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WILD BEE DECLINES AND CHANGES IN PLANT-POLLINATOR NETWORKS OVER 125 YEARS REVEALED THROUGH MUSEUM COLLECTIONS

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Abstract
Though recent literature highlights widespread bee declines, detailed information on local communities, plant-pollinator network interactions and individual species remains distressingly scarce. In order to accurately direct conservation initiatives and to evaluate the status of wild bees and their host plants, long-term data on these populations is critical. Examining pollinator communities across regional scales highlights small-scale changes that go undetected in larger investigations. In light of unknown effects of introduced species and cumulative range expansions of exotic taxa, monitoring wild communities closely and extensively over time is becoming increasingly important. The focus of this thesis is to investigate a regional wild bee plant-pollinator network to identify changes and correlates of change over 125 years (1891-2016) in the species that comprise the wild bee and plant communities of New Hampshire.

Shifts in regional wild bee community composition impact ecological relationships corresponding with the species that become more or less represented as a result of these shifts. This study analyzed 119 wild bee species in New Hampshire to reveal that 16 species are proportionally declining and 18 species are proportionally increasing. Over half of the species found in decline experienced a significant elevational or latitudinal range shift, many are regionally important crop pollinators, and all are native New Hampshire taxa. Neither genus nor guild affiliations were found to be indicators of change, suggesting that the requirements and behavior of individual species must be examined in order to evaluate the current and future state of the wild bee community.

The mutualistic interactions of plant-pollinator networks provide myriad economic, ecological, and cultural functions without which there would be severe environmental and societal consequences. Because of globally intensifying anthropogenic land use and climate change, plant-pollinator networks are becoming increasingly vulnerable to disturbance. The wild bee community interacts with a diverse array of flowering plants with specific environmental needs. Examining interactions between wild bees and floral hosts offers powerful insight into pollinator ecology and has potential to detect temporal network variation within the community.

This study revealed that changes in the wild bee plant-pollinator network over the past 125 years are characterized by a striking increase in exotic bee and plant taxa, which could have a destabilizing effect on mutualistic interactions in combination with increasing temperatures and habitat loss. Notable specialist interactions between native taxa that were recorded in historical networks have been lost, most likely due to host plant shifts and competition from recent species introductions. Subsequent monitoring and conservation efforts focused on habitat restoration for declining wild bee and plant taxa are fundamental to the future preservation of native biodiversity.

Keywords
Apoidea, Bee conservation, Bee declines, Biodiversity, Plant-Pollinator network, Pollination biology, Biology, Ecology, Entomology

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WILD BEE DECLINES AND CHANGES IN PLANT-POLLINATOR NETWORKS OVER 125 YEARS REVEALED THROUGH MUSEUM COLLECTIONS

BY

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THESIS

Submitted to the University of New Hampshire in Partial Fulfillment of the Requirements for the Degree of Master of Science in Biological Sciences: Integrative and Organismal Biology

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On April 18, 2018

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ABSTRACT

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By

Minna E. Mathiasson

University of New Hampshire, May, 2018

Though recent literature highlights widespread bee declines, detailed information on local communities, plant-pollinator network interactions and individual species remains distressingly scarce. In order to accurately direct conservation initiatives and to evaluate the status of wild bees and their host plants, long-term data on these populations is critical. Examining pollinator communities across regional scales highlights small-scale changes that go undetected in larger investigations. In light of unknown effects of introduced species and cumulative range expansions of exotic taxa, monitoring wild communities closely and extensively over time is becoming increasingly important. The focus of this thesis is to investigate a regional wild bee plant-pollinator network to identify changes and correlates of change over 125 years (1891-2016) in the species that comprise the wild bee and plant communities of New Hampshire.

Shifts in regional wild bee community composition impact ecological relationships corresponding with the species that become more or less represented as a result of these shifts. This study analyzed 119 wild bee species in New Hampshire to reveal that 16 species are proportionally declining and 18 species are proportionally increasing. Over half of the species found in decline experienced a significant elevational or latitudinal range shift, many are
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GENERAL INTRODUCTION

Wild bees play a vital role in our ecosystem. Bees provide the majority of global pollination services, worth approximately $217 billion in annual food crop production (Abrol et al. 2012). These pollination services ensure the reproductive success of almost 90% of angiosperms (flowering plants), of which there are currently an estimated 350,000 species, rendering them the foundation of innumerable other ecosystem services (Kearns et al. 1998; Kremen et al. 2007; Ollerton et al. 2011; Winfree et al. 2018). Ecosystem services are generally grouped into four categories: provision (obtained products and resources; e.g. food, medicine, energy), regulate (obtained benefits from processes; e.g. air quality, climate control, water purification), support (nutrient cycling, seed dispersal), and culture (nonmaterial benefit; e.g. recreation, spiritual enrichment) (Morelli 2011). In 1998, ecosystem services were conservatively valued at an annual $33 trillion (Kearns et al. 1998). Using the same estimation methods, the value of ecosystem services was updated in 2011 to an annual $125 trillion (Costanza et al. 2014). The services provided by insect communities span all of these four categories; pollination alone provides myriad benefits to ecosystems and thus to humans.

Pollination is crucial to successful crop production. A 2007 study revealed that 87 of the top worldwide food crops are dependent on animal pollination services, a majority of which are provided by bee species; moreover, insect pollination was shown to improve fruit and seed quality and quantity of 39 of the 57 leading single-crops (monocrops), which together account for 35% of global food production (Klein et al. 2007). To meet the growing demand for greater quantity, quality, and diversity of food in a diminishing environment (Garibaldi et al. 2009), the
value of these pollination services must be recognized as pollinator-dependent crops require sufficient pollinator availability. In recent years, there has been a disproportionate increase in pollinator-dependent cropland; increasing per capita demand of high-value, pollinator-dependent crops has mediated a respective growth in agriculture’s dependence on pollinators by 50% in the developed and 62% in the developing world between 1961 and 2006 (Aizen et al. 2009). If this trend continues to increase as expected, the need for pollination services will increase accordingly. The environmental conditions required to sustain thriving and diverse pollinator populations must be further evaluated in regional ecosystems. This information will be necessary to ensure the future need for pollination services as well as to better understand the global correlates of insect declines and to devise strategies for improvement.

**History and Presence of the European Honey Bee in the U.S.**

The dire plight of the European honey bee (*Apis mellifera*) has gained worldwide attention, particularly through the labeling of Colony Collapse Disorder (CCD). Yet, most are unaware of the history of this small creature, known affectionately as the “angel of agriculture,” that is now one of the most abundant insects on earth (Goulson 2003). This single species, *Apis mellifera* – not a native species to North America – was brought west in the mid-seventeenth century by English colonists. With the invention of moveable hives and management tools in the nineteenth century, commercial beekeeping took flight.

Though honey bees are managed primarily for honey production purposes, they provide pollination services as generalist pollinators as well (Aizen et al. 2009). Honey bees are widely considered to substitute the services of wild bees (Klein et al. 2007, Rucker et al. 2012), yet extensive study has shown that they are unable to replace the contributions of wild insects for a
broad range of agricultural crops (Greenleaf et al. 2006, Garibaldi et al. 2013, Rader et al. 2013). As a polylectic species, honey bees inclusively visit flowering plants as a generalist pollinator (Burger et al. 2013). Although it is impossible to expect a single species to exclusively provide the aforementioned pollination services required to maintain our ecosystems, the modern practice of honey bee commercial management seems to imply this expectation. Managed hives, which contain 10,000-40,000 individuals per hive (vanEngelsdorp et al. 2009) are transported, often recklessly, back and forth across the country to assure the abundant presence of honey bees during single crop flowering seasons. The past fifty years has witnessed a drastic decrease in the global honey bee population. In the United States, for instance, the number of honey-producing colonies has more than halved, from 5.9 million at its peak in 1947 down to 2.3 million by 2008. Similarly, European managed colonies decreased by 26.5% between 1961 and 2007.

Between 2006 and 2008, a condition known as Colony Collapse Disorder (CCD), characterized by sudden and cryptic death of a colony despite plentiful honey and pollen products in the hive, brought devastation to managed honey bee hives in the United States (vanEngelsdorp et al. 2008, 2009). Studies show that CCD could be the result of a variety of circumstances including *Nosema ceranae*, a highly infectious microsporidium (Higes et al. 2008), increased infestations of the parasitic mite *Varroa destructor*, and direct and sub-lethal effects of pesticides and agrochemicals (vanEngelsdorp et al. 2009).

The dramatic loss of honey bee populations during recent years has spurred questions of economics and sustainability. Moreover, native non-honey bee populations have started gaining more attention. Although humans have become highly reliant on honey bee pollination services, honey bees have been shown to be comparatively inefficient pollinators for many crops (vanEngelsdorp et al. 2009). According to leading entomologist Dr. Bryan Danforth, "An
individual visit by a native bee is actually worth far more than an individual visit by a honeybee. Honeybees are more interested in the nectar. They don't really want the pollen if they can avoid it. The wild, native bees are mostly pollen collectors. They are collecting the pollen to take back to their nests” (Gashler 2011). Furthermore, honey bees have been shown to limit reproductive success of native plant species in some cases due to their pollen removal strategies (Hargreaves et al. 2008). Consequently, though it is important to maintain the health of honey bee populations, it is just as important to look beyond this single species to the many other understudied yet critically valuable wild bees that inhabit our world.

Value of Wild Bee Services

It is little known that there are 4,000 bee species that are native to North America (Moisset & Buchmann 2010), collectively termed wild bees. These highly diverse populations are a vital alternative for pollination services. Wild bees differ from other bees in that they, unlike the domesticated honey bee for example, are unmanaged populations and are not used commercially for crop pollination. Beyond honey bees, managed bees include both non-native and native species such as stingless bees of the Meliponini tribe, bumble bees (Bombus spp.), leafcutter bees (Megachile spp.), and mason bees (Osmia spp.) (Garibaldi et al. 2013). The services provided by managed populations are considered commercial services, as compared with the genuine ecosystem services provided by wild pollinators (Allsopp et al. 2008). Similar to honey bees, the bumblebee Bombus terrestris and the alfalfa leaf-cutter bee Megachile rotundata have artificially extended ranges on a global scale, and have been shown to impact local wild bee fauna (Goulson 2003). Wild bees include unmanaged populations of the aforementioned managed species as well as native species including mining bees of the Andrenidae family, sweat bees of the Halictidae family, and carpenter bees (Xylocopa spp.) among many more (Rehan 2015). It has been shown
that in areas of low to moderate agricultural intensification where habitat diversity is high, unmanaged bee populations significantly enhance crop production (Aizen et al. 2009). From an evolutionary perspective, bee diversification most likely facilitated angiosperm diversification and vice versa (Danforth 2007); one result of this relationship is oligolectic wild bees that are specialized to effectively pollinate particular angiosperms with which they have co-evolved. The specialization and sheer diversity of wild bees make them more efficient global pollinators for a wide range of high-value crops and, as a result, fruit set is much higher in conjunction with wild bee pollination compared to honey bee pollination (Garibaldi et al. 2013). In a recent study, universally positive relationships between fruit set and wild pollinator floral visitation were found across 41 crop systems on six continents as compared with fruit set increases in conjunction with honey bee floral visitation of only 14% of these crop systems (Garibaldi et al. 2013).

