

Evaluating Pollinator Activity in a Native Plant Garden at the University of North Carolina Asheville

Matthew Jasper
Biology
The University of North Carolina at Asheville
One University Heights
Asheville, North Carolina 28804 USA

Faculty Advisor: Dr. Jennifer Rhode Ward

Abstract

Habitat loss and fragmentation as a result of urbanization and agriculture have led to considerable declines in populations of many North American native bee species. This decline has inspired the development of solutions intended to reduce pollinator habitat disruption, including incorporating plant species shown to enhance pollinator abundance into landscape design. The ability of heterogeneous landscapes to promote native bee abundance has been well studied; however, the complex nature of plant-pollinator mutualisms suggests that pollinator recruitment and reproductive success can be heavily influenced by the structure and density of floral neighborhoods. In the summer of 2015, pollinators were studied in a newly installed native plant habitat featuring herbaceous perennials native to the western North Carolina region or their cultivars. Visitor category, visit frequency, and visit duration were recorded and used to infer population-level demographic patterns regarding foraging behavior and plant preference within an artificial habitat. Field sampling time totaled 2,640 minutes in which visitor observations (n=2061) were made on six plant species: *Asclepias tuberosa* (butterfly milkweed), *Coreopsis verticillata* (whorled tickseed), *Helianthus flexuosus* (purple-headed sneeze weed), *Monarda fistulosa* (wild bergemont), *Penstemon digitalis* (foxglove beardtongue), *Sympheotrichum oblongifolium* (aeoromatic aster 'Raydon's favorite') from four families (Asteraceae, Apocynaceae, Lamiaceae, Plantaginaceae) in the summer of 2015. Visitor frequency and duration data were used in statistical analyses to assess visitor diversity and interaction strength across the six plant species. *Monarda fistulosa* received the highest diversity and abundance of total visitors, generating the highest relative interaction strength with bumblebees and butterflies among all visitor categories. *Penstemon digitalis* and *Coreopsis verticillata* generated stronger relative interaction strength with sweat bees and halictid bees among all visitor categories. Observations of visitor abundance were highly skewed toward bumblebees, while *Monarda fistulosa* received the most frequent and diverse visitor interactions of the six plant species. Summary statistics for *Monarda fistulosa* were generated using SAS showing significant differences in average foraging times in four out of 11 visitor categories, indicating weighted differences in the utilization of floral resources by the artificial habitat insect community assemblage. Developing methods such as these may illuminate the presence of a quantifiable optimum in keystone resource usage by insect pollinators, improving the effectiveness of small-scale pollinator refugia at promoting pollinator abundance in the wake of habitat fragmentation.

Keywords: Pollinator, Refuge Landscapes, Native Plants.

1. Introduction

Many plants rely on biotic vectors for the adequate transport of gametes for sexual reproduction. Likewise, many insects that provide these pollination services are solely dependent on floral structures as food sources and mating rendezvous sites, resulting in sensitive and complex mutualisms with substantial ecological influence. Species interactions within the plant - pollinator mutualistic network can be highly variable, generating complex weighted

systems through which resource acquisition variably influences reproductive success among participants²³, exercising critical influence over the stability, organization, and biodiversity of ecosystems¹². Many flower features such as floral depth, floral advertisement, or reward quality influence the behavior of pollinating insects¹¹, while pollen flow affects the reproductive success of plants, allowing pollinators to selectively regulate the evolution of floral structures²⁰. Solitary bee foraging behavior also greatly influences interactions between plants and honeybees by increasing competition for pollen and nectar resources, resulting in shorter, more frequent visits¹⁶. These relationships reflect the importance of plant biodiversity in the production of effective pollinator refugia illuminating potential strategies for making pollinator conservation initiatives more efficient.

The species diversity – area relationship is one of the most robust in pollinator ecology⁶, with loss of habitat strongly correlated with loss of pollinator diversity. One way pollinator conservation efforts can mitigate the effects of habitat loss is by increasing the availability of floral resources. The use of parks and ornamental landscapes can reduce the impacts of urbanization by providing access to pollinator resources in resource-isolated landscapes¹⁸. Though not equivalent to wild pollinator habitat, subsistent flower resources provided in urban landscapes can be sufficient to sustain an array of anthophilous insects²⁷. Plant population structure and composition within spatially isolated pollinator refugia can significantly enhance the efficiency of plant-pollinator interactions¹⁷, ultimately increasing pollinator resilience to habitat loss through the improved acquisition of floral resources. Animal recruitment to newly installed pollinator habitat occurs in a manner very similar to colonization of island ecosystems¹⁸, allowing for the application of similar methods (edge dynamics / interactions between mutualists) to be used for evaluating species network compositions⁹.

