5-31-2018

Direct and indirect controls on bee community composition

Caroline Marie DeVan
New Jersey Institute of Technology

Recommended Citation

DeVan, Caroline Marie, "Direct and indirect controls on bee community composition" (2018). *Dissertations*. 1590.
https://digitalcommons.njit.edu/dissertations/1590

ABSTRACT

DIRECT AND INDIRECT CONTROLS ON BEE COMMUNITY COMPOSITION

by

Caroline Marie DeVan

Bees are important pollinators, critical for the continued survival of plants in both natural and agricultural ecosystems. Diverse bee communities have been shown to increase richness in plant communities and plant reproduction depends upon bee community richness. Yet there is growing concern that pollinators, especially bees, are declining globally. This dissertation focuses on evaluating the mechanisms responsible for bee community composition in order to promote bee conservation in natural systems and their restoration in human-dominated urban and agricultural landscapes.

Bee populations are impacted directly by three things: floral resources, nesting resources and risk, primarily from natural enemies. Bees are indirectly affected by abiotic factors, like climate, that influence both their behavior and the resources available. Relationships between bees and their floral resources have received the most attention, providing evidence of floral resources structuring bee communities and controlling bee population dynamics. The first investigation described in this dissertation determines the universality of this relationship through a meta-analysis of the effects of plant community composition on bee community composition.

The second and third investigations described in this dissertation focus on the management of two species of cavity nesting bees, *Osmia cornifrons* and *O. taurus*, in terms of their utilization of artificial nesting substrate (Chapter 3) and the influence of temperature on their emergence timing (Chapter 4). This information is useful whether they need to be managed for their pollination services or to reduce their impacts as non-native species. The overall aim of this dissertation work is to promote bee restoration and conservation by adding to the understanding of the roles of both direct and indirect controls on bee community composition.

DIRECT AND INDIRECT CONTROLS ON BEE COMMUNITY COMPOSITION

by
Caroline Marie DeVan

A Dissertation
Submitted to the Faculty of
New Jersey Institute of Technology
in Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy in Biology

Federated Biological Sciences Department

May 2018

.

APPROVAL PAGE

DIRECT AND INDIRECT CONTROLS ON BEE COMMUNITY COMPOSITION

Caroline Marie DeVan

Dr. Daniel Bunker, Dissertation Advisor Date
Associate Professor of Biological Sciences, NJIT

Dr. Karen Goodell, Committee Member Date
Associate Professor of Evolution, Ecology and Organismal Biology, OSU

Dr. Claus Holzapfel Date
Associate Professor of Biological Sciences, Rutgers-Newark

Dr. Gareth Russell, Committee Member Date
Associate Professor of Biological Sciences, NJIT

Dr. Kimberly Russell, Committee Member Date
Assistant Professor, Ecology, Evolution, and Natural Resources, Rutgers-New Brunswick

Dr. Jessica Ware, Committee Member Date
Associate Professor of Biological Sciences, Rutgers-Newark

BIOGRAPHICAL SKETCH

Author:	Caroline Marie DeVan
Degree:	Doctor of Philosophy
Date:	May 2018

Undergraduate and Graduate Education:

- Doctor of Philosophy in Biology,
  New Jersey Institute of Technology, Newark, NJ, USA, 2017
- Bachelor of Arts in Environmental Studies and Spanish,
  University of Tennessee, Knoxville, TN, USA, 2004

Major:	Biological Sciences

Presentations and Publications:

Susan C. Lambrect, Louis Santiago, Caroline M. DeVan, Jose C. Cervera, Lee Buckingham, Sarah C. Pasquini. 2011. Plant water status and hydraulic conductance during flowering in the southern California coastal sage shrub *Salvia mellifera* (Lamiaceae*). American Journal of Botany* **98**(8): 1286-1292.

Meha Jain, Daniel Flynn, Case Prager, Georgia Hart, Caroline DeVan, Farshid Ahrestani, Matthew Palmer, Daniel Bunker, Johannes Knops, Claire Jouseau, Shahid Naeem, 2014. The importance of rare species: a trait based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecology and Evolution* **4**(1): 104-112.

.

I dedicate this thesis to my parents, Bill and Dorothy DeVan
and my grandparents, Jack and Margaret DeVan and Dorothy and Harold Ore
for their enduring love, support and encouragement.

And to the bees, thanks for teaching me so much.

ACKNOWLEDGMENT

I would like to thank Daniel Bunker, Ph.D, my dissertation adviser for bringing me into his lab and encouraging me to find and follow my own research interests. In addition, I would like to thank Dan and the rest of my dissertation committee, Karen Goodell, Ph.D, Claus Holzapfel, Ph.D, Gareth Russell, Ph.D, Kimberly Russell, Ph.D, and Jessica Ware, Ph.D., for their help and advice in making this research possible and their constructive edits on this document. I have learned an incredible amount from all of you, thank you!

I would like to acknowledge my funding support: The Garden Club of America and their Ecological Restoration Fellowship and the National Science Foundation for their funding of the C2PRISM – Computation and Communication: Promoting Research Integration in Science and Mathematics GK-12 Teaching Fellowship and the grant titled: EAGER: Climate Change and Phenological Mismatch – an Experimental Test with Cavity Nesting Bees, Cleptoparasites, and Floral Resources (DEB-1321265). I would further like to thank Bruce Bukiet, Ph.D, for the opportunities I received as a C2PRISM fellow.

This research was done in collaboration with several undergraduate students and I would like to acknowledge in particular, Miranda Bandeli and Karen Wang for their work on this project and the fun I had mentoring them. I learned so much from you! I also received technical support from Xueyang Fan and Jesse Weiland.

Key to my success at NJIT was the administrative support and leadership I received from the Federated Biology Department, including chairs Jorge Golowasch, Ph.D, and Gareth Russell, Ph.D. In particular I want to extend my gratitude to Karen

Roach, who has always advocated for me and provided important guidance throughout my graduate education.

Much of this research was done at Morristown National Historical Park (MORR) and I would like to thank the National Park Service, and staff at MORR for allowing me to put out nest boxes. Specifically, I would like to thank Robert Masson at MORR for his advice and guidance in selecting sites and the Northeast Temperate Network (NETN) and their crew for their plant data as used in Chapter 3.

I would like to thank John Ascher, Ph.D, University of Singapore, for help in identifying species and for teaching me the skills to identify my own specimens. I further learned about bee identification through participation in several workshops including the American Museum of Natural History Bee Course in Summer 2015 and I am exceedingly grateful for those opportunities.

Importantly, I have many friends and colleagues who have also made this work possible in direct and indirect ways. Thank you to Patrice Cole, Ph.D, Jake Weltzin, Ph.D, and Rich Norby, Ph.D, who helped me start my career in science. Thanks also to my wonderful friends without whom I would never have gotten his far: Kim Kennard, Cayenne Engel, Leslie Hamilton, Ph.D, Susan Geist, Mary Gound, Sonali Shukla, Ph.D, Lynn Sweet, Ph.D, Jennifer Riddell, Ph.D, Sara Jo Dickens, Ph.D, Matthew Valente, Meg Ereshefsky, and Connie Bucholz-Beahm. Thanks also to Melissa Sanchez Herrera, Ph.D, Tony Cullen, Manpreet Kohli, Will Kuhn, Ph.D, Dominic Evangelista, Ph.D, Kimberly Plank, Ph.D, Megan Litwhiler, Ph.D, Jessica Schnell, Ph.D, Sarah Kornbluth, Andrew Mashintonio, Ph.D, and Maria Stanko, Ph.D – getting to know you has been the best part of my time at NJIT.

Finally, I would like to thank my family, who has always given me their love and support and unending encouragement when I needed it most. I love you so much – Dorothy and Bill DeVan, Nick and Ashely Beth DeVan. Rachel, Wes and Eleanor Perrine, and Margaret DeVan and my entire extended family. I am so lucky to have you all in my life. Dorothy and Harold Ore, Jack DeVan, and Roger V.P. Anderson, I miss you very much!

TABLE OF CONTENTS

TABLE OF CONTENTS
(Continued)

Chapter **Page**

TABLE OF CONTENTS
(Continued)

TABLE OF CONTENTS
(Continued)

Chapter **Page**

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 Objective

The aim of my dissertation work is to promote bee restoration and conservation by adding to the understanding of the roles of both direct and indirect controls on bee community composition. My first chapter uses a meta-analytical approach to determine the relationship between plant diversity and pollinator diversity at the global scale. My second chapter explores the factors that influence the usage of artificial nesting substrate by wild bees. Finally, in my third chapter, I experimentally determine the influence of temperature on the emergence timing of bees which provides insight into potential impacts of climate change on wild bees.

1.2 Importance of Pollinators

Insect pollinators are critical for the continued survival of plants in both natural and agricultural ecosystems (National Research Council 2006, Klein *et al.* 2007, Thomann *et al.* 2013). The majority of all flowering plants are dependent on biotic pollination for reproduction. Ollerton *et al.* (2011) estimates that 308,006 angiosperm species (87.5% of all angiosperm species) utilize animal pollination. This ranges from 78% of all plants in temperate regions to 94% of all plants in tropical regions (Ollerton *et al.* 2011). Therefore, loss of pollinators increases pollen limitation and reduces the reproductive success for many plant species, potentially resulting in extinction of natural populations (Thomann *et al.* 2013). Pollination services also indirectly influence food sources for other, frugivorous animals, including humans and impact the habitat of many other animals (Ollerton *et al.* 2011; Thomann *et al.* 2013). Of the world's leading crops, over 75% depend on animal pollination (Klein *et al.* 2007, Winfree 2008). The economic value of pollination is estimated to be around $316 billion globally (Lautenbach *et al.* 2012) and pollinators are valued for non-economic reasons including aesthetics, their role in contributing to diverse wildflower communities (Hanley *et al.* 2015), and to human nutrition (Eilers *et al.* 2011).

The honey bee (*Apis mellifera*) is the world's primary managed pollinator and is declining in many parts of the globe due to the spread of *Varroa* mites and other pathogens, which can lead to Colony Collapse Disorder (CCD), as well as impacts from pesticides and reduced nutritional diversity (Kluser and Peduzzi 2007, vanEnglesdorp *et al.* 2010, Goulson *et al.* 2015, Sandhu *et al.* 2016). Managed honey bee decline is of huge concern worldwide due to its implications for agricultural production. However, recent studies indicate that non-managed pollinators, especially wild bees, are effective pollinators for a wide variety of crops, often providing pollination services equal to or greater than those of the managed honey bee *A. mellifera* (Kremen *et al.* 2002, Greenleaf and Kremen 2006, Winfree *et al.* 2007, Winfree *et al.* 2008, Brittain *et al.* 2013a, Brittain *et al.* 2013b, Garibaldi *et al.* 2013).

Diverse bee communities have been shown to increase richness in plant communities and plant reproduction depends upon bee community richness (Fontaine *et al.* 2006, Perfectti *et al.* 2009). Yet there is growing evidence that many wild, unmanaged pollinators, especially bees and butterflies, are also declining globally (Thomas and Abery 1995, Kearns *et al.* 1998. Maes and Van Dyck 2001, Thomas *et al.* 2004, Biesmeijer *et al.* 2006, Colla and Packer 2008, Goulson *et al.* 2008, Van Dyck *et al.* 2009, Potts *et al.* 2010, Cameron *et al.* 2011, Bommarco *et al.* 2012, Bartomeus *et al.* 2013a, Burkle *et al.* 2013, Fox 2013, Dirzo *et al.* 2014, Goulson *et al.* 2015, Koh *et al.* 2016). These declines stem from human activity, primarily habitat loss and resulting fragmentation, increasing pesticide use, reduction in quality and quantity of floral resources, introduction of alien species, high pathogen loads, and climate change – all of which are often occurring in concert with other factors, increasing their impacts through interactions (Goulson *et al.* 2008, Winfree *et al.* 2009, Potts *et al.* 2010, Winfree 2010, Vanbergen *et al.* 2013, Goulson *et al.* 2015).

1.3 Floral Resources Greatly Impact Bee Communities

An understanding of the mechanisms responsible for bee community composition is crucial for their conservation in natural systems and their restoration in human-dominated urban and agricultural landscapes (Dixon 2009, Roulston and Goodell 2011). Bee populations are impacted directly by three things: floral resources, nesting resources and risk, primarily from natural enemies (Roulston and Goodell 2011). Relationships between bees and their floral resources have received the most attention, providing evidence of floral resources structuring bee communities and controlling bee population dynamics (Potts *et al.* 2003b, Williams and Kremen 2007, Roulston and Goodell 2011). Although many plant-pollinator relationships are generalized, bees are often limited in space and time by available resources; which vary in richness, abundance and phenology (Waser *et al.* 1996, Bosch *et al.* 1997). Bees are also limited in food choice by their own physiology and morphology (Stang *et al.* 2009, Zurbuchen *et al.* 2010).

Pollinator restoration studies often focus on the importance of plant communities to the composition of bees and other pollinator studies. Therefore, my first chapter considers the generality of such claims through a meta-analytic approach that considers how richness of plants influences the richness of pollinators in ecosystems across the globe. Through this work, I have found that although plant richness does have a positive correlation to pollinator richness, it does not fully explain the patterns of bee biodiversity seen around the world nor local community composition. This is likely because bee populations are also influenced by other factors including nesting resources and risk, primarily from natural enemies (Roulston and Goodell 2011).

1.4 Bees as Potential Invasive Species

Although bees are generally considered to be positive actors in their ecosystems, there is an increasing number of bees that have been introduced to new ecosystems and in some cases, could be considered invasive species. My middle and last chapters focus on two non-native bee species, *Osmia taurus* and *O. cornifrons* that have become naturalized across the eastern seaboard. In these chapters I seek to determine how these bees may be influenced by the introduction of artificial nesting substrate and increasing temperatures due to climate change.

Invasive species are considered a major environmental problem (but see Davis *et al.* 2012) and a leading cause of biodiversity loss due to extinctions (Clavero and García-Berthou 2005, Pimental *et al.* 2005). Economic costs of invasive species in the United States alone have been estimated at $120 billion per year (Pimentel *et al.* 2005). However, it is also possible that some invasive species may provide beneficial ecosystem services or support native organisms. And not all non-native species are created equal: some non-native species do not become invasive, do not spread and remain at low abundances (Sakai *et al.* 2001, Schlaepfer *et al.* 2011, Davis *et al.* 2012).

Because of their pollination services and the honey provisioning from *Apis mellifera* (honey bees), the public considers most bees to be beneficial insects. This has led to the intentional introduction of non-native bees into new ecosystems for pollination purposes (e.g., *A. mellifera*, *Megachile rotundata*, *Osmia cornifrons*, and multiple bumblebee species like *Bombus terrestris* and *B. ruderatus*). In North America, of the 23 present non-native species, it is estimated that only 0.5% of bee species introductions were accidental (Ascher 2001, Cane 2003, Sheffield *et al.* 2011). The impacts of these introductions are of concern because although bees can provide pollination services, many studies have found negative effects from non-native bee introductions, with many species spreading beyond their introduced ranges (Goulson 2003).

Non-native bees have been documented to negatively impact native plants through decreased pollination efficiency, reduced visitation rates and changing pollen transport patterns. Such effects can reduce fitness of individual plants and change the genetic structure of populations. These impacts arise due to differences in the behaviors and morphologies of introduced species when compared to native pollinators which are more likely to have evolved in tandem with their floral hosts and have greater correspondence in morphology, behavior and phenology (Goulson 2003, Dohzono and Yokoyama 2010, Traveset and Richardson 2011, Goulson and Hughes 2015). Non-native bees, through competition with native bees, may also reduce the overall floral visitation rate to native plants if they either reduce native bee population abundances or directly prevent visitation by native bees (Aizen *et al.* 2008, Dohzono *et al.* 2008, Dohzono and Yokoyama 2010, Santos *et al.* 2012, Aizen *et al.* 2014, Sanguinetti and Bustos Singer 2014). Introduced bees may also harm plants indirectly via provisioning of pollination services to non-native plants (Goulson 2003, Barthell *et al.* 2001, Liu and Pemberton 2009, Aizen *et al.* 2014).

Invasive bees may have negative impacts on native bees through competition for nesting and floral resources, spread of parasites and pathogens, and hybridization resulting in reproductive disruptions (Hansen *et al.* 2002, Goulson 2003, Park *et al.* 2009, Dohzono and Yokoyama 2010, Santos *et al.* 2012, Morales *et al.* 2013, Sanguinetti and Bustos Singer 2014, Hedtke *et al.* 2015). These impacts are more likely to occur between closely related species and those species that are most similar to the non-native bee species in morphology, ecological niche or behavior (Thomson 2004, Ings *et al.* 2006, Dohzono and Yokoyama 2010, Goulson 2010, Morales *et al.* 2013).

North America is experiencing an increase in the number of non-native bees introduced over the past few decades and the impacts of these introductions are only beginning to be explored (e.g., *Anthidium manicatum* - Gibbs and Sheffield 2009). The ecological effects of these non-native bees in their introduced range is generally unknown. As described above, many studies indicate that that non-native bees generally have negative effects on native pollinators and plants. However, when floral resources are abundant and native bee communities are flexible in their foraging behaviors there may be little competition with invasive bees (Roubik and Villanueva-Gutierrez 2009). Furthermore, in select cases some non-native bees have been found to benefit native plants, providing efficient pollination services and increasing plant reproductive success, especially in light of declining native pollinator species (e.g., Junker *et al.* 2010, Sanguinetti and Bustos Singer 2014). It may also be that super-generalist non-native bees could provide resilience to plant-pollinator interaction webs in the face of disturbance and other environmental changes (Schlaepfer *et al.* 2011, Traveset *et al.* 2013).

1.5 *Osmia cornifrons* and *O. taurus*

1.5.1 Introduction of *Osmia cornifrons* and *O. taurus* to the United States

Osmia cornifrons was introduced to the United States in 1977 from Japan for managed pollination of fruit trees (Batra 1979, Abel and Wilson 1999, Goulson 2003), but has since escaped quarantine and spread across eastern North America with isolated populations in the Western US as well (Figure 1.1). *O. taurus* was unintentionally introduced to the US from Japan, likely at the same time as *O. cornifrons* (the two species look incredibly similar and are almost cryptic species) (Ascher 2001). *O. taurus* has also since spread across a similar range as *O. cornifrons* (Figure 1.1). Although *O. cornifrons* has been studied in both its native range (Miyamoto 1959, Sugiura and Maeta 1989, Kim *et al.* 2008, Matsumoto *et al.* 2009, Yoon *et al.* 2009, Ahn *et al.* 2014, Lee *et al.* 2015, Lee *et al.* 2016) and its introduced range (Abel and Wilson 1998, Wilson *et al.* 1999, Bosch and Kemp 2002, White *et al.* 2009, McKinney and Park 2012, Hedtke *et al.* 2015), there is very little information about *O. taurus* in either its introduced range or native range (but see Miyamoto 1959, Jeong *et al.* 2009, Yoon *et al.* 2009).

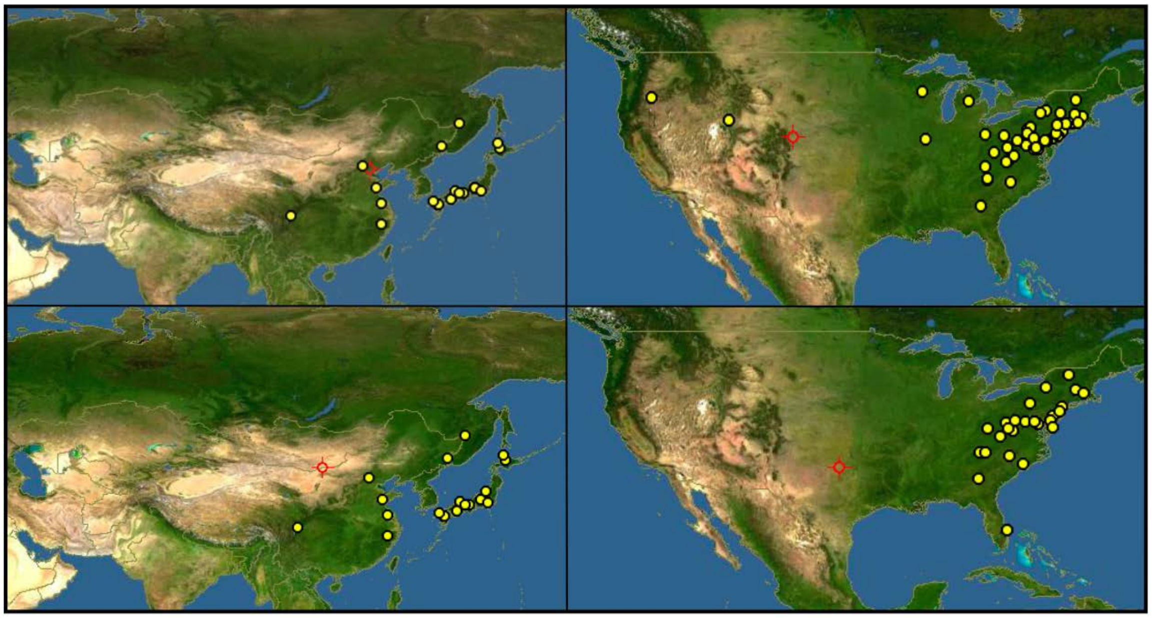

Figure 1.1 Both *Osmia cornifrons* and *O. taurus* have native ranges in north-eastern Asia including China, Japan and Korea and introduced ranges in eastern North America, top: *O. cornifrons* and bottom: *O. taurus* (left: native range, right: introduced range). These maps are taken from DiscoverLife (http://www.discoverlife.org) and indicate specimens in this database. They do not reflect the entire range of these species. Images taken 24 September 2016.

1.5.2 Natural History of *Osmia cornifrons* and *O. taurus*

O. cornifrons and *O. taurus*, are univoltine, solitary, cavity-nesting bees that nest in pre-existing cavities found primarily in wood (Bosch *et al.* 2001). They will also nest in artificial nesting substrate, including wooden nest boxes with holes drilled into them. After emerging from her natal nest, a female *Osmia* mates and upon finding a suitable cavity she founds her nest, lining it with mud. As solitary bees, *Osmia* females forage for pollen and nectar alone and without assistance from other bees (Bosch *et al.* 2001, McKinney and Park 2012). Both *Osmia cornifrons* and *O. taurus* are pollen generalists (Haider *et al.* 2014), possibly with a preference for plants within the Rosaceae family (Abel and Wilson 1999), and are active in spring (April to May) in both introduced and native ranges (Miyamoto 1959, C. DeVan, *pers. obs.*). An *Osmia* female provisions each individual egg with a pollen and nectar ball within its own cell, sealed off with mud (Bosch *et al*. 2001, McKinney and Park 2012). The size of the provision determines the size of the offspring as an adult, with female offspring generally being larger than males, and situated toward the back of the nest. Studies of *O. cornifrons* and related *Osmia* species have found that females can determine the sex of their young (Sugiura and Maeta 1989, Bosch and Vicens 2006, Radmacher and Strohm 2010). Each nest has between 8 to 22 cells (C. DeVan, *pers. obs*.) and one female can make more than one nest depending on the longevity, fecundity, and foraging efficiency of the female within the context of available floral resources and weather during the foraging season (Sugiura and Maeta 1989, Bosch and Vicens 2006, Radmacher and Strohm 2010).

For successful reproduction, these *Osmia* species require appropriate floral and nesting resources. Nesting resource availability has been found to influence the abundance of cavity nesting species (Steffan-Dewenter and Schiele 2008, Vickruck and Richards 2012) and overall bee community composition (Potts *et al.* 2005, Grundel *et al.* 2010). Appropriate nesting resources for cavity nesting bees are defined as holes of a reasonable size relative to their body size in quality substrate with a source of nest lining material (mud in the case of *Osmia cornifrons* and *O. taurus*) nearby (Morato and Martins 2006, Cane *et al.* 2007, McKinney and Park 2012). Microclimate also influences use of nesting resources (Everaars *et al.* 2011).

Furthermore, these nesting sites must have floral resources within their foraging range (Morato and Martins 2006, Guedot *et al.* 2009, Zurbuchen *et al.* 2010). Other studies have found floral resource availability has been a good predictor of nesting abundance for cavity nesting bees (Gathmann *et al.* 1994, Tscharntke *et al.* 1998, Goodell

2003, Guisse and Miller 2011, Ebeling *et al.* 2012). As pollen generalists both *O. cornifrons* and *O. taurus* are able to utilize a range of plant hosts, although there is some indication that they prefer plants in the Rosaceae family (Abel and Wilson 1999).

1.5.3 *Osmia cornifrons* and *O. taurus* in New Jersey

Most previous studies focus on the pollination potential of *Osmia cornifrons* and *O. taurus* and how to manage them for pollination purposes while little has been done to determine what ecological factors might limit their spread. Both *O. cornifrons* and *O. taurus* have demonstrated an ability to thrive in North America, including in central New Jersey, therefore it is important to understand what factors may limit their population sizes, in order to manage their potentially negative impacts on native ecosystems as well as the pollination services they may provide.

In general, bee populations are limited by the quantity and quality of floral and nesting resources as well as the presence of competitors and natural enemies (Murray *et al.* 2009, Roulston and Goodell 2011). In my third chapter, I seek to determine what factors influence the usage of artificial boxes by these two, non-native species. Recent work suggests introduction of nesting resources can benefit non-native species over native species (MacIvor and Packer 2015) and in my study site of Morristown, NJ, no native species were found to use my artificial nest boxes. Understanding what factors influence the usage of these nest boxes by *O. cornifrons* and *O. taurus* can help us better understand how to manage both wild and cultivated populations.

1.6 Climate Change Impacts on Spring Emergence of Bees

One of the most observable impacts of climate change on biological systems has been modification of the phenology of both plants and animals (Walther *et al.* 2002, Parmesan and Yohe 2003, Gordo and Sanz 2006, Parmesan 2006, Hegland *et al.* 2009). Phenology is the seasonal timing of organismal life history events and is especially sensitive to climatic variation. Elements of climate, including temperature, act as triggers for particular life stages in phenologically sensitive organisms (Menzel *et al.* 2006). As average temperatures have increased over the past few decades in temperate regions phenological shifts are being observed in plants and insects (Walther *et al.* 2002, Parmesan and Yohe 2003, Gordo and Sanz 2006, Parmesan 2006, Thackeray *et al.* 2010; Bartomeus *et al.* 2011).

My final study considers how earlier spring temperatures caused by climate change may influence both *O. cornifrons* and *O. taurus*. They have successfully expanded their range to large swaths of North America, and as their native range in Asia has a similar climate, it seems they are in effect pre-adapted to their new home. *O. cornifrons* has been shown to be phenologically sensitive (White *et al.* 2009), but little is known about the emergence timing of *O. taurus*. The northeastern United States has experienced an increase of 0.25°C per decade since the 1970s and is projected to increase by around 3-5°C over the next 50-100 years (Hayhoe *et al.* 2006, Dukes *et al.* 2009). With this increase in temperature, average spring temperatures in the northeast are also increasing and have resulted in advancing phenology of native bees and plants (Bartomeus *et al.* 2011). In my final chapter, I experimentally test whether non-native, spring emerging bees, like *O. cornifrons* and *O. taurus*, will advance their emergence in conjunction with the increasing spring temperatures likely to occur due to future climate change.