**Generalist and Specialist Plant-Pollinator Interactions**

In 1970, Dr. George Stebbins defined five principles that govern adaptive radiation (rapid diversification) for pollination. The “most effective pollinator” principle suggests that, given the quantitative nature of selection, the development of floral traits is greatly influenced by the most effective and frequent pollinator vectors. This principle recognizes that plant-pollinator selection and evolutionary modification is not exclusive, however, and that flowers have secondary vectors regardless of whether their form is influenced by these secondary vectors. The “selection along the lines of least resistance” principle suggests that the flower structure-pollinator vector relationship goes beyond visitation frequency and visitor abundance to structural and environmental limitations (Stebbins 1970).
In order to measure the strength of plant-pollinator interactions, complementary specializations and the evolutionary influence these relationships can have on floral traits, pollination effectiveness and pollination importance must be evaluated. Broadly speaking, pollination effectiveness can be defined as the number of seeds set by receptive flowers as a result of pollen deposition following a single visit by a pollination. Pollination importance measures both the effectiveness and the frequency of individual floral visitors to a flower. Morphological and physiological variation as well as differences in foraging behavior and strategy, specialist or generalist, can determine how effective and efficient different floral visitors are as pollinators. Natural selection is exemplified through insect foraging methods that serve to maximize the acquisition of floral rewards (Olsen 1996). Morphologically, the wild bee families Colletidae and Halictidae are phylogenetically oldest and possess the most primitive structures (Michener 1944). Variation in body length and abdomen can greatly influence a pollinator’s ability to remove or deposit pollen (Michener et al. 1994). Body shape plays a role in determining foraging range of a species and, in some cases, can prevent contact with floral reproductive structures. Visitors carrying the most pollen on their bodies are not always most efficient at depositing pollen on receptive stigmas (Adler & Irwin 2005), although this is often used as a measurement of pollinator efficiency given that measuring both body pollen and pollen deposition for an individual would be extremely difficult to assess (Huda et al. 2015; Howlett et al. 2011).

A study investigating the efficiency of different bees in pollinating onion flowers found that onion umbels visited by *Halictus farinosus*, native to the western U.S., set more seed per visit when compared to honey bee visits, which resulted in a significantly higher ratio of aborted seed. *Halictus farinosus* populations increased in conjunction with onion bloom, yet honey bee
relative abundance showed an inverse relationship, indicating that honey bees likely foraged on other plants during onion bloom. Although visitation rates for other bees stayed relatively constant throughout the day, *H. farinosus* activity peaked significantly at 1 p.m. and at 4 p.m. (Parker 1982). A 1992-1994 study in Nova Scotia found that honey bees pollinated low bush blueberry flowers at less than a quarter of the rate of pollination by *Bombus* spp. queens and *Andrena* spp. (Javorek et al. 2002). A 2006 study found that production of a field-grown hybrid cherry tomato variety greatly benefited from wild bee visitation. In this particular variety of tomato, the stigma extends beyond the anthers, a reproductive morphology that is likely favorable for insect pollination (Greenleaf & Kremen 2006). Floral morphology often controls bee species partitioning and complementary specialization, particularly the orientation of the flower’s stigma relative to the anthers as well as long and narrow nectar tubes that prevent entry by visitors that are too large or have a short proboscis (Blüthgen & Klein 2011).

Chemical signals, such as floral scent, are important means of communication between plants and floral visitors as well. These signals have evolved to attract wild pollinators, and may as effectively attract honey bees. Floral volatiles have been shown to mediate mutualisms between plants and specialized pollinators (De Vega et al. 2014). Among other cues, specialist bees use floral volatiles and taxon-specific olfactory cues to identify rewarding and non-rewarding flowers. Floral scent has been shown to influence long-range orientation and landing behavior in pollinators (Dötterl & Vereecken 2010; Raguso 2008; Burger et al. 2013). According to Stebbins’s “significance of character syndromes” principle, scent is likely the most attractive characteristic to pollinators and is even more valuable than shape or color (Stebbins 1970). A 2013 behavioral study compared the abilities of a generalist bee, *Apis mellifera*, and a specialist bee, *Andrena vaga*, to perceive floral volatiles. This study found that the specialist *Andrena vaga*
had more sensitive glomeruli, crucial to odorant signal transduction, which is likely responsible for the acute responsiveness that it exhibited to a behavior-mediating odorant, 1,4-dimethoxybenzene, of the *Salix* host flowers (Burger et al. 2013). A 2012 study similarly investigated the attraction of female oligolectic megachilid bees, *Hoplitis adunca*, to 1,4-benzoquinone, a floral volatile produced exclusively by host plants of *H. adunca* in the genera *Echium* (Asteraceae) and *Pontechium* (Boraginaceae), and found this plant-specific recognition cue to be essential in host plant identification (Burger et al. 2012).

**Complexity and Importance of Pollination Interaction Networks**

Plant-pollinator networks encompass mutualistic interactions requiring a complex array of requirements for both plants and pollinators. These interactions experience declines and compositional changes due to environmental alterations such as climate change, fluctuation in biodiversity, and habitat fragmentation, among other factors (Potts et al. 2010). Landscape changes have been shown to contribute to dominance by common taxa and correspondingly influence biodiversity (Carré et al. 2009). Research indicates that wild plant and bee diversity in addition to ecosystem stability are vulnerable as a result of these environmental disturbances and exotic species introductions (Goulson 2003; Potts et al. 2010; Nicolson & Wright 2017). Further exploration of the central requirements to support healthy pollination networks will be key to preventing additional declines. A 2013 study quantifying changes in plant-pollinator networks over 120 years in a forest understory habitat in Illinois found devastating losses of bee species (50% extirpation) and instability in the overall interaction network structure. The disruption in these plant-pollinator interactions could be attributed to a combination of overlapping factors including diverging temporality and phenology, changes in the landscape, and reduced spatial
co-occurrence of plants and pollinators (Burkle et al. 2013). The effects of temporal and phenological mismatches on plant-pollinator interactions have proven deleterious, corresponding to misalignment in peak activity times between floral hosts and their visitors as well as species extirpations. A 2016 study of northern New England wild bee pollination networks that investigated 197 unique plant-pollinator interactions over three seasons found that plant-pollinator structure is complex and diverse, yet plant-pollinator associations are poorly connected, which indicates their vulnerability to change. Weighted nestedness (Galeano et al. 2009) and connectance (Dunne et al. 2002) were evaluated at a community level in this study to measure species co-occurrence and the community’s resilience to species loss. Although species richness was found to be exceptionally high, the great variation in community composition over the collection period and the low measures of both weighted nestedness and connectance of plant-pollinator interactions suggests that the overall pollination network in this northern temperate region is susceptible to disturbance (Tucker & Rehan 2016). The intersection of high species richness yet fragile network structure is a concerning combination and underscores the urgency of further study and conservation of the wild bee and floral community structure in this region.

The mechanisms controlling wild bee and floral community structure (and pollination network structure) remain largely unknown. Floral functional specialization and insect pollination began gaining attention in the eighteenth century with German botanist Joseph Kölreuter’s description of plant sexuality and the role of insects in pollination (Mayr 1986). Discussion of patterns in functionality, plant phylogeny, and pollination syndromes has since persisted. Pollination syndromes are categorized based on floral trait selection influenced by selective pressures from specific pollinators or groups of specific pollinators (Fenster et al.
Plants retain or develop certain floral morphologies and characteristics due to the influence of a primary pollinator’s morphology and physiology, and foraging behavior. Although characteristics of pollinator syndromes are not exclusive prerequisites so as to preclude secondary pollinators, they are also not arbitrary or redundant (Faegri & van der Pijl 1979).

A 2011 study investigating pollination networks in Brazilian tropical grasslands found pollination network modules and plant-insect interactions to be associated with pollinator functional groups and syndromes (Danieli-Silva et al. 2011). A 2000 study on sclerophyllous vegetation in Tasmania found plant-pollinator interactions to be somewhat consistent with classically defined pollination syndromes yet, overall, floral visitation as predicted by syndromes was not consistent with the visitation observed (Hingston & Quillan 2000). There are mixed results in the reliability of pollinator syndromes as an accurate predictive tool. A global analysis found pollination syndromes to be accurate for approximately 30% of plant-pollinator communities that were included in the analysis (Ollerton et al. 2009; Rosas-Guerrero et al. 2014). A 2004 review of floral specialization and pollination syndromes concluded that although classic categories of pollination syndromes are not always inclusive and complete predictors of pollination networks, they should be viewed as adaptations influenced by selection created by functional groups of pollinators. Taking into account global plant and insect diversity, describing pollination syndromes simply and definitively is near impossible. Nevertheless, it is critically important to recognize the evolutionary and ecological role of specialization and functional interactions (Fenster et al. 2004). Moreover, when considering the authority of pollination syndromes, it is important to consider the change in its predictive value in pollinator populations compared with pollinator communities (Hernández-Yáñez et al. 2013; Ollerton et al. 2009).
There remains much to be discovered regarding the reasons for species additions to symbiotic mutualistic groups of plants and pollinators (Jordano et al. 2003).

In further breakdown of pollinator community networks, modules are composed of weakly connected species groups that are internally strongly connected internally usually by means of convergent taxonomical or functional traits (generally considered as co-evolutionary units). A modular network is characterized by groups (modules) of highly connected species to one another within a network and weak interactions that connect species within different modules. Understanding the level of modularity in a system yields greater insight into the basis and evolution of mutualistic plant-pollinator interactions (Olesen et al. 2007). Modularity is positively correlated with specialization in plant-pollinator interactions (Corbet 2000; Thompson 2005; Danieli-Silva et al. 2011) and it has been shown that larger networks are significantly more likely to be modular than smaller networks (Danieli-Silva et al. 2011). In a 2007 analysis of 51 pollination networks that included approximately 10,000 plant and pollinator species and 20,000 links, all networks with over 150 species were modular, while all networks with less than 50 species were not modular (Olesen et al. 2007).

Not all studies are consistent with those results. A 2013 pollination network study conducted in Veracruz, Mexico, found the pollination networks under study were overall more generalized than specialized, yet with a high level of modularity. The authors suggest that the reason for the high modularity in spite of low specialization may be a reflection of a pollinator’s pursuit of higher quality or quantity of floral resource, competitive exclusion, or phenology. The generalist nature of pollination revealed suggests that seasonality and food resource availability are the most compelling factors influencing the structure of plant-pollinator networks and that syndromes may be the basis of modules. The core plant species identified in the plant-pollinator
network had a range of flowering times throughout the year, indicating the extreme importance of temporality and phenology in a visitor’s foraging behavior. When a preferred floral host is unavailable, a pollinator will seek food and floral resources from a core floral host, which may be the mechanism for increased generalist behavior (Hernández-Yáñez et al. 2013).