Many plant – pollinator interactions are inherently asymmetric, with specialist plant species interacting with both specialist and generalist pollinator species²³. Distance from bee nesting sites can greatly influence the effectiveness of pollinator meadows at promoting increases in and abundance of bees. Bee foraging range is plastic within and among species, and is correlated with sex, body size, and sociality⁸. For instance, some large Hymenoptera bee species can forage several km from their nesting site, while smaller bees may only travel up to 50 m²⁴. Some solitary female bees only forage in close proximity to their nest, quickly returning to feed their larvae⁸. Thus, body size and species type are strongly correlated with home distance¹⁵. These differences in foraging behavior cause bee species to utilize isolated floral resources in different ways, influencing their sensitivity to habitat fragmentation at both the species and individual level. Pollinators may interact with isolated floral resources as only a fraction of their foraging range, or as the sole isolated resource for their entire developmental season⁶. Flower morphology also greatly impacts foraging range for bees via increased resource allocation to floral advertisement¹¹, allowing pollinators to detect foraging habitat over greater distances, encouraging resource exploration at the limits of their foraging range.

While plants and pollinators exhibit significant bidirectional impacts on each other in wild habitats²³, ignoring pollinator influence on plant dynamics, e.g. pollen limitation and genetic outcrossing, can allow urban planners to select ornamental landscapes specifically tailored to the conservation needs of individual bee species. Most current studies regarding the restoration of bee species assemblages focus on the mechanisms of reproduction, survival, and persistence in the wake of urban sprawl¹⁸. Increasing the availability of seasonal resources such as pollen and nectar in areas of reduced habitat at times of critical bee development can play an essential role in bee population sustainability and reproductive success²⁷. With the typical life span of many species of adult foraging bees limited to several weeks⁷, overlapping plant and pollinator phenologies provide resources at times of peak pollinator development. The availability of resources in conjunction with proximity to nesting sites can greatly strengthen bee community assemblages, and support bee resilience to habitat fragmentation.

In this study I researched the foraging behavior of pollinators within a recently installed dry adapted native plant meadow on the campus of University of North Carolina at Asheville (35.595623, -82.556907) designed to provide foraging habitat for native bees. I chose to focus on *Asclepias tuberosa* (butterfly milkweed), *Coreopsis verticillata* (whorled tickseed), *Helianthus flexuosum* (purple-headed sneeze weed), *Monarda fistulosa* (wild bergemont), *Penstemon digitalis* (foxglove beardtounge), *Symphyotrichum oblongifolium* (aeromatic aster ‘Raydons favorite’) based on their flowering phenologies, pollinator resource production, and diversity of pollinator specialization. The intent of this study was to characterize interactions between target plant species and visiting potential pollinators, providing quantifiable descriptions of plant resource contributions to specific insect categories. I hypothesized that plant species with larger resource allocation to advertisement and reward would have the greatest influence on pollinator recruitment and habitat dynamics. This magnet effect would translate to stronger visitor favoring interactions from less attractive plant species. I also hypothesized that there would be an inverse relationship between biodiversity and interaction strength, as increased biodiversity affected the foraging behavior of some visitor types.

2. Methods

2.1 planting

Plants native to western North Carolina or their cultivars were selected by landscape architect Randy Burroughs and incorporated into designs for wet and dry adapted meadow gardens on the University of North Carolina at Asheville campus. Plants were purchased as plugs and installed by UNC Asheville undergraduate research students in June 2015. Individual plants were installed in a grid pattern 0.5 meters apart, with native grass species *Andropogon ternarius* (split beard bluestem) and *Schizachyrium scoparium* interspersed as needed, allowing for ample growing space among neighboring plants. The meadow was situated on a hillside within a mowed grass landscape, physically isolated from other pollinator habitat by surrounding roads, buildings and parking lots, and spatially isolated from the nearest pollinator habitats by approximately 140 meters.