CHAPTER 2

PLANTS AND POLLINATORS SHOW STRONG CORRELATION IN DIVERSITY ACROSS TIME AND SPACE

2.1 Background

Insect pollinators are critical for the continued survival of plants in both natural and agricultural ecosystems (National Research Council 2006, Thomann *et al.* 2013). The majority of all flowering plants are dependent on biotic pollination for reproduction (Ollerton *et al.* 2011) and of the world's leading crops, over 75% depend on animal pollination (Klein *et al.* 2007, Winfree 2008). The economic value of pollination is estimated to be around $316 billion globally (Lautenbach *et al.* 2012) and pollinators are valued for non-economic reasons including aesthetics, their role in contributing to diverse wildflower communities (Hanley *et al.* 2015), and to human nutrition (Eilers *et al.* 2011).

However, the honey bee (*Apis mellifera*), the world's primary managed pollinator, is declining in many parts of the globe due to the spread of *Varroa* mites and other pathogens, which can lead to Colony Collapse Disorder (CCD), as well as impacts from pesticides and reduced nutritional diversity (Kluser and Peduzzi 2007, vanEnglesdorp *et al.* 2010, Goulson *et al.* 2015, Sandhu *et al.* 2016). Managed honey bee decline is of huge concern worldwide due to its implications for agricultural production. However, recent studies indicate that non-managed pollinators, especially wild bees, are effective pollinators for a wide variety of crops, often providing pollination services equal to or greater than those of the managed honey bee *A. mellifera* (Kremen *et al.* 2002, Greenleaf and Kremen 2006, Winfree *et al.* 2007, Winfree *et al.* 2008, Brittain *et al.* 2013a, Brittain *et al.* 2013b, Garibaldi *et al.* 2013). Yet there is growing evidence that many wild, unmanaged pollinators, especially bees and butterflies, are also declining globally (Thomas and Abery 1995, Maes and Van Dyck 2001, Thomas *et al.* 2004, Biesmeijer *et al.* 2006, Colla and Packer 2008, Goulson *et al.* 2008, Van Dyck *et al.* 2009, Potts *et al.* 2010, Cameron *et al.* 2011, Bommarco *et al.* 2012, Bartomeus *et al.* 2013a, Burkle *et al.* 2013, Fox 2013, Dirzo *et al.* 2014, Goulson *et al.* 2015, Koh *et al.* 2016). These declines stem from human activity, primarily habitat loss and resulting fragmentation, increasing pesticide use, reduction in quality and quantity of floral resources, introduction of alien species, high pathogen loads, and climate change – all of which are often occurring in concert with other factors, increasing their impacts through interactions (Goulson *et al.* 2008, Winfree *et al.* 2009, Potts *et al.* 2010, Winfree 2010, Vanbergen *et al.* 2013, Goulson *et al.* 2015).

Pollinator declines result in depauperate, homogenized communities dominated by the species that are tolerant of, or benefit from, human induced disturbances (Biesmeijer *et al.* 2006, Fründ *et al.* 2013, Vanbergen *et al.* 2013, Nielsen and Totland 2014; Kuhsel and Bluthgen 2015). Loss of diversity in pollinator communities has broader implications. Pollination services in managed and unmanaged ecosystems tend to increase with pollinator diversity, resulting in reduced pollen limitation and higher seed and fruit set (Albrecht *et al.* 2012, Bommarco *et al.* 2012, Davila *et al.* 2012, Brittain *et al.* 2013a, Brittain *et al.* 2013b, Fründ *et al.* 2013). Diversity may also serve as a buffer to the large temporal variability in individual pollinator populations ensuring adequate pollination year after year (Kremen *et al.* 2002) as well as reducing competition between plants for pollinators (Vamosi *et al.* 2006) and maintaining long term genetic diversity in plant populations (Benadi *et al.* 2013). Diverse pollinator communities are more likely to contain highly efficient pollinator species (Kleijn *et al.* 2015) and are also more resilient to disturbance ensuring pollination services even in the face of change (Winfree and Kremen 2009, Bartomeus *et al.* 2013b, Brittain *et al.* 2013a, Rader *et al.* 2013). But loss of diversity over time may reduce this resilience making it harder to maintain pollination services in the face of future changes (Burkle *et al.* 2013, Vanbergen *et al.* 2013, Koh *et al.* 2016).

Many animal-pollinated natural and agriculture systems across the globe are increasingly vulnerable to these pollinator losses (Calderone 2012, Leonhardt *et al.* 2013, Koh *et al.* 2016, although see Ghazoul 2005) and species endemic to biodiversity hotspots may be particularly at risk (Hoekstra *et al.* 2004, Vamosi *et al.* 2006). Therefore, in order to maintain global food supplies, as well as to preserve native plants we must determine which factors support diverse pollinator communities.

As all pollinators use flowering plants as a food source, either for the pollen or the nectar, for at least part of their life cycles, it has often been assumed that flowering plant communities structure pollinator communities (Potts *et al.* 2003b). Bees are considered the most important pollinator taxa globally (Winfree *et al.* 2008, Kleijn *et al.* 2015) in part because bees are completely dependent on flowers for food resources for their entire lives (O'Toole and Raw 1999). At the species level, it has been demonstrated that for some oligolectic bee species (bees whose larvae consume pollen from a narrow range of flowering species), availability and abundance of the host plant strongly predicts bee population size (Larsson and Franzen 2007). It has also been shown that for polylectic or generalist bee individuals, availability of native flowering plant species is positively associated with reproductive output (Williams and Kremen 2007). Furthermore, declines in butterflies have been linked to a reduction of nectar plants (Wallisdevries *et al.* 2012) and most studies analyzing declines in pollinator communities have found that bees with a narrow diet breadth are more likely to be impacted (Biesmeijer *et al.* 2006, Cane *et al.* 2006, Williams *et al.* 2010, Bartomeus *et al.* 2013a, Burkle *et al.* 2013, Weiner *et al.* 2014), suggesting that floral resources play a strong role in determining community composition of pollinator communities. However, it could also be hypothesized that pollinator species diversity may structure plant communities (Grundel *et al.* 2010), which may depend on functional complementarity between pollinators and their pollination efficiency (Perfectti *et al.* 2009, Fründ *et al.* 2013; but see Benadi *et al.* 2013). Loss of pollinators has also been found to lead to declines in plant populations (Biesmeijer *et al.* 2006, Leonhardt *et al.* 2013, Thomann *et a*l. 2013), with specialized interactions more likely to be impacted (Weiner *et al.* 2014, although see Benadi *et al.* 2013). Of course, it is also possible that there is no functional relationship between plant diversity and pollinator diversity and that rather these organisms co-vary in their richness and abundance due to similar responses to shared environmental conditions (Wolters *et al*. 2006; Castagneyrol and Jactel 2012).

Experiments can tease apart these relationships and determine the extent to which plant species diversity structures bee species diversity, or vice versa. However, empirical evidence is limited. The “Jena” experiment in Germany varied plant species richness and found that bee species richness was positively related to flowering plant species richness saturating at the highest levels of plant richness (Ebeling *et al.* 2008, Scherber *et al.* 2010). Ghazoul (2006) found an increase in pollinator visits to *Raphanus raphanistrum* when planted with other co-occuring flowering plant species of similar value to pollinators as compared to when part of a *R. raphanistrum* monoculture. Fontaine *et al.* (2006) demonstrated that increasing richness of pollinator species resulted in higher plant species richness in experimental communities and Fründ *et al.* (2013) and Albrecht *et al.* (2012) found higher seed production in plant communities visited by diverse pollinator communities than those visited by just one pollinator species.

For lack of experiments that could determine causality, I ask a simpler question: Are pollinator and plant species richness and abundance correlated in observational studies? A correlation (or congruence) between richness of taxa has been used to validate the use of surrogates in conservation efforts, with one taxa standing in for another (Castagneyrol and Jactel 2012). If plant and pollinator diversity are correlated, then plants, a well-studied taxon, could be used to plan and prioritize conservation efforts for pollinators. Previous studies on the correlation between different taxa (e.g., plants and various groups of animals) have found a greater correlation between the richness of two taxonomic groups when they share "close evolutionary bonds" including those that interact directly, like primary consumers (including pollinators) and producers (Wolters *et al.* 2006; Lewinsohn *et al.* 2008; Castagneyrol and Jactel 2012). Therefore, it is the aim of this paper to determine through a meta-analysis the relationship between the abundance and diversity of pollinators and flowering plants.

A number of observational surveys of natural, semi-natural, and human-impacted ecosystems have been undertaken that measure the diversity of plant communities and of pollinator or flower visitor communities. These studies are often focused not directly on how plant communities structure pollinator communities, but rather on natural, anthropogenic, or land management impacts on plant and pollinator communities. I rely on this larger body of literature for this meta-analysis. A comparison of these surveys could indicate the direction and strength of the relationship between bees and flowering plants in natural and managed ecosystems. A meta-analysis across sites from various ecosystems would also provide clues to whether such patterns are found globally or only in specific locales and to test which factors influence the strength of this relationship. Global patterns of plant and pollinator biodiversity have been found to vary by taxa (Castagneyrol and Jactel 2012) and by biome. For example, plant biodiversity has been found to be higher in the tropics than in temperate regions, but pollinator richness may show different patterns. Butterflies may also have a higher richness in the tropics, while bees may have greater richness in xeric areas (Michener 1979; Olesen and Jordano 2002; Schluening *et al.* 2012).

Therefore, I hypothesize that within communities, *pollinator species richness is positively correlated to plant species richness* and *pollinator abundance is positively correlated to plant abundance*. Furthermore, I predict that the strength of these meta-correlations will be higher for *pollinator taxa* that are dependent on plants for their entire life cycle rather than for only one life stage. I also hypothesize that this relationship between plants and pollinators is driven more by food availability than by overall habitat characteristics. Consequently, I predict that *type of plant* and *flowering status of plants* will impact the strength of correlation coefficients with higher correlations for flowering plants than for non-flowering and flowering plants combined. Because habitat characteristics can also influence these meta-correlations, I predict that *biome* will have an impact on the strength of the relationship between diversity of plants and pollinators with higher correlations occurring in biomes where both plants and pollinators have high richness. Finally, I predict that *sampling methods* for both *pollinators* and *plants* will impact the strength of correlations between plant and pollinator diversity.

2.2 Methods

2.2.1 Literature Search

I did a comprehensive search for articles that included pollinator and plant diversity measures. I primarily used Web of Science and Google Scholar for my search, combined with additional sources (primarily for older publications) pulled from the works cited pages of papers I had already identified. I used both general search terms (pollinat* AND plant* OR flower* AND rich* OR abund* OR divers*) and pollinator specific search terms in the place of pollinat* (bee*, apid*, hymenopter*, wasp*, dipt*, syrphid*, bombyllid*, lepidopt*, butterfl*, moth*). For the purposes of my paper, pollinator includes all invertebrate flower visitors, but does not include studies on life-stages that do not visit flowers, (e.g., caterpillars). I focused on the diversity measures of richness and abundance that are most commonly used (evenness, Simpson's Diversity Index, Shannon's Diversity Index). I concluded my search for papers in mid-2015.

2.2.2 Data Collection

For my analysis, I only included studies that contained direct correlation coefficients and sample sizes in either the text or figures. Papers that only contained multivariate analyses, multiple regressions, and structural equation models were not included. From these papers, I extracted correlation coefficients (Pearson's, Kendall's and Spearman's correlations), sample size (n) and other information relevant to my additional hypotheses. All correlation coefficients and ancillary data were extracted directly from the text where possible. When not directly presented, Pearson's correlation coefficient was calculated from data extracted from figures using Plot Digitizer™. Sometimes the number of data points visible in the figure differed from the stated sample size in the paper. In these cases, the sample size was determined based on the figure from which the data were extracted. Some correlation coefficients were transformed to r from F statistic and R^2 values using the standard conversions (Castagneyrol & Jactel 2012). Studies from the same location and time period but published in separate works were not considered as independent data.

2.2.3 Calculating Effect Size

I transformed each r value using Fisher's z transformation, where r is the correlation coefficient for each study, in order to calculate the effect size of each individual data point (Borenstein 2009, Castagneyrol and Jactel 2012).

$$z = 0.5 \log[(1 + r)/(1 - r)] \tag{2.1}$$

Positive z values indicate a positive correlation between pollinator and plant richness or abundance. All individual effect sizes are combined into a grand mean effect size per hypothesis (Gurevitch and Hedges 1999, Borenstein 2009). For the primary meta-regressions of the effect of plant richness on pollinator richness and plant abundance on pollinator abundance, each data point is either one study or independent values from the same study. Independent data points include individually reported correlations for different pollinator and plant taxonomic groupings and spatially separated locations. When multiple units of time (e.g., years, seasons, months) were reported individually for the same place they were averaged to create one data point. Where both flowering plants and all plant correlations were available for the same study, flowering plant correlation coefficients were used. Similarly, when data were available by specific pollinator taxa (e.g., hoverflies, bees, and butterflies) and by pollinator order, (e.g., Diptera, Hymenoptera and Lepidoptera), pollinator taxa, not pollinator order was used. This maximized the statistical power to determine effects of pollinator types and better reflected biological differences between pollinators, as orders may include pollinating and non-pollinating taxa (e.g., Hymenoptera includes bees, known as an important pollinator group and wasps which are not primarily known as pollinators).

2.2.4 Covariates

I also tested the importance of several covariates on the strength of the correlation between pollinator and plant community richness and abundance. I tested the impacts of pollinator type, plant type and flowering status, biome, and sampling methods for both plants and pollinators on my overall meta-correlations. Only covariate factors with $n \geq 1$ were used in the analysis.

Pollinator type. For each data point, pollinator taxa were noted as described in the published study. Studies that did not provide r values per individual pollinator taxon are coded as “mixed”. Analysis of the importance of pollinator taxa did not include the “mixed” group, meaning that each r value was associated with only one pollinator taxon.

Some pollinator taxa come from the same published study and therefore share plant communities. Analysis was also performed on pollinator grouping, comparing mixed pollinator groups to single pollinator taxa.

Plant type and flowering status. Plant taxon data points were also noted as described in the published study. If plant groups were specified in the publication they were categorized as either herbaceous (non-woody) or woody (trees, shrubs, lianas) otherwise they are coded as "plants." Analysis of the importance of plant type was performed with a data set that did not include the "plants" group, meaning that each *r* value was associated with only one plant type (woody or herbaceous). Some plant types come from the same published study and therefore share pollinator communities. Analysis was also performed on plant grouping, comparing groups of mixed plant types to a single plant type. Flowering status indicates whether the plants surveyed in the study included all plants or only the insect-pollinated plants in flower at the time. In this study, the term "flowering" includes all flowering plants pollinated by insects. Flowering plants that are have abiotic pollination or are pollinated by vertebrate animals are considered in this study to be "non-flowering." Terms used by authors and considered to indicate an insect-pollinated flowering status include "bee plants," "nectar plants," "insect pollinated plants," or "entomophilous plants." Where no mention was made, it was assumed that the survey included all plants in the area, not just those that were insect-pollinated. If correlations from both groupings were published, only the correlation with "flowering" plants was utilized.

Biome. All data points were mapped using the latitude/longitude provided in the published study. If a data point encompasses a latitudinal range, the middle point is used.

Where no latitude/longitude was available, studies were mapped based on the published location (e.g., Paris, France) using GoogleEarthPro. For all data points where location could be determined, I recorded the biome designation following Olsen *et al.* (2001), with the exception that all temperate and tropical forest types were combined into two broader categories of temperate forests and tropical forests.

Pollinator sampling methodology. Pollinators can be sampled by a variety of both passive and active methods. I broadly compared “active” sampling methods to “passive” sampling methods where “active” methods are defined as techniques that require the observer to be present and actively looking for pollinators (i.e., “observation” or “netting”) while “passive” techniques do not require the observer to be present (i.e., “traps”) or if the observer is present but they are not actively searching for pollinators (i.e., “sweep netting”). If a combination of “active” and “passive” methods are being used, I categorized the study as using “both.” I further distinguished between the specific sampling techniques used. Techniques included “traps” (e.g., light traps, bait traps, pan traps, Malaise traps, trap nests), “observation” where no samples were physically collected only visually observed, “netting” which refers to samples that are targeted (i.e., actively collected upon visual observation) and “sweep netting” which refers to samples collected by non-targeting netting (i.e., netting all samples in an area not focused on collecting specifically observed organisms) or a combination of these main methods.

Plant sampling methodology. Plants can also be sampled in a variety of ways including the use of both transects and plots. These sampling methods vary in both shape and sampling area. Therefore, I broadly compared transect sampling or “linear” sampling methods to both “circular” and “square” plot sampling. I also considered the overall size of sampling area (m^2) per study.

2.2.5 Analysis

To quantify the mean correlation between plant and pollinator diversity I implemented mixed random-effects models via the Metafor package (Viechtbauer 2010) in R (R Core Team 2012). Raw correlation coefficients were first converted to Fisher’s *z*-scores as described above. Transformation to Fisher’s *z* stabilizes the variance and also normalizes the data. Metafor uses inverse variance weights to combine study effect sizes into a summary effect size (Borenstein 2009, Viechtbauer 2010). Results were back-transformed to *r* for graphical presentation. Models were fit using restricted maximum likelihood (Viechtbauer 2005). Model fit was assessed by visual inspection of Q-Q normal plots. I quantified I^2 to assess potential variability among the true effect sizes (Higgins and Thompson 2002, Borenstein 2009). Overall model significance and significance of moderators was determined by Cochran’s Q-test (Viechtbauer 2010).

I tested for publication bias by inspection of funnel plots (Light and Pillemer 1984, Lewis and Clarke 2001, Sterne and Egger 2001, Rothstein *et al.* 2005). Funnel plots are plots of the effect size estimates per study against the standard error of the study. Studies with larger sample sizes should have higher precision and lower standard error and converge upon similar results assuming a true underlying treatment effect. In contrast, studies with small sample sizes will be less precise with higher standard errors and their results could vary more widely. Therefore, absent significant bias, when plotting effect size against sample size, an inverted funnel shape should result, with smaller sample size studies as the base of the funnel and larger sample size studies as the funnel tip. If the funnel plot is asymmetrical or skewed it indicates potential bias, with 'significant' correlations over-reported and 'non-significant' results under-reported. To test for asymmetry in the funnel plot I also performed a regression test (Egger *et al.* 1997).

2.3 Results

2.3.1 Overall Meta-Correlations

I identified 1461 papers in total, from which I was able to use 150 papers across all of my analyses (Appendix A). From these papers, I identified 165 independent data points for use in the plant richness – pollinator richness analyses and 84 independent data points for use in the plant abundance – pollinator abundance analyses. Only studies with an n > 4 were included in the meta-regressions. The studies in this meta-analysis span a 40-year period (1974 – 2014) and have global coverage including 37 countries on all continents except Antarctica. Temperate zones in Europe and North America were most commonly represented and bees and butterflies are the most commonly studied pollinator taxa. All analyses of congruence between diversity correlations of plants and pollinators showed significantly positive relationships (Table 2.1).

Table 2.1 Results of Plant-Pollinator Diversity Meta-Correlations: Effect Size (*r*), Sample Size (n), and 95% Confidence Intervals

Analysis	*r*	n	95% Confidence Interval
plant richness – pollinator richness	0.4537	127	0.3965 – 0.5075
plant abundance – pollinator abundance	0.4915	68	0.3034 – 0.5021

2.3.2 Heterogeneity and Covariates

My results also suggest significant and substantial variability due to heterogeneity in both analyses (Table 2.2). I tested several covariates as sources for this heterogeneity.

Table 2.2 Substantial Variability Due to Heterogeneity (I^2) was Found in Both Analyses

Analyses	**I^2**	**95% Confidence Interval**
plant richness – pollinator richness	65.94%	58.44% - 77.69%
plant abundance – pollinator abundance	78.18%	58.53% - 84.97%

Of the tested covariates, I found that plant type and flowering status, biome and pollinator sampling methods had a significant impact on the relationship between pollinator richness and plant richness. Only biome had a significant impact on the relationship between plant abundance and pollinator abundance. I did not find a significant impact of pollinator type or plant sampling methodology on my meta-correlations for either richness (Table 2.3) or abundance (Table 2.4).

Table 2.3 Significance of the Impact of Moderators on Plant Richness - Pollinator Richness Correlation Coefficients

Moderator	**QM**	**d. f.**	***p***
Pollinator type	1.8805	4	0.7577
Pollinator grouping	0.8015	1	0.3706
Plant type	15.1872	1	**<0.0001**
Plant grouping	8.0656	1	**0.0045**
Flowering status	5.5337	1	**0.0187**
Biome	24.8502	6	**0.0004**
Pollinator method	6.3437	2	**0.0419**
Pollinator method type	12.559	5	**0.0279**
Plant sampling method	3.4369	2	0.1793
Plant sampling area	0.0145	1	0.9041

Table 2.4 Significance of the Impact of Moderators on Plant Abundance - Pollinator Abundance Correlation Coefficients

Moderator	**QM**	**d. f.**	***p***
Pollinator type	6.4029	3	0.0936
Pollinator grouping	0.1224	1	0.7264
Plant type	0.9663	1	0.3256
Plant grouping	0.0726	1	0.7875
Flowering status	0.0606	1	0.8056
Biome	18.0595	6	**0.0061**
Pollinator method	1.3039	2	0.521
Pollinator method type	8.7699	5	0.1186
Plant sampling method	2.7580	2	0.6845
Plant sampling area	0.0690	1	0.7928

Pollinator type. There was no significant effect of pollinator taxa on the congruence of plant and pollinator richness nor on plant and pollinator abundance. Bees, butterflies and moths showed a significant positive relationship between plant and pollinator richness and plant and pollinator abundance. Analyses comparing congruence of the overall pollinator diversity (including all pollinator taxa in one group) to plant diversity, found similar correlation coefficients as analyses that compared individual taxa (e.g., bees or butterflies) to plant diversity (Figure 2.1).

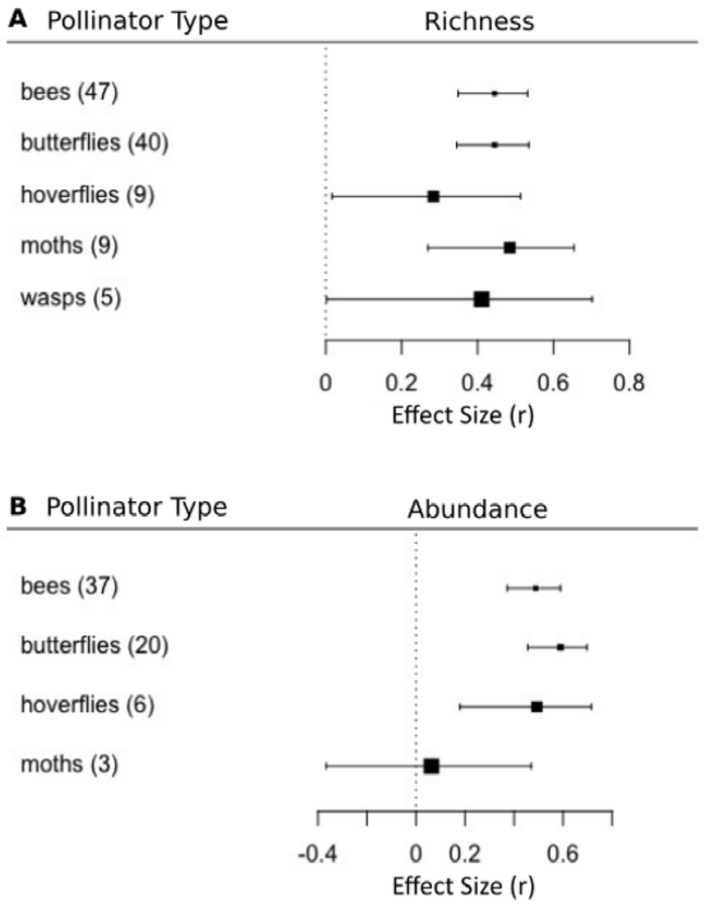

Figure 2.1 Forest plots indicating effect sizes (*r*) by pollinator taxon for pollinator richness – plant richness (A) and pollinator abundance – plant abundance (B). Error bars are 95% confidence intervals (CI) and observed effect size (represented by a square) is proportional to the precision of the estimate, with smaller squares indicating higher precision. Effects are considered significant when a CI does not overlap 0. Number of data points per pollinator type is indicated by the number in parentheses.

Plant type. There was a significant effect of plant type (plant richness – pollinator richness: QM = 15.1872, df = 1, $p < 0.0001$) on the relationship between plant and pollinator richness, with herbaceous plants having significantly higher correlation coefficient than woody plants. Congruence between plant richness and pollinator richness was also significantly higher when considering both woody and herbaceous plants together as compared to the congruence between only herbaceous plants and pollinators or only woody plants and pollinators (QM: 8.0656, df = 1, p = 0.0045). There were no significant effects of plant type on plant abundance – pollinator abundance correlations (Figure 2.2).

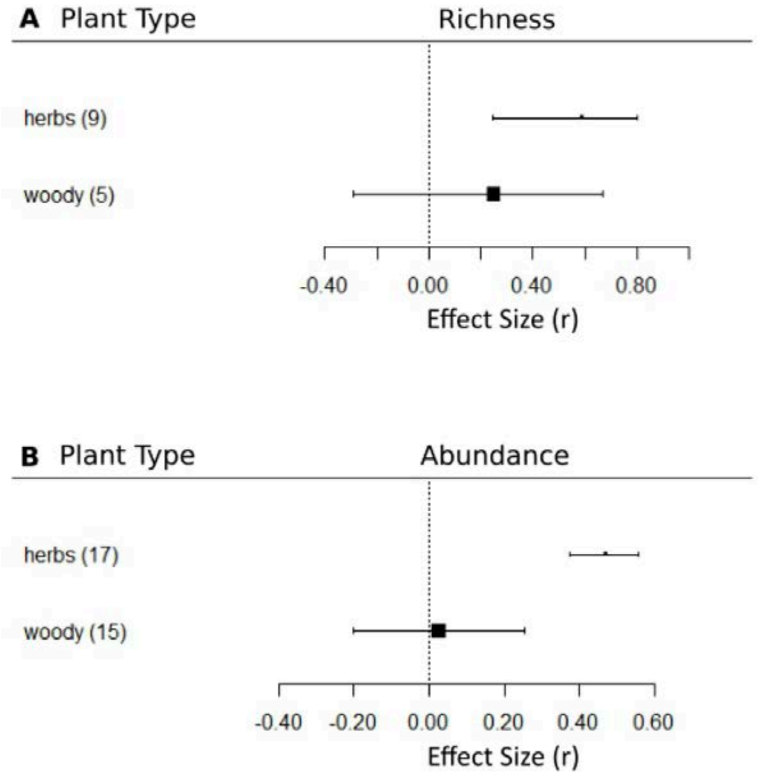

Figure 2.2 Forest plots indicating effect sizes (*r*) by plant type for pollinator richness – plant richness (A) and pollinator abundance – plant abundance (B). Error bars are 95% confidence intervals (CI) and observed effect size (represented by a square) is proportional to the precision of the estimate, with smaller squares indicating higher precision. Effects are considered significant when a CI does not overlap 0. Number of data points per plant type is indicated by the number in parentheses.

Plant Flowering Status. Flowering status has a significant effect on the overall congruence of plant richness and pollinator richness (QM = 5.5337, df = 1, p = 0.0187). Analyses considering only flowering plants had a stronger congruence between plant richness and pollinator richness than analyses considering all plants whether flowering or not. Flowering status did not have a significant effect on the overall congruence between plant abundance and pollinator abundance (Figure 2.3).