**Phenology of Pollination Networks**

Phenology (seasonal cycles) is a critical factor controlling the extent and possibility of a wild bee’s interaction with a floral host and influences network stability. Phenology also influences patterns of generalization and specialization and more significantly dictates interactions: if a plant and pollinator do not overlap phenologically, there is no opportunity for linkage (Jordano et al. 2003). Differing phenologies present a variety of scenarios, some of which have complementary effects and others that could result in phenological mismatch. The geographic co-occurrence of an early-flowering and late-flowering plant species could be an example of phenological complementarity if the early-flowering plant attracts a crucial pollinator that has a foraging period exceeding its flowering period. In this case, the pollinator could seek out the late-flowering plant, resulting in an effective mutualism between these sequentially blooming species (Baker 1963; Heinrich & Raven 1972; Waser & Real 1979; Blüthgen et al. 2011). Limited evidence exists to confirm increased plant-pollinator phenological mismatches (Goldstein & Ascher 2016), yet with mounting global climate change, phenological decoupling seems more likely than ever. A 2004 study in Scotland based on floral resources utilized by bumble bees in 30 plant communities showed that differing spatial and temporal patterns of resource availability could affect bumble bee distribution and survival (Devoto et al. 2004). Seasonality was shown to affect bee abundance and visitation to species of trees in the Legume
family (Fabaceae) in tropical rainforests in a 1990 study (Bawa 1990). In 1988, a study was conducted in southwest Germany on co-phenology of plants and anthophilous (flower frequenting) insects, observing 3600 anthophilous insects—1500 of which were bees—visiting 71 different plant species over 2 years. It was discovered that both the entomophilous (insect pollinated) plants and anthophilous (flower frequenting) insects were staggered continuously in flowering periods and flight times, respectively. Solitary bees such as *Andrena* and *Osmia* were dominant in spring whereas in summer, social bees such as *Bombus*, *Halictus*, and *Lasioglossum* were dominant. It is possible that in species-rich communities, staggered flight and blooming periods are caused not only by climatic factors but also by competitive exclusion (Kratochwil 1988). Though it has been revealed that bees exhibit plasticity in response to altered flowering times and adjust to avoid phenological mismatch (Bartomeus et al. 2011), previous studies have shown that changes in phenology, particularly in spring, contribute to network instability (Burkle et al. 2013; Robbirt et al. 2014). Springtime is most prone to phenological mismatch given the lifecycle of bees and plants and the increasing possibility of the early onset of spring (Kudo & Ida 2013). Knowledge of individual phenologies of flowering plants involved in plant-pollinator networks must also be considered for the optimal duration of the wild bee forage season.

**Effects of Competition and Environmental Change on Biodiversity**

Indisputable evidence that competition is occurring between native and introduced bee species is nearly impossible to obtain, as performing thorough competitive exclusion studies is exceedingly difficult. This lack of evidence, however, should not be equated to an absence of competition, given the information that does exist on the phenomena (Goulson 2003; Russo 2016). Exploitative competition (Schaffer et al. 1979; Balfour et al. 2015) and earlier foraging times of
larger bees such honey bees and bumble bees (Corbet et al. 1993; Dafni & Shmida 1996; Horskins & Turner 1999; Goulson 2003) threaten the food security of many wild and solitary bees.

Beyond competition between introduced and native species, anthropogenic factors, including climate change, are likely the primary culprits threatening wild bee biodiversity. Considerable changes in land use have occurred worldwide over the past 150 years: agricultural expansion, increased pesticide application, urbanization, and mass development of paved road systems. The ecological response to these changes is reflected in bee population dynamics corresponding to this period. Pollinator declines have been reported worldwide. Regardless of the large areas that remain to be surveyed, anthropogenic influence is increasing on a global scale. It is undeniable that disruption of pollinator networks is a global phenomenon, given the anthropogenic causes of these collapses (Kearns et al. 1998). Decreased habitat along with temporal, spatial, and phenological shifts that affect interactions between wild bees and their floral hosts are all possible negative outcomes of anthropogenic influence. Fitter & Fitter (2002) found that for 385 plant species the average initial flowering date has advanced by 4.5 days over the last ten years in Britain. Their data, which covers five sequential decades beginning with the 1950s, shows a major shift in first flowering date since the 1980s. They also found that insect-pollinated species are more likely to experience shifts in flowering times than wind-pollinated species (Fitter & Fitter 2002). Inouye (2008) found a significant relationship between snowmelt and flowering in montane wildflower populations, warning that climate change induced shifts in snowmelt increases risk of frost damage and flower bud mortality. Another 2008 study on flowering time shifts in Massachusetts plant communities found that flowering times are an average of seven days earlier than they were 150 years ago (Miller-Rushing & Primack 2008).
Increases in temperatures and CO$_2$ levels and their combined effects are affecting plant-pollinator interactions. Elevated CO$_2$ accelerates flowering time, changes leaf chemistry, and accelerates phenology (Springer & Ward 2007). Rising temperatures have been shown to reduce longevity in flowering plants and limit nectar production (DeLucia et al. 2012; Hoover et al. 2012). Using historical records, Miller-Rushing and Primack found that Concord, Massachusetts warmed 2.4° between 1852 and 2006 as a result of climate change and increased urbanization (Miller-Rushing & Primack 2008).

Habitat destruction and fragmentation have dire consequences for plant and insect communities. Kearns et al. (2011) discusses the biological effects of habitat fragmentation and its corresponding threats of intensified genetic drift, spatial isolation, and local extinction (Barrett & Kohn 1991; Menges 1995; Zayed 2009). Habitat loss and fragmentation have strong effects on bee decline on both solitary and social bee communities globally (Brown & Paxton 2009). Pollination services become at risk of limitation, which negatively impacts plant reproduction; inadequate pollen receipt limited female flowering plant fecundity by 62% in a 1994 study (Burd 1994). Bee richness changes reported by Biesmeijer et al. (2006) showed a 52% decline in Britain and ~67% in the Netherlands. Bees that were oligolectic had lower mobility, and required specific habitats showed greater relative decreases than generalist and more mobile bee species (Biesmeijer et al. 2006). Habitat fragmentation is a common result of increased agriculture (Potts et al. 2010). In a synthesis of 23 studies of landscape effects on crop pollination, significant decreases in bee richness and visitation rates were found with increased distance from natural habitat (Ricketts et al. 2008).

The positive relationship between decreased crop diversity (monoculture) and decreased pollinator biodiversity has been well documented (O’Toole 1993; Banaszak 1996; Kearns et al.
1998; Nicholls & Altieri 2013). A recent study conducted across 29 farms in New Jersey and Pennsylvania revealed that field size and diversity of crop and weed plants may be have greater effects than organic vs. conventional farming techniques. The wild bee visitation rates across those 29 farms were equally high between conventionally and organically managed farms because the crop and weed diversity were equal between both treatments (Winfree et al. 2008). Nevertheless, pesticide use and pathogen spillover from managed bee populations to wild populations have recently been associated with bee declines (Williams & Osborne 2009). Pesticide induced declines have been reported in the U.S. since the 1870’s (Johansen 1977). Findings from a 2009 Colorado study suggest that causes for decreased bee biodiversity and abundance go beyond the degree of urbanization and development to more specific conditions like grazing regime (Kearns & Oliveras 2009).

**Causes and Implications of Wild Bee Declines**

There is extensive research indicating that that the loss of wild bees would bring catastrophic devastation to ecosystems (Klein et al. 2007; Kearns & Oliveras 2009). Yet despite concerns about mass pollinator declines, there is a striking absence of information on wild bee species (Bartomeus et al. 2013), their regional specificity, and their response to the effects of stressors such as land use, anthropogenic climate change, increased chemical pesticides, and competition with introduced species. During this time of unprecedented human-induced environmental change, it is of pressing importance to understand the biological and ecological principles that directly affect the health and distribution of bees. To compensate for the lack of reliable baseline data for evaluating bee declines and changes in community composition, we must survey bee fauna in pristine refuge areas (Goldstein & Ascher 2016). Museum collections provide unique
insight into historical ecological trends and often reveal new species (Bartomeus et al. 2013), yet they remain greatly underutilized resources that contain a wealth of untapped knowledge (Suarez & Tsutsui 2004).

The research that does exist on wild bees documents concerning declines, particularly in the genus *Bombus* but also in other wild bee genera (Biesmeijer 2006; Goulson et al. 2008; Bartomeus et al. 2011). In a recent 120-year analysis of plant-pollinator networks, it was predicted that, although historic networks demonstrated a certain level of tolerance to disturbance, existing networks will be not be as resilient to future landscape changes (Burkle et al. 2013). There remains a lack of knowledge surrounding basic population ecology of angiosperms and bee taxa beyond well-known and model groups (Brown & Paxton 2009; Murray et al. 2009). Beyond the devastating ecological repercussions of reduced biodiversity, economic impact is significant: the loss of global ecosystem services between 1997 and 2011 is estimated between $4.3–20.2 trillion annually (Costanza et al. 2014). The following correlates of wild bee declines have been identified and are likely working both independently and synergistically: neonicotinoid pesticides (Woodcock et al. 2017), habitat fragmentation (Kearns et al. 1998; Brown & Paxton 2009), competition with exotic species (vanBergen 2013), climate change (Goulson et al. 2015), and loss of host plants (Schepet al. 2014). The effects of these stressors have varying impacts depending on morphology, lifestyle, habitat requirements, and pollination specialization of wild bees, each of which is exhibited differently by individual species. Gaining a greater understanding of drivers of wild bee biodiversity, floral associations, and pollination network structure requires multi-year studies of bee fauna (Goldstein & Ascher 2016), the analysis of spatial and temporal dynamics together (Ranta et al. 1981; Devoto et al. 2014), and individual species evaluations (Burkle et al. 2013; Koh et al. 2016).
**Research Objectives**

This study aims to investigate a regional community of wild bees and identify drivers of change over a 125-year period using museum specimens collected between 1891-2016. Given the inherent regional diversity across global ecosystems, exploring wild bee communities and variation in landscape, agriculture, and flora on local scales has the potential to detect wide-ranging pressures that are causing compositional shifts and declines worldwide. Chapter 1 focuses on status changes in wild bee community of New Hampshire over the 125-year period and ecological characteristics of individual species. Relative abundance measurements between a historical (1891-1987) and contemporary (1988-2016) period categorizes 119 bee species into groups that are proportionally decreasing, increasing, or stable in the entire community. Chapter 2 focuses on the plant-pollinator network of New Hampshire with a closer look at changes in the floral interactions of the wild bee species between historical and contemporary periods. Comparisons over the 125-year study period reveal that interactions that have been lost, progressive rarity of network plant species, specialist interactions, and exotic species introductions. A short conclusion summarizes the overall findings of this research as well as the topical importance of continued exploration of the wild bee community in order to conserve its invaluable biodiversity.
CHAPTER I:
STATUS CHANGES IN THE NEW HAMPSHIRE WILD BEE COMMUNITY
OVER 125 YEARS

INTRODUCTION

Wild bees provide essential pollination services to angiosperms, ensuring their reproductive success and endurance in both managed and unmanaged ecosystems globally (Ollerton et al. 2011). Yet the effects of continuous land development, pathogen spread, and climate shifts on the wild bee community remain understudied (Russo 2016). In order to support healthy bee pollination, ideal habitat conditions and behavior of the bee community within specific regions must first be established and subsequently monitored (Lebuhn et al. 2012). Further evaluation of these characteristics across various temporal, spatial, and taxonomic scales is essential to revealing previously undiscovered patterns and drivers of change in wild bee biodiversity to conservation policymakers.