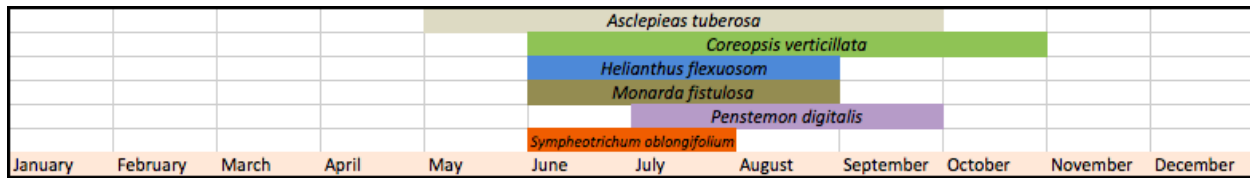


Figure 1: Description of flowering phenology

2.2 observation

Plants of the six target species with open flowers were randomly selected for observation on each day with at least 50% open sky. Observations were recorded for 2,640 minutes across 11 days from June 22nd to July 20th, 2015. Visitor identity and visit duration were recorded for each visit, and the number of visits were recorded as the visitation frequency. Pollinators were identified to the genus level in most cases based on physical characteristics using a field guide¹³ and the website insectidentification.org. Insect categories were then assigned using the Pennsylvania Native Bee Survey citizen science pollinator-monitoring guide.

2.3 statistical analyses

Observational data were used to generate histograms reflecting total floral visitation time among plant species, the number of unique floral visitor types among plant species, and the percentage of total floral visits made by a unique visitor category among each plant species. To calculate the species-wide visitation frequency for each plant, a species interaction matrix²³ was generated using both the number of visits (frequency) and the total visitation time (duration) per plant for each pollinator category. The subsequent interaction strength was used to assess the extent to which each pollinator category benefited from each plant species relative to other visitor categories. Statistical analyses on non-pollinating species were excluded. Summary statistics on mean foraging times among visitor categories for *Monarda fistulosa* were generated using SAS PROC GLM, Tukey-Kramer post HOC test. Biodiversity was calculated using the Shannon Diversity Index.

$$H = -\sum p_i \log p_i$$

3. Results

Hymenoptera and Lepidoptera were the most abundant orders of visitors, with nine families and 14 genera observed. The most common Hymenoptera species were the eusocial bees *Bombus* spp. and *Apis* spp., with semi-social halictid bees also present. Measurements of interaction strength with *Monarda fistulosa* appeared to favor the visiting insect

community the most among the six plant species. Measurements of interaction strength for *Coriopsis verticillata* (whorled tickseed) indicated that the plant produced its strongest interactions with smaller bees. *Monarda fistulosa* (wild bergemont) received the highest visitor frequency and Shannon-Weiner diversity score, receiving most interactions from the bumblebee and european honey bee visitor categories. Comparisons in mean visitation time to *M. fistulosa* (wild bergemont) showed significant difference between the Little Brown Moth and the Small Black Bee, Humming Bird Hawk Moth, and Yellow Sweat Bee categories, with Little Brown Moth exhibiting the highest mean foraging time among visitors.

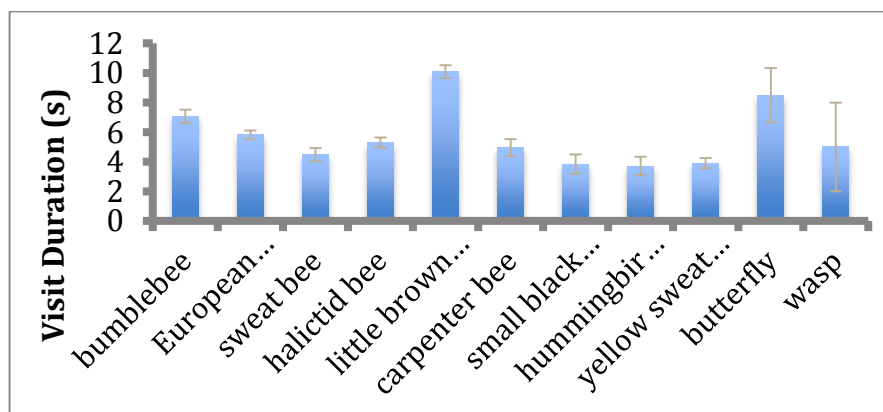


Figure 2: Histogram showing mean flower visitation time across 11 visitor categories for *Monarda fistulosa* (wild bergemont).