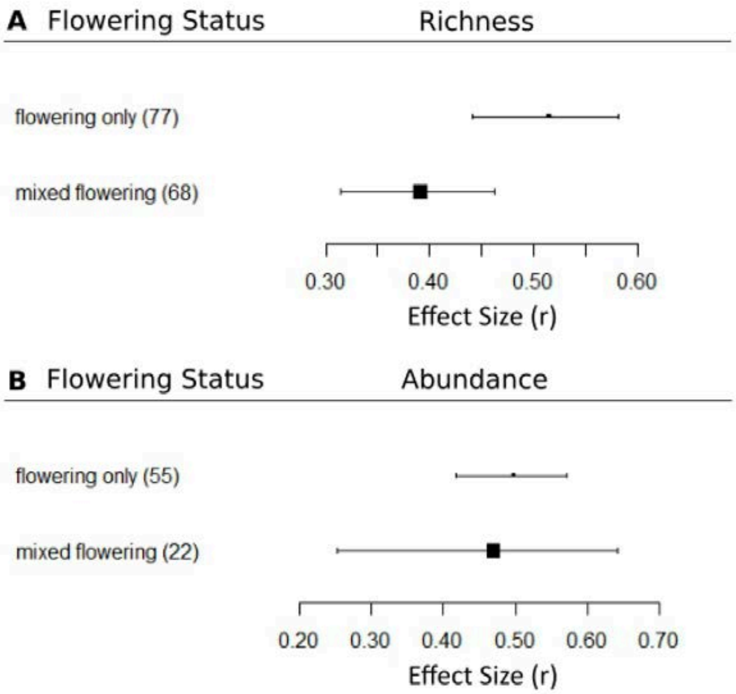

Figure 2.3 Forest plots indicating effect sizes (*r*) by flowering status for pollinator richness – plant richness (A) and pollinator abundance – plant abundance (B). Error bars are 95% confidence intervals (CI) and observed effect size (represented by a square) is proportional to the precision of the estimate, with smaller squares indicating higher precision. Effects are considered significant when a CI does not overlap 0. Number of data points per flowering status designation is indicated by the number in parentheses.

Biome. Biome has a significant effect on the overall congruence of plant richness and pollinator richness (QM = 24.8502, df = 6, $p = 0.0004$). Alpine biomes had the highest congruence between plant richness and pollinator richness, but with a very small sample size. Tropical forests, deserts and boreal forests had lower congruence between plant richness and pollinator richness, while Mediterranean and temperate forests and temperate grasslands had higher congruence for plant richness – pollinator richness. Similarly, congruence between plant abundance and pollinator abundance was also very high for alpine biomes (QM = 18.0595, df = 6, $p = 0.0061$), also with a small sample size.

However, all other biomes showed similar correlation coefficients between plant abundance and pollinator abundance (Figure 2.4).

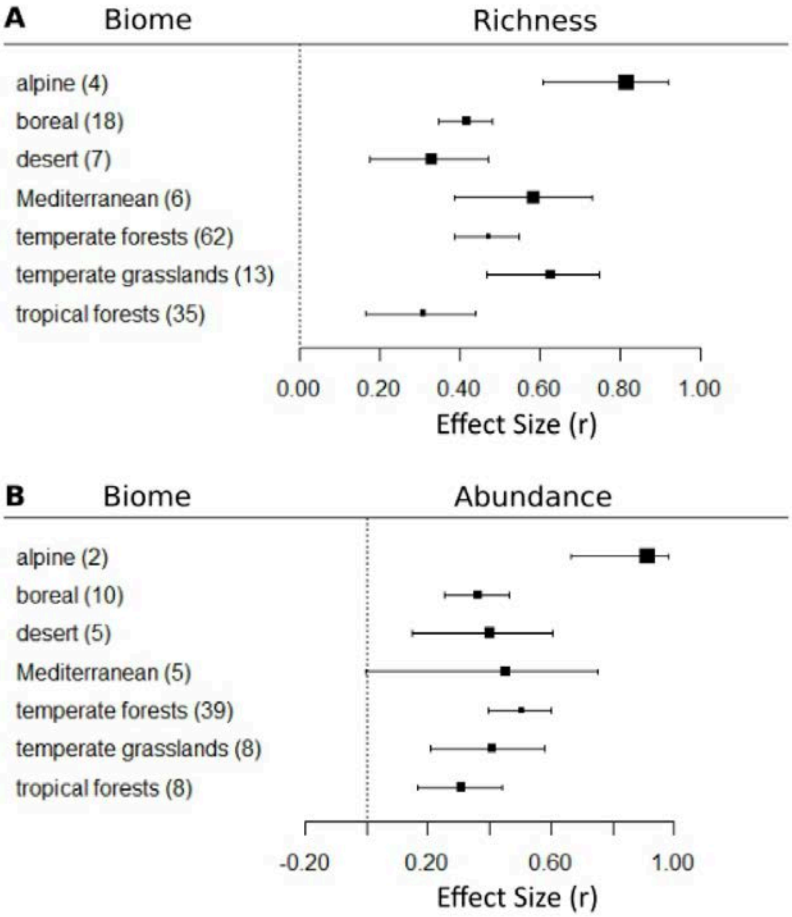

Figure 2.4 Forest plots indicating effect sizes (*r*) by biome for pollinator richness – plant richness (A) and pollinator abundance – plant abundance (B). Error bars are 95% confidence intervals (CI) and observed effect size (represented by a square) is proportional to the precision of the estimate, with smaller squares indicating higher precision. Effects are considered significant when a CI does not overlap 0. Number of data points per biome is indicated by the number in parentheses.

Pollinator sampling methodology. Pollinator sampling method (i.e., passive vs. active) had a significant effect on the congruence of plant richness and pollinator richness (QM = 6.3437, df = 2, p = 0.0419), but had no effect on the congruence between plant abundance and pollinator abundance. Active sampling methods were associated with stronger congruence between pollinator richness and plant richness than were passive sampling methods (Figure 2.5).

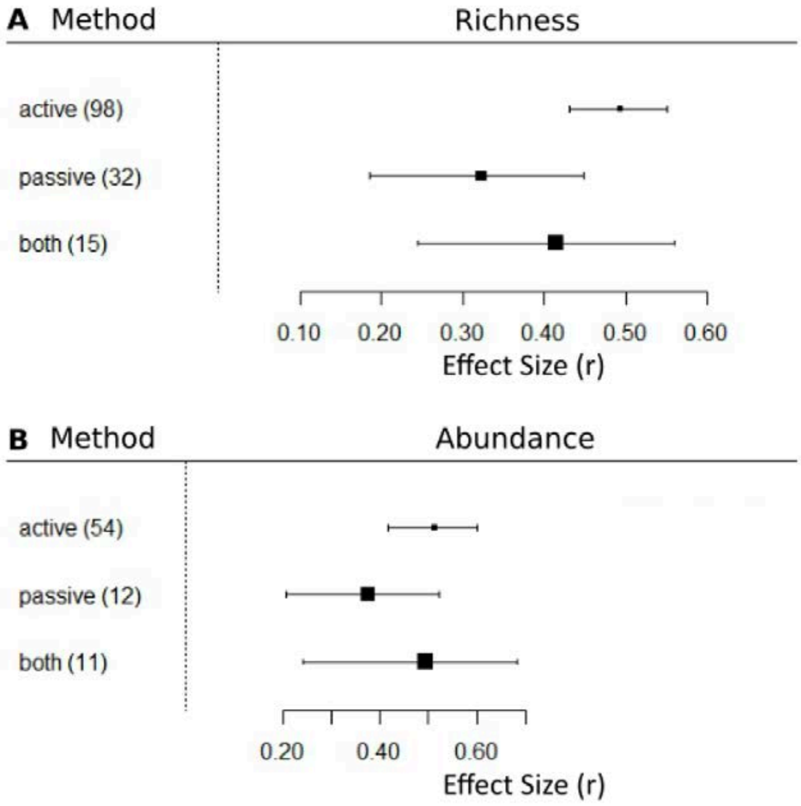

Figure 2.5 Forest plots indicating effect sizes (*r*) by pollinator sampling method for pollinator richness – plant richness (A) and pollinator abundance – plant abundance (B). Error bars are 95% confidence intervals (CI) and observed effect size (represented by a square) is proportional to the precision of the estimate, with smaller squares indicating higher precision. Effects are considered significant when a CI does not overlap 0. Number of data points per pollinator sampling method is indicated by the number in parentheses.

The specific techniques used for pollinator sampling also had a significant effect on the congruence of plant richness and pollinator richness (QM: 12.559, df = 5, p = 0.0279), but not on the congruence of plant abundance and pollinator abundance. Studies that utilized netting, an active sampling method, had the strongest association between pollinator richness and plant richness. Passive methods, like traps, resulted in lower congruence between plant and pollinator richness. Combined active and passive methods resulted in intermediate congruence between and richness of plants and pollinators (Figure 2.6).

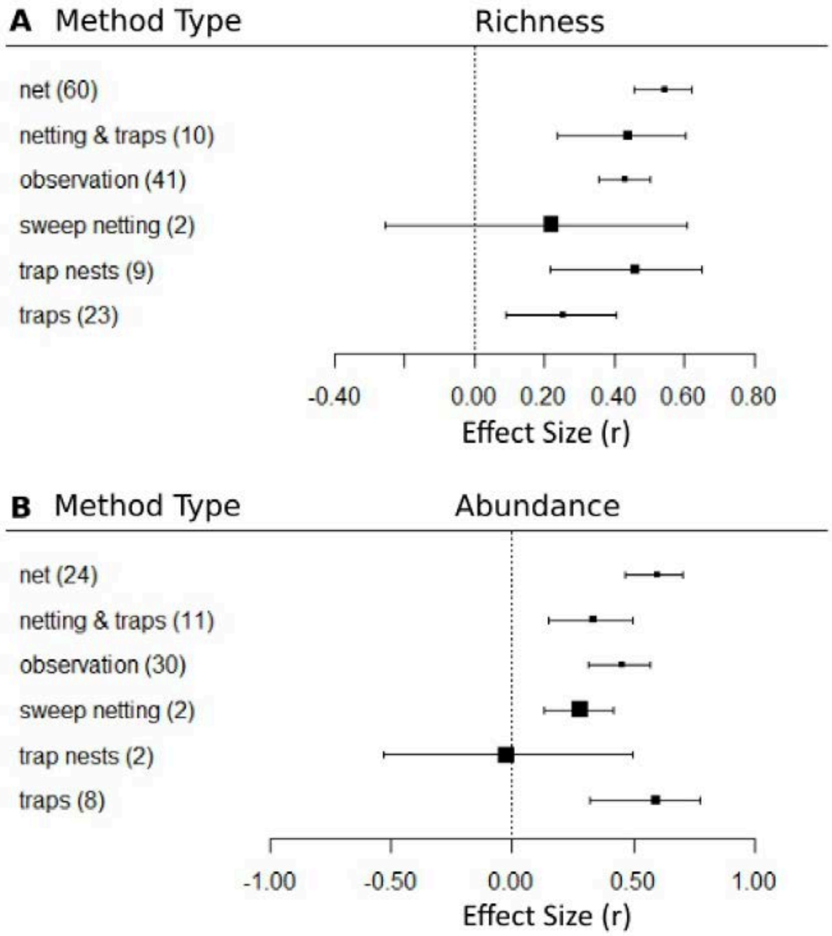

Figure 2.6 Forest plots indicating effect sizes (*r*) by pollinator sampling method type for pollinator richness – plant richness (A) and pollinator abundance – plant abundance (B). Error bars are 95% confidence intervals (CI) and observed effect size (represented by a square) is proportional to the precision of the estimate, with smaller squares indicating higher precision. Effects are considered significant when a CI does not overlap 0. Number of data points per pollinator sampling method type is indicated by the number in parentheses.

Plant sampling methodology. Plant sampling method (i.e., transects vs. plots) did not have a significant effect on the congruence of either plant richness (QM = 3.4369, df = 2, $p = 0.1793$) and pollinator richness (QM = 2.7580 , df = 2 , $p = 0.6845$). Sampling area also did not have a significant impact on the correlation between either plant richness

(QM = 0.0145, df = 1, *p* = 0.9041) or plant abundance and pollinator abundance (QM = 0.0690 , df = 1 , *p* = 0.7928).

2.3.3 No Evidence of Publication Bias

Inspection of funnel plots (Figure 2.7) as well as regression tests and rank correlation tests indicate no evidence of publication bias for either the plant richness and pollinator richness correlation (z = -7.0605, $p < 0.0001$; Kendall's tau = -0.2084, p = 0.0002) or the plant abundance and pollinator abundance correlation (z = -7.0798, $p < 0.0001$; Kendall's tau = -0.1784, p = 0.0216).

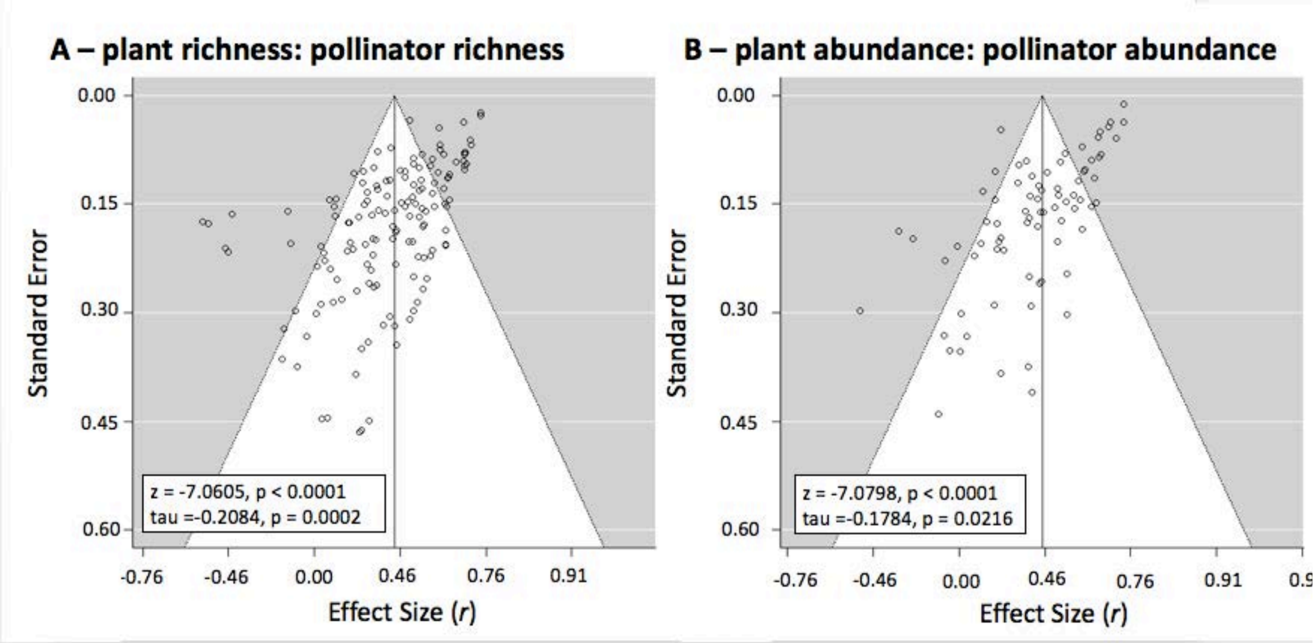

Figure 2.7 Funnel plots testing for publication bias for pollinator richness – plant richness (A) and pollinator abundance – plant abundance (B). Regression and rank correlation test results for each analysis in text boxes.

2.4 Discussion

2.4.1 Overall Meta-Correlations

My results indicate a strong positive correlation between plant richness and abundance and pollinator richness and abundance (Figure 2.1). This correlation between plants and pollinators was found across a wide range of studies performed over 40 years, including all major biomes, a large range of spatial scales, and across the spectrum of disturbance levels and types, indicating that it is very robust pattern. Publication bias does not appear to be evident in this study. Although a funnel plot of effect size versus standard error of the studies (Figure 2.7) was significantly asymmetric, the asymmetry was towards small studies having low effect sizes, confirming that negative correlations were as likely to be reported as positive correlations. I did not expect strong publication bias in this meta-analysis because many of the studies used in this meta-analysis were not originally designed to test the explicit hypothesis that plant and pollinator diversity are correlated. Rather, many of the included studies are instead focused on determining impacts of human activities and land management regimes and they take a variety of approaches from general surveys to network analyses.

Overall, the final correlation coefficients between plant richness - pollinator richness as well as for plant abundance - pollinator abundance remain strongly positive and significantly greater than zero. In fact, the overall correlation coefficient for plant richness – pollinator richness was similar to or greater than those found in previous meta-analyses of diversity congruence between taxa. Wolters *et al.* (2006) found an average correlation effect size (r) of 0.374 (95% CI: ± 0.0678) when comparing richness correlations between a wide range of taxa (e.g., plant richness to animal richness,

richness of one animal taxa to another). This effect size was larger, r ≈ 0.5 when considering only relationships comparing richness of plants to that of animals (extracted from Figure 3 in Wolters *et al.* 2006). Catagneyrol and Jactel (2012) found an overall effect size (r) of 0.45 (95% CI: 0.4-0.49) between plant richness and animal richness, including herps, birds, mammals, and arthropods. Finally, Westgate *et al.* (2014) found an average effect size (r) of 0.35 (s.d. = 0.36) across a global dataset including most major taxa. Taken together with my results, it seems that there is a relatively low congruence between different taxa globally (r = 0.35 - Westgate *et al.* 2014), however, when considering primary consumers and plants the congruence level increases (r = 0.49 - Castagneyrol and Jactel 2012). This suggests that many between-taxa relationships are context dependent but that richness congruence may be higher for organisms that interact directly via trophic relationships (i.e., primary animal consumers and the plants they consume). Pollinators could be considered a primary consumer as they consume plant resources for energetic and nutritional requirements during at least one life stage (Thomson 2003), explaining the similarity between this study (r = 0.45) and previous studies.

Although my results confirm a strong positive relationship between pollinator richness and plant richness, there is still a large amount of variability not explained by plant richness alone (Table 2.2). This may reflect the high levels of generalization found in most plant-pollinator communities (Waser *et al.* 1996, Bosch *et al.* 1997). Network studies of plant-pollinator interactions have consistently revealed highly asynchronous interactions between plants and pollinators with specialized pollinators interacting primarily with generalized plants and vice versa (Bascompte *et al.* 2006). Asynchrony would reduce the level of congruence between plant richness and pollinator richness. If both plants and pollinators were specialized, the correlation coefficient of plant richness and pollinator richness would be high, regardless of the number of species. If both taxa are specialized, as one species increases in number so would the other. The opposite is true for highly generalized relationships. If both species are generalists, they can vary in species richness independently. My moderately high global effect size could be explained by these network findings. My results also confirm a strong positive relationship between pollinator abundance and plant abundance, but similarly there is still a large amount of variability not explained by plant abundance alone.

My results also suggest significant and substantial variability due to heterogeneity in both analyses (Table 2.2). I tested several covariates as sources for this heterogeneity: plant type and flowering status, biome, and pollinator sampling methodology all had significant impacts on the overall correlation coefficient of the plant richness – pollinator richness analysis. Only biome has a significant impact on the overall correlation coefficient of the plant abundance – pollinator abundance analysis.

2.4.2 Effect of Pollinator Taxon Type on Plant-Pollinator Congruence

I expected pollinator identity to have an impact on the congruence of plants and pollinators due to taxon-specific life history differences. My study included all insect flower visitors, taxa that range in their dependence on flowering plants. I predicted that pollinator taxa that have a higher dependence on flowering plants, defined as the number of life stages that rely upon flower resources, would have a stronger correlation with plants. For example, bees require floral resources to complete their entire life cycle. Adults utilize nectar to gain energy and they provision larva with pollen packets

(Roulston and Goodell 2011). All other pollinators also rely upon flowers for energy as adults, but vary in their dependence on flowers for the provisions they provide their offspring. Juveniles of butterflies and moths (i.e., caterpillars) eat leaves, while wasps and flies primarily provision their juveniles with other arthropods through predation or scavenging (Bugg *et al.* 2008, Krenn 2010, Winfree *et al.* 2011, Danieli-Silva *et al.* 2012). Therefore, I expected that bees and Lepidoptera would have stronger correlation coefficients with plants than flies and wasps. However, there was not a significant impact of pollinator type on either plant richness – pollinator richness or plant abundance – pollinator abundance correlations (Table 2.1). This suggests a generalized relationship between plants and pollinators and supports the idea that congruence between taxa is limited by trophic level (Castagneyrol and Jactel 2012).

There is large within-taxa variability in traits of pollinators, including those that influence foraging behavior, which could limit the congruence between plant and pollinator diversity (Winfree *et al.* 2011). For example, some Lepidopteran species do not feed as adults (Krenn 2010) and cleptoparasitic bee species do not provision for their own offspring (Roulston and Goodell, Winfree 2010), resulting in missing or weak links to floral resources. Also, it is possible that specialist species have a stronger correlation with plant richness than generalist species, while generalist species may be more dependent on floral abundance than floral richness at the community level (Biesmeijer *et al.* 2006, Cane *et al.* 2006, Kleijn and Raemakers 2008). Phenology, sociality, mobility, distribution, body size, life-span and reproductive output of individual species determine both available resources and energetic and nutritional needs (Winfree *et al.* 2009, Ockinger *et al.* 2010, Potts *et al.* 2010, Williams *et al.* 2010) and should be taken into account when considering whether plant communities structure pollinator communities.

2.4.3 Effect of Plant Type and Flowering Status on Plant-Pollinator Congruence

My results indicate an impact of plant type on congruence between plant richness and pollinator richness. First, I found that there is a significantly higher effect size (r) when I consider all plants rather than considering just one plant type (i.e., herbaceous plants vs. woody plants). This indicates that a diversity of pollinators is better supported by the entire plant community rather than a subset of the plant community. However, when considering only one plant type, I found that there was a significantly stronger correlation between herbaceous plant richness and pollinator richness as compared to woody plant richness and pollinator richness. This is likely because for several of these studies, woody plants, especially trees, may be a better indication of habitat type or habitat structure than of available floral resources. A high diversity of trees may not facilitate a high diversity of pollinators if many of the trees are not insect pollinated. Furthermore, dense forest canopies are often negatively associated with diverse and abundant pollinator communities. For example, Hanula *et al.* (2015) found that both richness and abundance of bees was highest in cleared plots and open forests with an herbaceous understory as compared to dense pine forests in the southeastern United States.

I also found that when there is a higher correlation with richness of pollinators for flowering plants only when compared to correlation of pollinator richness to the entire plant community, which includes non-flowering species. This finding supports the hypothesis that congruence between plants and pollinators reflects their trophic relationship with higher congruence indicating a stronger dependence between taxa. As pollinators utilize floral resources (i.e., pollen and/or nectar) for their energy and nutrition requirements, measuring only plants in flower at the time of pollinator collections is likely a more accurate representation of available resources than considering the entire plant community.

2.4.4 Effect of Biome on Plant-Pollinator Congruence

Meta-correlations for plant richness and pollinator richness as well as plant abundance and pollinator abundance were significantly different depending on the biome in which the survey took place. Plant and pollinator diversity varies by biome, for example biotic pollination is greater in the tropics than in temperate regions (Bawa 1990). Plant and butterfly diversity are highest in tropical biomes (Willig *et al.* 2003, Kreft and Jetz á2007) and although bees are more abundant in tropical regions than temperate regions, they are most speciose in arid regions, especially those with high floristic diversity (Michener 1979, Schleuning *et al.* 2012). Species richness of Diptera increases with both latitude and elevational gradient (Elberling and Olesen 1999). Elevational gradients show similar patterns to latitudinal gradients with high latitudes and high elevations both generally showing a reduction in species richness of plants and associated animals (Currie 1991, Gaston 1992).

I found that the tropical forest biome had the lowest effect size (r) between plant richness and pollinator richness. This low congruence may be partially explained by the different latitudinal biodiversity patterns of plants and pollinators described above. Gaston (1992) found that the ratio of insect species to plant species decreases as plant richness increases. This could be due to an inverse relationship between plant richness and relative plant abundance. Therefore, in the tropics, flowering plants that are resources for pollinators may have low densities - resulting in longer search times for pollinators and thereby constraining specialization, according to optimal foraging theory (MacArthur and Pianka 1966, Albrecht *et al.* 2010a, Schleuning *et al.* 2012). This relationship between plant richness and relative plant abundance may contribute to the variability in interaction strength and level of specialization found within plant-pollinator networks. Olesen and Jordano (2002) found as latitude declined, the number of interactions with each plant also declined, suggesting that plant species are more specialized in tropical biomes. However, pollinators appear to be more generalized at lower latitudes (Gaston 19992, Olesen and Jordano 2002, Schleuning *et al.* 2012). This means that there is less niche differentiation and more overlap in resource use by pollinators in these tropical biomes (Schleuning *et al.* 2012). Together these studies suggest high levels of asynchrony in pollination networks in the tropics, which could result in a lower correlation coefficient between plant and pollinator richness.

In contrast, alpine biomes had the highest effect size (r) for both plant-pollinator richness and plant-pollinator abundance. Olesen and Jordano (2002) found that plant species are more specialized in alpine environments. Alpine ecosystems are highly seasonal with a short growing season for plants and activity season for pollinators (Olesen *et al.* 2008). Organisms with short activity phases are likely to have fewer interaction partners than organisms with long activity phases because there is less time for organisms to overlap (Olesen *et al.* 2008, Bosch *et al.* 2009, Kallimanis *et al.* 2009, Martín González *et al.* 2012). My results suggest that pollinators may also be more specialized at higher altitudes resulting in a stronger correlation between plant and pollinator diversity. High altitude communities, with their short growing season, extreme weather events and relatively low plant diversity may increase evolutionary pressure for specialization (Schleuning *et al.* 2012). It is also possible that due to the low sample size of alpine studies, these results are not generalizable.

All biomes, except alpine ecosystems, showed similar effect sizes for the relationship between plant abundance and pollinator abundance. Alpine biomes had a higher correlation coefficient for plant abundance and pollinator abundance when compared with all other biomes.

2.4.5 Effect of Pollinator Sampling Methods on Congruence

I found that pollinator sampling methods had a significant effect on the meta-correlation of plant richness with pollinator richness, but not for plant abundance and pollinator abundance. Active methods resulted in a higher correlation coefficient for plant richness – pollinator richness than using both active and passive methods or using only passive methods. This is likely because active methods of pollinator sampling, like netting, are more directly tied to the plant community, than passive methods like traps. Methods also vary by pollinator taxon, with butterflies being almost exclusively surveyed by active methods. Networks also generally use active methods.

These results indicate the importance of considering sampling methods when determining the relationship between plants and pollinators. It may be that measuring richness is more susceptible to sampling bias than measuring abundance, as the abundance meta-correlation was not significantly impacted by pollinator sampling method. Active methods have some observer bias as the skill level and style of the surveyor can vary. Passive methods may not have observer bias, but they use visual or scent based cues to attract pollinators and so could bring in additional individuals that wouldn't normally be in the study area, thereby underestimating the correlation between plant richness and pollinator richness. There has also been some indication that passive methods may be more effective where flowering plant abundance is lower or at greater distances from floral resources, creating further bias (Grundel *et al.* 2010).

