2012- 2013 (of 18)	Site B Winter Survival 2012- 2013 (of 18)	Site A Winter Survival 2013- 2014 (of 18)	Site B Winter Survival 2013- 2014 (of 18)	Total Percent Survival	z- value	df	p- value
ACH MIL	18	18	18	18	100	0.00	142	1.000
ACH STR	18	18	18	18	100			
AGA FOE	4	5	14	1	14	-3.34	142	0.001
AGA GOL	17	9	18	0	61.3			
ASC TUB	7	9	n/a	3	35	-3.14	70	0.002
ASC HEL	n/a	n/a	n/a	14	78			
BAP AUS	12	16	18	18	89	-0.27	142	0.785
BAP TWI	12	18	18	17	90.5			
HEL AUT	15	18	16	18	93	3.13	142	0.002
HEL MOE	3	16	17	17	74			
MON FIS	18	18	18	18	100	3.62	142	0.000
MON CLA	15	18	17	10	84			
PEN DIG	18	18	18	18	100	1.00	142	0.316
PEN HUS	18	18	18	17	99			
RUD FUL	1	16	n/a	5	41	-1.54	106	0.123
RUD GOL	3	15	n/a	12	55			
SYM NOV	18	18	18	18	100	2.03	142	0.043
SYM ALM	14	18	18	18	94.5			
TRA OHI	18	17	18	14	93	6.43	142	0.000
TRA RED	3	14	8	6	43			
VER VIR	17	18	18	18	99	4.78	142	0.000
VER LAV	12	14	18	18	86			

APPENDIX B.4 –INTERACTIONS INCLUDED IN MODELS NB = negative binomial distribution, P = Poisson distribution * model will not converge

ALL POLLINATORS									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH	NB	x	x	x	x	x	x	x	
AGA	P		x						x
ASC	P		x	x	x			x	
BAP	P	x	x	x	x	x	x	x	
HEL	P	x	x	x	x	x	x	x	
MON	P	x	x	x	x	x	x	x	
PEN	P	x	x	x	x	x	x	x	
RUD	P		x	x	x			x	
SYM	P	x	x	x	x	x	x	x	
TRA	P	x	x	x	x	x	x	x	
VER	NB	x	x	x	x	x	x	x	

ALL BEES									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH	P	x	x	x	x	x	x		
AGA	P		x		x				x
ASC	P		x	x	x			x	
BAP	P	x	x	x	x	x	x	x	
HEL	P	x	x	x	x	x	x	x	
MON	P	x	x	x	x	x	x	x	
PEN	P	x	x	x	x	x	x	x	
RUD	P		x	x	x			x	
SYM	P	x	x	x	x	x	x	x	
TRA	P	x	x	x	x	x	x	x	
VER	NB	x	x	x	x	x	x	x	

ALL NATIVE BEES									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH	P	x	x	x	x	x	x		
AGA	P		x		x				x
ASC	P		x	x	x			x	
BAP	P	x	x	x	x	x	x	x	
HEL	P	x	x	x	x	x	x	x	
MON	P	x	x	x	x	x	x	x	
PEN	P	x	x	x	x	x	x	x	
RUD	P		x	x	x			x	
SYM	P	x	x	x	x	x	x	x	
TRA	P	x	x	x	x	x	x	x	
VER	NB	x	x	x	x	x	x	x	

HONEY BEES									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH									
AGA	NB		x		x				x
ASC									
BAP									
HEL	P		x	x	x			x	
MON*									
PEN	P		x	x	x			x	
RUD									
SYM	P	x	x	x	x	x	x	x	
TRA	P		x	x	x			x	
VER	NB		x	x	x				

BUMBLE BEES									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH*									
AGA	NB		x		x				x
ASC	P		x	x	x				
BAP	NB	x	x	x	x	x	x	x	
HEL	P	x	x	x	x	x	x	x	
MON	P	x	x	x	x	x	x	x	
PEN	P	x	x	x	x	x	x	x	
RUD	P		x	x	x			x	
SYM	P	x	x	x	x	x	x	x	
TRA*									
VER	NB	x	x	x	x	x	x	x	

OTHER NATIVE BEES									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH	NB	x	x	x	x	x	x		
AGA*									
ASC*									
BAP	P	x	x	x	x	x	x	x	
HEL	P	x	x	x	x	x	x	x	
MON*									
PEN	P	x	x	x	x	x	x	x	
RUD	P		x	x	x			x	
SYM	P	x	x	x	x	x	x		
TRA*									
VER*									

BEETLES-BUGS									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH	P	x	x	x	x	x	x		
AGA	NB		x		x				
ASC*									
BAP*									
HEL*									
MON*									
PEN*									
RUD*									
SYM*									
TRA*									
VER*									

WASPS-ANTS									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH*									
AGA*									
ASC*									
BAP*									
HEL*									
MON*									
PEN*									
RUD*									
SYM*									
TRA*									
VER*									

BUTTERFLIES									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH*									
AGA*									
ASC*									
BAP*									
HEL*									
MON*									
PEN*									
RUD*									
SYM	P		x	x	x			x	
TRA*									
VER*									

FLIES									
	Dist.	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year	Type* Week
ACH	NB	x	x	x	x	x	x	x	
AGA*									
ASC	P		x	x	x				
BAP*									
HEL	P	x	x	x	x	x	x	x	
MON*									
PEN*									
RUD	P		x	x	x			x	
SYM*									
TRA	P	x	x	x	x	x	x	x	
VER*									

APPENDIX B.5

SUPPLEMENTAL RESULTS FOR CHAPTER 2

Supplemental results tables include Type III tests of fixed effects from the generalized linear mixed models (GLIMMIX), least squares means for plant types and other significant effects, differences of least squares means, T grouping for significant effects, and simple effect comparisons. Site A = Fairfax, Site B = Maidstone.

Achillea millefolium vs. *Achillea* 'Strawberry Selection'

ACH - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	1	0.39	0.6441
Type	1	44	119.04	<.0001
Site*Type	1	44	3.84	0.0563
year	1	44	19.65	<.0001
week(year)	6	25.84	2.08	0.0908
Site*year	1	44	37.94	<.0001
Type*year	1	44	0.44	0.5119

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.1538	0.1967	5.123	5.87	0.0019	3.1702	0.6235
Species	3.1059	0.1228	1	25.3	0.0251	22.3303	2.7414

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	2.675	0.1692	3.523	15.81	0.0002	14.512	2.4555
2014	1.5848	0.1984	2.938	7.99	0.0044	4.8782	0.9678

Site*year Least Squares Means						
Site	year	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	2013	3.044	0.1843	1.043	16.52	0.0345
Fairfax	2014	1.085	0.2135	1	5.08	0.1237
Maidstone	2013	2.3059	0.2351	3.638	9.81	0.001
Maidstone	2014	2.0846	0.2546	3.767	8.19	0.0016

T Grouping for Site*year Least Squares Means (Alpha=0.05)				
LS-means with the same letter are not significantly different.				
Site	year	Estimate		
Fairfax	2013	3.044		A
Maidstone	2013	2.3059	B	A
Maidstone	2014	2.0846	B	A
Fairfax	2014	1.085	B	

ACH - Other Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	1	0.54	0.5954
Type	1	45	137.5	<.0001
Site*Type	1	45	0.08	0.7853
year	1	45	3.38	0.0724
week(year)	6	45	7.29	<.0001
Site*year	1	45	140.47	<.0001

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-0.9328	0.2837	5.922	-3.29	0.017	0.3934	0.1116
Species	2.1502	0.1267	1	16.97	0.0375	8.5868	1.0883

ACH - Beetles and Bugs

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	44.9	0.36	0.5516
Type	1	44.96	10.91	0.0019
Site*Type	1	44.98	0.31	0.5792
year	1	44.92	0.04	0.8504
week(year)	6	31.97	1.92	0.1074
Site*year	1	43.71	1.61	0.2106

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-3.1643	8.7735	44.95	-0.36	0.72	0.04224	0.3706
Species	-0.7992	8.7452	44.92	-0.09	0.9276	0.4497	3.9324

ACH - Flies

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	44	0.51	0.4807
Type	1	44	0.85	0.3616
Site*Type	1	44	0.89	0.3508
year	1	44	6.22	0.0165
week(year)	6	44	1.59	0.1735
Site*year	1	44	1.07	0.306
Type*year	1	44	1.75	0.1924

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.5199	0.6008	44	2.53	0.0151	4.5719	2.7466
Species	2.1268	0.3972	44	5.35	<.0001	8.3882	3.3317

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	2.7916	0.5419	44	5.15	<.0001	16.3064	8.8361
2014	0.8552	0.5566	44	1.54	0.1316	2.3519	1.309

Differences of Year Least Squares Means						
year	_year	Estimate	Standard Error	DF	t Value	Pr > t
2013	2014	1.9363	0.7764	44	2.49	0.0165

***Agastache foeniculum* vs. *Agastache* 'Golden Jubilee'**

AGA - All Pollinators

One observation at week 6 removed

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	5.385	7.14	0.0411
week	5	16.19	6.55	0.0016
Type*week	5	16.19	0.78	0.5765

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.9972	0.2069	3.462	14.48	0.0003	20.0296	4.1447
Species	3.4363	0.195	2.813	17.62	0.0006	31.0733	6.0596

Week Least Squares Means							
week	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
0	2.42	0.2995	10.96	8.08	<.0001	11.2456	3.3686
1	2.8407	0.2605	7.5	10.91	<.0001	17.1285	4.4618
2	3.6032	0.2186	4.145	16.48	<.0001	36.7146	8.0252
3	3.8455	0.2056	3.301	18.7	0.0002	46.7817	9.6187
4	3.4268	0.225	4.603	15.23	<.0001	30.7788	6.9254
5	3.1645	0.2396	5.728	13.21	<.0001	23.676	5.6724

AGA - All Bees

One observation at week 6 removed

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	7.118	1.21	0.3076
week	5	16.88	5.83	0.0026
Type*week	5	16.88	0.64	0.6698

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.9248	0.2085	3.917	14.03	0.0002	18.6297	3.8834
Species	3.1402	0.206	3.755	15.24	0.0002	23.1074	4.7607

Week Least Squares Means							
week	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
0	2.1592	0.3519	16.68	6.14	<.0001	8.6639	3.0488
1	2.5109	0.309	13.14	8.13	<.0001	12.3159	3.8054
2	3.4128	0.2313	5.621	14.75	<.0001	30.3511	7.0214
3	3.7556	0.2104	3.978	17.85	<.0001	42.759	8.9985
4	3.3615	0.234	5.855	14.36	<.0001	28.8319	6.748
5	2.9948	0.2603	8.319	11.5	<.0001	19.9808	5.2016

AGA - All Native Bees
One observation at week 6 removed

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	10.12	0	0.98
week	5	16.28	8.02	0.0006
Type*week	5	16.28	0.17	0.9713

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.5878	0.1997	2.934	12.96	0.0011	13.3004	2.6563
Species	2.5915	0.2002	2.956	12.94	0.0011	13.3502	2.6727