Order	Family	Species	Category / Common Name
Coleoptera	Scarabaeidae	<i>Popillia</i> spp.	Beetle
Coleoptera	Nitidulidae	<i>Glischrochilus</i>	Green Striped Beetle
Coleoptera	Cantharidae	<i>Chauliognathus</i> spp.	Look- a-Like Lightning Bug
Diptera	Tabanidae		Horse Fly
Diptera	Mucidae	<i>Musca</i> spp.	Fly
Hemiptera	Lygaeidae	<i>Ocopeltus fasciatus</i>	Guard Beetle
Hymenoptera	Apidae	<i>Bombus</i> spp.	Bumblebee
Hymenoptera	Apidae	<i>Ceratina</i> spp.	Carpenter Bee
Hymenoptera	Formicidae	<i>Camponotus</i> spp.	Flying Ant
Hymenoptera	Halictidae	<i>Halictus</i> spp.	Halictid Bee
Hymenoptera	Apidae	<i>Apis mellifera</i>	Honeybee
Hymenoptera	Halictidae	<i>Dufourea</i> spp.	Small Black Bee
Hymenoptera	Halictidae	<i>Lassioglossum</i> spp.	Sweat Bee
Hymenoptera	Vespidae		Vespid Wasp
Hymenoptera	Halictidae		Yellow Sweat Bee
Lepidoptera	Pieridae	<i>Colias</i> spp.	Brown butterfly
Lepidoptera	Saturniidae	<i>Anisota</i> spp.	Brown moth
Lepidoptera	Sphingidae	<i>Macroglossum stellatarum</i>	Hummingbird Hawk Moth
Lepidoptera	Tortricidae		Little Brown Moth
Lepidoptera	Pieridae		White Butterfly

Figure 3: Table of identified insects, organized by Order.

Shannon Diversity Index	H
<i>Asclepias tuberosa</i>	0.50040242
<i>Coreopsis verticillata</i>	1.6578946
<i>Helianthus flexuosom</i>	1.17802321
<i>Monarda fistulosa</i>	1.9101241
<i>Penstemon digitalis</i>	1.23424495
<i>Sympheotrichum oblongifolium</i>	1.30860539

Figure 4: Shannon Diversity Index $H = -\sum p_i \log p_i$

Order	Category	<i>Asclepieas tuberosa</i>	<i>Coreopsis verticillata</i>	<i>Helianthus flexuosom</i>	<i>Monarda fistulosa</i>	<i>Penstemon digitalis</i>	<i>S. oblongifolium</i>
Hymenoptera	European Honey Bee		0.083	0.462	0.181	0.375	
Hymenoptera	Sweat Bee	0.101	0.116	0.417	0.226	0.064	
Hymenoptera	Halictid Bee		0.104	0.391	0.121	0.065	0.082
Lepidoptera	Little Brown Moth	0.103	0.401		0.098	0.201	
Hymenoptera	Carpenter Bee		0.071		0.193		
Hymenoptera	Small Black Bee		0.031	0.311	0.258		0.667
Lepidoptera	Hummingbird Hawk Moth			0.444	0.177		
Hymenoptera	Yellow Sweat Bee			0.125	0.266		
Lepidoptera	Butterflies		0.286		0.094		
Hymenoptera	Wasp		0.286	0.448	0.231		

Figure 5: Conditionally formatted matrix shows interaction strength excluding non-pollinating categories. Blue values indicate interactions that favor pollinators through lower frequency to duration foraging ratios. Red values indicate higher frequency to duration foraging ratio.

4. Discussion

Studies addressing species impacts within mutualistic networks have shown that the degree of influence for plants on their pollinator host populations is not just contingent on the frequency, but also the quality of visit interaction²³. For plants, interaction strength could be thought of as the contribution of a single visitation event to plant reproductive success, while for pollinators the duration of visits and availability of floral resources contributes to reproductive success via trophic exchange²³. By incorporating category-wide frequency and visit duration into a single value, this study approximated interaction strength between plants and pollinators. As shown, this interaction matrix can be used to approximate pollinator recruitment effectiveness among plant species within UNCA's pollinator garden.

Penstemon digitalis (Scrophulariaceae) is known to attract a variety of bees, providing sucrose- rich nectar as its primary pollinator reward¹¹. Large bees, such as members of the *Bombus* genus, are considered rare visitors of *Penstemon digitalis*¹¹, as the presence of the bristled staminode prevents access to its nectaries. In this study, smaller halictid and sweat bees reflected this trend, interacting strongly with *P. digitalis* (Figure 4), while bumblebees avoided the *P. digitalis* completely. The nectar resources of *P. digitalis* are largely uncontested by larger bee genera, allowing halictid and sweat bees to forage the resource unimpeded, resulting in interactions that favor pollinator resource acquisition.