The scope of current research on the bee community is largely focused on managed honey bee (Apis mellifera) and bumble bee (Bombus spp.) populations. Recent declines in both have been widely recorded across Europe and North America (Goulson et al. 2008; vanEngelsdorp et al. 2009; Colla et al. 2012; Bartomeus et al. 2013). These notable declines, along with recent evidence that wild bees are more effective pollinators than managed bees, have prompted investigation into possible declines beyond these well-studied species to the rest of the bee community (Garibaldi et al. 2013; Winfree et al. 2018). The global wild bee community is represented by approximately 20,000 species, almost all of which are unmanaged (Goulson 2003; Winfree 2010). North America alone hosts 4,000 of those species, each of which has
varied requirements for reproduction and survival (Cane & Tepedino 2001). In order to more fully understand individual species’ needs in addition to their contributions, assessments of the wild bee community must consider life history traits and guilds through long-term evaluation (Bartomeus et al. 2013; Burkle et al. 2013).

Due to the disproportionate legislative and agricultural support for honey bees, data on unmanaged wild bees is comparatively scarce (Colla & MacIvor 2017). In particular, there is a dearth of long-term data. Only recently has there been an upsurge in the amount of research focused on bees. Museum collections, however, are rich sources of insight into historic communities of flora and fauna worldwide (Bartomeus et al. 2013; Jacobson et al. 2018). Utilizing museum data is an important step towards generating fundamental information on wild bee populations.

This research is made all the more important by the increasing fluctuation in temperatures resulting from climate change, which poses a serious threat to ectothermic organisms like bees (Blanford et al. 2013). Even slight temperature changes have been shown to impact bee flight activity and foraging patterns (Heard & Hendrikz 1993; Stone 1994; Rader et al. 2013). Climate change has the potential to induce phenological mismatches between plant-pollinator pairings, which could reduce the diet breadth of bee species and hinder the mutualistic relationship between bees and host plants (Memmott et al. 2007; Robbirt et al. 2014). Under climate change models it is predicted that temperature will increase most along steep latitudinal temperature gradients in northern temperate areas (La Sorte et al. 2014). Non-migratory organisms that persist in these regions, such as wild bees, could be strongly affected by these changes, potentially inducing range shifts (Roth et al. 2014; Pyke et al. 2016). These effects paired with anthropogenic land use influences are likely to affect particular bee taxa more intensely than
others, especially when variable traits such as body size, diet breadth, sociality, and habitat preference are considered.

Investigating individual bee species’ responses to climate change and the overall community composition over time is important for identifying trends and for monitoring interactions between native and introduced species. Though some insect species have been intentionally introduced for services such as pollination or biocontrol, due to high international trade volume, many species are accidentally introduced to areas outside of their native ranges (Kobelt & Nentwig 2008; Shell & Rehan 2017). Introduced bee species comprise approximately 0.5% (21 species) of the bee species in North America and, apart from the few species introduced for crop pollination, most were introduced unintentionally (Cane 2003). Because of recent trade expansion and environmental modification, it is likely that there remain many undiscovered invasive species with unknown effects and ranges (Seebens et al. 2018). Introduced species are widely believed to threaten biodiversity and compete with native taxa (Vanbergen et al. 2018); however, they may also merit conservation value due to their ability to persist in unpredictable climates and supplement lost ecosystem services of extirpated taxa (Schlaepfer et al. 2011). Given the difficulties inherent in assessing the possible competition between such mobile organisms, conclusive evidence that exotic bee introductions have negative consequences is weak and requires more thorough evaluation (Goulson 2003). To further understand the effects of introduced species and to detect potential ecological invasions, the proportion of each species within regional communities should be compared over time.

In this study, we evaluate the wild bee community in New Hampshire over 125 years in order to assess changes in species composition by comparing historical (1891-1987) and contemporary (1988-2016) samples. Analyses are based on taxonomy, habitat preferences, range,
geography, and nesting biology. The northern temperate climate of New Hampshire and its
diverse geography and assortment of habitats make it an ideal location to fundamentally assess a
local wild bee community. The establishment of regional baseline data of the wild bee
community in New Hampshire is important to the evaluation of anthropogenic impacts (Marlin
& Laberge 2001) and to direct conservation policy. The aims of this work were twofold: first, to
assess the changes in status and range of the wild bee community over the past 125 years and
second, to determine the long-term stability of the wild bee community through individual
species assessments.

METHODS

Bee Specimen Database

A dataset of 17,043 non-\textit{Bombus} wild bee specimens collected over 125 years spanning the
period from 1891-2016 were included in this study. A recent study (Jacobson et al. 2018)
evaluated changes in New Hampshire \textit{Bombus} over 150 years. The present study therefore
focuses on the remainder of New Hampshire’s wild bee community. The full database was
obtained through a combination of museum specimens housed in the University of New
Hampshire Insect Collection (UNHC) collected between 1891-2012, specimens collected from
biodiversity field surveys conducted by the UNH Bee Lab from 2013-2016, and specimens from
the USGS Bee Inventory and Monitoring Lab in Maryland. Additional bee specimen information
was obtained through the collections of Michael Veit (Lawrence Academy, MA) and Joan Milam
(UMass Amherst, MA). All specimens were collected by means of bowl, net, or malaise
trapping. Although many historical museum specimens contained no supporting information on
collection method, it is likely that most historical specimens were collected by net as pan
trapping only came into consistent use in Hymenoptera sampling in the past 20 years (Aguiar & Sharkov 1997; Cane et al. 2000; Roulston et al. 2007). All UNH bee specimens were identified using taxonomic keys (Mitchell 1960, 1962; Gibbs 2011; Rehan and Sheffield 2011; DiscoverLife.org) and confirmed to species by professional taxonomists, given a unique UNH barcode ID, and entered into the database. Only specimens that had the following information were included in the final dataset: collection date, collection location, and species-level identification. Record locations ranged from 42.72° to 45.19° N latitude and -72.42° to -70.933° W longitude. Specimens were databased with geographic coordinates and repository information. Specimen record data can be downloaded from the online portal: https://unhcollection.unh.edu/database/.

**Collection Periods and Rarefaction**

In order to evaluate changes in the bee community composition, species richness and abundance over time, the data was divided into equally represented bins. Given the uncertainty of sampling effort in museum collections (Bartomeus et al. 2013), partitioning the data into equal time periods that each span an equal number of years would not be suitable. Rarefaction curves and statistics were calculated using species richness and specimen abundance as metrics for the binning scheme. Based on these curves, species richness proved most suitable for a primary regulator of equalization so that each bin contained roughly the same number of species and a rarefaction curve was generated with the ‘rarecurve’ function from the VEGAN package (Jari Oksanen et al. 2017) in R 3.3.2. The following two periods were established: 1891-1987 (historical) and 1988-2016 (contemporary). These two periods were additionally selected to reflect different temporalities: pre-urbanization and industrialization before the 1990s compared
with increasing roadways, urbanization and population gain between 1990 and the present (U.S. Census Bureau 2012) as well as to allow for an evaluation of long-term changes over the past 125 years (Colla et al. 2012; Jacobson et al. 2018). In tandem with agricultural expansion and land use change, there have been notable bee and pollinator declines in recent decades across Europe and the U.K., further signaling the importance of comparing changes within the North American the community during the past 30 years to detect possible corresponding declines (Wenzel et al. 2006; Goulson et al. 2008).

Species Richness Indices and Community Sampling Effectiveness

A species richness analysis determined species diversity indices to reveal how well the bee community was sampled in any given individual collection period. The true diversity of the community was approximated through point and confidence interval estimate computation (Wang 2011). Species diversity indices were generated for each time period using the SPECIES package (Wang 2011) in R 3.3.2. The following species richness estimates were calculated: Chao and Chao-1 with the function ‘chao1984’ (Chao 1984), ACE and ACE-1 with the function ‘chaolee1992’ (Chao & Lee 1992), and Jackknife with the function ‘jackknife’ (Burnham and Overton 1978). Each of these tests calculate a lower and upper bound estimate of species richness through which the effectivity of community sampling can be calculated by comparing the sampled to the estimated species richness.

Bee Abundance and Community Composition

After sorting the specimens into their respective collection time periods, the status of each bee species was evaluated using a relative abundance measurement to account for possible disparity
in sampling effort, especially during periods of low collection in the early 1900s. To ensure that species status evaluations were as conservative as possible, analyses were conducted at the genus level. The relative change of each genus was examined proportionally within a family between the two periods. As many species were represented by only a few specimens overall or sparsely and inconsistently over time, species were categorized as ‘data deficient’ if they did not meet the following requirements: species represented >1% of total collections within its genus, and species is represented by one or more specimens in each time period.

**Bee Abundance and Community Composition**

The qualified species were categorized by genus and a relative abundance measurement was made using the following equation to weight each time period by its total number of specimens collected:

\[
\text{Relative Abundance} = \frac{\# \text{ specimens collected of species within time period}}{\# \text{ total specimens collected in genus within time period}}
\]

A \( z \)-test was performed using XLSTAT (Version 2017.4.45491) comparing historical and contemporary samples, using the following equation with a 95% confidence interval:

\[
Z = \frac{\hat{p}_1 - \hat{p}_2}{\sqrt{\frac{\hat{p}_1 \cdot \hat{q}_1}{n_1} + \frac{\hat{p}_2 \cdot \hat{q}_2}{n_2}}}
\]

\( \hat{p}_1 \) = proportion of species within genus in historical sample  
\( \hat{p}_2 \) = proportion of species within genus in contemporary sample  
\( \hat{q}_1 = 1 - \hat{p}_1 \)  
\( \hat{q}_2 = 1 - \hat{p}_2 \)  
\( n_1 \) = total specimens within genus in historical sample  
\( n_2 \) = total specimens within genus in contemporary sample
As a z-test measures differences between two proportions, the ratio of qualified species within genus that were present in both the historical (1891-1987) and the contemporary (1988-2016) periods were compared. Using the relative abundance measurements and z-score calculations, each species was given a status determination based on any significant change (p<0.05) classified as one of the following: increase, decrease, or no change.