2.5 Conclusions

My results indicate that plant richness and abundance have a strong positive relationship to pollinator richness and abundance. This suggests that flowering plants could be used as surrogates for pollinators in conservation plans, although the effectiveness of this strategy would vary by biome. Impacts of sampling methodology used to determine effectiveness of any conservation or restoration strategies should also be considered. Although this study contains a large dataset including studies from all of the major terrestrial biomes, these biomes are not equally represented. More studies are needed in the tropics and polar/alpine regions. More studies in relatively undisturbed habitats are also needed, as most of these surveys come from disturbed or human impacted ecosystems.

Importantly, the correlations examined in the present study may suggest mechanisms, but they cannot demonstrate causation. It is possible that there is no causal relationship, but rather that pollinator and plant diversity are instead structured by common environmental factors such as soil fertility, net primary productivity, and various management activities. Pollinators are mobile organisms, able to move from place to place while foraging (Greenleaf *et al.* 2007, Zurbuchen *et al.* 2010). This mobility means that pollinator communities also respond to landscape variables, not just local floral richness. (Tylianakis *et al.* 2006, Sjodin *et al.* 2008, Carvalheiro *et al.* 2010, Carvalheiro *et al.* 2013, Jha and Kremen 2013, Scheper *et al.* 2013). Also, pollinator populations are likely limited by many factors in addition to floral diversity as not all pollinators exclusively depend on flowering plants for their entire life cycle (Winfree *et al.* 2011). Other factors including natural enemies and nest site availability are important to pollinator communities (Potts *et al.* 2005, Grundel *et al.* 2010, Winfree 2010, Roulston and Goodell 2011)

All my analyses had strongly positive overall effect sizes (r), suggesting that local flowering resources are one important factor in determining pollinator community composition. However, the causal mechanisms behind these correlations between flowering plant species richness and pollinator species richness and flowering plant abundance and pollinator abundance need to be explored further through more experiments that manipulate either floral diversity or pollinator diversity or both (e.g., Ebeling *et al.* 2008). My study also illustrates the limitations of using one taxon as a surrogate for another group of organisms, for there is large quantity of unexplained variability when using only plant richness and abundance to model pollinator diversity and abundance. Therefore, it is important that future studies continue to look beyond plants when determining the factors that best explain pollinator community composition.

CHAPTER 3

USE OF ARTIFICIAL NEST BOXES IN TEMPERATE FORESTS BY INTRODUCED *OSMIA* SPECIES

3.1 Background

The majority of bees are central place foragers, searching for food resources within flight range of their nests (Westrich 1996, O'Toole and Raw 1999, Knight *et al*. 2005, Williams and Kremen 2007, Zurbuchen *et al.* 2010). This means that nesting resources interact with floral resources to influence bee populations (Roulston and Goodell 2011). Most bee species make their own nests as a protected environment to raise their offspring, but many additional bee species are cleptoparasites, depositing their eggs in other bee species' nests (Westrich 1996, Michener 2000). Of those that make their own nests there are "renters" that utilize pre-existing cavities for their nests (e.g., existing holes or reappropriated burrows made by other organisms), while others are "excavators", creating the nest from scratch out of a chosen substrate (e.g., soil or wood). These nests can be built above-ground, generally in tree trunks or stems of plants, or below-ground, in the soil. These nests vary in size depending on the body-size of the bee species and the level of sociality (Michener 2000). These nesting traits influence both which nesting resources are limiting to a population and which risks these populations experience (Potts *et al.* 2005, Williams *et al.* 2010).

Osmia cornifrons and *O. taurus* are two species of cavity-nesting bee species that have been introduced to the eastern United States from Japan (see Section 1.6). Most *Osmia* species are cavity nesting bees, meaning they are "renters", utilizing pre-existing holes that are found above-ground, often in dead wood but also within other substrates including snail shells, stems, and artificial (human-made) materials. Many *Osmia* species then line these cavities and create nest cell partitions and plugs with masticated plant material or mud (Krombein 1967, Cane *et al.* 2007).

Available nesting resources have been found to structure bee communities (Potts *et al.* 2003b, Potts *et al.* 2005, Grundel *et al.* 2010) and influence bee population sizes (Julier and Roulston 2009, Gruber *et al.* 2011, Roulston and Goodell 2011, Artz *et al.* 2013, Dainese *et al.* 2017). Both quantity and quality of required nesting substrates and additional materials required for nest construction may vary in both time and space, limiting the size of bee populations (Cane 1991, Horne 1995, Sheffield *et al.* 2008, Steffan-Dewenter and Schiele 2008, Westphal *et al.* 2008). Indirect evidence for nest site limitation exists (Ricketts 2004, Potts *et al*. 2005, Cane *et al.* 2006, Kim *et al.* 2006, McFrederick and LeBuhn 2006, Klein *et al*. 2006, Sheffield *et al*. 2008, Moretti *et al*. 2009, Neame *et al.* 2013), but access to floral resources may be an equal or greater influence on nesting density (Eltz *et al.* 2003, Torné-Noguera *et al.* 2014). Also, nesting resources are often correlated with floral resources (Potts *et al.* 2003b, Campbell *et al.* 2007, Moretti *et al.* 2009), which makes it hard to determine the role of nesting resources on pollinator communities independent of flower availability (Roulston and Goodell 2011).

Finding natural nesting sites of bees can be very difficult (but see Potts *et al.* 2005 and Grundel *et al.* 2010), therefore, artificial nest boxes or trap nests have been used to sample for cavity nesting bees within an ecosystem (e.g., Krombein 1967, Jayasingh and Freeman 1980, Tscharntke *et al*. 1998, Wilson *et al.* 1999, Steffan and Schiele 2004, Giles *et al.* 2006, Steffan and Schiele 2008, Westphal *et al.* 2008, Forrest and Thomson

2011, Ebeling *et al.* 2012, MacIvor 2016). Usage of nest boxes by bees depends on both local and landscape factors. Landscape features, including proportion of various habitat types (e.g., forest vs. prairie and natural habitat vs. human influenced habitat) as well as patterns of fragmentation, can strongly influence both composition and abundance of cavity nesting bees in artificial nesting substrate (Gathmann *et al.* 1994, Klein *et al.* 2002, Kruess and Tscharntke 2002, Steffan-Dewenter 2002, Steffan-Dewenter 2003, Klein *et al.* 2006, Tylianakis *et al.* 2006, Taki *et al.* 2008, Schüepp *et al.* 2011, Loyola and Martins 2012, Steckel *et al.* 2014, MacIvor and Packer 2016, Dainese *et al.* 2017). Local factors including quantity and quality of natural nesting material and floral resources are also important. Both flowering plant richness and abundance are positively associated with colonization of trap nests (Tscharntke *et al.* 1998, Aguiar *et al.* 2005, Tylianakis *et al.* 2006, Taki *et al.* 2008, Dainese *et al.* 2017). Natural nesting substrate may compete with artificial nesting substrate for colonization (Sheffield *et al.* 2008, Roulston and Goodell 2011).

Nest box design also influences colonization rates (MacIvor 2016). Many cavity nesting bees have shown strong preference for specific cavity sizes (Krombein 1967, Budriené *et al.* 2004, Sheffield *et al.* 2008, Gruber *et al.* 2011, MacIvor 2016), as well as for specific substrates and nest lining material (Cane *et al.* 2007, MacIvor and Moore 2013, MacIvor 2016). Nest boxes also vary in quantity of potential nesting holes, affecting the nesting density and potential for competition experienced by nesting bees (Pitts-Singer and Bosch 2010, Artz *et al.* 2013). Nesting density also impacts the risks from natural enemies (Wcislo 1996, MacIvor and Packer 2015). Colonization rates can also be influenced by the visibility of the nest box or the ability of bees to distinguish their nests from others' nests (MacIvor 2016). Many cavity nesting bee species also exhibit philopatry which can influence colonization rates (Steffan-Dewenter and Schiele 2004, Pitts-Singer 2007, Steffan-Dewenter and Scheiele 2008).

In order to persist in their new homes, non-native bees, like *Osmia cornifrons* and *O. taurus* (see Section 1.6), must be able to find suitable nesting and foraging materials. *O. cornifrons* is a managed pollinator in the United States, but both species are also found as wild, non-managed bees, in wildlands throughout the eastern U.S. Both *O. cornifrons* and *O. taurus* have been found to nest in artificial nesting substrates, including wooden nesting blocks. However, the factors that influence the usage of artificial nest boxes for non-managed populations of these species are not well understood. In order to better understand how these species of non-native bees utilize artificial nesting substrate, I introduced wooden nest boxes to a temperate forest in New Jersey and determined the probability of nesting within individual nest holes within nest boxes. This study had three primary predictions: 1) Nesting is influenced by the number of available nesting cavities and probability of nesting will increase with increasing nesting cavity availability; 2) Nesting is influenced by the floral resource availability and probability of nesting will increase with increasing plant richness; and 3) Nest box design, specifically hole size and neighbor density, will influence probability of nesting in individual holes within a nest box.

3.2 Methods

3.2.1 Study Site

This study took place in Morristown National Historical Park (MORR), a federally managed park of approximately 690 ha, located in Morristown, NJ. MORR is part of the Lower New England/Northern Piedmont ecoregion and consists primarily of rolling hills and lowlands with an elevational range of 107-457m. It has a long history of human land-use including clearing land for agriculture and logging. Most famously MORR was home to the American Continental Army under George Washington over the winters of 1777 and 1779 during the Revolutionary War. It is dominated by mature second-growth forests of predominantly either mesic oak-beech forests or successional tuliptree forests with an understory dominated by invasive shrubs and the occasional ephemeral herb layer. Thin, well-drained sandy loam soils are intermixed with areas of rocky gneiss (Sneddon *et al.* 2008). Deer are very abundant in the park and have decimated the native understory in many areas (R. Masson, *pers. comm.)*.

3.2.2 Nest Box Experiment

Within the park, the Northeast Temperate Network (NETN) of the National Park Service has established 29 permanent forest monitoring plots, at random locations throughout the forested areas of MORR (Tierney *et al.* 2009). These 20 m x 20 m plots are intensively sampled biannually for vegetation, soil chemistry, light availability, coarse woody debris, and tree condition. These NETN surveys provide the vegetation data for my study including the richness and abundance of plants. I co-located my nest boxes (see Section 3.2.3) at 27 of these plots (Figure 3.1), in three treatment configurations: Treatment 1 (1 box per plot), Treatment 2 (2 boxes per plot), and Treatment 3 (1 box per plot with an additional box added approximately 1.5 months later. Nine NETN plots were randomly assigned to each treatment:

At each plot, nest boxes were attached to mature trees (> 10 cm diameter at breast height) with bungee cords at 1 m from the ground facing south-southeast. In Treatment 2, the lowest box was placed 1 m from the ground and the other box was placed just above it (but boxes did not come into physical contact with each other). In Treatment 3, half of the later boxes were attached above and the other half were attached below the existing box with random assignment of box placement. All boxes were placed in the field between 30-31 March 2013 except the additional box for Treatment 3 which were added 23 May 2013. Bee nesting activity began in early April 2013 and was completed by the beginning of June 2013. Nest boxes were left in the field until mid-January 2014 when they were brought to the Bunker Lab at New Jersey Institute of Technology, Newark, NJ where they were censused (see Section 3.2.4).

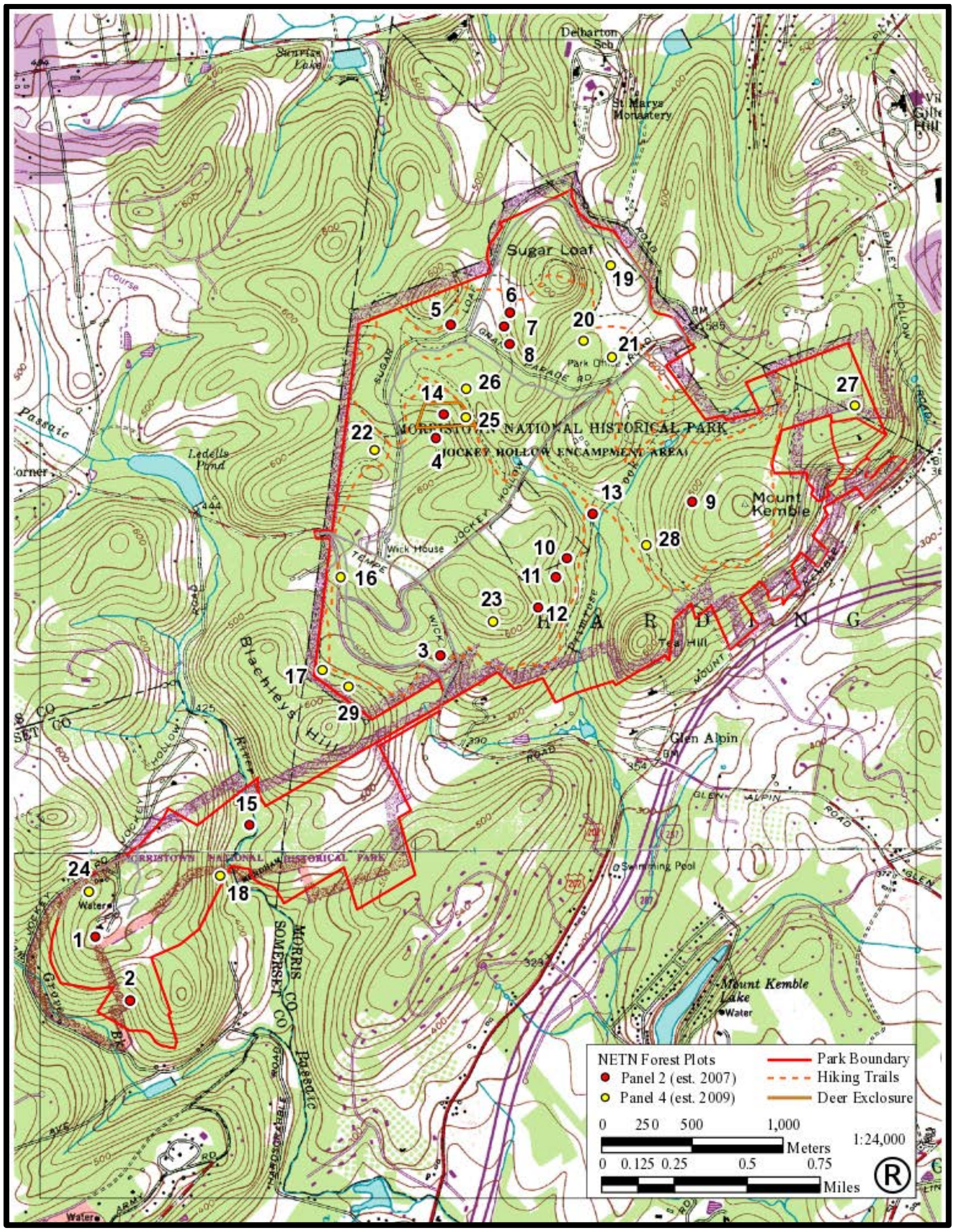

Figure 3.1 Map of the 29 permanent plots in Morristown National Historical Park monitored by the Northeast Temperate Network of the National Park Service. Bee boxes were placed at 27 of these sites from March 2013 to January 2014.

3.2.3 Nest Box Design

Each nest box was 30 cm wide by 28 cm deep by 13 cm high and consisted of four wooden trays with six holes per tray (24 holes per box). In each tray the six holes were equidistant from each other but varied on whether they were skewed towards the left side of the tray or towards the right side of the tray. Within each box, there were two trays with medium sized (7 mm diameter holes) and two trays with large (12 mm diameter holes). Trays alternated within the box such that every other tray had the same hole size and alignment, with random top tray assignment per box (Figure 3.2).

Figure 3.2 An example of a nest box used in this study. Although exact configuration of trays varied, in all cases boxes contained 24 holes in trays that alternated by hole size and hole alignment. Note: the mud-filled holes in the box indicate nests made by either *Osmia cornifrons* or *O. taurus*. Photo by Caroline DeVan.

3.2.4 Nest Box Census

Nest boxes were censused between January and March 2014 (Figure 3.3). The following attributes were recorded for all nest boxes: number of nests per box, number of cells per nest, male:female ratio per nest and the rate of parasitism or other cohabitants. At least one subsample per nest was removed for species identification. The species identity of the subsampled individual was assumed to represent the species of all individuals in the nest. Identifications were determined by C. DeVan with some confirmation by J. Ascher.

Figure 3.3 Colonized part of a tray from a nest box. For each bee nest found, the total number of nest cells and number of parasitized nest cells were counted. This photo was taken in the field in early summer 2013 before the bees in the nest had developed into adults. The yellow pollen provision is visible as are the bee larvae. The actual nest box census occurred in winter 2014 after the bees had matured into adults.

3.2.5 Plant Community

In order to determine the potential impact of the plant community on nesting I utilized plant community data collected by NETN in the summer of 2011 (NETN 2011). This survey was the most recent survey at the time of the experiment. Based on their survey data, I calculated total richness of trees, shrubs and herbaceous plants found in each NETN plot.

3.2.6 Analysis

I used repeated measures generalized linear mixed models (GLMM) with a binomial distribution and logit link function and a residual PL estimation technique in Mixed: GLMER of the R package LMER (LME-4) (RStudio v.1.0.153 - R Core Team 2012, Bates *et al.* 2015) to compare the likelihood of a nest box hole being colonized by a bee. *Osmia cornifrons* and *O. taurus* were considered together. Fixed effects included the categorical variables treatment and hole size and the continuous variables neighbor density (number of neighboring holes) and plant richness, and their interactions (treatment x plant richness, treatment x hole size, treatment x neighbor density, and hole size by neighbor density). Neighbor density (neighbor) and plant richness were centered prior to analysis. NETN plot was included as a random effect. Only two treatments were used in my analysis, Treatment 1 (one box) and Treatment 2 (two boxes). The second box in Treatment 3 had very low colonization rates and so nesting rates for Treatment 3 were not significantly different from Treatment 1. I therefore combined Treatments 1 with the first box from Treatment 3 in my analysis. The statistical significance of all effects were tested using likelihood ratio test (Bates *et al.* 2015).

3.3 Results

The full model, which included a random effect of nest box location (NETN site) and fixed effects of treatment, hole size, neighbor density, plant richness, and their associated interactions, had an AIC score of 990.2 and a BIC score of 1037.9. There was a significant effect of hole size ($X^2 = 4.75$, $p < 0.05$; Table 3.1) and number of neighboring holes ($X^2 = 9.58$, $p < 0.005$; Table 3.1) for the likelihood of a nest box hole being colonized by an *Osmia* species (*O. cornifrons* and *O. taurus* considered together). In addition, there was a significant effect of the interaction between hole size and number of neighboring holes ($X^2 = 4.39$, $p < 0.05$; Table 3.1). Treatment, overall plant richness, and their associated interactions had no effect on the likelihood of a nest box hole being colonized by either *Osmia* species (Table 3.1). The random effect of nest box location (NETN site) was also not significant.

Table 3.1. Effects of Treatment, Hole Size, Neighbor (Density of Neighboring Holes), Richness (Total Plant Richness) and their Interactions on the Likelihood of a Nest Box Hole Being Colonized in Spring 2013 in Morristown National Historical Park. Significant Effects are Noted in Italicized Bold. Full Model d.f. = 10

Effect	**d. f.**	**X^2**	***p***
Treatment	1	0.18	0.67
Hole size	1	4.75	***0.03***
Neighbor	1	9.58	***0.002***
Richness	1	0.95	0.33
Treatment x Richness	1	0.40	0.53
Treatment x Hole size	1	2.60	0.11
Treatment x Neighbor	1	2.22	0.14
Hole size x Neighbor	1	4.39	***0.04***

At the same neighbor density, the probability of colonization per nest box hole is higher for medium-sized (7 mm) holes than for large-sized (12 mm) holes. Higher neighbor density for any hole generally resulted in lower colonization rates for both hole sizes, but especially for the larger hole size (Figure 3.4).

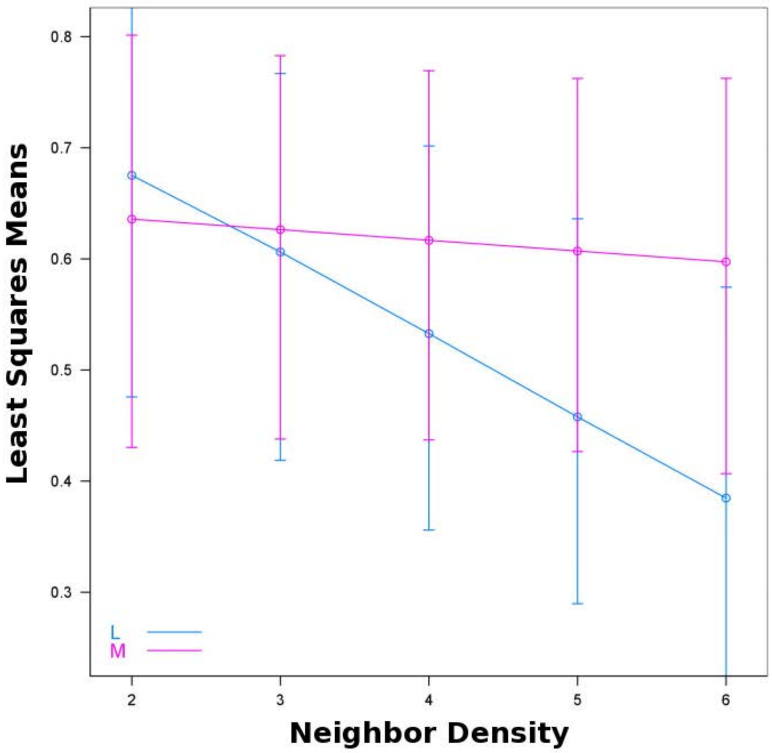

Figure 3.4. Least square means for probability of colonization based on hole size and neighbor density. Medium-sized holes, shown in purple, are 7 mm in diameter, while large-sized holes, shown in blue, are 12 mm in diameter. Error bars represent upper and lower confidence limits.

3.4 Discussion

3.4.1 Nest Box Experiment

The number of nest boxes at each nest site did not significantly affect the probability of colonization of any nest box hole by either *Osmia* species. This suggests that as the number of nest boxes and therefore availability of holes increases, the number of nests made by these cavity-nesting bees will also increase. This could indicate a limitation of natural nesting resources or it could simply mean that preference for artificial nesting resources are equivalent to or higher than natural nesting resources for these species (Roulston and Goodell 2011). Further studies would need to be done to determine causal mechanisms.

3.4.2 Floral Resources

The overall plant richness per site did not significantly affect the probability of colonization of any nest box hole by either *Osmia* species. This suggests that floral resources do not limit nesting of *Osmia cornifrons* and *O. taurus* at Morristown National Historical Park. This is not surprising as both *Osmia* species are known to be floral generalists and therefore should be able to utilize a wide range of floral resources (Haider *et al.* 2014). In a previous study, *Osmia cornifrons* was found to have a minimal foraging range of 500m (Guedot *et al.* 2009). As these two *Osmia* species are similar in size, it is likely they would have similar foraging ranges, as bee foraging ranges are positively related to their body size (Greenleaf *et al*. 2007). Therefore, both species are large enough to have a foraging range within MORR that should encompass some floral resources meaning that the spatial distribution of floral resources does not affect their nesting distribution.

Also, it could be that floral resources do not vary significantly between sites. I did not measure floral resources directly, and it is also possible that plant richness per nest box site does not accurately represent floral resource availability. Not all plants in the park are insect-pollinated or even flowering plants and flowering time for some bee pollinated plants may occur outside the nesting time for these species. Abundance of floral resources was also not measured and could have a large impact on bee populations (Dainese *et al.* 2017).

3.4.3 Nest Box Design

Hole size and neighbor density, as well as their interaction, affected the probability of colonization of any nest box hole by either *Osmia* species. In previous studies at MORR, both *O. cornifrons* and *O. taurus* were found to use a range of nest hole sizes, from 5 mm diameter to 12 mm diameter. (C. DeVan, *pers. obs*; Section 4.2). This suggests that while both species are flexible in their utility of different cavity sizes for nesting, both species are generally more likely to nest in the medium-sized (7 mm diameter) holes. This preference is likely related to their body size (Budriené *et al.* 2004) as preferred nest hole size for *Osmia* species has been found to be related to both the body size and sex of the offspring (Bosch *et al.* 2001, Radmacher and Stohm 2010, Marato and Martins 2012). I have noticed that small nests (5 mm diameter) tend to be biased towards males and large nests (12 mm diameter) biased towards females or sometimes subdivided to make smaller cells. Nests in 7 mm diameter holes include both males and females (C. DeVan, *pers. obs*).

Also, although both species will nest throughout my nest boxes, these model results suggest that increasing density of neighboring holes negatively influences nesting activity. This influence on nesting is more pronounced for large-sized (12 mm diameter) nest holes. These model results show that at low neighbor densities, probability of utilizing the large-sized and medium-sized holes is similar, but at higher neighbor density, the medium-sized holes are preferred. Neighbor density of a nest-box hole is related to the location of the hole within the box - holes along the edge of the box have fewer neighboring holes. Thus, selection of holes with lower neighbor density could be a result of density dependent limitations experienced by the bees, reducing the chance that a nest is next to other nests on all sides. Reducing density of nests could be an evolved response to the increased risk of natural enemies at high nest densities (Wcislo 1996, MacIvor and Packer 2015). However, Artz et al. (2013) found that *Osmia lignaria* females preferred to nest in high density nest boxes as compared to low density nest boxes. In some *Osmia* species, females can also create multiple nests within a single nest site and it may be that the same female would be more likely to place additional nests adjacent to previously made nests (Bosch and Vicens 2006).

It is also possible that edge holes may also be more visible or have a different microclimate than interior holes which could also influence preference for nesting in them. Everaars *et al.* (2011) found quantity of sun received by nest boxes was an important indicator for nesting of *O. bicornis*, a related European species. Nest boxes in sunnier sites were more likely to be colonized than those in shadier locations (Everaars *et al.* 2011, MacIvor 2016). Visibility has also been found to be important to nest site location for cavity-nesting bees (Krombein 1967, Guédot *et al.* 2006, Guédot *et al.* 2007, Artz *et al.* 2014).

3.4.4 Conclusions and Future Work

Artificial nest boxes are utilized by both *Osmia cornifrons* and *O. taurus* in temperate forests. I found that nest box design influenced the probability of a bee nesting within an artificial nest box more than quantity of nesting or floral resources. This suggests that usage of artificial nesting substrate, especially with preferred hole size and density, may assist these species in their establishment, which is positive if they are being managed for pollination efforts and negative if we want to reduce their abundances as a non-native species.

Abundance and distribution of species is not just related to food and shelter resources, species are also limited by their interactions with potential competitors and natural enemies (Goodell 2003, Budriené *et al.* 2004, Steffan-Dewenter and Scheile

2008, Roulston and Goodell 2011, Ebeling *et al.* 2012, Vickruck and Richards 2012, Dainese *et al.* 2017). *Osmia* species may compete for nesting or floral resources or they may avoid competition through niche differentiation. Using bee bowl sampling for a separate study, I found multiple species of *Osmia* in Morristown National Historical Park (MORR) during the springs of 2012 – 2014 (C. DeVan, *pers. obs.*). However, these other species are either much larger (*O. bucephala*) or smaller (*O. pumila* and *O. atriventris*) than either *O. cornifrons* and *O. taurus,* suggesting little competition for nesting resources. I did not find *Osmia lignaria*, a native bee of similar size to *O. cornifrons* and *O. taurus*, in my sampling, although its range suggests the possibility. *O. cornifrons* and *O. taurus* are of similar size and overlap in both their nesting and floral resources suggesting the possibility of competition between these species and with *O. lignaria*. Further work needs to be done to determine what interactions, if any, these species have with each other or the ability of these species to outcompete their native counterpart, *Osmia lignaria*.