Week Least Squares Means							
week	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
0	1.7652	0.3246	14.17	5.44	<.0001	5.8429	1.8968
1	2.0739	0.2922	10.89	7.1	<.0001	7.9555	2.3246
2	2.948	0.23	4.979	12.82	<.0001	19.0675	4.3849
3	3.2867	0.2145	3.84	15.32	0.0001	26.7556	5.7388
4	2.882	0.233	5.22	12.37	<.0001	17.8502	4.1586
5	2.5821	0.2509	6.781	10.29	<.0001	13.2253	3.3189

AGA - Honeybees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	12.02	8.96	0.0112
week	6	17.37	4.55	0.006
Type*week	5	16.12	3.51	0.0246

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.6013	0.2627	1	6.1	0.1035	4.9596	1.3028
Species	2.2009	0.2573	1	8.55	0.0741	9.033	2.3245

Week Least Squares Means							
week	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
0	1.0179	0.3575	2.912	2.85	0.0676	2.7673	0.9892
1	1.419	0.3367	2.31	4.21	0.0402	4.1328	1.3917
2	2.3938	0.3025	1.514	7.91	0.0327	10.9548	3.3136
3	2.6192	0.2966	1.401	8.83	0.0338	13.7241	4.0702
4	2.1744	0.3114	1.699	6.98	0.0301	8.797	2.7392
5	1.7783	0.3207	1.908	5.54	0.0344	5.9196	1.8985
6	2.2258	0.5824	12.51	3.82	0.0023	9.261	5.3935

AGA Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	11.8	0.6	0.4531
week	6	19.03	9.67	<.0001
Type*week	5	17.99	0.3	0.9084

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.433	0.1884	2.819	12.92	0.0014	11.3928	2.1462
Species	2.5104	0.186	2.697	13.5	0.0015	12.3105	2.2898

Week Least Squares Means							
week	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
0	1.5973	0.2691	12.35	5.94	<.0001	4.9398	1.3291
1	1.902	0.2549	10.32	7.46	<.0001	6.6993	1.7077
2	2.9805	0.2262	6.689	13.18	<.0001	19.6981	4.4561
3	3.2254	0.2225	6.278	14.5	<.0001	25.1626	5.5985
4	2.8143	0.2288	6.986	12.3	<.0001	16.6813	3.8172
5	2.3991	0.2383	8.127	10.07	<.0001	11.0128	2.6247
6	1.9809	0.49	24	4.04	0.0005	7.2495	3.5525

AGA - Beetles and Bugs

Cannot put type*week interaction in model

because of very sparse AGA GOL counts

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	3.704	20.3	0.0128
week	6	3.948	0.6	0.7279

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Cultivar	-1.1127	0.5852	3.819	-1.9	0.1334	0.3287	0.1923
Species	1.5321	0.3344	3.919	4.58	0.0107	4.6278	1.5477

***Asclepias tuberosa* vs. *Asclepias tuberosa* 'Hello Yellow'**

ASC - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	8.74	4.43	0.0655
year	1	8.695	25.12	0.0008
week(year)	1	6.842	8.61	0.0225
Type*year	1	8.74	0.68	0.4303

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.3879	0.1267	8.103	18.85	<.0001	10.8907	1.3799
Species	2.6996	0.1162	6.478	23.24	<.0001	14.8734	1.7279

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2014	2.172	0.147	10.61	14.77	<.0001	8.7761	1.2902
2015	2.9154	0.08932	2.761	32.64	0.0001	18.4571	1.6486

ASC - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	9.36	4.72	0.0568
year	1	9.32	22.3	0.001
week(year)	1	6.998	8.72	0.0213
Type*year	1	9.36	1.33	0.2772

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.3473	0.1333	7.853	17.61	<.0001	10.4571	1.3938
Species	2.6761	0.124	6.374	21.57	<.0001	14.5281	1.8021

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2014	2.1533	0.1561	10.37	13.79	<.0001	8.6132	1.3446
2015	2.8701	0.09403	2.587	30.52	0.0002	17.6384	1.6585

ASC - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	9.36	4.72	0.0568
year	1	9.32	22.3	0.001
week(year)	1	6.998	8.72	0.0213
Type*year	1	9.36	1.33	0.2772

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.3473	0.1333	7.853	17.61	<.0001	10.4571	1.3938
Species	2.6761	0.124	6.374	21.57	<.0001	14.5281	1.8021

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2014	2.1533	0.1561	10.37	13.79	<.0001	8.6132	1.3446
2015	2.8701	0.09403	2.587	30.52	0.0002	17.6384	1.6585

ASC - Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	9.143	5.24	0.0475
year	1	9.106	22.19	0.0011
week(year)	1	6.907	7.98	0.026
Type*year	1	9.143	1.53	0.2471

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Cultivar	2.332	0.128	7.916	18.21	<.0001	10.2987	1.3186
Species	2.6674	0.1188	6.376	22.45	<.0001	14.4019	1.7109

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
2014	2.1538	0.1496	10.4	14.4	<.0001	8.6174	1.2893
2015	2.8456	0.09039	2.637	31.48	0.0002	17.212	1.5558

***Baptisia australis* vs. *Baptisia* 'Twilite' Prairieblues**

BAP - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	26.96	0.28	0.604
Type	1	25.21	42.36	<.0001
Site*Type	1	25.79	7.07	0.0133
year	1	26.25	35.93	<.0001
week(year)	2	20.05	1.31	0.292
Site*year	1	27	0.17	0.6874
Type*year	1	25.73	0.61	0.4412

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.1363	0.1043	24.94	10.9	<.0001	3.1152	0.3248
Species	1.9474	0.07015	26.5	27.76	<.0001	7.0103	0.4918

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2014	1.1666	0.09172	23.88	12.72	<.0001	3.2111	0.2945
2015	1.9171	0.08632	27	22.21	<.0001	6.801	0.5871

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	1.3413	0.1412	26.34	9.5	<.0001
Fairfax	Species	1.8226	0.1139	26.08	16	<.0001
Maidstone	Cultivar	0.9313	0.1645	21.29	5.66	<.0001
Maidstone	Species	2.0722	0.1017	23.25	20.37	<.0001

BAP - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	26.96	0.08	0.7831
Type	1	25.22	36.35	<.0001
Site*Type	1	25.85	5.44	0.0278
year	1	26.22	31.41	<.0001
week(year)	2	20.09	0.97	0.3944
Site*year	1	27	0.06	0.8093
Type*year	1	25.65	0.95	0.3376

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.1203	0.1119	24.94	10.01	<.0001	3.0658	0.3432
Species	1.9281	0.07542	26.5	25.56	<.0001	6.8763	0.5186

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2014	1.147	0.09884	23.88	11.61	<.0001	3.1488	0.3112
2015	1.9014	0.09237	27	20.59	<.0001	6.6951	0.6184

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	1.2986	0.1532	26.39	8.48	<.0001
Fairfax	Species	1.7955	0.1227	26.14	14.63	<.0001
Maidstone	Cultivar	0.942	0.1753	21.31	5.37	<.0001
Maidstone	Species	2.0607	0.1095	23.35	18.83	<.0001

BAP - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	26.96	0.08	0.7831
Type	1	25.22	36.35	<.0001
Site*Type	1	25.85	5.44	0.0278
year	1	26.22	31.41	<.0001
week(year)	2	20.09	0.97	0.3944
Site*year	1	27	0.06	0.8093
Type*year	1	25.65	0.95	0.3376

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.1203	0.1119	24.94	10.01	<.0001	3.0658	0.3432
Species	1.9281	0.07542	26.5	25.56	<.0001	6.8763	0.5186

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2014	1.147	0.09884	23.88	11.61	<.0001	3.1488	0.3112
2015	1.9014	0.09237	27	20.59	<.0001	6.6951	0.6184

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	1.2986	0.1532	26.39	8.48	<.0001
Fairfax	Species	1.7955	0.1227	26.14	14.63	<.0001
Maidstone	Cultivar	0.942	0.1753	21.31	5.37	<.0001
Maidstone	Species	2.0607	0.1095	23.35	18.83	<.0001

BAP - Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	8.199	0.27	0.6177
Type	1	22.53	23.59	<.0001
Site*Type	1	20.8	10.85	0.0035
year	1	22.78	30	<.0001
week(year)	2	12.71	1.81	0.2028
Site*year	1	22.93	0.18	0.6739
Type*year	1	22.5	2.73	0.1125

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
C	1.0608	0.09968	13.6	10.64	<.0001	2.8885	0.2879
S	1.7063	0.09488	12.3	17.98	<.0001	5.5084	0.5227

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2014	1.0165	0.0842	7.943	12.07	<.0001	2.7634	0.2327
2015	1.7506	0.1095	18.31	15.98	<.0001	5.7578	0.6308

BAP - Other Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	24.77	1.96	0.1743
Type	1	23.49	15.78	0.0006
Site*Type	1	21.78	0.25	0.6229
year	1	26.44	0.76	0.3897
week(year)	2	18.85	0.78	0.4733
Site*year	1	26.98	0	0.9519
Type*year	1	26.68	0.89	0.3531

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
C	-1.9201	0.5269	23.89	-3.64	0.0013	0.1466	0.07723
S	0.2575	0.1772	25.19	1.45	0.1586	1.2937	0.2293

***Helenium autumnale* vs. *Helenium* 'Moerheim Beauty'**

HEL - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	33.28	16.25	0.0003
Type	1	34.82	238.01	<.0001
Site*Type	1	32.09	4.79	0.036
year	1	35.78	3.2	0.0819
week(year)	7	31.1	7.86	<.0001
Site*year	1	35.69	7.71	0.0087
Type*year	1	34.87	0	0.9977

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	2.1443	0.1139	35.08	18.83	<.0001	8.5357	0.9718
Maidstone	2.7006	0.1341	35.81	20.15	<.0001	14.8888	1.9959

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.2615	0.1134	31.34	11.12	<.0001	3.5309	0.4005
Species	3.5833	0.141	33.79	25.42	<.0001	35.9927	5.0737

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	1.1335	0.164	26.87	6.91	<.0001
Fairfax	Species	3.155	0.1493	35.03	21.13	<.0001
Maidstone	Cultivar	1.3896	0.1771	34.84	7.84	<.0001
Maidstone	Species	4.0116	0.1509	33.74	26.58	<.0001

T Grouping for Site*Type Least Squares Means (Alpha=0.05) significantly different			
Site	Type	Estimate	
Maidstone	Species	4.0116	A
Fairfax	Species	3.155	B
Maidstone	Cultivar	1.3896	C
Fairfax	Cultivar	1.1335	C

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-2.0215	0.2156	32.13	-9.37	<.0001
Site Maidstone	Cultivar	Species	-2.622	0.1909	35.24	-13.74	<.0001

HEL - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	32.97	14.49	0.0006
Type	1	34.82	212.46	<.0001
Site*Type	1	32.06	3.68	0.064
year	1	35.98	4.92	0.033
week(year)	7	31.27	7.93	<.0001
Site*year	1	35.66	8.5	0.0061
Type*year	1	34.87	0	0.9638

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	1.8843	0.1467	35.3	12.85	<.0001	6.5816	0.9653
Maidstone	2.481	0.1666	35.98	14.9	<.0001	11.9535	1.991