Habitat, Range, and Lifestyle Characteristics

For each species that was found to be either proportionately decreasing or increasing at the genus level, additional information on nesting habit (ground, stem, cavity), range (native or introduced), lifestyle (solitary, eusocial, cleptoparasitic), and pollinator type (generalist or specialist) was compiled. Average elevation and latitude were calculated for each species found in decline comparing the two samples. Descriptive statistics (mean and standard error) were calculated using the ‘describe’ function in the package PSYCH in R 3.3.2 (Revelle 2017) for both elevation and latitude. A heteroscedastic Welch’s two sample t-test for unequal variances was run using the ‘t.test’ function.

RESULTS

Bee Specimen Database

The 17,043 wild bee specimens in the full database represent six families, 36 genera, and 322 species (Table S1). As expected, the frequency distribution of bee species across the 125-year period (1891-2016) is uneven due to variation in population sizes of common and rare species (Bartomeus et al. 2013), and due to the uncertainty of historical sampling effort. Of the entire collection, 150 species were represented by more than 10 independent records, 26 species were
represented by over 100 independent records, and 46 species were represented by single specimen records. A total of 119 bee species met the requirements to be included in status assessment analyses (Table S1). Due to the terms of inclusion and because many species were not represented in both time bins, 203 species were excluded from analyses (Table S1). The collection location of specimens in both samples ranged widely across New Hampshire (Fig. 1).

Species Richness Indices and Community Sampling Effectiveness

The species richness analysis indicated that the bee community was effectively sampled and that there is a high bee species richness in New Hampshire (Fig. S1, Table S2). The number of species comprising the New Hampshire wild bee community during the 1891-1987 historical time period was estimated to be 233 by the ACE test lower bound (lb) estimate with 202 observed species, translating to a 90% sampling effectiveness. The other species richness indices calculated yielded similar results (Chao: 235 lb, 89% effectiveness; ACE-1: 241 lb, 87% effectiveness; Jackknife-1: 257 lb, 87% effectiveness). The number of species comprising the New Hampshire wild bee community during the 1988-2016 contemporary time period was estimated to be 333 by the ACE test lower bound estimate with 308 observed species, translating to a 97% sampling effectiveness. The other species richness indices calculated yielded similar results (Chao: 335 lb, 92% effectiveness; ACE-1: 319 lb, 97% effectiveness; Jackknife-1: 360 lb, 90% effectiveness).

Bee Abundance and Community Composition

Analyzing the relative proportion of the genera contained within each family revealed significant change in 16 genera (Fig. S2). Seven genera were found to be decreasing: *Andrena, Nomada,*
Hylaeus, Halictus, Sphecodes, Coelioxys, and Megachile. Nine genera were found to be increasing: Calliopsis, Psuedopanurgus, Ceratina, Melissodes, Colletes, Agapostemon, Lasioglossum, Anthidium, and Osmia.

All 119 species included in the analyses were assigned a status determination based on genus-level z-scores (Tables S3, S4 & S5). A total of 16 species were found to be in decline at the genus level (Table S4, Fig. 2). Seven species in the Andrenidae were found to be in decline: Andrena carlini, A. erythrogaster, A. forbesii, A. imitatrix, A. miserabilis, A. salictaria, and A. vicina. Two species in the Apidae were found to be in decline: Nomada bella and N. depressa. Five species in the Halictidae were found to be in decline: Agapostemon sericeus, Halictus rubicundus, Lasioglossum coriaceum, L. imitatum, and L. quebecense. Two species in the family Megachilidae were found to be in decline: Megachile brevis and M. montivaga. In contrast, 18 species were found to be increasing proportionally within their respective genera: Andrena commoda, A. cressonii, A. dunningi, A. melanochroa, A. nasonii, A. nubecula, A. placata, A. wilkella, Ceratina mikmaqi, Nomada articulata, Agapostemon virescens, Halictus ligatus, Lasioglossum cressonii, L. leucocomum, L. leucozonium, L. pilosum, Megachile relativa, and Osmia pumila (Table S5). The remaining 86 species were found to have experienced no significant proportional change at the genus level (Table S6).

Habitat, Range, and Lifestyle Characteristics

All species found to be in decline are native to New Hampshire. Out of the declining species, 14 are ground nesters and two are cavity-nesting. Four specialist pollinators (Andrena erythrogaster, A. salictaria, Nomada bella, and N. depressa) were found to be in decline. The remaining 12 declining species are generalist pollinators. Most declining species are solitary
nesters except for two cleptoparasitic species (Nomada bella, and N. depressa) and two eusocial species (Halictus rubicundus and Lasioglossum imitatum; Table 1).

Out of the 18 species found to be increasing, 15 species are ground nesters and three are stem or cavity-nesting species (Ceratina mikmaqi, Megachile relativa, and Osmia pumila). Two species (Andrena wilkella and Lasioglossum leucozonium) found to be increasing are introduced. The remaining 16 increasing species are native to New Hampshire. Two specialist pollinators (Andrena nubecula and A. placata) were found to be increasing and the other 16 increasing species are generalists. Most increasing species are solitary nesters apart from one cleptoparasitic species (Nomada articulata) and three eusocial species (Lasioglossum cressonii, L. leucocomum, and L. pilosum; Table S7).

Comparisons between the historical and contemporary samples of the average collection elevation of each species revealed significant differences for over half of the species found to be in decline (Welch’s T-tests, p<0.05; Table 2). Seven species experienced a significant increase in elevation: Andrena forbesii, A. miserabilis, Agapostemon sericeus, Halictus rubicundus, Lasioglossum coriaceum, L. imitatum, and Megachile montivaga. Three species experienced a significant decrease in elevation: A. imitatrix, Andrena vicina and Lasioglossum quebecense and six species experienced no significant change in elevation: Andrena carlini, A. erythrogaster, A. salictaria, Nomada bella, N. depressa, Megachile brevis.

Comparisons between the historical and contemporary samples of the average collection elevation of each species revealed significant differences for 8 of the 18 species found to be increasing (Welch’s T-tests, p<0.05; Table S8). Six species experienced a significant increase in elevation between historic and contemporary time periods: Andrena dunningi, A. nubecula, Lasioglossum leucozonium, L. pilosum, Megachile relativa and Osmia pumila. Two species
experienced a significant decrease in elevation: Halictus ligatus and Lasioglossum cressonii and ten species experienced no significant change in elevation (Table S8).

Comparisons between the historical and contemporary samples of the average collection latitude of each species revealed significant differences for over half of the species found to be in decline (Welch’s T-tests, p<0.05; Table 2). Eight species experienced a significant increase in collection latitude: Andrena forbesii, A. imitatrix, A. miserabilis, Agapostemon sericeus, Halictus rubicundus, Lasioglossum coriaceum, L. imitatum, and Megachile montivaga. The following two species experienced a significant decrease in collection latitude: L. quebecense and Megachile brevis and six species experienced no significant change in latitude (Table 2).

Comparisons between the historical and contemporary samples of the average collection latitude of each species revealed significant differences for a third of the species found to be increasing (Welch’s T-tests, p<0.05; Table S8). The following three species experienced a significant increase in collection latitude: Lasioglossum leucozonium, L. pilosum, and Osmia pumila. The following three species experienced a significant decrease in collection latitude: Andrena dunningi, Halictus ligatus, and Lasioglossum cressonii. A total of six species experienced no significant change in latitude (Table S8).

**DISCUSSION**

This study examined changes in the wild bee community over the span of 125 years (1891-2016) and potential drivers of change to explain proportional decreases or increases of species, genera and guilds. Genus-level species analyses that proportionally compared historical (1891-1987) and contemporary (1988-2016) samples revealed 16 declining species, 18 increasing species, and 86 species that experienced no change. Wild bees have been shown to be the most effective crop
pollinators and this study found many regionally important crop pollinators in decline (Adamson et al. 2012; Garibaldi et al. 2013). Explanatory characteristics such as habitat preferences, range, lifestyle, elevation and latitude were compiled for each species that experienced significant change.

**Diversity of the Wild Bee Community and Corresponding Studies**

A main objective of this study was to document the regional biodiversity and diverse ecology of wild bees that are often underappreciated and overshadowed by a few focal species selected for managed agricultural pollination (Cane 2001). Due to small sample sizes, many rare species were not analyzed, although they warrant future study (Bartomeus et al. 2013). Nevertheless, this study is an important step towards generating regionally specific status recommendations on the northern New England wild bee community and to highlight the individual importance of these species for further regionally focused study across North America.

Bartomeus et al. (2013) used a subset of the specimens from this study as well as records covering a broad section of the northeastern U.S. and found corresponding decreases in six species: *Andrena carlini, A. erythrogaster, A. salictaria, Halictus rubicundus, Lasioglossum imitatum*, and *Megachile brevis*. Consistent increases were found in three species: *Agapostemon virescens, Halictus ligatus*, and *Lasioglossum cressonii*. Our study revealed significant proportional shifts of 25 additional species in New Hampshire. This calculation indicates the importance of historic collections and demonstrates the power of regionally specific studies to detect finer-scale changes in the wild bee community. Many of the species in this study are widespread across North America. This study provides important species status assessments for
northern New England for comparison with future detailed studies in other ecoregions that could reveal habitat specificity and individual species declines and expansions on a broader scale.

**Ground-Nesting Species**

Most bees examined in this study are ground-nesting and all but two species found to be in decline are ground nesters. Though ground nesting biology is a shared trait among these species, there is great interspecific variation in nest diameter, soil moisture and texture, and nearby resources necessary for a female to build a suitable nest within each species (O’Toole & Raw 1991; Cane 2001). Nesting sites are a potential limiting resource and the availability of suitable nesting sites have been shown to influence community composition (Potts et al. 2005; Kremen et al. 2007). Ground nesting species, in contrast with cavity nesting species, have been shown to be especially sensitive to land use change and habitat fragmentation (Kremen & Ricketts 2000; Cane et al. 2006). Bee declines have been tied to large-scale agricultural intensification in North America (Grixti et al. 2009). The scale of agriculture has changed dramatically in recent decades shifting focus to intensive mass production, which has prompted a major increase in fertilizer use (Foley et al. 2005). Nitrogenous fertilizers contribute to soil acidification in agricultural areas (Schroder et al. 2011) whereas heavy metals contamination from traffic and industry is ubiquitous in urban soils (Alloway 2013). Ground nesting bees spend an appreciable amount of time interacting with the soil and are likely to suffer consequences due to soil pollution.

Unmanaged wild bee pollinators that are vital to major commercial crop production are widespread across eastern North America. Many species identified as declining in this study are regionally important ground-nesting crop pollinators. *Andrena carlini* and *A. vicina* are known to be of importance to blueberry pollination (Tuell & Isaacs 2010; Adamson et al. 2012; Bushmann
and Drummond 2015). *Andrena carlini, A. miserabilis, A. vicina,* and *Agapostemon sericeus* are important pollinators for apple (Adamson et al. 2012; Blitzer et al. 2016). *Halictus rubicundus* and *Lasioglossum coriaceum* are important for berry pollination (Nye et al. 1974; Adamson et al. 2012). *Lasioglossum imitatum* is a major pollinator of curcurbits as well as highbush blueberries (Tuell & Isaacs 2010; Adamson et al. 2012). Given the economic importance of each of these crops and for the benefit of sustained food security, the potential consequent loss of valuable pollination services because of bee declines is alarming and warrants further investigation into the habitat necessary to sustain these important crop pollinators (Bailes et al. 2015).