CHAPTER 4

OSMIA CORNIFRONS AND *O. TAURUS* EMERGE EARLIER UNDER SPRING WARMING TREATMENTS

4.1 Background

One of the most observable impacts of climate change on biological systems has been the shifting phenology of both plants and animals (Walther *et al.* 2002, Parmesan and Yohe 2003, Gordo and Sanz 2006, Parmesan 2006, Hegland *et al.* 2009). Phenology is the seasonal timing of organismal life history events and is especially sensitive to climatic variation. Elements of climate, including temperature, act as triggers for particular life stages in phenologically sensitive organisms (Menzel *et al.* 2006). As average temperatures have increased over the past few decades in temperate regions, phenological shifts are being observed in plants and insects (Walther *et al.* 2002, Parmesan and Yohe 2003, Gordo and Sanz 2006, Parmesan 2006, Thackeray *et al.* 2010; Bartomeus *et al.* 2011, Kudo and Ida 2013).

Bees are the most important pollinator taxa globally, providing pollination services to both agricultural and natural ecosystems (Potts *et al.* 2010). In exchange, all bee species are completely dependent on the floral resources of plants for their energy requirements (Roulston & Goodell 2011). Bees are phenologically sensitive organisms, requiring specific environmental conditions, to trigger each life stage. As many flowering plant species are also phenologically sensitive, concerns have been raised over the potential for a phenological or temporal mismatch between these important pollinators and their plant hosts under future climate scenarios. Such a mismatch could negatively impact reproduction of plants dependent on insect pollination and reduce bee populations that experience food shortages due to fewer available floral resources (Memmott *et al.* 2007, Tyliankis *et al.* 2008, Hegland *et al.* 2009, Potts *et al.* 2010, Yang and Rudolf 2010; Bartomeus *et al.* 2011).

Mismatches could potentially occur if organisms have differential sensitivity to environmental cues or if organisms utilize different environmental cues for their life events. For many species of bees their yearly emergence date, after overwintering in their natal nests, is sensitive to length of winter and both winter and spring temperatures. (Bosch and Blas 1994, Bosch and Kemp 2000, Kemp and Bosch 2001, Bosch and Kemp 2004, Gordo & Sanz 2006; Sgolastra *et al.* 2009, White *et al.* 2009; Sgolastra *et al.* 2012, Ahn *et al.* 2014, Walinga 2016). However, flowering time for plants can require both a change in day length and in temperature (Menzel *et al.* 2006).

The Northeastern US has experienced an increase of 0.25°C per decade since the 1970s (Hayhoe *et al.* 2006, Dukes *et al.* 2009). Models by Hayhoe *et al.* (2006) project an increase in average annual surface temperature of 2.9°C – 5.3°C by 2070-2099 relative to temperatures from 1961-1990. In conjunction, high temperature thresholds will be surpassed with increasing frequency and low temperature thresholds with decreasing frequency (DeGaetano and Allen 2002, Dukes *et al.* 2009). Bartomeus *et al.* (2011) found that average spring (mid-April) temperatures across the northeastern U.S. have increased since the 1880s, with the largest increases occurring since the 1970s. This warming trend corresponds with advancing phenology of ten native bee species and plants across the region. This suggests that phenological mismatches may be avoided or minimized for species that respond similarly to climate change. However, there is still potential for mismatches if phenologies of interacting organisms are not in sync (Bartomeus *et al.* 2011),

Osmia cornifrons and *O. taurus* are two non-native cavity-nesting bee species introduced from Japan into the United States. *O. cornifrons* was introduced as a managed pollinator while *O. taurus* was accidently introduced alongside *O. cornifrons* (Batra 1979, Abel and Wilson 1999, Goulson 2003). Both species have spread throughout the eastern United States (see Section 1.6). In their native ranges both *O. cornifrons* and *O. taurus* are active in early spring (Jeong *et al.* 2009, Ahn *et al*. 2014). In New Jersey, they both emerge around the same time in early spring and are active for about six weeks, generally from early to mid-April until late May in New Jersey with males preceding females by several days to a week (C. DeVan, *pers. obs*.), Little is known about what triggers emergence of *O. taurus*, however, *O. cornifrons* has been shown to have temperature dependent emergence (White *et al.* 2009; Ahn *et al.* 2014). Understanding how these species could respond to climate change scenarios has important implications for their management as either managed pollinators or as exotic species.

In this study, I experimentally tested the response of emergence time for *O. cornifrons* and *O. taurus* through manipulation of the spring temperatures experienced by a set of wild-caught bees. I hypothesized that *Osmia taurus*, like *O. cornifrons*, is sensitive to early spring temperatures and will emerge earlier when exposed to higher temperatures. To test this hypothesis, I manipulated the temperature experienced by diapausing *Osmia* beginning in late winter/early spring and predicted that emergence would accelerate under these experimental warming regimes. I also tested whether *O.*

cornifrons and *O. taurus* have different emergence times. They are both active around the same time (C. DeVan, *pers. obs.*), but their exact emergence timing may vary.

Mass of *Osmia* individuals is related to maternal provisions (Radmacher and Strohm 2010) with males being smaller than females due to sex-based resource allocation on the part of the mother. Eggs that become females are laid earlier and are therefore placed at the back of the nest. Males generally are laid later and are placed towards the front end of the nest. Bees emerge sequentially, front to back, from the nests meaning that generally males emerge earlier (Bosch 1994). Therefore, I predicted that smaller cocoons would be more likely to be males and to emerge earlier. I also predicted that bees found closer to the front of the nest would be more likely to emerge earlier than bees found farther back in the nest. Finally, I tested nest box, as a random effect, with the assumption that each nest box could vary in micro-habitat characteristics which are known to influence bee colonization rates (Everaars *et al.* 2011).

4.2 Methods

4.2.1 Collection of Study Organisms: *Osmia cornifrons* and *O. taurus*

Wooden nest boxes were placed out at Morristown National Historical Park (described in Section 3.2) in Morristown, NJ in February 2012 at 40 locations throughout the park. Nest boxes were 9.8 cm wide x 30.0 cm tall x 14.0 cm deep with twelve holes of 7 mm diameter and six holes of 5 mm diameter. Holes were in two columns, with all larger diameter holes above the smaller holes. Half of the 7 mm holes were lined with cardboard tubes and the other half were lined with parchment paper. All 5 mm holes were also lined with parchment paper. Nest boxes were attached approximately one meter off the ground, facing east-southeast, to mature trees (> 10 cm diameter at breast height) using zip-ties (Figure 4.1). Tree species varied. Nest boxes remained in the field until December 2012 when they were brought into the Bunker Lab at New Jersey Institute of Technology (NJIT) where they were placed on the roof of Colton Hall at NJIT. After one week, they were moved into a fridge where they were stored at 4°C until placed into an emergence treatment (see Section 4.2.3). Nest boxes were removed from the fridge for short periods of time for censusing.

Figure 4.1 Nest box design for spring 2012 with completed nests indicated by mud filled holes. Photo by C. DeVan.

4.2.2 Nest Box Census

Each nest box was individually censused and both nest boxes and nests were photographed (Figure 4.2).

Figure 4.2 Cocoons at the pupal stage from a nest that was removed from a nest box for censusing. Photo by C. DeVan.

In each box, I counted the total number of nests (holes occupied by bee cocoons) and noted the location of each nest in the box. The total number of cocoons per bee nest was recorded as well as the quantity and taxa of parasites if present. Over 1100 bee cocoons (containing un-emerged bees) from 215 randomly selected nests were weighed. For each bee nest, at least one individual was removed for species identification and sex determination. The species identity of the subsampled individual was assumed to represent the species of all individuals in the nest. Identifications were determined by C. DeVan with confirmation of a small subset of individuals by John Ascher.

4.2.3 Emergence Experiment

Bee cocoons were temporarily placed into gel capsules labeled with a unique identifying code based on the location where they were collected (e.g., nest box 1 – nest hole A– cocoon position C would be 1-A-C). Cocoons from different nests and nest boxes were mixed together and then randomly assigned to emergence treatments. Cocoons were then removed from labeled gel capsules and placed into well-plates with one cocoon per well (24 wells per plate). The unique identifying code of each cocoon and its position in the emergence tray was recorded. Emergence trays remained in storage (4°C) until emergence experiment began. Parasites and non-bee Hymenopteran found in nest boxes were not included in the emergence experiment.

Four emergence treatments were utilized in this experiment, corresponding to four different climate change scenarios for spring temperatures: 7WATT (5.0°C above ambient temperature), 4WATT (2.78°C above ambient temperature), CONTROL (ambient temperature) and DELAY (placed out nine days later, then kept at ambient temperature) (Figure 4.4). These spring treatments correspond to projected average yearly climate scenarios for the northeastern United States as modeled in Hayhoe *et al.* (2006): 7WATT to the maximum projected climate increase, 4WATT to the minimum projected climate increase; CONTROL to a no warming scenario where average temperatures remain at current levels. We also included DELAY as a scenario where warmer temperatures arrive later in the spring than currently. The warming treatments were created by utilizing reptile tank heaters (7 watt and 4 watt heaters respectively) in emergence boxes (coolers outfitted with racks to hold the cocoons and an emergence tube to allow bees to emerge). Control and delay treatments utilized the same design of emergence boxes but without any heaters (ambient temperature). These warming treatments apply to spring temperatures only.

The experiment began 12 March 2013 when emergence trays were randomly assigned a treatment and were placed into the 7WATT, 4WATT and CONTROL treatments. Nine days later (21 March 2013) the DELAY treatment trays were brought out of storage and placed into the CONTROL treatment boxes. Approximately 150 bee cocoons were placed into each of the 7WATT and 4WATT treatments, 100 bee cocoons into the DELAY treatment and 200 cocoons were placed in the control treatment. HOBO data loggers (Onset Computer Corporation, Bourne, MA, USA) were placed into each emergence box to measure air temperature and humidity within the box every 15 minutes.

Emergence boxes were monitored daily around 10am (always between 7am and 1pm) for bee emergence and for evidence of secondary attacks by natural enemies. A bee was considered emerged if the adult bee was fully outside of its cocoon or if there was only an empty cocoon left in the tray. Emerged bees were released after emergence. At the end of each census any empty cocoons were removed. Emergence boxes were censused daily (except 5 April and 14 April 2013 when no observations were made) from the beginning of the experiment (12 March 2013) until a week after the last bee emerged (20 April 2013). In order to make sure no other individuals had emerged, boxes continued to be checked periodically until the final census (1 June 2013). In the final census, all remaining cocoons were brought to the lab and dissected to determine their viability. I considered bees to be viable if when externally inspected they appeared to be fully developed adults without obvious signs of parasites. Survival rates were based on the number of emerged bees out of all viable bees. Parasitized cocoons and undeveloped bees were not included in calculations of survival rates.

4.2.4 Analysis

HOBO data loggers collected temperature measurements every 15 minutes throughout the experiment. I utilized this data to calculate daily average temperatures experienced by bees in each treatment for each day (24-hour period). Then, to determine the relationship between treatment and bee emergence date, I used an Analysis of Variance (ANOVA). Additional predictor variables tested were nest box and the location of each cocoon in the nest and their interactions. I tested these predictors on both the control treatment data set only and in conjunction with treatment for the entire data set.

To determine how average mass varied by sex for each species, I centered mass and used an Analysis of Variance (ANOVA). I also tested whether nest box hole size impacted mass of cocoons. I then tested whether either mass or species would impact emergence timing on both the control treatment data set only and in conjunction with treatment for the entire data set.

For all ANOVAs, I performed post-hoc analysis using Tukey's Honest Significant Difference (HSD) Tests. All analyses were performed using R v.3.3.1 and RStudio v.1.0.153 (R Core Team 2012).

4.3 Results

4.3.1 Results of Nest Box Census

Two non-native bee species, *Osmia cornifrons* and *O. taurus* (see Section 1.6), were found in the nest boxes, along with some Dipteran, Hymenopteran and fungal parasites and summer nesting Hymenoptera. Of the 242 nests made by bees, 64 nests (26%) were determined to be made by *O. cornifrons* and 107 nests (43%) were determined to made by *O. taurus*. The remainder (69 nests) were not identified to species but were either *O. cornifrons* or *O. taurus*.

Mass varied significantly by sex and by species, but there was no interaction between the two (Table 4.1). Overall males were smaller than females and *Osmia cornifrons* were smaller than *O. taurus* (Figure 4.3). Mass did not vary significantly by hole size (F = 12.063, df = 1, $p = 0.3$).

Table 4.1. Results of an ANOVA on the Influence of Sex (Male or Female) and Species (*O. cornifrons*, *O. taurus* or unknown) on Mass

Treatment	**d. f.**	**F value**	***p* value**
sex	1	43.67	<0.001
species	1	8.76	<0.01
sex x species	1	2.96	0.089
residuals	85		

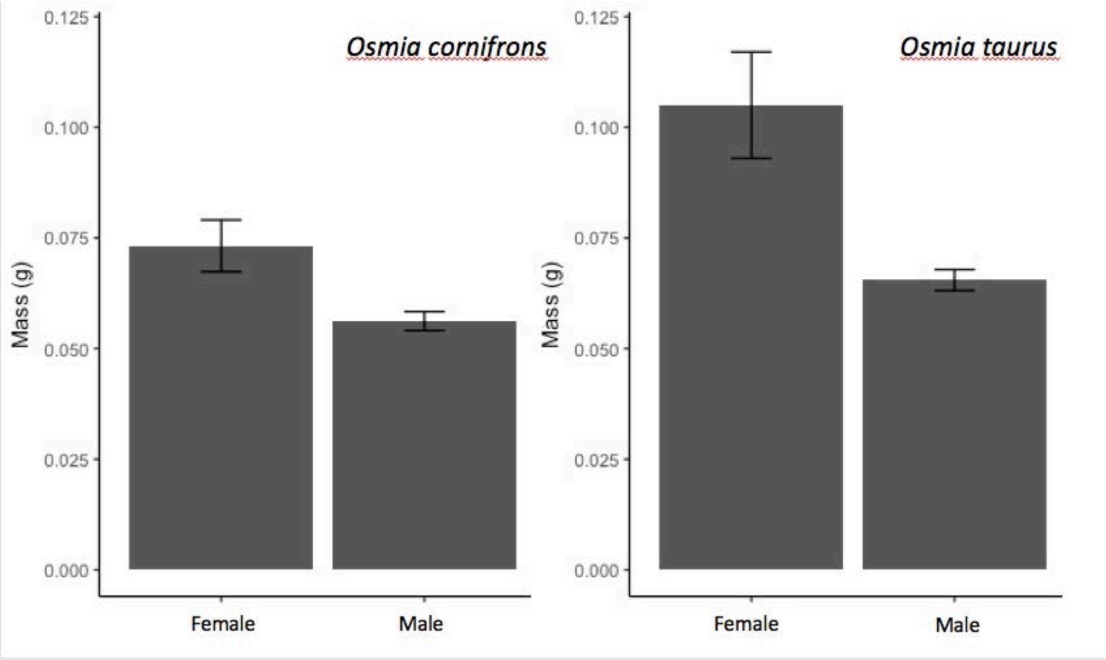

Figure 4.3 Females of both species were significantly larger than males and *Osmia taurus* females were significantly larger female *O. cornifrons*. Males of either species did not vary significantly in mass from all other males. This figure represents all the samples for which I had data for both sex and species (n=91). Of these, 14 were females and the rest (77) were males and 41 were *Osmia cornifrons* while 50 were *O. taurus*.

4.3.2 Warming Treatments: Bee Emergence and Survival

Throughout the experiment (5 Mar to 29 May), the warming treatments had higher average daily temperatures than the CONTROL treatment. The 7WATT treatment was on average 5.2°C above ambient temperature, while the 4WATT treatment was on average 2.3°C above the CONTROL (Figure 4.4).

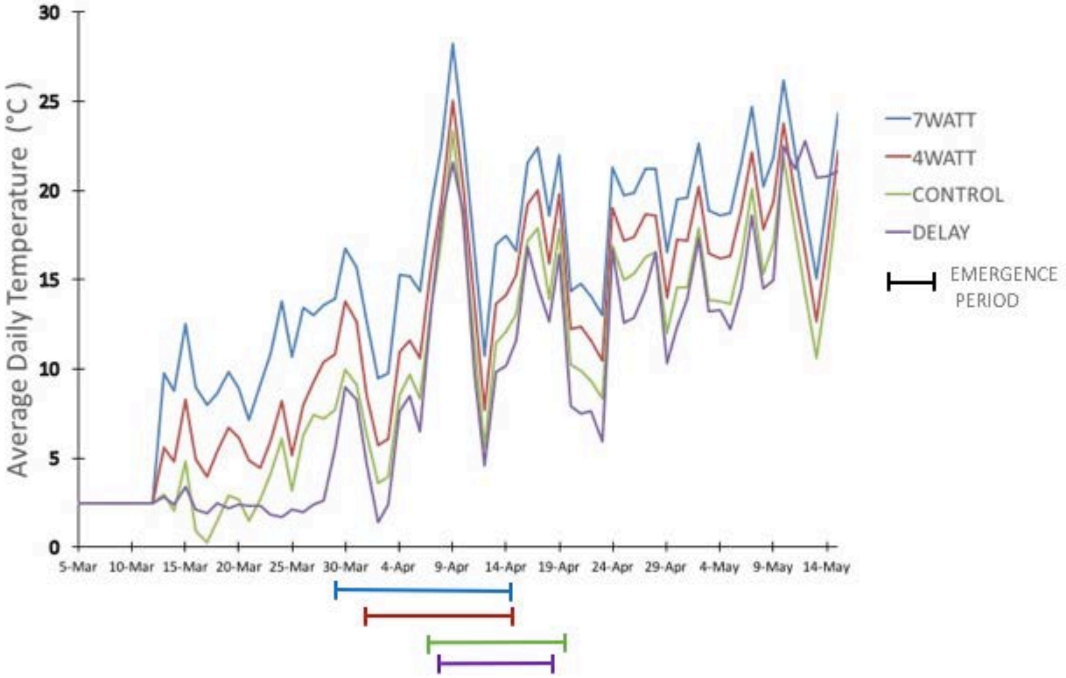

Figure 4.4 Average daily temperature (°C) from 5 Mar to 15 May 2013 in the four emergence treatments. Treatment temperatures indicated by different colored lines: 7WATT (+5.2°C) in blue, 4WATT (+2.3°C) in red, CONTROL (ambient) in green and DELAY in purple). Bee emergence began on 29 Mar and ended by 19 April. Emergence by treatment is indicated by the brackets under the x-axis, with treatment indicated by color.

Emergence time varied significantly by treatment (F = 265.69, df = 3, $p < 0.0001$; Table 4.2). Bees from the 7WATT treatment emerged first and emergence date was significantly different from all other treatments. Bees from the 4WATT treatment were next to emerge, followed by the CONTROL and DELAY treatments which had similar emergence times (Table 4.3, Figure 4.5).

Table 4.2 Results of an ANOVA on the Influence of Emergence Treatment on Emergence Timing

Treatment	**d. f.**	**F value**	***p* value**
treatment	3	265.69	<0.0001
residuals	538		

Table 4.3 Resulting *p*-values for Tukey's Honest Significant Difference (HSD) Tests Performed on Pairs of Emergence Treatments to Determine Whether Treatments Vary by Temperature. Significant Results are in Bold

Treatment Comparison (Tukey HSD)	**Emergence**
7WATT – 4WATT	**$p < 0.05$**
7WATT - CONTROL	**$p < 0.001$**
7WATT - DELAY	**$p < 0.001$**
4WATT - CONTROL	$p = 0.09$
4WATT - DELAY	**$p = 0.01$**
CONTROL - DELAY	$p = 0.9$

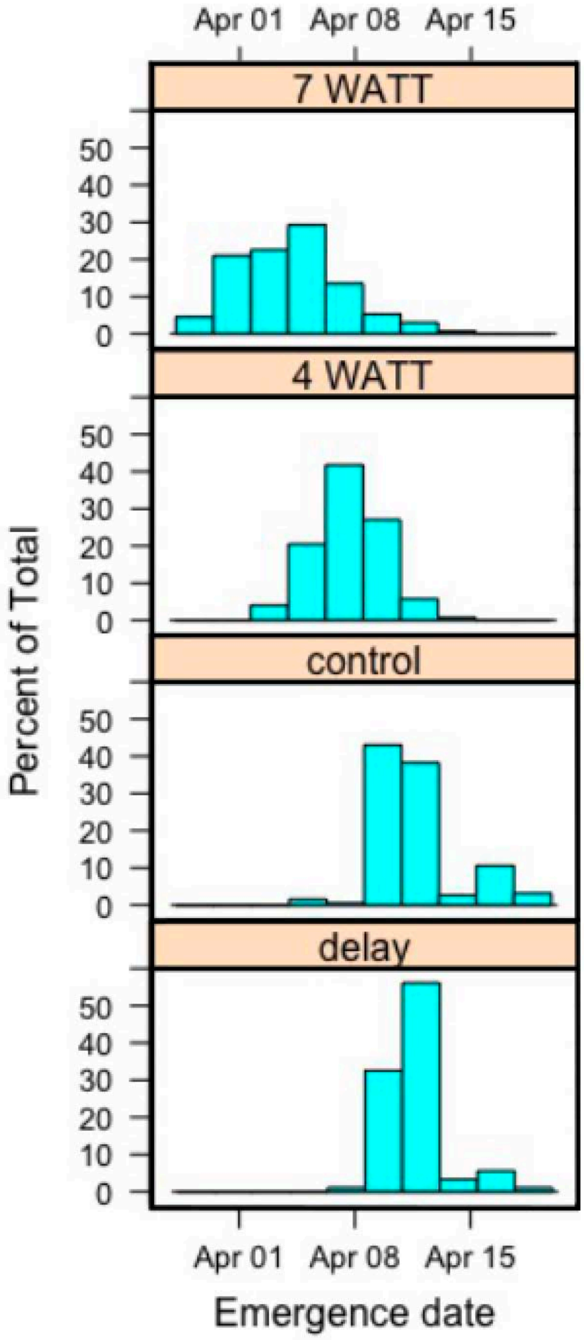

Figure 4.5 Emergence dates of both *Osmia cornifrons* and *O. taurus* combined for all emergence treatments (from top to bottom: 7WATT (+5.2°C), 4WATT (+2.3°C), CONTROL (ambient) and DELAY treatments). All bee emergence began on 29 Mar and ended by 19 April.

None of the predictors, mass, species, nest box or location in the nest, influenced emergence timing for the control treatment only or for the entire data set (see Appendix

B). Survival rates, defined as viable adults that emerged from their cocoons, were high for all treatments (92-95%) with ten or fewer bees per treatment that did not emerge and were found dead at the end of the experiment.

4.4 Discussion

4.4.1 Warming Treatments: Bee Emergence and Survival

My temperature treatments are similar to the projected changes in average surface temperature for the Northeastern United States and did in fact increase the temperature by 2.3°C (4WATT) and 5.2°C (7WATT). Warming treatments did result in earlier emergence times for *Osmia cornifrons* and *O. taurus*. This supports my hypothesis that these species of *Osmia* are phenologically sensitive and suggests that under future climate scenarios these bees will emerge earlier in the spring. DELAY and CONTROL experiments did not vary in emergence timing. Other studies have found that once the minimum length of diapause has occurred, bees will emerge readily when warmed (Krunic and Stanisavljevic 2000) and emergence will occur more quickly the longer the overwintering period (Vicens *et al.* 1994). This may explain why in my experiment there was no difference in the timing of emergence from CONTROL and DELAY treatments. There was no effect of warming on overall survival suggesting that warmer spring temperatures will not have an adverse effect on diapausing bees.

4.4.2 Factors Influencing Bee Emergence

None of the additional predictor variables I tested had a significant impact on bee emergence. Even though, as expected, males were significantly smaller than females for both species and *Osmia cornifrons* was significantly smaller than *O. taurus*. This result was somewhat surprising since these factors have been known to affect emergence in other *Osmia* species (Bosch 1994). Emergence did occur within each treatment over a relatively short period of time (less than two weeks), which may make detection of emergence timing difficult. Also, my nest boxes had two different sized holes, which could have added some noise to my data set, even though cocoon mass was not significantly affected by nest box hole size.

4.4.3 Climate Change and Phenology

Bees are important pollinators and therefore understanding their response to projected climate change scenarios helps us understand the potential impacts of climate change on pollination services. My study confirms previous studies that have found other species of *Osmia* to be phenologically sensitive, suggesting that with warmer spring temperatures, many spring active *Osmia* species will emerge earlier. It is not clear whether floral resources will also advance their warming at the same rate as bees. Flowering time in plants is also affected by length of daylight, not just temperature and is species specific (Menzel *et al.* 2006). If flowering times do not advance at the same rate as bee emergence then there could be phenological mismatches resulting in population declines for both plants and bees (Forrest and Thomson 2011). However, both *O. cornifrons* and *O. taurus* are generalist bee species, able to utilize multiple plant species (Wilson *et al.* 1999, Haider *et al.* 2014), which could provide some resilience in a changing climate. For example, Bartomeus *et al*. (2011) did not find a phenological mismatch between 10 species of generalist spring emerging northeastern North American bees and insect-pollinated plants. And a recent study found that bees with larger dietary breadth and smaller body sizes were less likely to have declined over the past 140 years (Bartomeus *et al.* 2013a)

This study also provides evidence that many *Osmia* species, not just *O. lignaria* (Pitts-Singer *et al.* 2008) and *O. cornifrons* (White *et al.* 2009) could be manipulated for early spring crop pollination. *Osmia lignaria* have been shown to have geographic variation in emergence timing when reared in a common environment (Pitts-Singer *et al.* 2014). This may also be true of *O. taurus* and *O. cornifrons*, for they are not native to North America, but thriving in this new range. Both their native and introduced ranges are fairly large, suggesting some inherent genetic variability and possibly also some flexibility in the timing of their emergence. This study also suggests that if climate change results in warmer temperatures at more northern latitudes, both *O. cornifrons* and *O. taurus*, could further expand their range in both their native and their non-native homes.

4.4.4 Future Studies

Although recent papers suggest some resiliency in the phenology of plant-pollinator interactions under changing climate regimes (Forrest and Thomson 2011, Bartomeus *et al.* 2011, Bartomeus *et al.* 2013b), further research is needed (Forrest 2015). Climate change will affect the emergence of bees in different ways – winter length and winter temperatures are also predictors of survival and spring emergence (Walinga 2016) and should be manipulated in future studies. Studies have also shown the importance of a short pre-wintering (fall) period for spring emerging bees to reduce critical energy/mass loss during diapause (Bosch and Kemp 2004, Bosch *et al.* 2010, Sgolastra *et al.* 2012). Without this period of cooling before over-wintering, higher rates of mortality during winter occur (Torchio *et al.* 1987, Sgolastra *et al.* 2011). This is likely because if bees do not experience a cooler pre-wintering period or are exposed to higher temperatures while overwintering, bees remain metabolically active and can use up important energy stores that are required to make it through winter diapause. In fact, earlier spring emergence and shorter periods of diapause are one potential response of *Osmia* species that have been exposed to warmer fall and winter temperatures (Bosch and Kemp 2003, Sgolastra *et al.* 2011, Waling 2016).