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	0.9257	0.1468	31.6	6.31	<.0001	2.5237	0.3705
Species	3.4396	0.174	34.21	19.76	<.0001	31.1734	5.4256

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	1.8819	0.2418	35.83	7.78	<.0001	6.5657	1.5876
2014	2.4835	0.1237	35.43	20.07	<.0001	11.9825	1.4824

Site*Year Least Squares Means						
Site	year	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	2013	1.7345	0.2533	36	6.85	<.0001
Fairfax	2014	2.034	0.1361	30.91	14.94	<.0001
Maidstone	2013	2.0292	0.2722	35.87	7.45	<.0001
Maidstone	2014	2.9329	0.1613	35.98	18.18	<.0001

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	0.7774	0.2022	28.16	3.85	0.0006
Fairfax	Species	2.9912	0.1816	35.03	16.47	<.0001
Maidstone	Cultivar	1.0741	0.2128	34.35	5.05	<.0001
Maidstone	Species	3.888	0.1833	34.18	21.22	<.0001

T Grouping for Site*Type Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Site	Type	Estimate	
Maidstone	Species	3.888	A
Fairfax	Species	2.9912	B
Maidstone	Cultivar	1.0741	C
Fairfax	Cultivar	0.7774	C

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-2.2138	0.2484	32.32	-8.91	<.0001
Site Maidstone	Cultivar	Species	-2.8139	0.2162	35.14	-13.02	<.0001

HEL - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	32.95	68.53	<.0001
Type	1	33.68	165.44	<.0001
Site*Type	1	30.27	14.79	0.0006
year	1	35.96	1.77	0.1915
week(year)	7	30.35	1.48	0.2119
Site*year	1	34.9	13.1	0.0009
Type*year	1	34.36	4.07	0.0515

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	1.2271	0.1343	34.17	9.14	<.0001	3.4114	0.458
Maidstone	2.3779	0.1488	35.96	15.98	<.0001	10.7821	1.604

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	SE Mean
Cultivar	0.8393	0.131	30.43	6.41	<.0001	2.3148	0.3033
Species	2.7657	0.1567	34.96	17.65	<.0001	15.8902	2.4897

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	SE Mean
2013	1.6376	0.1994	35.92	8.21	<.0001	5.1427	1.0253
2014	1.9674	0.1464	35.16	13.43	<.0001	7.1523	1.0474

Site*year Least Squares Means						
Site	year	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	2013	1.2619	0.2158	35.86	5.85	<.0001
Fairfax	2014	1.1924	0.1554	29.76	7.67	<.0001
Maidstone	2013	2.0133	0.2278	35.91	8.84	<.0001
Maidstone	2014	2.7425	0.1769	35.99	15.5	<.0001

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	0.5283	0.1801	25.83	2.93	0.0069
Fairfax	Species	1.9259	0.1721	35.97	11.19	<.0001
Maidstone	Cultivar	1.1503	0.1814	34.48	6.34	<.0001
Maidstone	Species	3.6055	0.1634	34.2	22.07	<.0001

T Grouping for Site*Type Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Site	Type	Estimate	
Maidstone	Species	3.6055	A
Fairfax	Species	1.9259	B
Maidstone	Cultivar	1.1503	C
Fairfax	Cultivar	0.5283	D

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-1.3976	0.228	30.04	-6.13	<.0001
Site Maidstone	Cultivar	Species	-2.4552	0.1752	35.03	-14.01	<.0001

Type*Year Least Squares Means						
Type	year	Estimate	Standard Error	DF	t Value	Pr > t
Cultivar	2013	0.5275	0.2016	29.13	2.62	0.014
Cultivar	2014	1.1511	0.1714	32.22	6.72	<.0001
Species	2013	2.7476	0.2662	33.11	10.32	<.0001
Species	2014	2.7838	0.1584	35.39	17.57	<.0001

**HEL - Honeybees
Fairfax only**

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	19.76	92.9	<.0001
year	1	14.24	2.06	0.1727
week(year)	6	16.08	27.55	<.0001
Type*year	1	19.76	0.93	0.3467

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-0.7756	0.2552	14.67	-3.04	0.0085	0.4604	0.1175
Species	2.5531	0.2873	21.38	8.88	<.0001	12.8463	3.6914

HEL - Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	31.94	70.88	<.0001
Type	1	32.18	137.79	<.0001
Site*Type	1	30.42	0.71	0.4073
year	1	35.99	3.72	0.0615
week(year)	7	30.26	1.31	0.2784
Site*year	1	35.17	14.2	0.0006
Type*year	1	34.75	0.27	0.6057

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	SE Mean
Fairfax	0.5891	0.1951	33.34	3.02	0.0048	1.8024	0.3516
Maidstone	2.3094	0.2207	35.54	10.46	<.0001	10.0687	2.2226

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	SE Mean
Cultivar	0.2383	0.1916	30.29	1.24	0.2233	1.269	0.2432
Species	2.6603	0.2247	34.22	11.84	<.0001	14.3002	3.2126

Site*Type Least Squares Means								
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	SE Mean
Fairfax	Cultivar	0.5366	0.2926	24.86	-1.83	0.0787	0.5848	0.1711
Fairfax	Species	1.7148	0.2378	35.43	7.21	<.0001	5.5554	1.3211
Maidstone	Cultivar	1.0131	0.2487	35.73	4.07	0.0002	2.7541	0.6849
Maidstone	Species	3.6058	0.2311	33.61	15.6	<.0001	36.8104	8.5078

T Grouping for Site*Type Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Site	Type	Estimate	
Maidstone	Species	3.6058	A
Fairfax	Species	1.7148	B
Maidstone	Cultivar	1.0131	C
Fairfax	Cultivar	-0.5366	D

Simple Effect Comparisons of Site*Type Least Squares Means By Site

Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-2.2513	0.3634	29.89	-6.19	<.0001
Site Maidstone	Cultivar	Species	-2.5927	0.1887	35.29	-13.74	<.0001

HEL - Other Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	11.5	6.47	0.0265
Type	1	28.83	0.17	0.6788
Site*Type	1	26.15	0.01	0.9319
year	1	29.05	0	0.984
week(year)	7	28.63	1.7	0.149
Site*year	1	28.87	3.23	0.0829
Type*year	1	26.86	4.66	0.0399

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	SE Mean
Fairfax	-1.2036	73.7425	29.05	-0.02	0.9871	0.3001	22.1317
Maidstone	-2.1874	73.7443	29.05	-0.03	0.9765	0.1122	8.2745

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	SE Mean
C	-1.7624	73.7441	29.05	-0.02	0.9811	0.1716	12.6567
S	-1.6286	73.7426	29.05	-0.02	0.9825	0.1962	14.4688

Site*Type Least Squares Means								
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	SE Mean
Fairfax	Cultivar	-1.2822	73.7445	29.05	-0.02	0.9862	0.2774	20.4595
Fairfax	Species	-1.125	73.7409	29.05	-0.02	0.9879	0.3247	23.9407
Maidstone	Cultivar	-2.2427	73.7444	29.05	-0.03	0.9759	0.1062	7.8299
Maidstone	Species	-2.1322	73.7451	29.05	-0.03	0.9771	0.1186	8.7444

T Grouping for Site*Type Least Squares Means (Alpha=0.05)				
LS-means with the same letter are not significantly different.				
Site	Type	Estimate		
Fairfax	Species	-1.125		A
Fairfax	Cultivar	-1.2822	B	A
Maidstone	Species	-2.1322	B	
Maidstone	Cultivar	-2.2427	B	

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.1572	0.3183	25.48	-0.49	0.6257
Site Maidstone	Cultivar	Species	-0.1105	0.4998	28.65	-0.22	0.8267

HEL - Flies

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	25.41	1.2	0.2827
Type	1	25.79	0.17	0.6835
Site*Type	1	24.03	1.21	0.2825
year	1	30.94	0.22	0.6392
week(year)	7	26.16	0.61	0.7417
Site*year	1	25.34	0.81	0.3755
Type*year	1	26.03	0.37	0.5492

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-0.2714	0.3865	20.1	-0.7	0.4906	0.7623	0.2947
Species	-0.5563	0.5817	31.16	-0.96	0.3463	0.5733	0.3335

***Monarda fistulosa* vs. *Monarda fistulosa* 'Claire Grace'**

MON - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	46.77	33.32	<.0001
Type	1	46.35	2.87	0.097
Site*Type	1	47.97	4.47	0.0397
year	1	47.32	60.39	<.0001
week(year)	5	34.32	36.25	<.0001
Site*year	1	46.77	1.61	0.2109
Type*year	1	33.21	6.27	0.0174

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Fairfax	2.5376	0.05145	29.17	49.32	<.0001	12.6491	0.6508
Maidstone	1.9758	0.09887	41.74	19.98	<.0001	7.2123	0.7131

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Cultivar	2.1832	0.07551	47.99	28.91	<.0001	8.8751	0.6702
Species	2.3301	0.07579	47.98	30.75	<.0001	10.2792	0.779

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
2013	1.7747	0.1136	47.44	15.62	<.0001	5.8982	0.6699
2014	2.7387	0.04982	46.66	54.98	<.0001	15.467	0.7705

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	2.3901	0.06818	28	35.06	<.0001
Fairfax	Species	2.685	0.06379	29.15	42.09	<.0001
Maidstone	Cultivar	1.9764	0.1187	43.2	16.65	<.0001
Maidstone	Species	1.9752	0.1202	43.87	16.43	<.0001

T Grouping for Site*Type Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Site	Type	Estimate	
Fairfax	Species	2.685	A
Fairfax	Cultivar	2.3901	B
Maidstone	Cultivar	1.9764	C
Maidstone	Species	1.9752	C

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.2949	0.08274	27.55	-3.56	0.0014
Site Maidstone	Cultivar	Species	0.001182	0.1341	46.57	0.01	0.993

MON - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	23.29	25.65	<.0001
Type	1	32.8	2.3	0.1391
Site*Type	1	30.99	4.01	0.054
year	1	41.61	50.75	<.0001
week(year)	5	33.63	42.05	<.0001
Site*year	1	41.41	0.7	0.4077
Type*year	1	26.85	4.49	0.0434

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	2.4256	0.06469	12.86	37.5	<.0001	11.3094	0.7316
Maidstone	1.8608	0.1065	38.24	17.47	<.0001	6.4291	0.6847

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.0666	0.08475	42.17	24.38	<.0001	7.8982	0.6694
Species	2.2198	0.08503	42.47	26.11	<.0001	9.2058	0.7828

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	1.6649	0.1232	46.71	13.51	<.0001	5.2852	0.6513
2014	2.6215	0.05602	24.47	46.8	<.0001	13.757	0.7707

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	2.2703	0.08593	22.78	26.42	<.0001
Fairfax	Species	2.581	0.07974	20.95	32.37	<.0001
Maidstone	Cultivar	1.863	0.1286	45.67	14.49	<.0001
Maidstone	Species	1.8587	0.131	45.99	14.19	<.0001

T Grouping for Site*Type Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Site	Type	Estimate	
Fairfax	Species	2.581	A
Fairfax	Cultivar	2.2703	B
Maidstone	Cultivar	1.863	C
Maidstone	Species	1.8587	C