There are mixed conclusions as to the influence of agriculture and other habitat disturbance on wild bee species: certain ground-nesting bees benefit from moderate human disturbance (Kremen et al. 2007), yet other ground nesters suffer habitat loss with increasing urbanization as a result of soil compaction (Kremen & Ricketts 2000). Consequently, agricultural intensification, causing a reduction in semi-natural landscapes, has been shown to shift community composition in favor of common taxa in Europe (Carré et al. 2009). Monitoring the wild bee species that have changed in proportion within the community, taking into consideration their individual biology such as nesting habit, after periods of general agricultural expansion, will be important to future studies that focus on the effects of specific types of agricultural practices on the wild bee community and habitat availability.

**Cleptoparasitic Species**

Cleptoparasitic species are particularly important as bioindicators due to their reliance on other bee species for survival (Sheffield et al. 2013). *Nomada* spp., the largest genus of cleptoparasitic bees, has been shown to decline correspondingly with host decline, which are
primarily *Andrena* species (Westrich 1996). Proportional changes in cleptoparasitic bee species could reveal changes not only in their respective host species, but in the stability and abundance of the overall bee community (Sheffield et al. 2013). A study examining an Illinois bee community over 120 years found disproportionate declines in *Nomada* species (Burkle 2013). This study found two *Nomada* species to be decreasing (*Nomada bella* and *N. depressa*) and one *Nomada* species (*N. articulata*) to be increasing. Declines in cleptoparastic species could signal ecosystem instability as they are known to be community stabilizers (Sheffield et al. 2013).

**Conservation Consideration**

Poleward latitudinal range shifts of non-migratory organisms have been documented in the northern hemisphere because of warming climates (Parmesan et al. 1999; Lenoir and Svenning 2013), which contribute to range shifts in bee communities (Kuhlmann et al. 2012). Of the bee species found to be in decline in this study, 50% showed upward latitudinal and elevational range shifts. One third of the species found to be increasing also experienced upward latitudinal range shifts over the 125-year period. Given predictions for continued climate change, continued monitoring the relocation patterns of species across regions is important. Synthesizing information on regional species lists, land use, and the ecology of pollinator communities is an essential future step to generating appropriate landscape management and conservation policy recommendations. This study exemplifies the complexity and vulnerability of the bee community within a region and provides important baseline information for future wild bee community ecology research.
### CHAPTER I TABLES AND FIGURES

**Table 1.** Declining New Hampshire wild bee species with additional characteristics.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Subgenus</th>
<th>Nesting Habit</th>
<th>Lifestyle</th>
<th>Range (Northeast)</th>
<th>Pollinator Type</th>
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<tbody>
<tr>
<td>Andrenidae</td>
<td><em>Andrena carlini</em> †</td>
<td><em>Melandrena</em></td>
<td>Ground</td>
<td>Solitary</td>
<td>Native</td>
<td>Generalist</td>
</tr>
<tr>
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<td><em>Tylandrena</em></td>
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<td>Native</td>
<td>Specialist</td>
</tr>
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<td><em>Trachandrena</em></td>
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<tr>
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<td><em>Scrapteropsis</em></td>
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<td>Solitary</td>
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<td>Generalist</td>
</tr>
<tr>
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<td><em>Larandrena</em></td>
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<td>Native</td>
<td>Generalist</td>
</tr>
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<td>Specialist</td>
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<td>Native</td>
<td>Generalist</td>
</tr>
<tr>
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<td><em>Halictus rubicundus</em> †</td>
<td><em>Halictus</em></td>
<td>Ground</td>
<td>Eusocial &amp; Solitary</td>
<td>Native</td>
<td>Generalist</td>
</tr>
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<td>Cavity/Stem</td>
<td>Solitary</td>
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</table>

† Found to be in decline in Northeast U.S. by Bartomeus et al. 2013 *(note: this study used a subset of UNHC bee specimens)*

* Associated with nesting habit, but did not construct nest
Table 2. Average elevation and latitude for declining New Hampshire wild bee species comparing historical (1891-1987) and contemporary (1988-2016) samples (elevation data found with Geoplaner V2.7).

<table>
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<td>-</td>
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<td>-19.19</td>
<td>10</td>
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† Found to be in decline in Northeast U.S. by Bartomeus et al. 2013 (note: this study used a subset of UNHC bee specimens)
* p<0.05
- data insufficient to conduct a T-test

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<tr>
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<td>165.36</td>
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<td>318.70</td>
<td>0.00</td>
<td>-9.39</td>
<td>10</td>
<td>&lt;0.001*</td>
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</table>
**Figure 1.** Map of study database specimen locations across New Hampshire, U.S.A. (generated using QGIS 2.18.13 Las Palmas)
Figure 2. Relative abundance (proportion of species within genus) of New Hampshire wild bee species found to be in decline based on significant (p<0.05) z-scores compared between historical (1891-1987) and contemporary (1988-2016) periods.
CHAPTER II:
WILD BEE PLANT-POLLINATOR NETWORK CHANGES IN NEW HAMPSHIRE OVER 125 YEARS

INTRODUCTION

Plant-pollinator networks are composed of interactions among thousands of species with individualized needs for survival. It is likely that these interactions occurring between both native and introduced flora and fauna have been impacted by changes in climate, habitat availability, and exotic species introductions. Though there is speculation in existing literature regarding the positive or negative effects of species introductions, these effects are often unquantified (Russo 2016). Rapid range expansions and accidental introductions of exotic species invite notions of competition-induced consequences for native species’ food sources and habitat availability. Though antagonism by introduced species is difficult to observe in a natural environment, what information can be parsed concerning the effects of introduced species on native species interactions is important to document as a reference point for future research.

The network of interactions between plants and their pollinators is characterized by mutualism and coevolution; by the same measure, it is a complex and fragile system. Pollination is often viewed through the lens of ecosystem services, a quantification of the beneficial services provided to humans by ecosystems (Morelli 2011). Consequently, the importance of pollination to the global crop economy was recently valued at $217 billion annually (Abrol 2012). Wild bees represent the top contributors of pollination services (Free 1993; Javorek et al. 2002; Garibaldi et al. 2013) and are believed to pollinate a majority of the 87.5% of angiosperms that are animal-
pollinated, which encompasses 308,006 species of flowering plants (Ollerton 2011). Many of these species are economically important commercial crops (Klein et al. 2007) and compose the diverse array of human foods. In the U.S. alone, wild bee pollination services were estimated to be worth $3.07 billion in 2006 (Losey & Vaughan 2006). The value today is likely to be much higher, considering the increase in pollinator-dependent crop plants over the past decade (Russo et al. 2013).

Beyond the clear economic importance of wild bee pollination lies a wealth of ecological value flowing from plant-pollinator relationships. Recent worldwide bee declines have brought attention to the stability and resistance of plant-pollinator interactions to species and habitat loss and the corresponding effects these losses may have on pollination services and consequently food security (Winfree et al. 2008; Potts et al. 2010; Brosi et al. 2013; Burkle et al. 2013). The subtleties of plant-pollinator relationships are extensive and subject to change. Wide gaps in knowledge surrounding these complex networks still exist, yet biodiversity has been shown to be fundamental to a functional plant-pollinator network (Blüthgen & Klein 2010; Winfree et al. 2018). Wild bees are a highly diverse group of pollinators, encompassing a wide range of morphologies, nesting habits, lifestyles (solitary - social) and foraging patterns (specialist - generalist). Bees forage in a variety of ways for pollen and nectar from flowering plants for food and nest provisions. Specialist bees are either monolectic (uncommon) or oligolectic pollinators that visit the same or related plants, whereas generalist bees are polylectic bees that visit many unrelated plant taxa (Michener 2000). Specialization of pollinators serves an important role in the structure and evolution of insect and plant communities, yet these specializations go far beyond the notion of linked extinction, in which case the loss of a plant species results in the loss of an animal species. Pollination interactions may be more accurately defined as well connected
“interaction webs” that experience shifts due to temporal and geographic changes (Kearns et al. 1998, Memmott et al. 2004). As ectothermic organisms, pollinators are particularly susceptible to experiencing decreased fitness as a result of temperature variation (Paaijmans et al. 2013). In order to protect these critical plant-pollinator interactions, there is an urgent need to gain a deeper understanding of the environmental circumstances affecting these wild pollinator populations and their specialized, evolutionary relationships with plant communities. Given that plant-pollinator webs are dependent on changes in the landscape, investigating the fundamental aspects that shape these networks is of great importance and must be inclusive of all regional habitats in order to evaluate geographic variation.

A 2004 study (Memmott et al. 2004) that simulated pollinator extinction from plant-pollinator networks found solitary bees to be among the most linked pollinators, and recommended they receive increased conservation attention in temperate regions. A recent long-term study of the northeastern U.S. bee community found that wild bee declines were linked ecologically to smaller diet breadth (specialists) and shorter foraging phenologies (Bartomeus et al. 2013). Recent analyses of 119 wild bee species over 125 years in New England found 16 species in decline (Chapter 1), all of which are native taxa and over half of which experienced significant range (latitude and elevation) shifts. Similarly, a study of 120 years of plant-pollinator networks in Illinois revealed a disproportionate loss of specialist bee species (Burkle et al. 2013). However, the inability to distinguish between small diet breadth and species rarity implies that species loss could be due to specialization, rarity, or both factors in combination (Burkle et al. 2013).

Identifying changes in the structure of these bipartite networks could clarify drivers of bee declines, such as competition between native and exotic flora and fauna, phenological shifts
and mismatch, pollination specialization vs. generalization, and habitat requirements. Bipartite networks are illustrative of the ecological relationships that have been formed within the plant-pollinator community and are able to highlight the strengths and vulnerabilities of individual species interactions (Memmott 1999; Olesen et al. 2008; Russo et al. 2013; Russo 2016). Relating the outcome of focal studies to comparative studies between historical and contemporary wild bee communities (Bartomeus et al. 2013; Burkle et al. 2013) has the power to illuminate connections between global temperate regions.