The flowers of *Monarda fistulosa* are protandrous, with stamens that mature before female reproductive organs. This drives the asynchronous flowering of this species and encourages simultaneous foraging on multiple flowers on the same capitula by pollinators, making it an extremely effective magnet species. *Bombus* spp. are common visitors to *Monarda fistulosa*¹⁰ and were found to be the most frequent visitors throughout this study. Lepidopterans are occasional visitors as well¹⁰, and the long duration visits observed in this study indicate that *M. fistulosa* acts as

substantial foraging resource for moths and butterflies. Smaller bees tend to avoid *Monarda fistulosa*¹⁰, likely favoring more accessible flowers with less competition for resources⁵.

Asclepias tuberosa is frequently pollinated by honeybees, bumblebees, and carpenter bees, which utilize it as a nectar resource²⁷. The pollen of *A. tuberosa* is contained within pollinia, making it inaccessible as a feeding resource for foraging florivorous bees⁴. Unlike *M. fistulosa*, which contains an extremely productive nectary as well as abundant pollen food resources, the nectary of *A. tuberosa* promotes the high frequency, short duration visits from most nectar loving bees^{3,21} and wasps²⁵, which act as important pollinia vectors. The erratic foraging behavior of *Bombus* spp. and *Apis mellifera* on *A. tuberosa* likely encourages smaller bees to seek less competitive foraging sites during peak foraging times⁵. *A. tuberosa* provides a valuable nectar resource for Monarch butterflies, as well as edible foliage for its larval form caterpillar, although these are not common pollen dispersal agents for the plant⁴. This mutualism is inherently asymmetric, as Monarchs are poor contributors to the reproductive success of *A. tuberosa*.

Other plants from this study tended to show less distinctive patterns of pollinator recruitment. The nectaries of *Sympheotrichum oblongifolium*, *Helianthus flexuosom*, and *Coriopsis verticilata* are easily accessed by many types of bees, allowing it to attract a wide range of pollinators who do not require specialized proboscides to feed. Future research could ascertain the degree to which other nearby plants affected pollinator foraging patterns on these plants as the habitat becomes more established.

With the continuous rise in urbanization, factors including habitat fragmentation and environmental changes routinely threaten the persistence of plant - pollinator mutualisms, as well as global species diversity and abundance²⁶. Bee census data¹⁹ clearly shows several North American bumblebee species to be absent from their former range, as well significant population declines for the North American honey bee, *Apis mellifera*¹⁹, which suffers large seasonal die offs as a result of the introduced parasitic mite, *Varroa destructor*. The development of pollinator refuge conservation projects in the wake of bee population decline can be of great benefit to many industries, including agriculture, which rely heavily on bees for pollination services. By implementing simple changes in the ornamental landscape design, biodiversity of pollinator communities can be increased, resulting in positive structural changes within the refuge and the surrounding landscape. Solitary and non-apis bees, such as those in the *Bombus* genus, can influence the foraging behavior of smaller honeybees when managed in close proximity to agriculture, improving the pollination efficiency per bee among many crop types. Conversely, the emerging trend of using pollinator meadows in urban landscapes can generate areas that require less maintenance, reducing the cost of upkeep associated with open grass or mulch areas¹⁸.

As the scientific communities understanding of using plant installations to drive pollinator population growth continues to improve, recognizing the influence of plant structure and density within pollinator meadow refuges on specific pollinators can allow for the development of more efficient meadow designs. Plants requiring biotic pollen vectors have evolved strategies unique to their environmental niche by which to ensure the most genetic outcrossing¹⁴, and exploiting these adaptations can aid in the targeted recruitment of specific pollinators. While some plants rely heavily on advertisement to attract pollinators, pollination success relies heavily on the amount and frequency of visitations. Plants with higher allocation to rewards such as nectar, pollen, chemical signals, or mating rendezvous are likely to procure longer visits from pollinators¹⁴, resulting in stronger interactions and higher resource uptake to the pollinator. The proximity of plants with contrasting pollinator recruitment strategies to one another can have significant bidirectional impacts on reproductive processes², strengthening codependence within the refuge. As pollinator foraging distance is inherently linked to floral advertisement²³, plants with preferred floral morphologies or stronger allocation to floral advertisement can act as pollinator magnets for plants with high reward investment but a discrete floral advertisement.