It is also critical to know what happens to bees after they emerge. It may be that bees emerging earlier do not have as high a rate of survival post-emergence or their reproductive success may be reduced, due to either lack of floral resources or higher physiological stress. This is especially possible if springs aren't just warmer, but rather are more variable in their high and low temperatures (Bosch *et al.* 2006). Although earlier emergence may reduce parasite load if parasites emerge later (Wcislo *et al.* 1994).

Osmia cornifrons and *O. taurus* are quickly expanding their range in the United States. The jury is still out on what impacts they have on local bee and plant communities, but this study has important implications for the population growth of these species in a warming world. A better understanding of their emergence patterns allows better management of these species, whether for pollination services or to minimizes any harmful impacts caused by their introduction to a new ecological community.

CHAPTER 5

SYNTHESIS AND CONCLUSIONS

Bees and other pollinators are critical for the continued survival of plants in both natural and man-made ecosystems. Diverse pollinator communities have been shown to increase richness in plant communities and plant reproduction depends upon pollinator community composition (National Research Council 2006, Klein *et al.* 2007, Ollerton *et al.* 2011, Thomann *et al.* 2013). Yet there is growing concern that pollinators, especially bees, are declining globally (Potts *et al.* 2010, Vanbergen *et al.* 2013, Goulson *et al.* 2015). This dissertation evaluates potential mechanisms responsible for bee and pollinator community composition in order to promote pollinator conservation in natural systems and their restoration in human-dominated urban and agricultural landscapes.

Previous work has found evidence of floral resources structuring pollinator communities and controlling pollinator population dynamics (Potts *et al.* 2003, Roulston and Goodell 2011). My meta-analysis confirmed these previous studies as I found strong positive correlations between plant and pollinator diversity and abundance across all major terrestrial ecosystems. These results suggest that flowering plants could be used as surrogates for pollinators in conservation plans, although the effectiveness of this strategy would vary by biome. Impacts of sampling methodology used to determine effectiveness of any conservation or restoration strategies should also be considered. Direct experimental tests of any restoration or conservation interventions are also still needed as even strong correlations do not prove causal mechanisms.

Bee populations are impacted directly not just by floral resources, but also by nesting resources and risk, primarily from natural enemies (Roulston and Goodell 2011). Bees are also indirectly affected by abiotic factors, like climate, that influence both their behavior and the resources available. My work on *Osmia cornfirons* and *O. taurus* confirm that nesting resources and climate can influence bee populations. I found that usage of artificial nesting substrate by these bees is affected by the design of nest boxes, especially cavity hole size and density of neighboring cavities. I also found that both of these species are phenologically sensitive and therefore may be affected by warmer spring temperatures caused by climate change. This information is useful whether *O. cornifrons* and *O. taurus* need to be managed for their pollination services or to reduce their impacts as non-native species.

In conclusion, the scientific investigations in this dissertation have shown that generally plant diversity and abundance correlates with pollinator diversity and abundance across the world in at a global scale, with some variation in the strength of this relationship based on biome and sampling method. These investigations also show that management of two cavity-nesting bees, *Osmia cornifrons* and *O. taurus*, for pollination or as non-native species can be done through artificial nesting substrate and manipulating their spring temperatures.

APPENDIX A

List of studies utilized in the meta-correlation analyses of plant and pollinator richness (R) and/or in the meta-correlation analyses of plant and pollinator abundance (A).

Abrahamczyk and Kessler 2010 (R, A)
Abrahamczyk *et al.* 2011(R)
Albrecht *et al.* 2007a (R)
Albrecht *et al.* 2007b (R, A)
Albrecht *et al*. 2010a (R)
Albrecht *et al.* 2010b (R)
Albrecht *et al*. 2014 (R)
Anderson *et al.* 2014
Bartomeus *et al.* 2008 (R)
Bartomeus *et al.* 2010 (R)
Batary *et al.* 2010 (R)
Benadi et al. 2014 (R)
Bhardwaj *et al.* 2012 (R, A)
Blaauw and Isaacs 2014 (R)
Bock *et al.* 2007 (R, A)
Brehm *et al.* 2007 (R)
Brosi *et al.* 2007 (R, A)
Brosi *et al.* 2008 (R, A)
Carper *et al.* 2014 (R, A)
Carstensen *et al.* 2014 (R)
Carvell 2002 (R, A)
Castro-Urgal and Traveset 2014 (R)
Castro-Urgal *et al.* 2012 (R)
Chamberlain *et al.* 2014 (R)
Chettri 2010 (R)
Chmura *et al.* 2013 (R, A)
Cremene *et al.* 2005 (R)
Croxton *et al.* 2005 (R)
Dallimer *et al.* 2012 (R)
Dauber *et al.* 2003 (R)
Devoto *et al.* 2005 (R)
Ebeling *et al.* 2008 (R)
Ebeling *et al.* 2012 (R)
Ekroos *et al.* 2008 (A)
Ekroos *et al.* 2013 (R)
Fang and Huang 2012 (R)
Forup and Memmott 2005 (R, A)
Forup *et al.* 2008 (R)
Fründ *et al.* 2010 (R)
Gathmann *et al*. 1994 (R)
Gibson *et al.* 2011 (R)
Gikungu 2006 (R)
Grass *et al.* 2013 (R, A)
Grill *et al.* 2005 (R)
Haenke *et al.* 2009 (A)
Hagen and Kraemer 2010 (R, A)
Hannon and Sisk 2009 (R)
Hanula and Horn 2011
Hauck *et al.* 2014 (R)
Hegland and Boeke 2006 (R)
Heithaus 1974 (R)
Hendrix *et al.* 2010 (R, A)
Henning and Ghazoul (A)
Holl 1996 (R, A)
Holzschuh *et al.* 2007 (R)
Holzschuh *et al.* 2011 (R)
Holzschuh *et al.* 2012 (A)
Hopwood 2008 (R, A)
Horner-Devine *et al.* 2003 (R, A)
Hudewenz *et al.* 2012 (R)
Hudson *et al.* 2013 (A)
Kaiser-Bunbury *et al.* 2011 (R)
Kitahara and Watanabe 2003 (R)
Kitahara 2004 (R)
Kitahara *et al.* 2008 (R)
Kivinen et al. 2006 (R)
Kleijn and van Langevelde 2006 (A)
Kleijn *et al.* 2004 (R)
Kleintjes *et al.* 2004 (R, A)
Knop *et al.* 2006 (R)
Koch *et al.* 2013 (R, A)
Kohler *et al.* 2007 (R, A)
Kremen 1992 (R)
Kunte *et al.* 1999 (R, A)
Kuussaari *et al.* 2011 (R)
Locatelli and Machado 2000 (R)
Love 2010 (R, A)
Lowenstein *et al.* 2014 (R, A)
Loyola and Martins 2008 (A)
Maccherini *et al.* 2009 (R)
Mandelik *et al.* 2012 (R, A)
Marini *et al.* 2009 (R)

APPENDIX A
(CONTINUED)

Marrero *et al.* 2014 (R)
McIntyre and Hostetler 2001 (R)
Mello *et al.* 2011 (R)
Meng *et al.* 2012 (R)
Meyer *et al.* 2009 (R, A)
Moldenke 1975 (R, A)
Morandin and Kremen 2013 (A)
Munguira and Thomas 1992 (A)
Myers *et al.* 2012 (R, A)
Nielsen and Totland 2014 (R)
Noordiijk *et al.* 2009 (A)
Ochoa-Hueso *et al.* 2014 (A)
Ockinger and Smith 2006 (R, A)
Ockinger and Smith 2007 (R, A)
Ockinger *et al.* 2006 (R)
Osborn *et al.* 1999 (R)
Popic *et al.* 2013 (R, A)
Potts *et al.* 2000 (R, A)
Potts *et al.* 2003a (R, A)
Potts *et al.* 2003b (R, A)
Potts *et al.* 2004 (R)
Potts *et al.* 2006 (R)
Power and Stout 2011 (R, A)
Proches and Cowling 2006 (R)
Pryke and Samways 2003 (R, A)
Redpath-Downing *et al.* 2013 (A)
Reed 1993 (R)
Richards *et al.* 2011 (A)
Rickert *et al.* 2012 (R, A)
Romey *et al.* 2007 (R, A)
Rutgers-Kelly and Richards 2013 (R, A)
Saarinen *et al.* 2005 (R, A)
Sajjad and Saeed 2010 (A)
Santi *et al.* 2010 (R)
Santos *et al.* 2012 (R)
Sarospataki *et al.* 2009 (R, A)
Scherber *et al.* 2010 (R)
Schulze *et al.* 2004 (R)
Schwartz *et al.* 2013 (R)
Shuey *et al.* 2012 (R)
Simonson *et al.* 2001 (R)
Sjodin *et al.* 2008 (A)
Smith *et al.* 2008 (R)
Steffan-Dewenter and Tscharntke 1997 (R)
Steffan-Dewenter and Tscharntke 2000 (A)
Steffan-Dewenter and Tscharntke 2001 (R,A)
Stout and Casey 2014 (R)
Sutherland *et al.* 2001 (A)
Syndenham *et al.* 2014 (R, A)
Taki *et al.* 2008 (R)
Taki *et al.* 2010 (R, A)
Tarrant *et al.* 2013 (R)
Tepedino and Stanton 1981 (R)
Torné-Noguera *et al.* 2014 (R, A)
Traveset *et al.* 2013 (R)
Tscharntke *et al.* 1998 (R)
Tylianakis *et al.* 2006 (R)
Usher and Keiller 1998 (R)
Vazquez and Aizen 2003 (R)
Vessby *et al.* 2002 (R)
Weibull *et al.* 2003 (R)
Werling *et al.* 2014 (R)
Williams *et al.* 2011 (R, A)
Yamamoto *et al.* 2007 (R, A)
Yamaura *et al.* 2012 (R, A)

APPENDIX B

Results of ANOVAs on the influence of predictors on the emergence timing of *Osmia* bees from the CONTROL treatment data set. Predictors were also analyzed for their influence on *Osmia* bee emergence for the entire data set, but were not significant, data not shown.

Table B.1 Results of an ANOVA on the influence of sex (male or female) and species (*O. cornifrons, O. taurus* or unknown) on emergence timing of the control data set

Predictors	d. f.	F value	*p* value
species	1	0.1067	0.7603
mass	1	0.6801	0.4559
mass x species	1	0.0144	0.9102
residuals	4		

Table B.2 Results of an ANOVA on the influence of nest box and location in the nest (i.e. nest cell) on emergence timing of the control data set

Predictors	d. f.	F value	*p* value
nest cell	10	0.7014	0.7193
nest box	29	1.2259	0.2491
nest cell x nest box	88	1.1065	0.3410
residuals	60		

REFERENCES

Abel, C. A. and R. L. Wilson. 1998. The use of diverse plant species for increasing *Osmia cornifrons* (Hymenoptera: Megachilidae) in field cases. *Journal of Kansas Entomological Society* **71**:23-28.

Abrahamczyk, S. and M. Kessler. 2010. Hummingbird diversity, food niche characters, and assemblage, composition along a latitudinal precipitation gradient in the Bolivian lowlands. *Journal of Ornithology* **151**:615-625.

Abrahamczyk, S., P. Gottleuber, C. Matauschek, and M. Kessler. 2011. Diversity and community composition of euglossine bee assemblages (Hymenoptera: Apidae) in western Amazonia. *Biodiversity and Conservation* **20**:2981-3001.

Aguiar, C. M., C. A. Garófalo, and G. F. Almeida. 2005. Trap-nesting bees (Hymenoptera, Apoidea) in areas of dry semideciduous forest and caatinga, Bahia, Brazil. *Revista Brasileira de Zoologia* **22**:1030-1038.

Ahn, J. J., Y.-L. Park, C. Jung. 2014. Modeling spring emergence of *Osmia cornifrons* Radoszkowski (Hymenoptera: Megachilidae) females in Korea. *Journal of Asia-Pacific Entomology* **17**:901-905.

Aizen, M. A., C. L. Morales, and J. M. Morales. 2008. Invasive mutualists erode native pollination webs. 2008. *PLoS Biology* **6**:e31.

Aizen, M.A., C. L. Morales, D. P. Vázquez, L. A. Garibaldi, A. Sáez, and L. D. Harder. 2014. When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. *New Phytologist* **204**:322-328.

Albrecht, M., P. Duelli, C. Müller, D. Kleijn, and B. Schmid. 2007a. The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology* **44**:813-822.

Albrecht, M., P. Duelli, B. Schmid, and C. B. Müller. 2007b. Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *Journal of Animal Ecology* **76**:1015-1025.

Albrecht, M., M. Riesen, and B. Schmid. 2010a. Plant-pollinator network assembly along the chronosequence of a glacier foreland. *Oikos* **119**:1610-1624.

Albrecht, M., B. Schmid, Y. Hautier, and C. B. Muller. 2012. Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B-Biological Sciences* **279**:4845-4852.

Albrecht, M., B. Schmid, M. K. Obrist, B. Schüpbach, D. Kleijn, and P. Duelli. 2010b. Effects of ecological compensation meadows on arthropod diversity in adjacent intensively managed grasslands. *Biological Conservation* **143**:642-649.

Albrecht, J. D. G. Berens, B. Jaroszewicz, N. Selva, R. Brandl, and N. Farwig. 2014. Correlated loss of ecosystem services in coupled mutualistic networks. *Nature Communications* **5**:3810-3818.

Anderson, P. M. L, G. Avlonitis, and H. Ernstson. 2014. Ecological outcomes of civic and expert-led urban greening projects using indigenous plant species in Cape Town, South Africa. *Landscape and Urban Planning* **127**:104-113.

Artz, D. R., M. J. Allan, G. I. Wardell, and T. L. Pitts-Singer. 2013. Nesting site density and distribution affect Osmia lignaria (Hymenoptera: Megachilidae) reproductive success and almond yield in a commercial orchard. *Insect Conservation and Diversity* **6**:715-724.

Artz, D. R., M. J. Allan, G. I. Wardell, and T. L. Pitts-Singer. 2014. Influence of nest box color and release sites on *Osmia lignaria* (Hymenoptera: Megachilidae) reproductive success in a commercial almond orchard. *Journal of Economic Entomology* **107**:2045–2054.

Ascher, J. S. 2001. *Hylaeus hylinatus* Smith, a European bee new to North America, with notes on other adventive bees (Hymenoptera: Apoidea). *Proceedings of the Entomological Society Washington* **103**:184-190.

Barthell, J. F., J. M. Randall, R. W. Thorp, and A. M. Wenner. 2001. Promotion of seed set in yellow-star-thistle by honey bees: evidence of an invasive mutualism. *Ecological Applications* **11**:1870-1883.

Bartomeus, I., J. S. Ascher, J. Gibbs, B. N. Danforth, D. L. Wagner, S. M. Hedtke, and R. Winfree. 2013a. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences of the United States of America* **110**:4656-4660.

Bartomeus, I., J. S. Ascher, D. Wagner, B. N. Danforth, S. Colla, S. Kornbluth, and R. Winfree. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences of the United States of America* **108**:20645-20649.

Bartomeus, I., M. G. Park, J. Gibbs, B. N. Danforth, A. N. Lakso, and R. Winfree. 2013b. Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecology Letters* **16**:1331-1338.

Bartomeus, I., M. Vilà, and L. Santamaría. 2008. Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia* **155**:761-770.

Bartomeus, I., M. Vilà, and I. Steffan-Dewenter. 2010. Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *Journal of Ecology* **98**:440-450.

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**:431-433.

Batáry, P., A. Báldi, M. Sárospataki, F. Kohler, J. Verhulst, E. Knop, F. Herzog, and D. Kleijn. 2010. Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agriculture, Ecosystems and Environment* ***136****:35-39.*

Bates, D., B. Bolker, M. Mächler, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**:1-48.

Batras, S. W. T. 1979. *Osmia cornifrons* and *Pithitis smaragula*, two Asian bees introduced into the United States for crop pollination. *Maryland Agricultural Experiment Station Special Miscellaneous Publications* **1**:307-312.

Bawa, K. S. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* **21**:399-422.

Benadi, G., N. Blüthgen, T. Hovestadt, and H.-J. Poethke. 2013. Contrasting specialization–stability relationships in plant–animal mutualistic systems. *Ecological Modelling* **258**:65-73.

Benadi, G., T. Hovestadt, H.-J. Poethke, and N. Blüthgen. 2014. Specialization and phenological synchrony of plant-pollinator interactions along an altitudinal gradient. *Journal of Animal Ecology* **83**:639-650.

Bhardwaj, M., V. P. Uniyal, A. K. Sanyal, and A. P. Singh. 2012. Butterfly communities along an elevational gradient in the Tons valley, Western Himalayas: implications of rapid assessment for insect conservation. *Journal of Asia-Pacific Entmology* **15**:207-217.

Biesmeijer, J. C., S. P. Roberts, M. Reemer, R. Ohlemuller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**:351-354.

Blaauw, B. R. and R. Isaacs. 2014. Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. *Basic and Applied Ecology* **15**:701-711.

Bock, C. E., R. A. Bailowitz, D. W. Danforth, Z. F. Jones, and J. H. Bock. 2007. Butterflies and exurban development in southeastern Arizona. *Landscape and Urban Planning* **80**:34-44.

Bommarco, R., O. Lundin, H. G. Smith, and M. Rundlof. 2012. Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society B - Biological Science* **279**:309-315.

Borenstein, M. 2009. Effect sizes for continuous data. In: H. Cooper LVH, J.C. Valentine (ed.) The Handbook of Research Synthesis and Meta-Analysis, 2nd edn. Russell Sage Foundation, New York, p. 221-235.

Bosch, J. 1994a. Improvement of field management of *Osmia cornuta* (Latreille) (Hymenoptera, Megachilidae) to pollinate almond. *Apidologie* **25**:71-83.

Bosch, J. 1994b. *Osmia cornuta* Latr. (Hymenoptera, Megachilidae) as a potential pollinator in almond orchards. *Journal of Applied Entomology* **117**:151-157.

Bosch, J and M. Blas. 1994. Effect of over-wintering and incubation temperatures on adult emergence in *Osmia cornuta* Latr (Hymenoptera, Megachilidae). *Apidologie* **25**:265-277.

Bosch, J. and W. P. Kemp. 2000. Development and emergence of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environmental Entomology* **29**:8-13.

Bosch, J. and W. P. Kemp. 2003. Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environmental Entomology* **32**:711-716.

Bosch, J. and W. P. Kemp. 2004. Effect of pre-wintering and winter temperature regimes on weight loss, survival, and emergence time in the mason bee *Osmia cornuta* (Hymenoptera: Megachilidae). *Apidologie* **35**:469-479.

Bosch, J., W. P. Kemp, and G. E. Trostle. 2006. Bee population returns and cherry yields in an orchard pollinated with *Osmia lignaria* (Hymenoptera: Megachilidae). Journal of *Economic Entomology* **99**:408-413.

Bosch, J., Y. Maeta, and R. Rust. 2001. A phylogenetic analysis of nesting behavior in the Genus *Osmia* (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America* **94**:617-627.

Bosch, J., A. M. Martín Gonzalez, A. Rodrigo, and D. Navarro. Plant-pollinator networks: adding the pollinator’s perspective. *Ecology Letters* **12**:409-419.

Bosch, J. J. Retana, and X. Cerdá. 1997. Flowering phenology, floral traits and pollinator composition. *Oecologia* **109**:583-591.

Bosch, J., F. Sgolastra, and W. P. Kemp. 2010. Timing of eclosion affects diapause development, fat body consumption and longevity in Osmia lignaria, a univoltine, adult-wintering solitary bee. *Journal of Insect Physiology* **56**:1949-1957.

Bosch, J. and N. Vicens. 2006. Relationship between body size, provisioning rate, longevity and reproductive success in females of the solitary bee *Osmia cornuta*. *Behavioral Ecology and Sociobiology* **60**:26-33.

Brehm, G., R. K. Caldwell, and J. Kluge. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography* **16**:205-219.

Brittain, C., C. Kremen, and A. M. Klein. 2013a. Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology* **19**:540-547.

Brittain, C., N. Williams, C. Kremen, and A. M. Klein. 2013b. Synergistic effects of non-Apis bees and honey bees for pollination services. *Proceedings of the Royal Society B - Biological Sciences* **280**:20122767.

Brosi, B. J., G. C. Daily, and P. R. Ehrlich. 2007. Bee community shifts with landscape context in a tropical countryside. *Ecological Applications* **17**:418-430.

Brosi, B. J., G. C. Daily, T. M. Shih, F. Oviedo, and G. Durán. 2008. The effects of forest fragmentation on bee communities in tropical countryside. *Journal of Applied Ecology* **45**:773-783.

Budriené, A. E. Budrys, and Z. Nevronyté. 2004. Solitary Hymenoptera Aculeata inhabitating trap-nests in Lithuania: nesting cavity choice and niche overlap. *Latvijas Entomologs* **41**:19-31.

Bugg, R. L., R. G. Colfer, W. E. Chaney, H. A. Smith, and J. Cannon. 2008. Flower flies (Syrphidae) and other biological control agents for aphids in vegetable crops. *ANR Publication* **8285**:1-25.

Burkle, L. A., J. C. Martin, and T. M. Knight. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence and function. *Science* **339**:1611-1615.

Calderone, N. W. 2012. Insect pollinated crops, insect pollinators and US agriculture: trend analysis of aggregate data for the period 1992-2009. *PLoS One* **7**:e37235.

Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America* **108**:662-667.

Campbell, J.W., J. L. Hanula, and T. A. Waldrop. 2007. Effects of prescribed fire and fire surrogates on floral visiting insects of the blue ridge province in North Carolina. *Biological Conservation* **134**:393–404

Cane, J. H. 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society* **64**:406-413.

Cane, J. H. 2003. Exotic nonsocial bees (Hymenoptera: Apiformes) in North America: ecological implications. In: K. Strickler, J. H. Cane (eds.) For Nonnative Crops, Whence Pollinators of the Future. Lanham: Proceedings of the Entomological Society of America, pp.113-126.

Cane, J. H., T. Griswold, and F. D. Parker. 2007. Substrates and materials used for nesting by North American *Osmia* bees (Hymenoptera: Apiformes: Megachilidae). *Annals of the Entomological Society of America* **100**:350-358.

Cane, J. H., R. L. Minckley, L. J. Kervin, T. H. Roulston, and N. M. Williams. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications* **16**:632-644.

Carper, A. L., L. S. Adler, P. S. Warren, and R. E. Irwin. 2014. Effects of surburanization on forest bee communities. *Environmental Entomology* **43**:252-262.

Carstensen, D. W., M. Sabatino, K. TrØjelsgaard, and L. P. C. Morellato. 2014. Beta diversity of plant-pollinator networks and the spatial turnover of pairwise interactions. *PLoS One* **9**:e112903.

Carvalheiro, L. G., W. E. Kunin, P. Keil, J. Aguirre-Gutierrez, W. N. Ellis, R. Fox, Q. Groom, S. Hennekens, W. Van Landuyt, D. Maes, F. Van de Meutter, D. Michez, P. Rasmont, B. Ode, S. G. Potts, M. Reemer, S. P. Roberts, J. Schaminee, M. F. WallisDeVries, and J. C. Biesmeijer. 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecology Letters* **16**:870-878.

Carvalheiro, L. G., C. L. Seymour, R. Veldtman, and S. W. Nicolson. 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology* **47**:810-820.

Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation* **103**:33-49.

Castagneyrol, B. and H. Jactel. 2012. Unraveling plant-animal diversity relationships: a meta-regression analysis. *Ecology* **93**:2115-2124.

Castro-Urgal, R. and A. Traveset. 2014. Differences in flower visitation networks between an oceanic and a continental island. *Botanical Journal of the Linnean Society* **174**:478-488.

Chamberlain, S., D. P. Vázquez, L. Carvalheiro, E. Elle, and J. C. Vamosi. 2014. Phylogenetic tree shape and the structure of mutualistic networks. *Journal of Ecology* **102**:1234-1243.

Chettri, N. 2010. Cross-taxon congruence in a trekking corridor of Sikkim Himalayas: surrogate analysis for conservation planning. *Journal for Nature Conservation* **18**:75-88.

Chmura, D., P. Adamski, and Z. Denisiuk. 2013. How do plant communities and flower visitors relate? A case study of semi-natural xerothermic grasslands. *Acta Societatis Botanicorum Poloniae* **82**:99-105.

Clavero, M. and E. García-Berthou. 2005. Invasive species are a leading cause of animal extinctions. *TRENDS in Ecology and Evolution* **20**:110.

Colla, S. R., and L. Packer. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on Bombus affinis Cresson. *Biodiversity and Conservation* **17**:1379-1391.

Cremene, C., G. Groza, L. Rakosy, A. A. Schileyko, A. Baur, A. Erhardt, and B. Baur. 2005. Alternations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspot. *Conservation Biology* **19**:1606-1618.

Croxton, P. J., J. P. Hann, J. N. Greatorex-Davies, and T. H. Sparks. 2005. Linear hotspots? The floral and butterfly diversity of green lanes. *Biological Conservation* **121**:579-584.

Currie, D. J. 1991. Energy and larg-scale patterns of animal- and plant-species richness. *The American Naturalist* **137**:27-49.

Dainese, M., V. Riedinger, A. Holzschuh, D. Kleijn, J. Scheper, and I. Steffan-Dewenter. 2017. Managing trap-nesting bees as crop pollinators: spatiotemporal effects of floral resources and antagonists. *Journal of Applied Ecology* **00**:1-10.

Dallimer, M., J. R. Rouquette, A. M. J. Skinner, P. R. Armsworth, L. M. Maltby, P. H. Warren, and K. J. Gaston. 2012. Contrasting patterns in species richness of birds, butterflies and plants along riparian corridors in an urban landscape. *Diversity and Distribution* **18**:742-753.

Danieli-Silva, A., J. M. T. de Souza, A. J. Donatti, R. P. Campos, J. Vicente-Silva, L. Freitas, and I. G. Varassin. 2012. Do pollination syndromes cause modularity and predict interactions in a pollination network in a tropical high-altitude grasslands? *Oikos* **121**:35-43.

Dauber, J., M. Hirsch, D. Simmering, R. Waldhardt, A. Otte, and V. Wolters. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture, Ecosystems and Environment* **98**:321-329.

Davila, Y. C., E. Elle, J. C. Vamosi, L. Hermanutz, J. T. Kerr, C. J. Lortie, A. R. Westwood, T. S. Woodcock, and A. C. Worley. 2012. Ecosystem services of pollinator diversity: a review of the relationship with pollen limitation of plant reproduction. *Botany* **90**:535-543.

Davis, E. S., N. Reid, and R. J. Paxton. 2012. Quantifying forage specialization in polyphagic insects: the polylectic and rare solitary bee, Colletes floralis (Hymenoptera: Colletidae). *Insect Conservation and Diversity* **5**:289-297.

DeGaetano, A. T. and R. J. Allen. 2002. Trends in twentieth-century extremes across the United States. *Journal of Climate* **15**:3188-3205.

Devoto, M., D. Medan, and N. H. Montaldo. 2005. Patterns of interaction between plants and pollinators along an environmental gradient. *Oikos* **109**:461-472.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* **345**:401-406.

Dixon, K. W. 2009. Pollination and restoration. *Science* **31**:571-573.