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.3107	0.1037	22.15	-3	0.0066
Site Maidstone	Cultivar	Species	0.004336	0.1485	37.38	0.03	0.9769

MON - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	21.25	17.81	0.0004
Type	1	33.12	2.15	0.1523
Site*Type	1	31.1	4.41	0.0439
year	1	41.84	45.62	<.0001
week(year)	5	33.52	36.9	<.0001
Site*year	1	41.66	0.18	0.6738
Type*year	1	27.69	4.75	0.0379

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	2.3879	0.07061	11.56	33.82	<.0001	10.8911	0.769
Maidstone	1.8813	0.1121	36.17	16.78	<.0001	6.5619	0.7355

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.0565	0.08919	40.01	23.06	<.0001	7.8185	0.6974
Species	2.2127	0.08987	40.45	24.62	<.0001	9.1407	0.8215

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	1.664	0.1283	46.54	12.97	<.0001	5.2803	0.6777
2014	2.6052	0.05987	21.56	43.51	<.0001	13.5345	0.8103

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	2.2235	0.09307	20.95	23.89	<.0001
Fairfax	Species	2.5524	0.08632	18.96	29.57	<.0001
Maidstone	Cultivar	1.8895	0.1345	44.19	14.04	<.0001
Maidstone	Species	1.8731	0.1379	44.73	13.58	<.0001

T Grouping for Site*Type Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Site	Type	Estimate	
Fairfax	Species	2.5524	A
Fairfax	Cultivar	2.2235	B
Maidstone	Cultivar	1.8895	C
Maidstone	Species	1.8731	C

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.3289	0.1108	22.8	-2.97	0.0069
Site Maidstone	Cultivar	Species	0.01643	0.1548	37.62	0.11	0.9161

MON - Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	23.85	26.69	<.0001
Type	1	40.69	3.92	0.0544
Site*Type	1	33.51	9.46	0.0042
year	2	45.3	26.25	<.0001
week(year)	5	35.41	43.14	<.0001
Site*year	1	44.86	1.98	0.1663
Type*year	2	36.27	4.32	0.0208

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	2.5315	0.05493	4.898	46.09	<.0001	12.5727	0.6906
Maidstone	2.1889	0.07209	13.34	30.36	<.0001	8.925	0.6434

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.2696	0.05945	17.65	38.18	<.0001	9.6755	0.5752
Species	2.5442	0.05591	15.46	45.5	<.0001	12.7336	0.712

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
2013	1.8009	0.09945	36.36	18.11	<.0001	6.055	0.6022
2014	2.7078	0.04653	7.145	58.2	<.0001	14.9961	0.6977
2015	2.119	0.1382	47.77	15.34	<.0001	8.3228	1.1499

Site*Type Least Squares Means							
Site - Type	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Fairfax - Cultivar	2.3156	0.07476	12.77	30.97	<.0001	10.1315	0.7574
Fairfax - Species	2.7474	0.06542	8.956	42	<.0001	15.6021	1.0207
Maidstone - Cultivar	2.189	0.09638	30.65	22.71	<.0001	8.9263	0.8603
Maidstone - Species	2.1887	0.09718	31.08	22.52	<.0001	8.9237	0.8672

T Grouping for Site*Type Least Squares Means (Alpha=0.05)

LS-means with the same letter are not significantly different.

Site	Type	Estimate	
Fairfax	Species	2.7474	A
Fairfax	Cultivar	2.3156	B
Maidstone	Cultivar	2.189	B
Maidstone	Species	2.1887	B

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.4318	0.08758	19.47	-4.93	<.0001
Site Maidstone	Cultivar	Species	0.00029	0.1291	42.35	0	0.9982

***Penstemon digitalis* vs. *Penstemon digitalis* ‘Husker Red’**

PEN - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	18.89	0.01	0.9116
Type	1	32.52	4	0.054
Site*Type	1	28.59	2.29	0.1408
year	1	30.08	1.49	0.2321
week(year)	3	22.47	2.76	0.0661
Site*year	1	28.06	0.7	0.41
Type*year	1	16.11	2.64	0.1238

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.2247	0.15	24.24	8.16	<.0001	3.4031	0.5106
Species	1.578	0.1426	21.64	11.06	<.0001	4.8452	0.6911

PEN - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	16.73	0.03	0.8631
Type	1	35.26	3.53	0.0684
Site*Type	1	34.75	3.08	0.0882
year	1	34.18	0.57	0.4559
week(year)	3	22.26	2.67	0.0726
Site*year	1	32.42	0.18	0.6759
Type*year	1	15.33	3.1	0.0981

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	1.3198	0.1219	4.49	10.83	0.0002	3.7428	0.4561
Maidstone	1.2732	0.2181	19.9	5.84	<.0001	3.5724	0.7791

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.1319	0.1481	23.39	7.64	<.0001	3.1015	0.4593
Species	1.4612	0.1429	21.02	10.22	<.0001	4.3111	0.6162

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	1.0104	0.1576	10.44	6.41	<.0001
Fairfax	Species	1.6292	0.1339	6.374	12.17	<.0001
Maidstone	Cultivar	1.2533	0.2648	24.52	4.73	<.0001
Maidstone	Species	1.2931	0.2643	25.35	4.89	<.0001

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.6188	0.1616	11.24	-3.83	0.0027
Site Maidstone	Cultivar	Species	-0.03981	0.2995	28.54	-0.13	0.8952

PEN - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	15.15	0.94	0.3471
Type	1	33.27	1.74	0.1967
Site*Type	1	34.02	1.31	0.26
year	1	35.04	0.04	0.8346
week(year)	3	19.82	3.47	0.0357
Site*year	1	33.63	0.64	0.4287
Type*year	1	12.76	2.57	0.1335

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	1.0759	0.1211	5.012	8.89	0.0003	2.9327	0.355
Maidstone	1.3287	0.2052	15.4	6.48	<.0001	3.7761	0.7748

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.0934	0.1366	20.44	8.01	<.0001	2.9843	0.4076
Species	1.3112	0.1336	18.74	9.81	<.0001	3.7107	0.4958

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	0.8784	0.156	11.79	5.63	0.0001
Fairfax	Species	1.2734	0.1397	8.649	9.11	<.0001
Maidstone	Cultivar	1.3083	0.2458	20.63	5.32	<.0001
Maidstone	Species	1.3491	0.2459	21.59	5.49	<.0001

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.395	0.1707	8.345	-2.31	0.0481
Site Maidstone	Cultivar	Species	-0.04074	0.2709	30.77	-0.15	0.8815

PEN - Honeybees - Fairfax only

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	9.525	9.31	0.0129
year	1	9.845	1.23	0.2945
week(year)	3	13.78	1.4	0.284
Type*year	1	9.525	0	0.9629

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-1.4643	0.5392	9.625	-2.72	0.0224	0.2312	0.1247
Species	0.3035	0.2273	10.04	1.33	0.2114	1.3546	0.3079

PEN - Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	7.004	8.84	0.0207
Type	1	19.24	0.48	0.4976
Site*Type	1	15.24	0	0.9817
year	1	31.68	6.71	0.0144
week(year)	3	19.46	0.18	0.9099
Site*year	1	33.42	0.06	0.8123
Type*year	1	25.14	0.22	0.6463

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
C	-0.2385	0.2596	12.63	-0.92	0.3755	0.7878	0.2045
S	-0.06988	0.2458	10.48	-0.28	0.7818	0.9325	0.2293

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	-0.5549	0.3228	23.28	-1.72	0.0989	0.5741	0.1853
2014	0.2465	0.2043	5.261	1.21	0.2789	1.2796	0.2614

PEN - Other Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	22.59	1.78	0.1957
Type	1	33	1.72	0.1989
Site*Type	1	32.49	0.27	0.6093
year	1	33.33	1.31	0.2612
week(year)	3	22.73	3.2	0.0427
Site*year	1	31.92	1.94	0.1731
Type*year	1	13.7	4.37	0.0558

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
C	0.4465	0.2104	28.66	2.12	0.0425	1.5629	0.3288
S	0.7961	0.1925	26.35	4.14	0.0003	2.2168	0.4267

***Rudbeckia fulgida* vs. *Rudbeckia fulgida* 'Goldsturm'**

RUD - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	5.954	0.22	0.6565
year	1	7.436	0.18	0.6819
week(year)	1	5.935	0.21	0.6657

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.6339	0.1203	4.335	13.58	0.0001	5.124	0.6164
Species	1.5687	0.1229	4.663	12.76	<.0001	4.8006	0.59

RUD - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	6.229	0.01	0.9097
year	1	13.92	0.24	0.6339
week(year)	1	8.418	2.96	0.1218

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	0.8413	0.1074	12.62	7.83	<.0001	2.3193	0.2492
Species	0.8255	0.1081	12.55	7.64	<.0001	2.283	0.2468

RUD - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	6.229	0.01	0.9097
year	1	13.92	0.24	0.6339
week(year)	1	8.418	2.96	0.1218

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	0.8413	0.1074	12.62	7.83	<.0001	2.3193	0.2492
Species	0.8255	0.1081	12.55	7.64	<.0001	2.283	0.2468

RUD - Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	9.609	0.18	0.6814
year	1	9.467	0.54	0.48
week(year)	1	7.285	1.71	0.2302
Type*year	1	9.609	0.75	0.4062

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-1.1369	0.3627	6.361	-3.13	0.0187	0.3208	0.1164
Species	-1.364	0.4424	9.848	-3.08	0.0118	0.2556	0.1131

RUD - Other Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	12.1	1.16	0.3029
year	1	12.11	0.17	0.6834
week(year)	1	8.642	2.28	0.1671
Type*year	1	12.1	3.58	0.0828

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	0.5912	0.1248	11.84	4.74	0.0005	1.8061	0.2254
Species	0.7642	0.102	12.45	7.5	<.0001	2.1472	0.2189

RUD - Flies

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	5.267	0.18	0.6882
year	1	5.179	2.58	0.167
week(year)	1	5.573	2.38	0.1775
Type*year	1	5.267	1.42	0.2847

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Cultivar	0.9309	0.1848	3.595	5.04	0.0096	2.5367	0.4688
Species	0.8505	0.1878	3.889	4.53	0.0113	2.3409	0.4396

***Symphotrichum novae-angliae* vs. *S. novae-angliae* 'Alma Potschke'**

SYM - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	18.86	52.78	<.0001
Type	1	16.09	687.49	<.0001
Site*Type	1	15.6	6.53	0.0215
year	1	15.61	5.91	0.0275
week(year)	1	8.652	43.22	0.0001
Site*year	1	17.07	3.82	0.0671
Type*year	1	14.49	0.11	0.7504

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Fairfax	3.0433	0.04923	11.71	61.82	<.0001	20.975	1.0326
Maidstone	2.392	0.07609	21.44	31.44	<.0001	10.9356	0.8321

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Cultivar	1.6058	0.08267	19.44	19.42	<.0001	4.9817	0.4119
Species	3.8296	0.03094	7.697	123.79	<.0001	46.0432	1.4244

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
2013	2.6205	0.06568	21.28	39.9	<.0001	13.7427	0.9026
2014	2.8149	0.05549	19.73	50.73	<.0001	16.6907	0.9261