Northern New England is represented by a diverse assortment of plant species and habitats to support its approximately 300 wild bee species, making it an ideal location to assess plant-pollinator relations (Tucker & Rehan 2016; Jacobson et al. 2018). Using a collection of wild bee specimens with floral association records covering a period of 125 years, we evaluate structural change in the plant-pollinator network between historical and contemporary periods taking into consideration the conservation status of native wild bee and plant species that compose the plant-pollinator community. This study intends to fill knowledge gaps in our understanding of the drivers of change within plant-pollinator relationships that characterize long-term network stability or vulnerability. Here we identify plant and bee species that are critically important ecological resources to plant-pollinator networks. This study serves as an important historical assessment of the plant-pollinator networks of northern New England, which are more broadly representative of northeastern North America. The aims of this study are threefold: first, to determine the plant-pollinator network in New Hampshire over the past 125 years; second, to evaluate if changes in the network over that period could be attributed to loss of specialists, exotic species introductions, and range expansions; and third, to investigate shifts in the bee species and floral hosts of critical importance to the network.
METHODS

Bee and Plant Databases

The bee specimens evaluated in this study are housed in the University of New Hampshire Insect Collection (UNHC) and databased in the open access UNHC archives [https://unhcollection.unh.edu/database/]. The full database is composed of 17,043 non-\textit{Bombus} wild bee specimens collected between 1891-2016 and expertly identified to the species level (Mitchell 1960, 1962; Gibbs 2011; Rehan & Sheffield 2011; DiscoverLife.org). Range information was obtained from DiscoverLife and The Very Handy Manual (Droege 2015). The specimens in this database contain supporting data on taxonomy, geographic coordinates, repository information, collection method, and floral associations as available. Of the total wild bee specimens other than \textit{Bombus}, 2,497 (15\%) contained records of floral host associations and were included in analyses for this study.

Prior analyses on species-level status assessments of this northeastern North American wild bee community documented significant change in relative abundance (Chapter 1). Accordingly, each species was given a status determination of increase, decrease, or no change (stable) based on relative comparison calculations between historical (1891-1987) and contemporary (1988-2016) sample periods. As this study builds on prior species status assessments, the same time periods were used to compare the historical (1891-1987) and contemporary (1988-2016) plant-pollinator networks. These time points were determined to be the most suitable binning scheme by rarefaction and a species diversity analysis. Time periods focusing on points before and after the late 1980’s have been used in similar bee decline studies (Biesmeijer et al. 2006; Colla et al. 2008) and are additionally based on the ecological and
environmental differences that divide these periods. Neonicotinoid insecticides became commercially available in 1985 and gained widespread use shortly thereafter (Kollmeyer et al. 1999), annual temperatures reached a record high in 1987 and have since been increasing and consistently above average (NOAA 2018), invasive bee species introductions have increased dramatically in North America since the 1980s (Russo 2016), and the great majority of agricultural and urban expansion occurred within the past 30 years in our study region (USDA 2012; Sundquist and Stevens 1999).

All floral host entries were verified from original specimen labels and accompanying collection information. To ensure accuracy of the plant data, any floral associations that could be determined only to family, based on collection notes and field surveys, were excluded. Taxonomic and range information was obtained using identification keys and distribution records on The New England Wild Flower Society website [gobotany.newenglandwild.org], Flora Novae Angliae: A Manual for the Identification of Native and Naturalized Higher Vascular Plants of New England (Haines et al. 2011), the USDA PLANTS database (USDA 2018), and The Consortium of Northeastern Herbaria portal (Consortium of Northeastern Herbaria 2018). Information on the plant species of rare or imperiled status was obtained from the Native Plant Protection Act (New Hampshire Natural Heritage Bureau 2013).

**Plant-Pollinator Network Construction and Species-Level Analyses**

To evaluate change and interrelatedness in the plant-pollinator interaction network over the 125-year study period, a network analysis was conducted using the 2,497 wild bee specimens with accompanying floral data. All specimens with floral information were collected by sweep net as other trapping methods do not explicitly consider floral associations. The ‘plotweb’ function
from the bipartite package (Memmott 1999; Dormann et al. 2009) in R 3.3.2 was used to build interaction network figures for the historical (1891-1987) and contemporary (1988-2016) periods, as well as for the overall 125-year period and subsets to illustrate key groups of conservation concern. Flowering plant and bee species were used as the two sets of nodes, with connections drawn between them to evaluate the degree of assortativity, the extent to which nodes are interconnected in that network (Noldus & Mieghem 2015). The networks constitute weighted representations of the plant-pollinator interactions. Thus, the boxes representing the nodes are proportionally scaled by the abundance of unique interactions.

The function ‘networklevel’ from the bipartite package (Dormann et al. 2009) calculated measures of nestedness, weighted nestedness, and connectance for the network, all of which are considered to be markers of co-evolution (Bascompte et al. 2003; Dormann et al. 2008). Nestedness is an organized network-level structure in which species are organized by decreasing numbers of interactions in a community where 0 represents a total lack of nestedness (no co-occurrence) and 1 represents maximum nestedness (high co-occurrence) (Atmar & Patterson 1993; Bascompte et al. 2003; Dormann et al. 2009). Weighted nestedness weights the nestedness measurement by considering interaction frequency to determine species co-occurrence (Galeano et al. 2009). A plant-pollinator network would be considered highly nested if, within the entire network of plants that interact with generalist bees, a group of specialist bees interacted with a subset of those plants of the larger network (Nielsen & Bascompte 2007; Bascompte et al. 2003). Conversely, little overlap between generalist and specialist species would results in a network with low nestedness. Unlike other network measures, nestedness values are not affected by network size (Nielsen & Bascompte 2007). Connectance calculates the proportion of realized links in a network out of all conceivable links to measure community resilience to species loss.
(Dunne et al. 2002; Dormann et al. 2008, 2009). In theory, a highly connected system (connectance = 1) is less likely to suffer from individual species loss than a poorly connected system (connectance = 0) (Jordano 1987; Kearns et al. 1998).

The function ‘specieslevel’ from the bipartite package (Dormann et al. 2009) calculated degree, normalized degree, and pollinator service index (PSI) values for each individual bee and plant species within the interaction network. Degree is a measurement of species links: the unique interactions per individual species (Jordano et al. 2003; Dormann et al. 2009). In this study, the bee species degree value represents the diet breadth for each bee species as a measurement of the number of floral hosts visited by that individual species. The plant species degree value represents the number of individual bee species that visited that particular species. To calculate the normalized degree value, the degree value for each species is weighted relative to the total number of conceivable links between all species (Dormann et al. 2016; Tucker & Rehan 2016). The individual importance of each pollinator species within the entire community is measured by its pollinator service index (PSI) value. This index cannot be used to evaluate the importance of each plant species (Dormann et al. 2008). The PSI is calculated based on visitation rates of bee species to plant species and the diversity of visitors for each plant species. A PSI value of 1 indicates an individual bee species’ critical role within the network whereas a PSI value of 0 indicates a nonessential role. Bee species were categorized as specialists (oligolectic) or generalists (polylectic) based on degree measurements. Specialists were classified as having fewer than four preferred floral hosts during all collection periods whereas generalists had a diet breadth of greater than four floral hosts.
RESULTS

Plant-Pollinator Network Communities

The 2,497 plant-pollinator interactions used in this study occurred between 40 angiosperm (flowering plant) and six bee families over the 125-year period (1891-2016) and were represented by 124 flowering plant and 222 wild bee species. Of the 222 bee species in the full network, 74 (33%) interacted with only one floral host, likely as specialist pollinators, whereas 127 (57%) exhibited more generalist interactions (between 2-10 floral hosts). Only 21 generalist species (9%) interacted with 10 or more floral hosts (Table S1).

The historical plant-pollinator interaction network includes 110 unique interactions. Tracing these interactions to the contemporary period revealed an interaction loss of 94% (103/110). The loss of 30% of the (33/110) interactions is likely due to bee or plant extirpations or declines, such that neither bee nor plant species exists in the contemporary network. The other 64% (70/110) loss is attributed to mismatch between bee and plant species that both still exist in the network yet do not interact. This mismatch includes lack of spatial co-occurrence between bee and plant species, phenological mismatch, or sampling bias. The remaining 6% (7/110) of interactions were maintained from the historical period to the present (Fig. 1, Table S2).

At the community level, the nestedness measure, which is not affected by network size, was highest during the historical period (5.39), indicating the most co-occurrence between generalist and specialist bee and plant species at that time. The nestedness was lowest for the overall (2.25) and slightly higher for the contemporary (2.68) network. Connectance was lowest in the overall network (0.033), with a slightly higher value during the contemporary period (0.041) and the highest value during the historical period (0.047; Table S3).
Exotic Species Introductions and Expansions

Overall, six exotic bee species are present in the network: *Andrena wilkella*, *Hylaeus leptocephalus*, *Lasioglossum leucozonium*, *Lasioglossum zonulum*, *Anthidium oblongatum*, and *Megachile sculpturalis*. During the historical period, four interactions involving exotic bee species were recorded whereas 114 interactions involving exotic bee species were documented in the contemporary plant-pollinator network (Table S4).

The ranges of the 124 flowering plants in the network include taxa that are native (N), introduced (E), or are mixed native and introduced (N/E) such that both native and exotic species belong to a genus. Of these 124 plants, 30% (37/124) are exotic taxa, 54% (67/124) are native taxa, and 16% (20/124) are mixed native and exotic. The historical network contained 112 unique interactions (207 total interactions) that were made up of associations between wild bee species and floral hosts with the following ranges: 76% native plants (85/112), 10% exotic plants (11/112), and 14% mixed native and exotic plants (16/112). The contemporary network contained 841 unique interactions (2290 total interactions) that were made up of associations between wild bee species and plant hosts with the following ranges: 44% native plants (369/841), 40% exotic plants (333/841), and 16% mixed native and exotic plants (39/841) (Table S5).

Eight rare or imperiled native plant species are present in the interactions recorded in this study (Table 1). Six of these species have not had wild bee visitations recorded since 1990: *Eutrochium fistulosum* (Joe-Pye weed), *Nabalus boottii* (Boott’s rattlesnake root), *Solidago leiocarpa* (Cutler’s alpine goldenrod), *Diapensia lapponica* (pincushion plant), *Rhododendron lapponicum* (Lapland rosebay), and *Cypripedium parviflorum* (yellow lady’s slipper). These eight rare and endangered species were involved in 11 unique interactions that were lost between
the historical and contemporary time periods based on the museum specimen floral association data (Table S2).

**Floral Hosts of Critical Importance**

The importance of individual floral host species importance was evaluated in each network based on node measurements of diet breadth (degree) in order to identify key species to the network. Degree measures the unique diversity of visitors to a floral host. There was no overlap in the plant species revealed to be of critical importance in the historical and contemporary networks. The average historical degree of floral hosts was 2.78 (0.047 normalized degree) and the average contemporary degree was 9.16 (0.040 normalized degree) (Table S6).

During the historical period, four native plant species held the highest degree values: *Chamerion angustifolium* (narrow-leaved fireweed), *Rhus glabra* (smooth sumac), *Rhus typhina* (staghorn sumac), and *Spiraea alba* (broadleaf meadowsweet). During the contemporary period, the four highest degree values were held by all exotic plant species: *Fagopyrum esculentum* (buckwheat), *Barbarea vulgaris* (yellow-rocket), *Trifolium repens* (white clover), and *T. pratense* (red clover).

The floral genera that supported the highest wild bee diversity and abundance also changed entirely between the historical and contemporary networks. During the historical period, the highest species diversity was supported by the following four genera: *Rhus* (sumac, Native/Exotic), *Spiraea* (spirea, N/E), *Chamerion* (fireweed, N), and *Salix* (willow, N/E). Historically, the genera that received the most bee visitations were *Rhus, Salix, Solidago* (goldenrod, N), and *Chamerion* (Table S7). During the contemporary period, the following four
genera supported both the highest bee species diversity and visitor abundance: *Solidago*, *Rubus* (blackberry, N/E), *Trifolium* (clover, E), and *Fagopyrum* (buckwheat, E) (Table S7).