Dohzono, I., Y. K. Kunitake, J. Yokoyama, and K. Goka. 2008. Alien bumble bee affects native plant reproduction through interactions with native bumble bees. *Ecology* **89**:3082-3092.

Dohzono, I. and J. Yokoyama. 2010. Impacts of alien bees on native plant-pollinator relationships: a review with special emphasis on plant reproduction. *Applied Entomological Zoology* **45**:37-47.

Dukes, J. S., J. Pontius, D. Orwig, J. R. Garnas, V. L. Rodgers, N. Brazee, B. Cooke, K. A. Theoharides, E. E. Stange, R. Harrington, J. Ehrenfeld, J. Gurevitch, M. Lerdau, K. Stinson, R. Wick, and M. Ayres. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? *Canadian Journal for Forest Research* **39**:231-248.

Ebeling, A., A-M. Klein, J. Schumacher, W. W. Weisser, and T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* **117**:1808-1815.

Ebeling, A., A.-M. Klein, W. W. Weisser, and T. Tscharntke. 2012. Multitrophic effects of experimetnal changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. *Oecologia* **169**:453-464.

Egger, M., G. D. Smith, M. Schneider, and C. Minder. 1997. Bias in meta-analysis detected by a simple, graphical test. *British Medical Journal* **315**:629-634.

Eilers, E. J., C. Kremen, S. Smith Greenleaf, A. K. Garber, and A. M. Klein. 2011. Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS One* **6**:e21363.

Ekroos, J. M. Kuussaari, J. Tiainen, J. Heiölä, T. Seimola, and J. Helenius. Correlations in species richness between taxa depend on habitat, scale and landscape context. *Ecological Indicators* **34**:528-535.

Ekroos, J., M. Piha, and J. Tiainen. 2008. Role of organic and conventional field boundaries on boreal bumblebees and butterflies. *Agriculture, Ecosystems and Environment* **124**:155-159.

Elberling, H. and J. M. Olesen. 1999. The structure of high latitude plant-flower visitor system: the dominance of flies. *Ecography* **22**:314-323.

Eltz, T., C. A. Bruhl, Z. Imiyabir, K. E. Linsenmair. 2003. Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management. *Forest Ecological Management* **172**:301–313

Everaars, J., M. W. Strohbach, B. Gruber, C. F. Dormann. 2011. Microsite conditions dominate habitat selection of the red mason bees (*Osmia bicornis*, Hymenoptera: Megachilidae) in an urban environment: a case study from Leipzig, Germany. *Landscape and Urban Planning* **103**:15-23.

Fang, Q. and S.-Q. Huang. 2012. Relative stability of core groups in pollination networks in a biodiversity hotspot over four years. *PLoS One* **7**:e32663.

Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PloS Biology* **4**:129-135.

Forrest, J. R. K. 2015. Plant-pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? *Oikos* **124**:4-13.

Forrest, J. R. K. and J. D. Thomson. 2011. An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecological Monographs* **81**:469-491.

Forup, M. L., K. S. E. Henson, P. G. Craze, and J. Memmott. 2008. The restoration of ecological interactions: plant-pollinator networks on ancient and restored heatlands. *Journal of Applied Ecology* **45**:742-752.

Forup, M. L. and J. Memmott. 2005. The restoration of plant-pollinator interactions in hay meadows. *Restoration Ecology* **13**:265-274.

Fox, R. 2013. The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* **6**:5-19.

Fründ, J., C. F. Dormann, A. Holzschuh, and T. Tscharntke. 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology* **94**:2042-2054.

Fründ, J., K. E. Linsenmair, and N. Blüthgen. 2010. Pollinator diversity and specialization in relation to flower diversity. *Oikos* **119**:1581-1590.

Gallai, N., J.-M. Salles, J. Settele, and B. E. Vaissière. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* **68**:810-821.

Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, L. G. Carvalheiro, L. D. Harder, O. Afik, I. Bartomeus, F. Benjamin, V. Boreux, D. Cariveau, N. P. Chacoff, J. H. Dudenhöffer, B. M. Freitas, J. Ghazoul, S. Greenleaf, J. Hipólito, A. Holzschuh, B. Howlett, R. Isaacs, S. K. Javorek, C. M. Kennedy, K. M. Krewnka, S. Krishnan, Y. Mandelik, M. M. Mayfield, I. Motzke, T. Munyuli, B. A. Nault, M. Otieno, J. Petersen, G. Pisanty, S. G. Potts, R. Rader, T. H. Ricketts, M. Rundlöf, C. L. Seymour, C. Schüepp, H. Szentgyörgyi, H. Taki, T. Tscharntke, C. H. Vergara, B. F. Viana, T. C. Wanger, C. Westphal, N. Williams, and A. M. Klein. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339**:1608-1611.

Gason, K. J. 1992. Regional numbers of insect and plant species. *Functional Ecology* **6**:243-247.

Gathmann, A., H.-J. Greiler, and T. Tscharntke. 1994. Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia* **98**:8-14.

Ghazoul, J. 2005. Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology and Evolution* **20**:367-373.

Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. *Journal of Ecology* **94**:295-304.

Gibbs, J. and C. S. Sheffield. 2009. Rapid range expansion of the wool-carder bee, *Anthidium manicatum* (Linnaeus) (Hymenoptera: Megachilidae), in North America. *Journal of the Kansas Entomological Society* **82**:21-29.

Gibson, R., B. Knott, T. Eberlein, and J. Memmott. 2011. Sampling method influences the structure of plant-pollinator networks. *Oikos* **120**:822-831.

Gikungu, M. W. 2006. Bee diversity and some aspects of their ecological interactions with plants in a successional tropical community. Rheinischen Friedrich-Wilhelms-Universität Bonn. Dissertation.

Giles, V. and J. S. Ascher. 2006. A survey of the bees of the Black Rock Forest Preserve, New York (Hymenoptera: Apoidea). *Journal of Hymenopteran Research* **15**:208-231.

Goodell, K. 2003. Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia* **134**:518-527.

Gordo, O. and J. J. Sanz. 2006. Temporal trends in phenology of the honey bee *Apis mellifera* (L.) and the small white *Pieris rapae* (L.) in the Iberian Peninsula (1952-2004). *Ecological Entomology* **31**:261-268.

Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **34**:1-26.

Goulson, D. 2010. Impacts of non-native bumblebees in Western Europe and North America. *Applied Entomological Zoology* **45**:7-12.

Goulson, D. and W. O. H. Hughes. 2015. Mitigating the anthropogenic spread of bee parasites to protect wild pollinators. *Biological Conservation* **191**:10-19.

Goulson, D., G. C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. *Annual Review of Entomology* **53**:191-208.

Goulson, D., E. Nicholls, C. Botias, and E. L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* **347**:1255957.

Grass, I., D. G. Berens, F. Peter, and N. Farwig. 2013. Additive effects of exotic plant abundance and land-use intensity on plant-pollinator interactions. *Oecologia* **173**:913-923.

Greenleaf, S. S., and C. Kremen. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation* **133**:81-87.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* **153**:589-596.

Grill, A., B. Knoflach, D. F. R. Cleary, and V. Kati. 2005. Butterfly, spider, and plant communities in different land-use types in Sardinia, Italy. *Biodiversity and Conservation* **14**:1281-1300.

Gruber, B., K. Eckel, J. Everaars, and C. F. Dormann. 2011. On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie* **42**:564.

Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and N. B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications* **20**:1678-1692.

Guédot, C., J. Bosch, and W. P. Kemp. 2007. Effect of three-dimension and color contrast on nest localization performance of two solitary bees (Hymenoptera: Megachilidae). *Journal of Kansas Entomological Society* **80**:90-104.

Guédot, C., J. Bosch, and W. P. Kemp. 2009. Relationship between body size and homing ability in the genus *Osmia* (Hymenoptera; Megachilidae). *Ecological Entomology* **34**:158-161.

Guédot C., T. L. Pitts-Singer, J. S. Buckner, J. Bosch, and W. P. Kemp. 2006. Olfactory cues and nest recognition in the solitary bee *Osmia lignaria*. *Physiological Entomology* **31**:110–119.

Guisse, J. K. and D. G. Miller III. 2011. Distribution and habitat preferences of *Osmia lignaria* (Hymenoptera: Megachilidae) and associated cavity-nesting insects in California's Sierra Nevada foothills adjacent to the Sacramento Valley. *The Pan-Pacific Entomologist* **87**:188-195.

Gurevitch, J. and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. *Ecology* **80**: 1142-1149.

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

Hagen, M. and M. Kraemer. 2010. Agricultural surroundings support flower-visitor networks in an Afrotropical rain forest. *Biological Conservation* **143**:1654-1663.

Haider, M., S. Dorn, C. Sedivy, and A. Müller. 2014. Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (Megachilidae: Osmiini). *Biological Journal of the Linnean Society* **111**:78-91.

Hanley, N., T. D. Breeze, C. Ellis, and D. Goulson. 2015. Measuring the economic value of pollination services: principles, evidence and knowledge gaps. *Ecosystem Services* **14**:124-132.

Hannon, L. and T. D. Sisk. 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. *Biological Conservation* **142**:2140-2154.

Hansen, D. M., J. M. Olesen, and C. G. Jones. 2002. Trees, birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds? *Journal of Biogeography* **29**:721-734.

Hanula, J. L. and S. Horn. 2011. Removing an invasive shrub (Chinese privet) increases native bee diversity and abundance in riparian forests of the southeastern United States. *Insect Conservation and Diversity* **4**:275-283.

Hanula, J. L., S. Horn, and J. J. O'Brien. 2015. Have changing forest conditions contributed to pollinator decline in the southeastern United States? *Forest Ecology and Management* **348***:*142-152.

Hauck, M., C. Dulamsuren, B. Bayartogtokh, K. Ulykpan, U. D. Burkitbaeva, E. Otgonjargal, S. V. Titov, T. Enkhbayar, A. K. Sundetpaev, U. Beket, and C. Leuschner. 2014. Relationships between the diversity patterns of vascular plants, lichens and invertebrates in the Central Asian forest-steppe ecotone. *Biodiversity and Conservation* **23**:1105-1117.

Hayhoe, K., C. Wake, B. Anderson, X.-Z. Liang, E. Maurer, J. Zhu, J. Bradbury, A. DeGaetano, A. Hertel, D. Wuebbles. 2006. *Regional climate change projections for the Northeast U.S. Mitigation and Adaptation Strategies for Global Change* **13**:425-436.

Hedtke, S. M., E. J. Blitzer, G. A. Montgomery and B. N. Danforth. 2015. Introduction of non-native pollinators can lead to trans-continental movement of bee-associated fungi. *PLoS One* **10**:e0130560.

Hegland, S. J. and L. Boeke. 2006. Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology* **31**:532-538.

Hegland, S. J., A. Nielsen, A. Lázaro, A.-L. Bjerknes and Ø. Totland. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* **12**:184-195.

Heithaus, R. E. 1974. The role of plant-pollinator interactions in determining community structure. *Annals of the Missouri Botanical Garden* **61**:675-691.

Hendrix, S. D., K. S. Kwaiser, and S. B. Heard. 2010. Bee communities (Hymenoptera: Apoidea) of small Iowa hill prairies are as diverse and rich as those of large prairie preserves. *Biodiversity Conservation* **19**:1699-1709.

Henning, E. I. and J. Ghazoul. 2012. Pollinating animals in the urban environment. *Urban Ecosystems* **15**:149-166.

Higgins, J. P. T. and S. G. Thompson. 2002. Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine* **21**:1539-1558.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2004. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* **8**:23-29.

Holl, K. D. 1996. The effect of coal surface mine reclamation on diurnal Lepidopteran conservation. *Journal of Applied Ecology* **33**:225-236.

Holzschuh, A., C. F. Dormann, T. Tscharntke, and I. Steffan-Dewenter. 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B – Biological Sciences* **278**:3444-3451.

Holzschuh, A., J.-H. Dudenhöffer, and T. Tscharntke. 2012. Landscape with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation* **153**:101-107.

Holzschuh, A., I. Steffan-Dewenter, D. Kleijn, and T. Tscharntke. 2007. Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology* **44**:41-49.

Hopwood, J. 2008. The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation* **141**:2632-2640.

Horne, M. 1995. Leaf area and toughness: effects on nesting material preferences of *Megachile rotundata* (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America* **88**:868–875.

Horner-Devine, M. Claire, G. C. Daily, P. R. Ehrlich, and C. L. Boggs. 2003. Countryside biogeography of tropical butterflies. *Conservation Biology* **17**:168-177.

Hudewenz, A. A.-M. Klein, C. Scherber, L. Stanke, T. Tscharntke, A. Vogel, A. Weigelt, W. W. Weisser, and A. Ebeling. 2012. Herbivore and pollinator responses to grassland management intensity along experimental changes in plant species richness. *Biological Conservation* **150**:42-52.

Hudson, J. R., J. L. Hanula, and S. Horn. 2013. Removing Chinese privet from riparian forests still benefits pollinators five years later. *Biological Conservation* **167**:355-362.

Ings, T. C., N. L. Ward, and L. Chittka. 2006. Can commercially imported bumble bees out-compete their native conspecifics? *Journal of Applied Ecology* **43:**940-948.

Jayasingh, D. B. and B. E. Freeman. 1980. The comparative population dynamics of eight solitary bees and wasps (Aculeata: Apocrita: Hymenoptera) trap-nesting in Jamaica. *Biotropica* **12**:214-219.

Jeong, G., K. Lee, J. Choi, S. Hwang, B. Park, W. Kim, Y. Choi, I. Park, and J. Kim. 2009. Incidence of *Wolbachia* and *Cardinium* endosymbionts in the Osmia community in Korea. *The Journal of Microbiology* **47**:28-32.

Jha, S. and C. Kremen. 2013. Resource diversity and landscape-level homogenization drive native bee foraging. *Proceedings of the National Academy of Science of the United States* **110**:555-558.

Julier, H. E. and T. H. Roulston. 2009. Wild bee abundance and pollination service in cultivated pumpkins: farm management, nesting behavior and landscape effects. *Journal of Economic Entomology* **10**:563-573.

Junker, R. R., R. Bleil, C. C. Daehler, and N. Blüthgen. 2010. Intra-floral resource partitioning between endemic and invasive flower visitors: consequences for pollinator effectiveness. *Ecological Entomology* **35:**760-767.

Kaiser-Bunbury, C. N., T. Valentin, J. Mougal, D. Matatiken, and J. Ghazoul. 2011. The tolerance of island plant-pollinator networks to alien plants. *Journal of Ecology* **99**:202-213.

Kallimanis, A. S., T. Petanidou, J. Tzanopoulos, J. D. Pantis, and S. P. Sgardelis. 2009. Do plant-pollinator interaction networks result from stochastic processes? *Ecological Modelling* **220**:684-693.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* **29**:83-112.

Kemp, W. P. and J. Bosch. 2001. Post-cocooning temperatures and diapause in the alfalfa pollinator *Megachile rotunda* (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America* **94**:244-250.

Kim, J., N. Williams, C. Kremen. 2006. Effects of cultivation and proximity to natural habitat on ground- nesting native bees in California sunflower fields. *Journal of Kansas Entomological Society* **79**:309–320.

Kim, H. Y., K. Y. Lee, S. B. Lee, S. R. Kim. 2008. Mitochondrial DNA sequence variation of the mason bee, *Osmia cornifrons* (Hymenoptera: Megachilidae). *International Journal of Industrial Entomology* **16**:75-86.

Kitahara, M. 2004. Butterfly community composition and conservation in and around a primary woodland of Mount Fuji, central Japan. *Biodiversity and Conservation* **13**:917-942.

Kitahara, M. and M. Watanabe. 2003. Diversity and rarity hotspots and conservation of butterfly communities in and around the Aokigahara woodland of Mount Fuji, central Japan. *Ecological Research* **18**:503-522.

Kitahara, M., M. Yumoto, and T. Kobayashi. 2008. Relationship of butterfly diversity with nectar plant species richness in and around the Aokigahara primary woodland of Mount Fuji, central Japan. *Biodiversity and Conservation* **17**:2713-2734.

Kivinen, S., M. Luoto, M. Kuussaari, and J. Helenius. 2006. Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical location. *Journal of Biogeography* **33**:862-875.

Kleijn, D., F. Berendse, R. Smit, N. Gilissen, J. Smit, B. Brak, and R. Groeneveld. 2004. Ecological effectiveness of agri-environment schemes in different agricultural landscapes in the Netherlands. *Conservation Biology* **18**:775-786.

Kleijn, D. and I. Raemakers. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology* **89**:1811-1823.

Kleijn, D. and F. van Langevelde. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology* **7**:201-214.

Kleijn, D., R. Winfree, I. Bartomeus, L. G. Carvalheiro, M. Henry, R. Isaacs, A. M. Klein, C. Kremen, L. K. M'Gonigle, R. Rader, T. H. Ricketts, N. M. Williams, N. Lee Adamson, J. S. Ascher, A. Baldi, P. Batary, F. Benjamin, J. C. Biesmeijer, E. J. Blitzer, R. Bommarco, M. R. Brand, V. Bretagnolle, L. Button, D. P. Cariveau, R. Chifflet, J. F. Colville, B. N. Danforth, E. Elle, M. P. Garratt, F. Herzog, A. Holzschuh, B. G. Howlett, F. Jauker, S. Jha, E. Knop, K. M. Krewenka, V. Le Feon, Y. Mandelik, E. A. May, M. G. Park, G. Pisanty, M. Reemer, V. Riedinger, O. Rollin, M. Rundlof, H. S. Sardinas, J. Scheper, A. R. Sciligo, H. G. Smith, I. Steffan-Dewenter, R. Thorp, T. Tscharntke, J. Verhulst, B. F. Viana, B. E. Vaissiere, R. Veldtman, K. L. Ward, C. Westphal, and S. G. Potts. 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications* **6**:7414.

Klein, A.-M., I. Steffan-Dewenter, D. Buchori, and T. Tscharntke. 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology* **16**:1003-1014.

Klein, A.-M., I. Steffan-Dewenter and T. Tscharntke. 2006. Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. *Journal of Animal Ecology* **75**:315-323.

Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B - Biological Sciences* **274**:303-313.

Kleintjes, P. K. and B. F. Jacobs, and S. M. Fettig. 2004. Intial response of butterflies to an overstory reduction and slash mulching treatment of a degraded piñon-juniper woodland. *Restoration Ecology* **12**:231-238.

Kluser, S. and P. Peduzzi. 2007. Global pollinator decline: a literature review. UNEP/GRID-Europe.

Knight, M. E., M. A. P. Martin, S. Bishop, J. L. Osborne, R. J. Hale, R. A. Sanderson, and D. Goulson. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (Bombus) species. *Molecular Ecology* **14**:1811-1820.

Knop, E., D. Kleijn, F. Herzog, and B. Schmid. 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology* **43**:120-127.

Koch, B., P. J. Edwards, W. U. Blanckenhorn, S. Buholzer, T. Walter, R. O. Wüest, and G. Hofer. 2013. Vascular plants as surrogates on butterfly and grasshopper diversity on two Swiss subalpine summer pasture. *Biodiversity Conservation* **22**:1451-1465.

Koh, I., E. V. Lonsdorf, N. M. Williams, C. Brittain, R. Isaacs, J. Gibbs, and T. H. Ricketts. 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Acadmey of Sciences of the United States of America* **113**:140-145.

Kohler, F., J. Verhulst, E. Knop, F. Herzog, and D. Kleijn. 2007. Indirect effects of grassland extensification schemes on pollinators in two contrasting European countries. *Biological Conservation* **135**:302-307.

Kreft, H. and W. Jetz. 2007. Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Science of the United States of the America* **104**:5925-5930.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**:203-217.

Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America* **99**:16812-16816.

Krenn, H. W. 2010. Feeding mechanisms of adult Lepidoptera: structure, function, and evolution of mouthparts. *Annual Review of Entomology* **55**:307-327.

Krombein, K. V. 1967. Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Institutional Press, Washington, D.C.

Kruess, A. and T. Tscharntke. 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology* **16**:1570-1580.

Krunic, M., L. Stanisavljevic, M. Pinzauti, and A. Felicioli. 2005. The accompanying fauna of *Osmia cornuta* and *Osmia rufa* and effective measures of protection. *Bulletin of Insectology* **58**:141-152.

Kudo, G. and T. Y. Ida. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* **94**:2311-2320.

Kuhsel, S., and N. Bluthgen. 2015. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. *Nature Communications* **6**:7989.

Kunte, K., A. Joglekar, G. Utkarsh, and P. Pramod. 1999. Patterns of butterfly, bird and tree diversity in the Western Ghats. *Current Science* 1-19.

Kuussaari, M., T. Hyvönen, and O. Härmä. 2011. Pollinator insects benefit from rotational fallows. *Agriculture, Ecosystems and Environment* **143**:28-36.

Larsson, M., and M. Franzen. 2007. Critical resource levels of pollen for the declining bee *Andrena hattorfiana* (Hymenoptera, Andrenidae). *Biological Conservation* **134**:405-414.

Lautenbach, S., R. Seppelt, J. Liebscher, and C. F. Dormann. 2012. Spatial and temporal trends of global pollination benefit. *PLoS ONE* **7**:e35954.

Lee, K. Y., K. S. Lee, H. J. Yoon, and B. R. Jin. 2015. Ovarian development and secretion of vitellogenin protein during the wintering period and after emergence in the hornfaced bee, *Osmia cornifrons*. *Journal of Asia-Pacific Entomology* **18**:515-523.

Lee, K. Y., H. J. Yoon, K. S. Lee, and B. R. Jin. 2016. Development and mating behavior of Osmia cornifrons (Hymenoptera: Megachilidae) in the constant temperature. *Journal of Asia-Pacific Entomology* **19**:281-287.

Leonhardt, S. D., N. Gallai, L. A. Garibaldi, M. Kuhlmann, and A.-M. Klein. 2013. Economic gain, stability of pollination and bee diversity decrease from southern to northern Europe. *Basic and Applied Ecology* **14**:461-471.

Lewinsohn, T. M., P. I. Prado, P. Jordano, J. Bascompte, and J. M. Olesen. 2006. Structure in plant-animal assemblages. *Oikos* **113**:174-184.

Lewis, S., and M. Clarke. 2001. Forest plots: trying to see the wood and the trees. *British Medical Journal* **322**:1479-1480.

Light, R., and D. Pillemer. 1984. Summing Up: The Science of Reviewing Research. Harvard University Press, Cambridge.

Liu, H. and R. W. Pemberton. 2009. Solitary invasive orchid bee outperforms co-occuring native bees to promote fruit set of an invasive Solanum. *Oecologia* **159**:515-525.

Locatelli, E. and I. C. Machado. 2000. Bee diversity and their floral resources in a fragment of a tropical altitudinal wet forest (“brejos de altitude”) in northeastern Brazil. *Acta Horticultura* **561**:317-325.

Love, B. 2010. The bees of the American and Cosumnes rivers in Sacramento County, California: effects of land use on native bee diversity. California State University, Scramento, Thesis.

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

Loyola, R. D. and R. P. Martins. 2008. Habitat structure components are effective predictors of trap-nesting Hymenoptera diversity. *Basic and Applied Ecology* **9**:735-742.

Loyola, R. D. and R. P. Martins. 2012. Habitat structure components are effective predictors of trap-nesting Hymenoptera diversity. *Basic and Applied Ecology* **9**:735-742.

MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist* **100**:603-609.

Maccagnani, B., E. Ladurner, F. Santi, and G. Burgio. 2003. *Osmia cornuta* (Hymenoptera, Megachilidae) as a pollinator of pear (*Pyrus communis*): fruit- and seed-set. *Apidologie* **34**:207-216.

Maccherini, S., G. Bacaro, L. Favilli, S. Piazzini, E. Santi, and M. Marignani. 2009. Congruence among vascular plants and butterflies in the evaluation of grassland restoration success. *Acta Oecologia* **35**:311-317.

MacIvor, J. S. 2016. Cavity-nest boxes for solitary bees: a century of design and research. *Apidologie* **48**:311-327.

MacIvor, J. S. and L. Packer. 2015. ‘Bee hotels’ as tools for native pollinator conservation: a premature verdict? *PLoS One* **10**:e0122126.

MacIvor, J. S., and L. Packer. 2016. The bees among us: modelling occupancy of solitary bees. *PLoS One* **11**:e0164764.

Mader , E., M. Spivak, E. Elaine. 2010. Managing Alternative Pollinators: A Handbook for Beekeepers, Growers, and Conservationists, SARE Handbook 11. Natural Resource, Agriculture, and Engineering Service (NRAES).

Maes, D. and H. V. Dyck. 2001. Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation* **99**:263-276.

Mandelik, Y., R. Winfree, T. Neeson, and C. Kremen. 2012. Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications* **22**:1535-1546.

Marini, L., P. Fontana, A. Battisti, and K. J. Gaston. 2009. Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland-forest mosaic: a multi-scale approach. *Insect Conservation and Diversity* **2**:213-220.

Marrero, H. J., J. P. Torretta, and D. Medan. 2014. Effect of land use intensification on specialization in plant-floral visitor interaction networks in the Pampas of Argentina. *Agriculture, Ecosystems and Environment* **188**:63-71.

Martín González, A. M., S. Allesina, A. Rodrigo, and J. Bosch. 2012. Drivers of compartmentalization in a Mediterranean pollination network. *Oikos* **121**:2001-2013.

Matsumoto, S., A. Abe, and T. Maejima. 2009. Foraging behavior of *Osmia cornifrons* in an apple orchard. *Scientia Horticulturae* **121**:73-79.

Matsumoto, S. and T. Maejima. 2010. Several new aspects of the foraging behavior of *Osmia cornifrons* in an apple orchard. *Psyche* 1-6.

McFrederick, Q. S. and G. LeBuhn. 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)?

McIntyre, N. E. and M. E. Hostetler. 2001. Effects of urban land use on pollinator (Hymenoptera: Apoidea) communities in a desert metropolis. *Basic and Applied Ecology* **2**:209-218.

McKinney, M. L. and Y.-L. Park. 2012. Nesting activity and behavior of *Osmia cornifrons* (Hymenoptera: Megachilidae) elucidated using videography. *Psyche* 1-8.

Mello, M. A. R., G. M. d. M. Santos, M. R. Mechi, and M. G. Hermes. 2011. High generalization in flower-visiting networks of social wasps. *Acta Oecologica* **37**:37-42.

Memmott, J., P. G. Craze, N. M. Waser and M. V. Price. 2007. Global warming and the disruption of plant-pollinator interactions. *Ecology Letters* **10**:710-717.

Meng, L.-Z., K. Martin, J.-X. Liu, F. Burger, and J. Chen. 2012. Contrasting responses of hoverflies and wild bees to habitat structure and land use change in a tropical landscape (southern Yunnan, SW China). *Insect Science* **19**:666-676.

Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kübler, P. Bissolli, O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatczak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remisova, H. Scheifinger, M. Striz, A. Susnik, A. J. H. Van Vliet, F.-E.Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**:1969-1976.

Meyer, B., F. Jauker, and I. Steffan-Dewenter. 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology* **10**:178-186.

Michener, C. D. 1979. Biogeography of the bees. *Annals of the Missouri Botanical Garden* **66**: 277-347.

Michener, C. D. 2000. Bees of the World, 2nd Edition. The Johns Hopkins University Press, Baltimore, MD.