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	2.0374	0.0854	16.86	23.86	<.0001
Fairfax	Species	4.0492	0.03757	4.594	107.79	<.0001
Maidstone	Cultivar	1.1741	0.1396	19.56	8.41	<.0001
Maidstone	Species	3.6099	0.04823	10.11	74.84	<.0001

T Grouping for Site*Type Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Site	Type	Estimate	
Fairfax	Species	4.0492	A
Maidstone	Species	3.6099	B
Fairfax	Cultivar	2.0374	C
Maidstone	Cultivar	1.1741	D

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-2.0118	0.08783	12.28	-22.91	<.0001
Site Maidstone	Cultivar	Species	-2.4358	0.143	17.07	-17.04	<.0001

SYM - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	19.54	56.71	<.0001
Type	1	15.18	690.19	<.0001
Site*Type	1	14.71	5.46	0.034
year	1	14.78	7.09	0.0179
week(year)	1	8.333	46.46	0.0001
Site*year	1	16.16	3.61	0.0754
Type*year	1	13.79	0.21	0.654

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	3.011	0.04698	13.1	64.09	<.0001	20.3078	0.9541
Maidstone	2.3672	0.07251	21.48	32.65	<.0001	10.6672	0.7735

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.5965	0.0802	18.37	19.91	<.0001	4.9355	0.3958
Species	3.7817	0.02896	8.123	130.59	<.0001	43.8915	1.271

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	2.5839	0.06353	20.53	40.67	<.0001	13.249	0.8417
2014	2.7943	0.05381	19.29	51.93	<.0001	16.3504	0.8798

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	2.0136	0.08427	16.32	23.89	<.0001
Fairfax	Species	4.0084	0.03467	4.66	115.6	<.0001
Maidstone	Cultivar	1.1793	0.1346	18.58	8.76	<.0001
Maidstone	Species	3.5551	0.04548	10.79	78.17	<.0001

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-1.9947	0.0882	11.92	-22.62	<.0001
Site Maidstone	Cultivar	Species	-2.3758	0.1391	16.15	-17.08	<.0001

SYM - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	20.72	5.1	0.0349
Type	1	20.2	447.65	<.0001
Site*Type	1	20.31	13.9	0.0013
year	1	20.21	13.99	0.0013
week(year)	1	8.253	1.31	0.2845
Site*year	1	21.16	24.01	<.0001
Type*year	1	19.77	4.21	0.0536

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	2.3743	0.06459	18.35	36.76	<.0001	10.7439	0.6939
Maidstone	2.1181	0.09296	21.45	22.79	<.0001	8.3153	0.7729

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.0718	0.1066	20.35	10.05	<.0001	2.9207	0.3115
Species	3.4206	0.03407	21.07	100.41	<.0001	30.5882	1.042

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	2.0457	0.08388	21.16	24.39	<.0001	7.7342	0.6487
2014	2.4468	0.07132	19.18	34.31	<.0001	11.551	0.8239

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	1.4085	0.1183	17.79	11.91	<.0001
Fairfax	Species	3.3402	0.0485	19.4	68.87	<.0001
Maidstone	Cultivar	0.7351	0.1785	21.25	4.12	0.0005
Maidstone	Species	3.5011	0.04741	21.95	73.85	<.0001

T Grouping for Site*Type Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Site	Type	Estimate	
Maidstone	Species	3.5011	A
Fairfax	Species	3.3402	B
Fairfax	Cultivar	1.4085	C
Maidstone	Cultivar	0.7351	D

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-1.9316	0.1265	17.69	-15.27	<.0001
Site Maidstone	Cultivar	Species	-2.766	0.1835	21.17	-15.07	<.0001

SYM - Honeybees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	19.7	131.94	<.0001
Type	1	19.84	150.89	<.0001
Site*Type	1	19.14	10.57	0.0042
year	1	19.68	1.06	0.3151
week(year)	1	6.702	127.69	<.0001
Site*year	1	20.26	1.29	0.2685
Type*year	1	17.81	2.45	0.1348

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	2.1439	0.06412	15.53	33.44	<.0001	8.533	0.5471
Maidstone	0.661	0.1157	20.9	5.71	<.0001	1.9367	0.2241

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	0.6059	0.1173	19.88	5.16	<.0001	1.8329	0.2151
Species	2.199	0.06174	20.25	35.62	<.0001	9.0162	0.5567

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-2.0087	0.1271	16.64	-15.81	<.0001
Site Maidstone	Cultivar	Species	-1.1776	0.224	20.24	-5.26	<.0001

SYM - Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	20.13	4.36	0.0497
Type	1	19.58	393.59	<.0001
Site*Type	1	19.75	14.04	0.0013
year	1	19.57	11.33	0.0031
week(year)	1	7.537	1.41	0.2707
Site*year	1	20.55	21.86	0.0001
Type*year	1	19.17	4.86	0.04

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	2.3476	0.06924	18	33.91	<.0001	10.4609	0.7243
Maidstone	2.0947	0.09891	20.87	21.18	<.0001	8.1226	0.8034

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.0448	0.1138	19.72	9.18	<.0001	2.843	0.3236
Species	3.3975	0.03618	20.44	93.89	<.0001	29.8878	1.0815

Site*Type Least Squares Means							
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean
Fairfax	Cultivar	1.396	0.1268	17.55	11.01	<.0001	4.0392
Fairfax	Species	3.2993	0.05254	18.89	62.79	<.0001	27.0924
Maidstone	Cultivar	0.6937	0.1906	20.64	3.64	0.0016	2.001
Maidstone	Species	3.4957	0.0493	21.63	70.91	<.0001	32.9718

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-1.9032	0.1361	17.5	-13.98	<.0001
Site Maidstone	Cultivar	Species	-2.802	0.1959	20.55	-14.3	<.0001

SYM - Other Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	22.08	2.56	0.1239
Type	1	15	6.04	0.0267
Site*Type	1	15	1.82	0.1978
year	1	19.4	0.01	0.9297
week(year)	1	8.435	0.06	0.8103
Site*year	1	19.4	1.39	0.2528

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-2.4494	0.5506	17.74	-4.45	0.0003	0.08635	0.04755
Species	-0.9144	0.3498	22.35	-2.61	0.0157	0.4008	0.1402

SYM - Butterflies and Moths

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	23.8	11.95	0.0021
year	1	23.48	0.01	0.908
week(year)	1	18.98	2.3	0.1459
Type*year	1	23.8	0	0.9864

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-2.4451	0.7484	23.72	-3.27	0.0033	0.08672	0.0649
Species	0.2071	0.2219	22.69	0.93	0.3604	1.2301	0.2729

***Tradescantia ohiensis* vs. *Tradescantia* 'Red Grape'**

TRA - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	20.84	6.85	0.0162
Type	1	33.94	19.5	<.0001
Site*Type	1	46.05	3.88	0.0549
year	1	46.8	8.14	0.0064
week(year)	6	38.45	6.39	<.0001
Site*year	1	46.88	0.85	0.3605
Type*year	1	45.27	0.77	0.3838

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	1.6733	0.1368	19.69	12.23	<.0001	5.3296	0.7292
Maidstone	1.1561	0.1653	30.97	7	<.0001	3.1775	0.5251

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.1528	0.1275	35.92	9.04	<.0001	3.1671	0.4038
Species	1.6765	0.1315	36.49	12.75	<.0001	5.347	0.7031

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	1.1146	0.199	49.12	5.6	<.0001	3.0483	0.6065
2014	1.7148	0.09509	18.87	18.03	<.0001	5.5555	0.5283

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	1.2903	0.1572	28.31	8.21	<.0001
Fairfax	Species	2.0562	0.1583	28.31	12.99	<.0001
Maidstone	Cultivar	1.0153	0.1961	40.31	5.18	<.0001
Maidstone	Species	1.2969	0.1817	35.84	7.14	<.0001

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.7659	0.157	38.83	-4.88	<.0001
Site Maidstone	Cultivar	Species	-0.2816	0.1836	43.02	-1.53	0.1325

TRA - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	25.03	12.18	0.0018
Type	1	39.24	16.87	0.0002
Site*Type	1	44.46	0.04	0.8374
year	1	45.59	11.19	0.0017
week(year)	6	38.57	4.41	0.0017
Site*year	1	47.53	0.16	0.6879
Type*year	1	44.28	0.23	0.6356

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	1.2373	0.1718	22.88	7.2	<.0001	3.4462	0.5922
Maidstone	0.3609	0.226	36.91	1.6	0.1189	1.4346	0.3243

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	0.362	0.1996	43.63	1.81	0.0766	1.4362	0.2867
Species	1.2362	0.1786	41.27	6.92	<.0001	3.4424	0.6148

Year Least Squares Means							
Year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	0.3199	0.2686	47.45	1.19	0.2395	1.377	0.3699
2014	1.2782	0.134	29.37	9.54	<.0001	3.5903	0.4813

Site*Type Least Squares Means						
Site	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	0.8206	0.2	32.51	4.1	0.0003
Fairfax	Species	1.654	0.2027	32.8	8.16	<.0001
Maidstone	Cultivar	-0.09654	0.3271	45.15	-0.3	0.7693
Maidstone	Species	0.8183	0.2396	38.13	3.42	0.0015

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	Cultivar	Species	-0.8334	0.2099	41.58	-3.97	0.0003
Site Maidstone	Cultivar	Species	-0.9149	0.3528	41.98	-2.59	0.013

Type*year Least Squares Means						
Type	year	Estimate	Standard Error	DF	t Value	Pr > t
Cultivar	2013	-0.07081	0.3139	46.1	-0.23	0.8225
Cultivar	2014	0.7949	0.1999	44.78	3.98	0.0003
Species	2013	0.7107	0.3253	46.8	2.18	0.0339
Species	2014	1.7616	0.1374	30.84	12.82	<.0001

TRA - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	27.92	1.9	0.1785
Type	1	25.97	8.92	0.0061
Site*Type	1	40.11	1.8	0.1876
year	1	45.83	10.34	0.0024
week(year)	6	33.15	2.43	0.0464
Site*year	1	46.83	3.48	0.0685
Type*year	1	36.6	0.72	0.4002

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-0.1989	0.2242	42.45	-0.89	0.38	0.8196	0.1838
Species	0.5359	0.2231	41.49	2.4	0.0209	1.709	0.3813

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	-0.4032	0.3391	48.6	-1.19	0.2402	0.6682	0.2266
2014	0.7401	0.1342	21.09	5.52	<.0001	2.0962	0.2813

TRA - Honeybees - Fairfax only

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	22.85	19.52	0.0002
year	1	25.49	2.65	0.116
week(year)	5	20.99	5.39	0.0024
Type*year	1	22.85	4.82	0.0386

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	0.3294	0.2087	14.34	1.58	0.1363	1.3901	0.2901
Species	1.294	0.2191	23.46	5.91	<.0001	3.6475	0.7991

TRA - Flies

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	36.84	1.19	0.282
Type	1	17.69	0.02	0.8856
Site*Type	1	18.95	1.14	0.2995
year	1	43.19	0.14	0.7123
week(year)	6	34.12	7.85	<.0001
Site*year	1	36.94	6.47	0.0153
Type*year	1	29.79	0.54	0.4677