Many closely related bee species also exhibit different foraging behaviors. Social bee species tend to be mesolectic, exhibiting generalist feeding habits on a multitude of floral hosts, while many solitary and bumble bee species tend to be oligolectic, with very specific pollen host requirements⁸. This trend was largely reflected in our study with observations of *M. fistulosa*, which showed highest visitation frequency from bumblebees (*Bombus*). Social bees *Lassioglossum* spp. and *D. monardae* tended to have the widest range of plant preference, although were much less abundant. One likely reason for the higher abundance of *Bombus* species was the correlation between body size and the proximity of the study site to adjacent pollinator habitat, which may have exceeded the foraging range of smaller Hymenoptera species.

While overlapping pollinator recruitment strategies can increase pollinator visitation frequency, overlapping plant phenologies can ensure access to pollinator resources during times of peak development across a range of pollinator species. The plants selected for the University of North Carolina at Asheville garden provide foraging resources for 8/12 months annually. Flowers with the widest temporal contribution to the meadow are *Penstemon smallii* and *Coriopsis verticilata*, whose floral structures provide easily accessed food resources for smaller pollinators with a

shorter foraging range. Planting strategies that promote resource availability to these insects can increase the species evenness within the refuge, resulting in more diverse assemblages with higher resistance to disturbance.

The integration of Smart Growth Planning Concepts¹ around western North Carolina should include urban planting strategies that provide integrated resource alternatives to displaced pollinator habitat. Bees have disappeared in large cities where urban sprawl is prevalent, and the early implementation of pollinator conservation models can preserve indigenous pollinators rather than recruiting new populations. As more data is collected on bee population demography around University of North Carolina at Asheville, information on extirpated or endangered pollinator species can be used to guide future installations in the region. If increasing the population and biodiversity of pollinating insects in urban areas is a goal of urban planners, than a fluid understanding of plant pollination strategy, phenology, and interaction strength can significantly influence the effectiveness and ecological productivity of artificial meadow design.

5. Acknowledgements

I would like to thank Dr. Jennifer Rhode Ward for her outstanding mentorship and edits on this paper, Dr. H. David Clarke and the UNCA botany research group, Melisa Acker, Bethany Beliveau, Chava Krivchenia, Phyllis Stiles for her work acquiring the Burt's Bees grant which provided funding for this project, Burt's Bees, the UNCA Grounds crew, and Sam Powel from the UNCA math department.

6. Sources

1. Asheville City Council. Smart Growth Planning Concepts. http://www.ashevollenc.gov/portals/0/city-documents/Planning/matrix_1.pdf
2. Baskett, C.A., Emery, S.M., Rudgers, J.A. 2016. Pollinator visits to threatened species are restored following invasive plant removal. *International Journal of Chicago Press*. Vol. 172, No. 3 (March/April 2011), pp. 411-422
3. Betz, R. F., Struven, R.D., Wall, J.E. and Heitler, F.B. 1994. Insect pollinators of 12 milkweed (*Asclepias*) species. In Proceedings of the Thirteenth North American Prairie Conference: Spirit of the Land, Our Prairie Legacy 45-60
4. Borders, B and Lee-Mader, E. 2014. Milkweeds: a conservation practitioner's guide. 146 pp. Portland, OR. The Xerces Society for Invertebrate Conservation.
5. Brittain, C., Williams, N., Kremen, C., Klein, A.M. 2013 Synergistic effects of non-*Apis* bees and honey bees for pollination services. *Proc R Soc B* 280: 20122767. <http://dx.doi.org/10.1098/rspb.2012.2767>
6. Burkle, L. A., and Knight, T. M. 2012. Shifts in pollinator composition and behavior cause slow interaction accumulation with area in plant-pollinator networks. *Ecology*, 93(11), 2329–2335. <http://0-www.jstor.org.wncln.wncln.org/stable/41739304>
7. Cane, J. H., Minckley, R. L., Kervin, L. J., Roulston, T. H., & Williams, N. M. 2006. Complex responses within a desert bee guild (hymenoptera: apiformes) to urban habitat fragmentation. *Ecological Applications*, 16(2), 632–644. <http://0-www.jstor.org.wncln.wncln.org/stable/40061683>
8. Cane, J.H. and Spies, S. 2006. Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. *Biological Conservation*. 99-112 The University of Chicago Press. 1x-435 pp.
9. Corso, G., Britton, N.F. 2014. Comparisons and contrasts between asymmetry and nestedness in interacting ecological networks. *Open Journal of Ecology*, 2014, 4, 653-661
10. Cruden, R. W., Hermanutz, L., & Shuttleworth, J. 1984. The pollination biology and breeding system of *Monarda fistulosa* (Labiatae). *Oecologia*, 64(1), 104–110. <http://0-www.jstor.org.wncln.wncln.org/stable/421742>
11. Dieringer, G., and Cabrera L.R. 2002. The interaction between pollinator size and the bristle staminode of *Penstemon digitalis* (Scrophulariaceae). *American Journal of Botany*, 89(6), 991–997. Retrieved from <http://0-www.jstor.org.wncln.wncln.org/stable/4131391>
12. Ferreira, P.A., Boscolob, D., Viana, B.F. 2012. What do we know about the effects of landscape changes on plant–pollinator interaction networks? *Ecological Indicators* 31 (2013) 35-40
13. Eaton, E. & Kaufman, K. 2006. Kaufman Field Guide to Insects of North America. Houghton Mifflin, ISBN: 0618153101 Cite: 15572
14. Fishman, M.A., Hadany, L. 2012. Pollinators' mating rendezvous and the evolution of floral advertisement. *Journal of Theoretical Biology* 316 (2013) 99–106

15. Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia*, 153(3), 589–596. Retrieved from <http://0-www.jstor.org.wncln.wncln.org/stable/40213008>
16. Greenleaf, S. S., & Kremen, C. 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences of the United States of America*, 103(37), 13890–13895. <http://0-www.jstor.org.wncln.wncln.org/stable/30050351>
17. Jakobsson, A., Lázaro, A. and Totland, O. 2009. Relationships between the floral neighborhood and individual pollen limitation in two self-incompatible herbs. *Oecologia*, Vol. 160, No. 4 (Jul., 2009), pp. 707–719
18. McFrederick, M.S., LeBuhn, G. 2005. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biological Conservation* 129 (2006) 372–82
19. NRC [U.S. National Research Council]. 2007. Status of Council]. Pollinators in North America. The National Academies Press, Washington, D.C.
20. Snow, A. A., and Lewis, P. O. 1993. Reproductive traits and male fertility in plants: empirical approaches. *Annual Review of Ecology and Systematics*, 24, 331–351. <http://0-www.jstor.org.wncln.wncln.org/stable/2097182>
21. Theiss, K., S. Kephart, and C. T. Ivey. 2007. Pollinator effectiveness on co-occurring milkweeds (*Asclepias*; Apocynaceae, Asclepiadoideae). *Annals of the Missouri Botanical Garden* 94:505–516
22. Vanbergen, A.J. 2014. Landscape alteration and habitat modification: impacts on plant–pollinator systems. *Current Opinion in Insect Science* 2014, 5:44–49
23. Vázquez, D. P., Lomáscolo, S. B., Maldonado, M. B., Chacoff, N. P., Dorado, J., Stevani, E. L., & Vitale, N. L. 2012. The strength of plant-pollinator interactions. *Ecology*, 93(4), 719–725. <http://0-www.jstor.org.wncln.wncln.org/stable/23213720>
24. Walther-Hellwig, K., Frankl, R. 2000. Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Entomol.* 124(7-8), 299–306
25. Wilson, M.W., Bertin, R.I., and Price, P.W. 1979. Nectar production and flower visitors of *Asclepias verticillata*. *American Midland Naturalist* 102: 23–35
26. Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G. and Aizen, M.A. (2009) A meta-analysis of bees' responses to anthropogenic disturbance ecology. Vol. 90, No. 8 (Aug., 2009), pp. 2068–2076
27. Wojcik, V. A., Frankie, G.W., Thorp, R.W., and Hernandez, J. L. (2008). Seasonality in bees and their floral resource plants at a constructed urban bee habitat in Berkeley, California. *Journal of the Kansas Entomological Society*, 81(1), 15–28. Retrieved from <http://0-www.jstor.org.wncln.wncln.org/stable/25086414>
28. Wyatt, R. (1981). The reproductive biology of *Asclepias tuberosa*. II. factors determining fruit-set. *The New Phytologist*, 88(2), 375–385. <http://0-www.jstor.org.wncln.wncln.org/stable/2431812>