Mitchell, B. R., G. Shriver, F. Dieffenbach, T. Moore, D. Faber-Langendoen, G. Tierney, P. Lombard, and J. Gibbs. 2011. Northeast Temperate Network Vital Signs Monitoring Plan. Technical Report NPS/NER/NRTR—2006/059.

Miyamoto, S. 1959. Biological studies on Japanese bees – XII. Flower relationships of five species of bees belonging to the Genus *Osmia* (Hymenoptera: Megachilidae). *Science Reports of the Hyogo University of Agriculture* **4**:35-40.

Moldenke, A. R. 1975. Niche specialization and species diversity along a California transect. *Oecologia* **21**:219-242.

Morales, C. L., M. P. Arbetman, S. A. Cameron, and M. A. Aizen. 2013. Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment* **11**:529-534.

Morandin, L. A. and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications* **23**:829-839.

Morato, E. F. and R. P. Martins. 2006. An overview of proximate factors affecting the nesting behavior of solitary wasps and bees (Hymenoptera: Aculeata) in preexisting cavities in wood. *Neotropical Entomology* **35**:285-298.

Moretti, M., F. de Bello, S. P. M. Roberts, and S. G. Potts. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology* **78**:98-108.

Monzón, V., J. Bosch, and J. Retana. 2004. Foraging behavior and pollinating effectiveness of *Osmia cornuta* (Hymenoptera: Megachilidae) and *Apis mellifera* (Hymenoptera: Apidae) on “Comice” pear. *Apidologie* **35**:575-585.

Munguira, M. L. and J. A. Thomas. 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. *Journal of Applied Ecology* **29**:316-329.

Murray, T. E., M. Kuhlmann, and S. G. Potts. 2009. Conservation ecology of bees: populations, species and communities. *Apidologie* **40**:211-236.

Myers, M. C., B. J. Hoksch, and J. T. Mason. 2012. Butterfly response to floral resources during early establishment at a heterogeneous prairie biomass production site in Iowa, USA. *Journal of Insect Conservation* **16**:457-472.

National Research Council. 2007. Status of Pollinators in North America. Washington, DC: The National Academies Press. DOI: 10.17226/11761.

Neame, L. A., T. Griswold, and E. Elle. 2013. Pollinator nesting guilds respond differently to urban habitat fragmentation in an oak-savannah ecosystem. *Insect Conservation and Diversity* **6**:57-66.

Nielsen, A., and Ø. Totland. 2014. Structural properties of mutualistic networks withstand habitat degradation while species functional roles might change. *Oikos* **123**:323-333.

Noordiijk, J., K. Delille, A. P. Schaffers, and K. V. Sykora. 2009. Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation* **142**:2097-2103.

O'Toole, C., and A. Raw. 1999. Bees of the World. Blandford, London.

Ochoa-Hueso, R., D. de la Puente Ranea, and J. L. Viejo. 2014. Comparison of trends in habitat and resource selection by the Spanish festoon, Zerynthia rumina, and the whole butterfly community in a semi-arid Mediterranean ecosystem. *Journal of Insect Science* **14**:1-14.

Öckinger, E., A. E. Eriksson, and H. G. Smith. 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biological Conservation* **133**:291-300.

Öckinger, E. and H. G. Smith. 2006. Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologi*a **149**:526-534.

Öckinger, E. and H. G. Smith. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology* **44**:50-59.

Olesen, J. M, J. Bascompte, H. Elberling, and P. Jordano. 2008. Temporal dynamics in a pollinator network. *Ecology* **89**:1573-1582.

Olesen, J. M. and P. Jordano. 2002. Geographic patterns in plant-pollinator mutualistic networks. *Ecology* **83**:2416-2424.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* **120**:321-326.

Olsen, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial Ecoregions of the world: a new map of life on earth. *BioScience* **51**:933-938.

Osborn, F., W. Goitia, M. Cabrera, and K. Jaffé 1999. Ants, plants and butterflies as diversity indicators: comparisons between strata in six neotropical forest sites. *Studies of Neotropical Fauna and Environment* **34**:59-64.

Park, Y.-L., V. Kondo, J. White, T. West, B. McConnell, and T. McCutcheon. 2009. Nest-to-nest dispersal of Chaetodactylus krombeini (Acari, Chaetodactylidae) associated with Osmia cornifrons (Hymenoptera: Megachilidae). *Journal of Applied Entomology* **133**:174-180.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**:637-669.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37-42.

Perfectti, F., J. M. Gómez, and J. Bosch. 2009. The functional consequences of diversity in plant-pollinator interactions. *Oikos* **118**:1430-1440.

Pimental, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**: 273-288.

Pitts-Singer, T. L. 2007. Olfactory response of megachilid bees, *Osmia lignaria*, *Megachile rotundata*, and *M. pugnata*, to individual cues from old nest cavities. *Environmental Entomology* **36**:402-408.

Pitts-Singer, T. L. and J. Bosch. 2010. Nest establishment, pollination efficiency, and reproductive success of *Megachile rotundata* (Hymenoptera: Megachilidae) in relation to resource availability in field enclosures. *Environmental Entomology* **39**:149-158.

Pitts-Singer, T. L., J. Bosch, W. P. Kemp, and G. E. Trostle. 2008. Field use of an incubation box for improved emergence timing of *Osmia lignaria* populations used for orchard pollination. *Apidologie* **39**:235-246.

Pitts-Singer, T. L., J. H. Cane, and G. Trostle. 2014. Progeny of *Osmia lignaria* from distinct regions differ in developmental phenology and survival under a common thermal regime. *Journal of Insect Physiology* **67**:9-19.

Popic, T. J., G. M. Wardle, and Y. C. Davila. 2013. Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology* **38**:76-86.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution* **25**:345-353.

Potts, S. G. T. Petanidou, S. Roberts, C. O'Toole, A. Hulbert, and P. Willmer. 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biological Conservation* **129**:519-529.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'emen, C. O'Toole, S. Roberts and P. Willmer. 2003a. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* **101**:103-112.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003b. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84:2628-2642.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'emen, and P. Willmer. 2004. Nectar resource diversity organises flower-visitor community structure. *Entomologia Experimentalis et Applicata* **113**:103-107.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'emen, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology* **30**:78-85.

Potts, S. G., P. Willmer, A. Dafni, and G. Ne'eman. 2000. The utility of fundamental ecological research of plant-pollinator interactions as the basis for landscape management practices. *Acta Horticultura* **561**:141-152.

Power, E. F. and J. C. Stout. 2011. Organic dairy farming: impacts on insect-flower interaction networks and pollination. *Journal of Applied Ecology* **48**:561-569.

Proches, S. and R. M. Cowling. 2006. Insect diversity in Cape fynbos and neighboring South African vegetation. *Global Ecology and Biogeography* **15**:445-451.

Pryke, S. R. and M. J. Samways. 2003. Quality of remnant indigenous grassland linkages for adult butterflies (Lepidoptera) in an afforested African landscape. *Biodiversity and Conservation* **12**:1985-2004.

R Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rader, R., J. Reilly, I. Bartomeus, and R. Winfree. 2013. Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Biology* **19**:3103-3110.

Radmacher, S. and E. Strohm 2010. Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). *Apidologie* **41**:169-177.

Redpath-Downing, N. A., D. Beaumont, K. Park, and D. Goulson. 2013. Restoration and management of machair grassland for the conservation of bumblebees. *Journal of Insect Conservation* **17**:491-502.

Reed, C. 1993. Reconstruction of pollinator communities on restored prairies in eastern Minnesota: final report to the Minnesota Department of Natural Resources Nongame Wildlife Program. Conservation Biology Research Grants Program. Division of Ecological Services, Minnesota Department of Natural Resources.

Richards, M. H., A. Rutgers-Kelly, J. Gibbs, J. L. Vickruck, S. M. Rehan, and C. S. Sheffield. 2011. Bee diversity in naturalizing patches of Carolinian grasslands in southern Ontario, Canada. *Canadian Entomology* **143**:279-299.

Rickert, C., A. Fichtner, R. van Klink, and J. P. Bakker. 2012. Alpha- and beta-diversity in moth communities in salt marshes is driven by grazing management. *Biological Conservation* **146**:24-31.

Ricketts, T. H. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology* **18**:1262-1271.

Romey, W. L., J. S. Ascher, D. A. Powell, and M. Yanek. 2007. Impacts of logging on midsummer diversity of native bees (Apoidea) in a northern hardwood forest. *Journal of the Kansas Entomological Society* **80**:327-338.

Rothstein, H., A. Sutton, and M. Borenstein, editors. 2005. Publication Bias in Meta-Analysis: Prevention, Assessment, and Adjustments. John Wiley & Sons, Chichester, England.

Roubik, D. W. and R. Villanueva-Gutiérrez. 2009. Invasive Africanized honey bee impact on native solitary bees: a pollen resource and trap nest analysis. *Biological Journal of the Linnean Society* **98**:152-160.

Roulston, T. a. H., and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology* **56**:293-312.

Rutgers-Kelly, A. C. and M. H. Richards. 2013. Effect of meadow regeneration on bee (Hymenoptera: Apoidea) abundance and diversity in souther Ontario, Canada. *Canada Entomology* **145**:655-667.

Saarinen, K., A. Valtonen, J. Jantunen, and S. Saarnio. 2005. Butterflies and diurnal moths along road verges: does road type affect diversity and abundance? *Biological Conservation* **123**:403-412.

Sajjad, A. and S. Saeed. 2010. Floral hosts plant range of syrphid flies (Syrphidae: Diptera) under natural conditions in southern Punjab, Pakistan. *Pakistan Journal of Botany* **42**:1187-1200

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* **32**: 305-332.

Sandhu, H., B. Waterhouse, S. Boyer, and S. Wratten. 2016. Scarcity of ecosystem services: an expeirmental manipulation of declining pollination rates and its economic consequences for agriculture. *PeerJ* **4**:e2099.

Sanguinetti, A. and R. Bustos Singer. 2014. Invasive bees promote high reproductive success in Andean orchids. *Biological Conservation* **175**:10-20.

Santi, E., S. Maccherini, D. Rocchini, I. Bonini, G. Brunialti, L. Favilli, C. Perini, F. Pezzo, S. Piazzini, E. Rota, E. Salerni, and A. Chiarucci. 2010. Simple to sample: vascular plants as surrogate group in nature reserve. *Journal for Nature Conservation* **18**:2-11.

Santos, G. M. de M., C. M. L. Aguiar, J. Genini, C. F. Martins, F. C. V. Zanella, M. A. R. Mello. 2012. Invasive Africanized honeybees change the structure of native pollination networks in Brazil. *Biological Invasions* **14**:2369-2378.

Sárospataki, M., A. Báldi, P. Batáry, Z. Józan, S. Erdös, and T. Rédei. 2009. Factors affecting the structure of bee assemblages in extensively and intensively grazed grasslands in Hungary. *Community Ecology* **10**:182-188.

Scheper, J., A. Holzschuh, M. Kuussaari, S. G. Potts, M. Rundlöf, H. G. Smith, and D. Kleijn. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. *Ecology Letters* **16**:912-920.

Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E-D. Schulze, C. Roscher, A. Weigelt, E. Allan, H. Beßler, M. Bonkowski, N. Buchmann, F. Buscot, L. W. Clement, A. Ebeling, C. Engels, S. Halle, I. Kertscher, A-M. Klein, R. Koller, S. König, E. Kowalski, V. Kummer, A. Kuu, M. Lange, D. Lauterbach, C. Middelhoff, V. D. Migunova, A. Milcu, R. Müller, S. Partsch, J. S. petermann, C. Renker, T. Rottstock, A. Sabais, S. Scheu, J. Schumacher, V. M. Temperton, and T. Tscharntke. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**:553-556.

Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The potential conservation value of non-native species. *Conservation Biology* **25**:428-437.

Schleuning, M. J. Fründ, A-M. Klein, S. Abrahamczyk, R. Alarcón, M. Albrecht, G. K. S. Andersson, S. Bazarian, K. Böhning-Gaese, R. Bommarco, B. Dalsgaard, D. M. Dehling, A. Gotlieb, M. Hagen, T. Hickler, A. Holzschuh, C. N. Kaiser-Bunbury, H. Kreft, R. J. Morris, B. Sandel, W. J. Sutherland, J-C. Svenning, T. Tscharntke, S. Watts, C. N. Weiner, M. Werner, N. M. Williams, C. Winqvist, C. Dormann, and N. Blüthgen. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology* **22**: 1925-1931.

Schüepp, C., J. D. Herrmann, F. Herzog, and M. H. Schmidt-Entling. 2011. Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia* **165**:713-721.

Schulze, C. H., M. Waltert, P. J. A. Kessler, R. Pitopang Shahabuddin, D. Veddeler, M. Mühlenberg, S. R. Gradstein, C. Leuschner, I. Steffan-Dewenter, and T. Tscharntke. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications* **14**:1321-1333.

Schwartz, A, A. Muratet, L. Simon, and R. Julliard. 2013. Local and management variables outweigh landscape effects in enhancing the diversity of different taxa in a big metropolis. *Biological Conservation* **157**:285-292.

Sgolastra, F., J. Bosch, R. Molowny-Horas, S. Maini, and W. P. Kemp. 2009. Effect of temperature regime on diapause intensity in an adult-wintering Hymenopteran with obligate diapause. *Journal of Insect Physiology* **56**:185-194.

Sgolastra, F., W. P. Kemp, J. S. Buckner, T. L. Pitts-Singer, S. Maini, and J. Bosch. 2011. The long summer: pre-wintering temperatures affect metabolic expenditure and winter survival in a solitary bee. *Journal of Insect Physiology* **57**:1651-1659.

Sgolastra, F., W. P Kemp, S. Maini, and J. Bosch. 2012. Duration of prepupal summer dormancy regulates synchronization of adult diapause with winter temperatures in bees in the genus *Osmia*. *Journal of Insect Physiology* **58**:924-933.

Shuey, J. A., E. H. Metzler, and K. Tungesvick. 2012. Moth communities correspond with plant communities in midwestern (Indian, USA) sand prairies and oak barrens and their degradation endpoints. *American Midland Naturalist* **167**:273-284.

Sheffield, C. S., P. G. Kevan, S. M. Westby, and R. F. Smith. 2008. Diversity of cavity-nesting bees (Hymenoptera: Apoidea) within apple orchards and wild habitats in the Annapolis Valley, Nova Scotia, Canada. *Canadian Entomologist* **140**:253-249.

Sheffield, C. S., S. Dumesh, and M. Cheryomina. 2011. *Hylaeus punctatus* (Hymenoptera: Colletidae), a bee species new to Canada, with notes on other non-native species. *Journal of Entomological Society of Ontario* **142**:29-43.

Simonson, S., P. A. Opler, T. J. Stohlgren, and G. W. Chong. 2001. Rapid assessment of butterfly diversity in a montane landscape. *Biodiversity and Conservation* **10**:1369-1386.

Sjodin, N. E., J. Bengtsson, and B. Ekbom. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology* **45**:763-772.

Smith, G. F., T. Gittings, M. Wilson, L. French, A. Oxbrough, S. O'Donoghue, J. O'Halloran, D. L. Kelly, F. J. G. Mitchell, T. Kelly, S. Iremonger, A.-M. McKee, and P. Giller. 2008. Identifying practical indicators of biodiversity for stand-level management of plantation forests. *Biodiversity Conservation* **17**:991-1015.

Sneddon, L., R. E. Zaremba, E. Largay, G. Podniesinski, S. Perles, and J. Thompson. 2008. Vegetation classification and mapping of Morristown National Historical Park, New Jersey. Technical Report NPS/NER/NRTR – 2008/116.

Stang, M., P. G. L. Klinkhamer, N. M. Waser, I. Stang, and E. van der Meijden. 2009. Size-specific interaction patterns and size matching in a plant-pollinator interaction web. *Annals of Botany* **103**:1459-1469.

Steckel, J., C. Westphal, M. K. Peters, M. Bellach, C. Rothenwoehrer, S. Erasmi, C. Scherber, T. Tscharntke, and I. Steffan-Dewenter. 2014. Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biological Conservation* **172**:56-64.

Steffan-Dewenter, I. 2002. Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology* **27**:631-637.

Steffan-Dewenter, I. 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology* **17**:1036-1044.

Steffan-Dewenter, I. and S. Schiele. 2004. Nest-site fidelity, body weight and population size of the red mason bee, *Osmia rufa* (Hymenoptera: Megachilidae), evaluated by mark-recapture experiments. *Entomology General* **27**:123-131.

Steffan-Dewenter, I., and S. Schiele. 2008. Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology* **89**:1375-1387.

Steffan-Dewenter, I. and T. Tscharntke. 1997. Early successin of butterfly and plant communities on set-aside fields. *Oecologia* **109**:294-302.

Steffan-Dewenter, I. and T. Tscharntke. 2001. Succession of bee communities on fallows. *Ecography* **24**:83-92.

Sterne, J. A. C., and M. Egger. 2001. Funnel plots for detecting bias in meta-analysis: Guidelines on choice of axis. *Journal of Clinical Epidemiology* **54**:1046-1055.

Stout, J. C. and L. M. Casey. 2014. Relative abundance of an invasive alien plant affects insect-flower interaction networks in Ireland. *Acta Oecologica* **55**:78-85.

Sugiura, N. and Y. Maeta. 1989. Parental investment and offspring sex ratio in a solitary mason bee, *Osmia cornifrons* (Radoszkowski) (Hymenoptera, Megachilidae). *Japanese Journal of Entmology* **57**:861-875.

Sutherland, J. P., M. S. Sullivan, and G. M. Poppy. 2001. Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agricultural and Forest Entomology* **3**:57-64.

Syndenham, M. A. K., S. R. Moe, Ø. Totland, and K. Eldegard. 2014. Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? *Ecography* **37**:1-14.

Taki, H., B. F. Viana, P. G. Kevan, F. O. Silva, and M. Buck. 2008. Does forest loss affect the communities of trap-nesting wasps (Hymenoptera: Aculeata) in forests? landscape vs. local habitat conditions. *Journal of Insect Conservation* **12**:15-21.

Taki, H., T. Inoue, H. Tanaka, H. Makihara, M. Sueyoshi, M. Isono, and K. Okabe. 2010. Respnoses of community structure, diversity, and abundance of understory plants and insect assemblages to thinning in plantations. *Forest Ecology and Management* **259**:607-613.

Tarrant, S., J. Ollerton, M. L. Rahman, J. Tarrant, and D. McCollin. 2013. Grassland restoration on landfill sites in the East Midlands, United Kingdom: an evaluation of floral resources and pollinating insects. *Restoration Ecology* **21**:560-568.

Tepedino, V. J. and N. L. Stanton. 1981. Diversity and competition in bee-plant communities on short-grass prairie. *Oikos* **36**:35-44.

Thackeray, S. J., T. H. Sparks, M. Frederiksen, S. Burthe, P. J. Bacon, J. R. Bell, M. S. Botham, T. M. Brereton, P. W. Bright, L. Carvalho, T. Clutton-Brock, A. Dawson, M. Edwards, J. M. Elliott, R. Harrington, D. Johns, I. D. Jones, J. T. Jones, D. I. Leech, D. B. Roy, W. A. Scott, M. Smith, R. J. Smithers, I. J. Winfield and S. Wanless. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* **16**:3304-3313.

Thomann, M., E. Imbert, C. Devaux, and P. O. Cheptou. 2013. Flowering plants under global pollinator decline. *Trends of Plant Science* **18**:353-359.

Thomas, C. D. and J. C. G. Abery. 1995. Estimating rates of butterfly decline from distribution maps: the effect of scale. *Biological Conservation* **73**:59-65.

Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher, R. Fox, R. T. Clarke, and J. H. Lawton. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**:1879-1881.

Thomson, J. 2003. When is it mutualism? *The American Naturalist* **162**:S1-S9.

Thomson, D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* **85**:458-470.

Tierney, G. L., D. Faber-Langendoen, B. R. Mitchell, W. G. Shriver, and J. P. Gibbs. 2009. *Frontiers in Ecology and the Environment* **7**:308-316.

Torné-Noguera, A., A. Rodrigo, X. Arnan, S. Osorio, H. Barril-Graells, L. C. da Rocha-Filho, and J. Bosch. 2014. Determinants of spatial distribution in a bee community: nesting resources, flower resources, and body size. *PLoS One* **9**:e97255.

Torchio, P. F., E. Asensio, and R. W. Thorp. 1987. Introduction of the European bee, *Osmia cornuta*, into California almond orchards (Hymenoptera: Megachilidae). *Environmental Entomology* **16**:664-667.

Traveset, A., R. Heleno, S. Chamorro, P. Vargas, C. K. McMullen, R. Castro-Urgal, M. Nogales, H. W. Herrera, and J. M. Olesen. 2013. Invaders of pollination networks in the Galápagos Islands: emergence of novel communities. *Proceedings of the Royal Society B – Biological Sciences* **280**:20123040

Traveset, A. and D. M. Richardson. 2011. Mutualisms: key drivers of invasions… key casualties of invasions. In: D. M. Richardson (ed.). Fifty Years of Invasion Ecology: The Legacy of Charles Elton, 1st ed. Blackwell Publishing Ltd, pp.143-160.

Tscharntke, T., A. Gathmann, and I. Steffan-Dewenter. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology* **35**:708-719.

Tylianakis, J. M., R. K. Didham, J. Bascompte and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* **11**:1351-1363.

Tylianakis, J. M., A. M. Klein, T. Lozada, and T. Tscharntke. 2006. Spatial scale of observation affects alpha, beta and gamma diversity of cavity-nesting bees and wasps across a tropical land-use gradient. *Journal of Biogeography* **33**:1295-1304.

Usher, M. B. and S. W. Keiller. 1998. The macrolepidoptera of farm woodlands: determinants of diversity and community structure. *Biodiversity and Conservation* **7**:725-748.

Vamosi, J. C., T. M. Knight, J. A. Steets, S. J. Mazer, M. Burd, and T. L. Ashman. 2006. Pollination decays in biodiversity hotspots. *Proceeding of the National Academy of Science in the United States of America* **103**:956-961.

Van Dyck, H., A. J. Van Strien, D. Maes, and C. A. M. Van Swaay. 2009. Declines in common, widespread butterflies in a landscape under intense human use. *Conservation Biology* **23**:957-965.

Vanbergen, A. J., and t. I. P. Initiative. 2013. Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment* **11**:251-259.

vanEngelsdorp, D., J. Hayes Jr., R. M. Underwood, and J. S. Pettis. A survey of honey bee colony losses in the United States, fall 2008 to spring 2009. *Journal of Apicultural Research* **49**:7-14.

Vazquez, D. P. and M. A. Aizen. 2003. Null model analyses of specialization in plant-pollinator interactions. *Ecology* **84**:2493-2501.

Vessby, K., B. Söderström, A. Glimskär, and B. Svensson. 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology* **16**:430-439.

Vicens, N., J. Bosch and M. Blas. 1994. Biology and population structure of *Osmia tricornis* Latreille (Hymenoptera: Megachilidae). *Journal of Applied Entomology* **117**:300-306.

Vickruck, J. L. and M. H. Richards. 2012. Niche partitioning based on nest site selection in the small carpenter bees *Ceratina mikmaqi* and *C. calcarata*. *Animal Behavior* **83**:1083-1089.

Viechtbauer, W. 2005. Bias and efficiency of Meta-Analytic variance estimators in the random-effects model. *Journal of Educational and Behavioral Statistics* **30**:261-293.

Viechtbauer, W. 2010. Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software* **36**:1-48.

Walinga, C. P. 2016. The effects of changing spring tempertures on fuel use, mass loss, emergence time, and chill coma recovery in solitary mason bees (*Osmia* spp.). Thesis – University of Ottawa.

Wallisdevries, M. F., C. A. M. Van Swaay, and C. L. Plate. 2012. Changes in nectar supply: A possible cause of widespread butterfly decline. *Current Zoology* **58**:384-391.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**:389-395.

Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems and why it matters. *Ecology* **77**:1043-1060.

Wcislo, W. T. 1996. Parasitism rates in relation to nest site in bees and wasps (Hymenoptera: Apoidea). *Journal of Insect Behavior* **9**:643-656.

Wcislo, W. T., R. L. Minckley, R. A. B. Leschen, and S. Reyes. 1994. Rates of parasitism by natural enemies of a solitary bee, *Dieunomia triangulifera* (Hymenoptera, Coleoptera and Diptera) in relation to phenologies. *Sociobiology* **23**:265-273.

Wei, S.-G., R. Wang, M. J. Smirle, and H.-L. Xu. 2002. Release of *Osmia excavata* and *Osmia jacoti* (Hymenoptera: Megachilidae) for apple pollination. *The Canadian Entomologist* **134**:369-380.

Weibull, A.-C., O. Ostman, and A. Granqvist. 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation* **12**:1335-1355.

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

Westgate, M. J., P. S. Barton, P. W. Lane, and D. B. Lindenmayer. 2014. Global meta-analysis reveals low consistency of biodiversity congruence relationships. *Nature Communications* **5**:3899.

Westphal, C., R. Bommarco, G. Carré, E. Lamborn, N. Morison, T. Petanidou, S. G. Potts, S. P. M. Roberts, H. Szengyörgyi, T. Tscheulin, B. E. Vaissière, M. Woyciechowski, J. C. Biesmeijer, W. E. Kunin, J. Settele, and I. Steffan-Dewenter. 2008. Measuring bee diversity in different European habitats and biogoegraphical regions. *Ecological Monographs* **78**:653-671.

Westrich, P. 1996. "Habitat requirements of central European bees and the problems of partial habitats." In: A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams. The Conservation of Bees, Vol. 18. The Linnean Society of London and The International Bee Research Association. Academic Press, pp. 1-16.

White, J., Y. Son and Y.-L. Park. 2009. Temperature-dependent emergence of *Osmia cornifrons* (Hymenoptera: Megachilidae) adults. *Journal of Economic Entomology* **102**:2026-2032.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* **143**:2280-2291.

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

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Synthesis* **34**: 273-309.

Wilson, R. L, C. A. Abel, and S. G. McClurg. 1999. *Osmia* spp. Reared in artificial nesting sites in a backyard environment. *Journal of the Iowa Academy of Science* **106**:4-7.

Winfree, R. 2008. Pollinator-dependent crops: an increasingly risky business. *Current Biology* **18**:R968-R969.

Winfree, R. 2010. The conservation and restoration of wild bees. In: R. S. Ostfeld and W. H. Schlesinger (eds). Year in Ecology and Conservation Biology 2010. Wiley-Blackwell, Malden, pp. 169-197.

Winfree, R., R. Aguilar, D. P. Vazquez, G. LeBuhn, and M. A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* **90**:2068-2076.

Winfree, R., I. Bartomeus, and D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution and Systematics* **42**:1-22.

Winfree, R., and C. Kremen. 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B - Biological Sciences* **276**:229-237.

Winfree, R., N. M. Williams, J. Dushoff, and C. Kremen. 2007. Native bees provide insurance against ongoing honey bee losses. *Ecology Letters* **10**:1105-1113.

Winfree, R. N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* **45**:793-802.

Wolters, V., J. Bengtsson, and A. S. Zaitsev. 2006. Relationship among the species richness of different taxa. *Ecology* **87**:1886-1895.

Yang, L. H. and V. H. W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters* **13**:1-10.

Yoon, H. J., K. Y. Lee, S. B. Lee, and I. G. Park. 2008. Research on the current status of insect pollinator use in Korea. *Han'gug yangbong haghoeji*:1-9

Zurbuchen, A., L. Landert, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation* **143**:669-676.