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	-1.0918	2.5564	42.42	-0.43	0.6715	0.3356	0.8579
Species	-1.0624	2.5593	43.71	-0.42	0.6801	0.3456	0.8846

***Veronicastrum virginicum* vs. *Veronicastrum virginicum* 'Lavendelturm'**

VER - All Pollinators

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	32.19	12.62	0.0012
Type	1	20.68	6.65	0.0176
Site*Type	1	25.84	2.32	0.14
year	2	28.23	36.74	<.0001
week(year)	5	21.31	9.58	<.0001
Site*year	1	28.88	2.57	0.1195
Type*year	1	29.24	0.77	0.3888

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Fairfax	2.9542	0.07412	4.38	39.86	<.0001	19.1858	1.422
Maidstone	2.9329	0.09557	10.99	30.69	<.0001	18.7826	1.795

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Cultivar	3.3088	0.0642	8.516	51.54	<.0001	27.3532	1.7561
Species	2.6642	0.07677	13.05	34.7	<.0001	14.3559	1.1021

Site*Type Least Squares Means							
Site - Type	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
Fairfax - Cultivar	3.2161	0.08706	7.282	36.94	<.0001	24.9298	2.1703
Fairfax - Species	2.7796	0.08867	7.852	31.35	<.0001	16.1121	1.4287
Maidstone - Cultivar	3.4325	0.09469	10.58	36.25	<.0001	30.9546	2.9312
Maidstone - Species	2.4333	0.1469	28.98	16.56	<.0001	11.3969	1.6747

Simple Effect Comparisons of Site*Type Least Squares Means By Site							
Simple Effect Level	Type	Type	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Cultivar	Species	0.4365	0.09695	9.73	4.5	0.0012
Site Maidstone	Cultivar	Species	0.9992	0.1568	28.16	6.37	<.0001

VER - All Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	34.59	3.49	0.0703
Type	1	23.24	7.74	0.0105
Site*Type	1	28.35	3.06	0.0909
year	2	29.59	24.64	<.0001
week(year)	5	21.59	8.82	0.0001
Site*year	1	30.65	0.14	0.7156
Type*year	1	30.81	0.7	0.4089

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	3.2695	0.05528	11.03	59.14	<.0001	26.2975	1.4539
Species	2.5048	0.07577	21.05	33.06	<.0001	12.2414	0.9275

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	1.7718	0.1759	27.83	10.08	<.0001	5.8813	1.0342
2014	2.88	0.05576	7.466	51.65	<.0001	17.8144	0.9934
2015	3.7714	0.06668	6.924	56.56	<.0001	43.4427	2.8969

VER - All Native Bees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	34.81	0.61	0.4384
Type	1	13.83	8.52	0.0113
Site*Type	1	20.33	3.83	0.0642
year	2	23.76	26.19	<.0001
week(year)	5	21.45	3.31	0.0229
Site*year	1	26.26	1.25	0.2733
Type*year	1	26.93	0.53	0.4735

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.9467	0.07774	8.053	37.91	<.0001	19.0433	1.4804
Species	1.9382	0.1139	20.68	17.02	<.0001	6.9466	0.7912

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	1.0577	0.2617	18.32	4.04	0.0007	2.8798	0.7538
2014	2.3584	0.08453	6.33	27.9	<.0001	10.5738	0.8938
2015	3.7714	0.08609	2.28	43.81	0.0002	43.4419	3.7399

VER - Honeybees - Fairfax only

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Type	1	23	3.58	0.071
year	1	23	8.32	0.0084
week(year)	4	23	15.76	<.0001

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	1.7218	0.2447	23	7.04	<.0001	5.5948	1.369
Species	1.3338	0.1995	23	6.68	<.0001	3.7953	0.7573

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	0.9522	0.3841	23	2.48	0.0209	2.5914	0.9954
2014	2.1034	0.1036	23	20.3	<.0001	8.1939	0.849

VER - Bumblebees

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Site	1	6.851	0.06	0.8174
Type	1	18.25	0.23	0.64
Site*Type	1	18.42	0.22	0.6476
year	2	20.68	3.53	0.0479
week(year)	5	15.06	0.27	0.9218
Site*year	1	21.41	0.15	0.6985
Type*year	1	21.77	0.04	0.8497

Type Least Squares Means							
Type	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Cultivar	2.7863	0.2745	1.997	10.15	0.0096	16.2215	4.4535
Species	1.7816	0.2603	1.666	6.84	0.0325	5.9396	1.5461

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	0.7441	0.4961	7.037	1.5	0.1771	2.1045	1.0441
2014	2.2106	0.2315	1	9.55	0.0664	9.1212	2.1117
2015	3.7337	0.4139	2.77	9.02	0.0039	41.8321	17.3147

APPENDIX C.1 –INTERACTIONS INCLUDED IN ECHINACEA MODELS

Interactions included in models for analysis of pollinator visitation to *Echinacea purpurea*, *Echinacea purpurea* ‘White Swan,’ *Echinacea purpurea* ‘Pink Double Delight,’ and *Echinacea* ‘Sunrise.’

P = Poisson distribution

* Models could not converge

	Distribution	Site	Type	Year	Week (year)	Site * Type	Site * Year	Type * Year
All Bees	P	X	X	X	X	X	X	X
All Non-Bees	P	X	X	X	X	X	X	X
Honey Bees	P		X	X	X			
Bumble Bees	P	X	X	X	X	X	X	X
Other Native Bees	P	X	X	X	X	X	X	
Beetles/Bugs*								
Wasps/Ants*								
Butterflies	P	X	X	X	X	X	X	X
Flies	P	X	X	X	X	X	X	

APPENDIX C.2

SUPPLEMENTAL RESULTS FOR CHAPTER 3

Supplemental results tables include significance of effects included in the generalized linear mixed models (GLIMMIX), least squares means for plant types and other significant effects, differences of least squares mean, T grouping for significant effects, and simple effect comparisons. Site A = Fairfax (F), Site B = Maidstone (M).

***Echinacea purpurea* (ECH PUR), *Echinacea purpurea* ‘White Swan’ (ECH WHI), *Echinacea purpurea* ‘Pink Double Delight’ (ECH PIN) and *Echinacea* ‘Sunrise’ (ECH SUN)**

All Bees

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	1.5789	0.241	93.58	6.55	<.0001	4.8498	1.1688
Maidstone	0.3406	0.2304	84.56	1.48	0.1431	1.4058	0.3239

Differences of Site Least Squares Means						
Site	Site	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Maidstone	1.2383	0.2964	82.81	4.18	<.0001

T Grouping for Site Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
Site	Estimate	
Fairfax	1.5789	A
Maidstone	0.3406	B

Plant_Name Least Squares Means							
Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
ECH PIN	-0.6063	0.3824	72.75	-1.59	0.1172	0.5454	0.2085
ECH PUR	2.4591	0.2435	96.31	10.1	<.0001	11.6944	2.8478
ECH SUN	0.5156	0.3449	83.52	1.49	0.1387	1.6746	0.5775
ECH WHI	1.4707	0.2811	90.55	5.23	<.0001	4.3521	1.2236

Differences of Plant_Name Least Squares Means						
Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
ECH PIN	ECH PUR	-3.0654	0.5135	80.6	-5.97	<.0001
ECH PIN	ECH SUN	-1.1218	0.5683	78.58	-1.97	0.0519
ECH PIN	ECH WHI	-2.0769	0.5323	79.91	-3.9	0.0002
ECH PUR	ECH SUN	1.9436	0.2747	69.46	7.08	<.0001
ECH PUR	ECH WHI	0.9885	0.1903	69.89	5.19	<.0001
ECH SUN	ECH WHI	-0.9551	0.3072	68.92	-3.11	0.0027

T Grouping for Plant_Name Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
Plant Name	Estimate	
ECH PUR	2.4591	A
ECH WHI	1.4707	B
ECH SUN	0.5156	C
ECH PIN	-0.6063	C

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	1.1446	0.3586	100.8	3.19	0.0019	3.1411	1.1264
2014	0.775	0.1822	75.12	4.25	<.0001	2.1705	0.3955

Differences of year Least Squares Means						
year	_year	Estimate	Standard Error	DF	t Value	Pr > t
2013	2014	0.3696	0.4348	99.12	0.85	0.3973

T Grouping for year Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
year	Estimate	
2013	1.1446	A
2014	0.775	A

Site*Plant_Name Least Squares Means							
Site - Plant Name	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
F ECH PIN	0.3466	0.3701	64.77	0.94	0.3526	1.4142	0.5234
F ECH PUR	2.6708	0.2542	93.91	10.51	<.0001	14.4509	3.6738
F ECH SUN	1.084	0.3318	76.26	3.27	0.0016	2.9566	0.9809
F ECH WHI	2.2144	0.2624	89.63	8.44	<.0001	9.1557	2.4025
M ECH PIN	-1.5591	0.7678	81.99	-2.03	0.0455	0.2103	0.1615
M ECH PUR	2.2475	0.2672	94.69	8.41	<.0001	9.4638	2.5288
M ECH SUN	-0.05293	0.499	78.78	-0.11	0.9158	0.9484	0.4733
M ECH WHI	0.7269	0.3759	84.21	1.93	0.0565	2.0687	0.7776

T Grouping for Site*Plant_Name Least Squares Means (Alpha=0.05)

LS-means with the same letter are not significantly different.

Site	Plant Name	Estimate		
Fairfax	ECH PUR	2.6708		A
Maidstone	ECH PUR	2.2475		B
Fairfax	ECH WHI	2.2144		B
Fairfax	ECH SUN	1.084		C
Maidstone	ECH WHI	0.7269	D	C
Fairfax	ECH PIN	0.3466	D	C
Maidstone	ECH SUN	-0.05293	D	E
Maidstone	ECH PIN	-1.5591		E

Simple Effect Comparisons of Site*Plant_Name Least Squares Means By Site

Simple Effect Level	Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	ECH PIN	ECH PUR	-2.3242	0.3544	54.04	-6.56	<.0001
Site Fairfax	ECH PIN	ECH SUN	-0.7375	0.4141	54.1	-1.78	0.0805
Site Fairfax	ECH PIN	ECH WHI	-1.8678	0.3637	54.1	-5.14	<.0001
Site Fairfax	ECH PUR	ECH SUN	1.5867	0.2553	52.24	6.22	<.0001
Site Fairfax	ECH PUR	ECH WHI	0.4564	0.1613	50.6	2.83	0.0067
Site Fairfax	ECH SUN	ECH WHI	-1.1303	0.2689	52.91	-4.2	0.0001
Site Maidstone	ECH PIN	ECH PUR	-3.8065	0.9163	85.31	-4.15	<.0001
Site Maidstone	ECH PIN	ECH SUN	-1.5061	1.0085	83.02	-1.49	0.1391
Site Maidstone	ECH PIN	ECH WHI	-2.286	0.9523	84.39	-2.4	0.0186
Site Maidstone	ECH PUR	ECH SUN	2.3004	0.461	71.99	4.99	<.0001
Site Maidstone	ECH PUR	ECH WHI	1.5205	0.32	71.44	4.75	<.0001
Site Maidstone	ECH SUN	ECH WHI	-0.7799	0.5263	70.82	-1.48	0.1429

All Non Bees

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	0.1813	0.2499	17.55	0.73	0.4778	1.1988	0.2996
Maidstone	-1.1395	0.2815	27.06	-4.05	0.0004	0.32	0.09009

Differences of Site Least Squares Means						
Site	Site	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Maidstone	1.3208	0.3018	10.09	4.38	0.0014

T Grouping for Site Least Squares Means (Alpha=0.05)
LS-means with the same letter are not significantly different.

Site	Estimate	
Fairfax	0.1813	A
Maidstone	-1.1395	B

Plant_Name Least Squares Means							
Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
ECH PIN	-0.5115	0.2424	44.92	-2.11	0.0404	0.5996	0.1453
ECH PUR	-0.3414	0.268	54.37	-1.27	0.2082	0.7108	0.1905
ECH SUN	-0.7812	0.3172	71.35	-2.46	0.0162	0.4578	0.1452
ECH WHI	-0.2823	0.2831	62.81	-1	0.3225	0.7541	0.2135

Differences of Plant_Name Least Squares Means						
Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
ECH PIN	ECH PUR	-0.1702	0.2577	80.15	-0.66	0.511
ECH PIN	ECH SUN	0.2697	0.307	83.33	0.88	0.3822
ECH PIN	ECH WHI	-0.2292	0.2726	85.31	-0.84	0.4027
ECH PUR	ECH SUN	0.4399	0.2903	77.19	1.52	0.1338
ECH PUR	ECH WHI	-0.05909	0.2552	78.52	-0.23	0.8175
ECH SUN	ECH WHI	-0.499	0.3026	81.99	-1.65	0.103

T Grouping for Plant_Name Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
Plant Name	Estimate	
ECH WHI	-0.2823	A
ECH PUR	-0.3414	A
ECH PIN	-0.5115	A
ECH SUN	-0.7812	A

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
2013	-0.7217	0.3547	84.62	-2.03	0.045	0.4859	0.1724
2014	-0.2365	0.2052	26.4	-1.15	0.2594	0.7894	0.1619

Differences of year Least Squares Means						
year	_year	Estimate	Standard Error	DF	t Value	Pr > t
2013	2014	-0.4852	0.3788	86.27	-1.28	0.2036

T Grouping for year Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
year	Estimate	
2014	-0.2365	A
2013	-0.7217	A

Site*Plant_Name Least Squares Means							
Site - Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
F ECH PIN	-0.06246	0.2942	28.78	-0.21	0.8334	0.9394	0.2764
F ECH PUR	0.1909	0.2885	27.33	0.66	0.5137	1.2104	0.3492
F ECH SUN	-0.01591	0.3084	32.31	-0.05	0.9592	0.9842	0.3036
F ECH WHI	0.6126	0.2657	21.45	2.31	0.0312	1.8452	0.4903
M ECH PIN	-0.9606	0.3491	49.63	-2.75	0.0083	0.3827	0.1336
M ECH PUR	-0.8737	0.3596	49.28	-2.43	0.0188	0.4174	0.1501
M ECH SUN	-1.5466	0.4807	79.37	-3.22	0.0019	0.213	0.1024
M ECH WHI	-1.1772	0.4291	70.96	-2.74	0.0077	0.3081	0.1322

T Grouping for Site*Plant_Name Least Squares Means (Alpha=0.05)				
LS-means with the same letter are not significantly different.				
Site	Plant Name	Estimate		
Fairfax	ECH WHI	0.6126		A
Fairfax	ECH PUR	0.1909		B
Fairfax	ECH SUN	-0.01591		B
Fairfax	ECH PIN	-0.06246	C	B
Maidstone	ECH PUR	-0.8737	C	D
Maidstone	ECH PIN	-0.9606		D
Maidstone	ECH WHI	-1.1772		D
Maidstone	ECH SUN	-1.5466		D

Simple Effect Comparisons of Site*Plant_Name Least Squares Means By Site							
Simple Effect Level	Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	ECH PIN	ECH PUR	-0.2534	0.2441	48.66	-1.04	0.3043
Site Fairfax	ECH PIN	ECH SUN	0.04655	0.2693	50.91	-0.17	0.8634
Site Fairfax	ECH PIN	ECH WHI	-0.6751	0.2258	49.65	-2.99	0.0043
Site Fairfax	ECH PUR	ECH SUN	0.2068	0.2497	45.48	0.83	0.4117
Site Fairfax	ECH PUR	ECH WHI	-0.4217	0.2052	45.55	-2.05	0.0457
Site Fairfax	ECH SUN	ECH WHI	-0.6285	0.2346	48.41	-2.68	0.0101
Site Maidstone	ECH PIN	ECH PUR	0.08694	0.4173	85.38	-0.21	0.8354
Site Maidstone	ECH PIN	ECH SUN	0.586	0.5247	90.22	1.12	0.267
Site Maidstone	ECH PIN	ECH WHI	0.2166	0.4781	91.39	0.45	0.6516
Site Maidstone	ECH PUR	ECH SUN	0.6729	0.4884	82.07	1.38	0.172
Site Maidstone	ECH PUR	ECH WHI	0.3035	0.4376	81.4	0.69	0.4899
Site Maidstone	ECH SUN	ECH WHI	-0.3694	0.5378	86.35	-0.69	0.494

Honeybees - Fairfax only

Plant_Name Least Squares Means							
Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
ECH PIN	-1.1935	0.6177	26.14	-1.93	0.0642	0.3031	0.1873
ECH PUR	0.6145	0.2568	24.88	2.39	0.0246	1.8487	0.4748
ECH SUN	-1.7703	0.946	19.5	-1.87	0.0764	0.1703	0.1611
ECH WHI	0.4067	0.27	22.19	1.51	0.1462	1.5018	0.4055

Differences of Plant_Name Least Squares Means						
Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
ECH PIN	ECH PUR	-1.808	0.6463	25.79	-2.8	0.0096
ECH PIN	ECH SUN	0.5767	1.115	21.18	0.52	0.6103
ECH PIN	ECH WHI	-1.6002	0.6571	25.82	-2.44	0.0221
ECH PUR	ECH SUN	2.3848	0.9625	19.48	2.48	0.0225
ECH PUR	ECH WHI	0.2078	0.3434	24.48	0.61	0.5506
ECH SUN	ECH WHI	-2.177	0.9725	19.75	-2.24	0.0369

T Grouping for Plant_Name Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
Plant Name	Estimate	
ECH PUR	0.6145	A
ECH WHI	0.4067	A
ECH PIN	-1.1935	B
ECH SUN	-1.7703	B

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t 	Mean	Standard Error Mean
2013	-0.04241	0.3521	26.59	-0.12	0.905	0.9585	0.3375
2014	-0.9289	0.5202	19.71	-1.79	0.0896	0.395	0.2055

T Grouping for year Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
year	Estimate	
2013	-0.04241	A
2014	-0.9289	A

Bumblebees

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	0.9448	0.4359	95.1	2.17	0.0327	2.5723	1.1213
Maidstone	-0.1078	0.3466	78.16	-0.31	0.7565	0.8978	0.3112

Differences of Site Least Squares Means						
Site	Site	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Maidstone	1.0526	0.5414	85.09	1.94	0.0552

T Grouping for Site Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
Site	Estimate	
Fairfax	0.9448	A
Maidstone	-0.1078	A

Plant_Name Least Squares Means							
Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
ECH PIN	-1.8247	0.7407	73.18	-2.46	0.0161	0.1613	0.1194
ECH PUR	2.2039	0.411	101.5	5.36	<.0001	9.0603	3.7234
ECH SUN	0.2065	0.5054	92.96	0.41	0.6838	1.2294	0.6213
ECH WHI	1.0883	0.4455	98.45	2.44	0.0164	2.9692	1.3229

Differences of Plant_Name Least Squares Means						
Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
ECH PIN	ECH PUR	-4.0287	0.9931	83.95	-4.06	0.0001
ECH PIN	ECH SUN	-2.0312	1.0358	82.79	-1.96	0.0532
ECH PIN	ECH WHI	-2.913	1.0084	83.53	-2.89	0.0049
ECH PUR	ECH SUN	1.9974	0.331	69.04	6.03	<.0001
ECH PUR	ECH WHI	1.1156	0.2318	69.22	4.81	<.0001
ECH SUN	ECH WHI	-0.8818	0.3708	68.25	-2.38	0.0202

T Grouping for Plant_Name Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
Plant Name	Estimate	
ECH PUR	2.2039	A
ECH WHI	1.0883	B
ECH SUN	0.2065	C
ECH PIN	-1.8247	C

year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	0.6769	0.5959	102.4	1.14	0.2587	1.9677	1.1726
2014	0.1601	0.3261	75.83	0.49	0.6249	1.1736	0.3827

Differences of year Least Squares Means						
year	_year	Estimate	Standard Error	DF	t Value	Pr > t
2013	2014	0.5168	0.7718	98.87	0.67	0.5047

Other Native Bees

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	-0.09793	0.2843	91.87	-0.34	0.7312	0.9067	0.2577
Maidstone	-1.3719	0.3495	104	-3.92	0.0002	0.2536	0.08865

Differences of Site Least Squares Means						
Site	Site	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Maidstone	1.274	0.4222	103.1	3.02	0.0032

T Grouping for Site Least Squares Means (Alpha=0.05)		
LS-means with the same letter are not significantly different.		
Site	Estimate	
Fairfax	-0.09793	A
Maidstone	-1.3719	B

Plant_Name Least Squares Means							
Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
ECH PIN	-1.131	0.3615	100	-3.13	0.0023	0.3227	0.1167
ECH PUR	0.001598	0.2906	96.27	0.01	0.9956	1.0016	0.291
ECH SUN	-1.2407	0.4644	97.35	-2.67	0.0089	0.2892	0.1343
ECH WHI	-0.5696	0.4297	102.7	-1.33	0.1879	0.5657	0.2431

Differences of Plant_Name Least Squares Means						
Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
ECH PIN	ECH PUR	-1.1326	0.4754	100.5	-2.38	0.0191
ECH PIN	ECH SUN	0.1098	0.5949	99.41	0.18	0.854
ECH PIN	ECH WHI	-0.5613	0.5676	102.2	-0.99	0.325
ECH PUR	ECH SUN	1.2423	0.4399	91.93	2.82	0.0058
ECH PUR	ECH WHI	0.5712	0.4065	100.1	1.41	0.163
ECH SUN	ECH WHI	-0.6711	0.5387	98.93	-1.25	0.2158

T Grouping for Plant_Name Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Plant Name	Estimate		
ECH PUR	0.001598		A
ECH WHI	-0.5696	B	A
ECH PIN	-1.131	B	
ECH SUN	-1.2407	B	

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	-0.897	0.4414	102.3	-2.03	0.0447	0.4078	0.18
2014	-0.5729	0.2052	93.98	-2.79	0.0064	0.5639	0.1157

Differences of year Least Squares Means						
year	_year	Estimate	Standard Error	DF	t Value	Pr > t
2013	2014	-0.3241	0.4962	102.2	-0.65	0.5151

Site*Plant_Name Least Squares Means							
Site - Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
F ECH PIN	-0.4	0.3889	79.15	-1.03	0.3068	0.6703	0.2607
F ECH PUR	0.3088	0.3075	81.16	1	0.3183	1.3618	0.4188
F ECH SUN	-0.8214	0.4557	61.05	-1.8	0.0764	0.4398	0.2004
F ECH WHI	0.5209	0.3013	86	1.73	0.0874	1.6835	0.5072
M ECH PIN	-1.8619	0.7146	103.9	-2.61	0.0105	0.1554	0.111
M ECH PUR	-0.3056	0.4085	100.7	-0.75	0.4562	0.7367	0.301
M ECH SUN	-1.6601	0.7529	103.7	-2.2	0.0297	0.1901	0.1431
M ECH WHI	-1.6602	0.7529	103.7	-2.2	0.0297	0.1901	0.1431

T Grouping for Site*Plant_Name Least Squares Means (Alpha=0.05)				
LS-means with the same letter are not significantly different.				
Site	Plant Name	Estimate		
Fairfax	ECH WHI	0.5209		A
Fairfax	ECH PUR	0.3088		A
Maidstone	ECH PUR	-0.3056	B	A
Fairfax	ECH PIN	-0.4	B	
Fairfax	ECH SUN	-0.8214	B	
Maidstone	ECH SUN	-1.6601	B	
Maidstone	ECH WHI	-1.6602	B	
Maidstone	ECH PIN	-1.8619	B	

Simple Effect Comparisons of Site*Plant_Name Least Squares Means By Site							
Simple Effect Level	Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	ECH PIN	ECH PUR	-0.7088	0.3498	55.4	-2.03	0.0476
Site Fairfax	ECH PIN	ECH SUN	0.4213	0.487	53.23	0.87	0.3908
Site Fairfax	ECH PIN	ECH WHI	-0.9209	0.3433	57.35	-2.68	0.0095
Site Fairfax	ECH PUR	ECH SUN	1.1302	0.4164	42.16	2.71	0.0096
Site Fairfax	ECH PUR	ECH WHI	-0.2121	0.241	40.92	-0.88	0.3841
Site Fairfax	ECH SUN	ECH WHI	-1.3423	0.4188	46.27	-3.21	0.0024
Site Maidstone	ECH PIN	ECH PUR	-1.5563	0.8778	103.3	-1.77	0.0792
Site Maidstone	ECH PIN	ECH SUN	-0.2018	1.082	103.7	-0.19	0.8524
Site Maidstone	ECH PIN	ECH WHI	-0.2017	1.082	103.7	-0.19	0.8525
Site Maidstone	ECH PUR	ECH SUN	1.3545	0.7723	102.9	1.75	0.0824
Site Maidstone	ECH PUR	ECH WHI	1.3545	0.7723	102.9	1.75	0.0824
Site Maidstone	ECH SUN	ECH WHI	0.000093	0.9926	103.5	0	0.9999

Butterflies and Moths

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	-2.8192	7.6391	93.82	-0.37	0.7129	0.05965	0.4557
Maidstone	-4.8355	7.6467	92.74	-0.63	0.5287	0.007943	0.06074

Differences of Site Least Squares Means						
Site	Site	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Maidstone	2.0162	0.5853	16.48	3.44	0.0032

Plant_Name Least Squares Means							
Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
ECH PIN	-4.3725	7.6504	91.88	-0.57	0.569	0.01262	0.09654
ECH PUR	-3.0085	7.6399	93.6	-0.39	0.6946	0.04937	0.3772
ECH SUN	-4.0566	7.648	93.59	-0.53	0.5971	0.01731	0.1324
ECH WHI	-3.8718	7.6519	93.55	-0.51	0.6141	0.02082	0.1593

Differences of Plant_Name Least Squares Means						
Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
ECH PIN	ECH PUR	-1.364	0.6379	89.21	-2.14	0.0352
ECH PIN	ECH SUN	-0.3159	0.7253	87.21	-0.44	0.6642
ECH PIN	ECH WHI	-0.5007	0.7681	86.84	-0.65	0.5162
ECH PUR	ECH SUN	1.0481	0.4962	76.32	2.11	0.038
ECH PUR	ECH WHI	0.8634	0.5567	77.72	1.55	0.125
ECH SUN	ECH WHI	-0.1847	0.653	78.64	-0.28	0.778

T Grouping for Plant_Name Least Squares Means (Alpha=0.05)			
LS-means with the same letter are not significantly different.			
Plant	Estimate		
ECH PUR	-3.0085		A
ECH WHI	-3.8718	B	A
ECH SUN	-4.0566	B	
ECH PIN	-4.3725	B	

Year Least Squares Means							
year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	-3.876	14.0462	95.68	-0.28	0.7832	0.02073	0.2912
2014	-3.7787	5.9957	76.11	-0.63	0.5304	0.02285	0.137

Differences of year Least Squares Means						
year	_year	Estimate	Standard Error	DF	t Value	Pr > t
2013	2014	-0.09737	15.27	93.29	-0.01	0.9949

Site*Plant_Name Least Squares Means							
Site - Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
F ECH PIN	-3.4103	7.6476	93.88	-0.45	0.6567	0.03303	0.2526
F ECH PUR	-2.2452	7.6397	93.82	-0.29	0.7695	0.1059	0.8091
F ECH SUN	-3.2157	7.645	93.72	-0.42	0.675	0.04013	0.3068
F ECH WHI	-2.4058	7.6401	93.72	-0.31	0.7535	0.09019	0.6891
M ECH PIN	-5.3347	7.701	89.97	-0.69	0.4903	0.004821	0.03713
M ECH PUR	-3.7718	7.6529	93.54	-0.49	0.6233	0.02301	0.1761
M ECH SUN	-4.8975	7.6801	93.57	-0.64	0.5252	0.007465	0.05734
M ECH WHI	-5.3379	7.7008	93.48	-0.69	0.4899	0.004806	0.03701

Simple Effect Comparisons of Site*Plant_Name Least Squares Means By Site							
Simple Effect Level	Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
Site Fairfax	ECH PIN	ECH PUR	-1.1651	0.4147	55.81	-2.81	0.0068
Site Fairfax	ECH PIN	ECH SUN	-0.1946	0.496	54.47	-0.39	0.6963
Site Fairfax	ECH PIN	ECH WHI	-1.0045	0.4232	55.61	-2.37	0.0211
Site Fairfax	ECH PUR	ECH SUN	0.9705	0.3833	48.31	2.53	0.0146
Site Fairfax	ECH PUR	ECH WHI	0.1606	0.2872	51.93	0.56	0.5784
Site Fairfax	ECH SUN	ECH WHI	-0.8098	0.3961	51.8	-2.04	0.046
Site Maidstone	ECH PIN	ECH PUR	-1.563	1.2054	91.62	-1.3	0.198
Site Maidstone	ECH PIN	ECH SUN	-0.4372	1.3669	90.51	-0.32	0.7498
Site Maidstone	ECH PIN	ECH WHI	0.00314	1.4794	88.75	0	0.9983
Site Maidstone	ECH PUR	ECH SUN	1.1257	0.9215	77.75	1.22	0.2256
Site Maidstone	ECH PUR	ECH WHI	1.5661	1.0725	76.97	1.46	0.1483
Site Maidstone	ECH SUN	ECH WHI	0.4404	1.2529	79.63	0.35	0.7261

Simple Effect Comparisons of Plant_Name*year Least Squares Means By year							
Simple Effect Level	Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
year 2013	ECH PIN	ECH PUR	-0.9262	0.7298	87.75	-1.27	0.2077
year 2013	ECH PIN	ECH SUN	-0.1041	0.8422	87.03	-0.12	0.9019
year 2013	ECH PIN	ECH WHI	-0.2005	0.8554	86.28	-0.23	0.8152
year 2013	ECH PUR	ECH SUN	0.8221	0.6386	79.62	1.29	0.2017
year 2013	ECH PUR	ECH WHI	0.7257	0.6484	77.93	1.12	0.2664
year 2013	ECH SUN	ECH WHI	-0.0963	0.7748	79.99	-0.12	0.9013
year 2014	ECH PIN	ECH PUR	-1.8018	0.7701	74.62	-2.34	0.022
year 2014	ECH PIN	ECH SUN	-0.5278	0.8853	70.07	-0.6	0.553
year 2014	ECH PIN	ECH WHI	-0.8008	0.8835	74.68	-0.91	0.3676
year 2014	ECH PUR	ECH SUN	1.2741	0.5844	54.29	2.18	0.0336
year 2014	ECH PUR	ECH WHI	1.001	0.596	67.04	1.68	0.0977
year 2014	ECH SUN	ECH WHI	-0.2731	0.7329	63.76	-0.37	0.7107

Flies

Site Least Squares Means							
Site	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
Fairfax	-1.3103	0.3464	77.38	-3.78	0.0003	0.2697	0.09343
Maidstone	-1.3545	0.3542	106.5	-3.82	0.0002	0.2581	0.0914

Differences of Site Least Squares Means						
Site	Site	Estimate	Standard Error	DF	t Value	Pr > t
Fairfax	Maidstone	0.04419	0.4468	105.9	0.1	0.9214

Plant_Name Least Squares Means							
Plant Name	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
ECH PIN	-1.6371	0.3502	89.88	-4.68	<.0001	0.1945	0.06812
ECH PUR	-1.2573	0.3438	87.41	-3.66	0.0004	0.2844	0.09779
ECH SUN	-1.5839	0.4838	98.92	-3.27	0.0015	0.2052	0.09927
ECH WHI	-0.8511	0.3321	98.68	-2.56	0.0119	0.4269	0.1418

Differences of Plant_Name Least Squares Means						
Plant Name	Plant Name	Estimate	Standard Error	DF	t Value	Pr > t
ECH PIN	ECH PUR	-0.3798	0.4063	92.61	-0.93	0.3523
ECH PIN	ECH SUN	-0.05318	0.5333	99.08	-0.1	0.9208
ECH PIN	ECH WHI	-0.786	0.3999	96.37	-1.97	0.0523
ECH PUR	ECH SUN	0.3267	0.4843	94.05	0.67	0.5016
ECH PUR	ECH WHI	-0.4061	0.3339	89.77	-1.22	0.227
ECH SUN	ECH WHI	-0.7328	0.47	99.53	-1.56	0.1221

**T Grouping for Plant_Name
Least Squares Means
(Alpha=0.05)**

LS-means with the same letter are not significantly different.

Plant Name	Estimate	
ECH WHI	-0.8511	A
ECH PUR	-1.2573	A
ECH SUN	-1.5839	A
ECH PIN	-1.6371	A

Year Least Squares Means

year	Estimate	Standard Error	DF	t Value	Pr > t	Mean	Standard Error Mean
2013	-1.7107	0.4736	98	-3.61	0.0005	0.1807	0.08559
2014	-0.954	0.2461	80.2	-3.88	0.0002	0.3852	0.0948

Differences of Year Least Squares Means

year	_year	Estimate	Standard Error	DF	t Value	Pr > t
2013	2014	-0.7567	0.5277	95.58	-1.43	0.1549