**Wild Bee Species of Critical Importance**

Individual species importance was evaluated in each network based on node measurements of diet breadth (degree) and pollinator service indices (PSI) in order to identify key species to the network. Degree measures the unique diversity of plant hosts visited by an individual species whereas PSI values synthesize visitation rates with the diversity of visitors for each plant species to reveal species contributing essential service to the network. Aside from *Anthidiellum notatum* as an overall key species, there was otherwise no overlap in the wild bee species revealed to be of critical importance in the historical and contemporary networks. The average historical degree of bee species was 1.95 (0.048 normalized degree) and the average contemporary degree was 3.84 (0.041 normalized degree) (Table S1).

During the historical period, degree values revealed 34 species that interacted with only one floral host as specialists. Bee species in the family Megachilidae were most well represented during this period and correspondingly had the broadest diet breadth. *Megachile brevis* interacted with six unique floral hosts, and the following three species each interacted with five floral hosts: *Coelioxys rufitarsis*, *Hoplitis producta*, and *Megachile latimanus*. *Lasioglossum quebecense* (Halictidae) interacted with the most floral hosts (seven) historically. Three of the seven historical floral host species visited by *Lasioglossum quebecense* that had no recorded interactions since 1981 are extremely rare and endangered specialized native flora (*Nabalus boottii*, *Solidago leiocarpa*, *Cypripedium parviflorum*). Seven native bee species had PSI values
of 1.0 during the historical period: *Andrena algida, Andrena w-scripta, Epeoloides pilosulus, Anthidiellum notatum, Heriades carinata, Megachile inermis*, and *Osmia virga* (Table S1).

During the contemporary period, degree values revealed a total of 81 species that interacted with only one floral host as specialists. Bee species in the Halictidae were the most well represented during this period and correspondingly had the greatest diet breadth. Of the nine bee species that had diet breadths greater than 15 unique floral hosts, *Ceratina calcarata* (Apidae) is the only species that is not part of the Halictidae. *Halictus ligatus* interacted with the most floral hosts (31), followed by *Halictus confusus* (29), *Lasioglossum versatum* (24), *Ceratina calcarata* (23) and *Agapostemon virescens* (22). Six native bee species all had the highest PSI values: *Andrena kalmiae* (1.0), *Dufourea novaeangliae* (1.0), *Anthidiellum notatum* (1.0), *Andrena ziziae* (0.83), *Macropis ciliata* (0.80), and *Halictus ligatus* (0.65) (Table S1).

**Floral Interactions of Declining Wild Bee Species**

Ten of the 16 declining wild bee species have records of floral interactions during both time periods, whereas six species did not and, thus, these six species were excluded from further analyses. In comparing the normalized degree values, which measures the diet breadth relative to all possible interactions between bee species and floral hosts, six species experienced a decrease in diet breadth (normalized degree) from the historical to contemporary periods: *Andrena erythrogaster, Agapostemon sericeus, Lasioglossum imitatum, Lasioglossum quebecense, Megachile brevis*, and *Megachile montivaga*. By contrast, four declining species experienced an increase in diet breadth: *Andrena carlini, Andrena miserabilis, Andrena vicina*, and *Halictus rubicundus*. The pollinator service indices revealed that five declining species with relatively high PSI values during the historical period experienced drastic decreases in PSI value in the
contemporary period: *Andrena carlini, Andrena miserabilis, Lasioglossum quebecense, Megachile brevis* and *Megachile montivaga* (Fig. 2, Table 2).

**DISCUSSION**

The overall changes in the plant-pollinator network revealed general network expansion, potential competition between native and exotic bee fauna for floral resources, and a substantial increase in exotic taxa over time. In recent years, the network has grown to include many exotic wild bees and plants. This network expansion has likely caused certain interactions to be lost due to host plant shifts or competition. Exotic taxa are often adaptable in unfavorable environments and invade areas opportunistically (Goulson 2003; Richards et al. 2006; Crawford et al. 2009). Exotic plants have the potential to spread quickly to extensively cover areas; yet, when given a choice, it has been shown that bee species prefer native to exotic co-occurring flora (Williams et al. 2011; Morandin & Kremen 2013). Combined with natural and anthropogenic disturbance, range expansions of exotic taxa could be a driver of network instability. A nested network is characterized by specialist interactions as a subset of generalist interactions and corresponds to stability in mutualistic networks (Bascompte et al. 2003; Valdovinos et al. 2016). In this study, the nestedness value was significantly highest for the historical network, indicating that the contemporary network will be more vulnerable to disturbance (Table S3). Related studies have similarly found that interaction networks weaken in response to current anthropogenic climate change (Memmott et al. 2007; Burkle et al. 2013). This study highlights the need for long-term data to reveal changes in the plant-pollinator community.
Effects of Specialization and Exotic Species Introductions

Two recent studies on long-term wild bee communities (Bartomeus et al. 2013; Burkle et al. 2013) found a disproportionate loss of specialist species and species with smaller diet breadths over time. In this study, we found interactions with rare and imperiled native flora were more likely to be lost with specialist pollinators than generalist pollinators. Most of these floral species are also specialized either in morphology (Asclepias tuberosa, butterfly milkweed; Cypripedium parviflorum, yellow lady’s slipper) or by alpine habitat requirements (Nabalus boottii, Boott’s rattlesnake root; Solidago leiocarpa, Cutler’s alpine goldenrod; Diapensia lapponica, pincushion plant; Rhododendron lapponicum, Lapland rosebay) (Haines et al. 2011).

Loss of generalist species has been proven to constitute dire imperilment to an interaction network (Memmott et al. 2004). Megachile brevis has not been observed in the contemporary network since 2011 and experienced a decline in both abundance and floral host interactions since the historical period. The unique floral hosts that Megachile brevis interacted with decreased from primarily native floral hosts (Chamerion angustifolium, N; Smilax ornata, E; Asclepias sp., N; Eupatorium album, N; Eutrochium fistulosum, N, Spiraea sp. N/E) to one exotic floral host (Vicia sp., E). In previous recent studies, this bee species was found to be in decline in the northeastern U.S. (Bartomeus et al. 2013) and extirpated in Illinois (Burkle et al. 2013).

The introduction of the notorious Anthidium oblongatum, an exotic megachilid with a rapidly expanding range, to the plant-pollinator network appears to have induced a host plant shift for native Anthidiellum notatum. During the historic period, Anthidiellum notatum exclusively foraged on Lotus corniculatus (birdsfoot trefoil) whereas during the contemporary period, Anthidium oblongatum was the sole visitor to this plant species. Anthidium oblongatum
was first found in the northeastern U.S. in 1994 (Hoebeke & Wheeler 1999; Maier 2009) and has been consistently linked to *Lotus corniculatus* in this region (Ascher 2001; Maier 2009). *Lotus corniculatus* was introduced to the U.S. in the 1800’s as cattle forage and was found in New England as early as 1880 (Consortium of Northeastern Herbaria 2018). Though the behavior of *Anthidium oblongatum* has not yet been well studied, its congener *Anthidium manicatum* exhibits extremely aggressive territorial behavior and is known to attack and kill intruders that attempt to visit flowers within their territory (Wirtz et al. 1988; Hicks 2011).

The range expansions and integration of exotic species is evidenced by the increase in exotic wild bee and floral hosts in network interactions. In this study, exotic bee species composed only four of the network interactions during the historical period in contrast to 114 exotic bee species interactions in the contemporary network. The historical interactions of exotic bee species occurred with native plant taxa, yet the contemporary exotic bee species interactions were dominated by exotic plant taxa (Table S2). Previous studies have similarly detected exotic bee preferences for exotic flora (Goulson 2003; Hanley & Goulson 2003; MacIvor et al. 2015). Congruent with the increased presence of exotic bee species, exotic plant taxa involved in network interactions increased dramatically between the two sampling periods with only 10% of unique interactions involving exotic floral hosts during the historical period compared with 40% of unique interactions in the contemporary period. This increase in interaction frequency for exotic plant taxa corresponded to a decrease for native plant taxa, with 76% of historical unique interactions involving native flora falling to only 44% of unique interactions during the contemporary period (Table S2). In terms of abundance, however, native plant taxa are strongly represented in the contemporary network with 60% of total interactions involving native plant taxa and 34% involving exotic plant taxa. Similarly, the most important genus to the
contemporary network is *Solidago* (goldenrod, native), comprising 19% of total contemporary interactions. *Solidago* has additionally been shown to be an incredibly important floral resource to *Bombus* species (Jacobson et al. 2018) as well as generally to the wild bee fauna of the northeastern U.S. (Ginsberg 1983; Fowler 2016).

**Conclusion and Future Research Recommendations**

Consistent future monitoring of shifts in plant-pollinator networks is of vital importance to wild bee stability and endurance. Climate change and an increase in disturbed habitat due to agricultural expansion and urbanization over the past 30 years are likely drivers of network instability and are expected to continue in the future (Tylianakis et al. 2008; La Sorte et al. 2014; Oakleaf et al. 2015). Increased habitat restoration combined with native floral enhancement of agricultural landscapes has been proven critical to wild bee biodiversity (Williams et al. 2015; Tonietto et al. 2017). The findings of this study provide additional support for focus on landscape restoration and promoting native flora plantings as a promising amelioration for the health of the wild bee community.
**CHAPTER II TABLES AND FIGURES**

**Table 1.** Rare plants of the New Hampshire wild bee plant-pollinator network. Plant conservation status obtained from NH Heritage records of the Native Plant Protection Act.

<table>
<thead>
<tr>
<th>Family</th>
<th>Flower species binomial</th>
<th>Common Name</th>
<th>Native New England (N) or Introduced (E)</th>
<th>NH Conservation Status</th>
<th>Bee Species Associations</th>
<th>Bee Abundance</th>
<th>Year of last recorded interaction</th>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td><em>Asclepias tuberosa</em></td>
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<td>N</td>
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<td>6</td>
<td>8</td>
<td>2014</td>
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<td></td>
<td><em>Eutrochium fistulosum</em></td>
<td>Joe-Pye Weed</td>
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<td>2</td>
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<td>8</td>
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<td></td>
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<td>Cutler's alpine goldenrod</td>
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<td>1981</td>
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<td>24</td>
<td>2016</td>
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<td><em>Rhododendron lapponicum</em></td>
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<td></td>
<td><em>Cypripedium parviflorum</em></td>
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<td>5</td>
<td>1981</td>
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Table 2. Species-level network statistics for declining New Hampshire wild bee species

<table>
<thead>
<tr>
<th>Family</th>
<th>Bee species binomial</th>
<th>Nesting Habit</th>
<th>Diet Breadth (Degree)</th>
<th>Diet Breadth (Normalized Degree)</th>
<th>Pollinator Service Index (PSI)</th>
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<td></td>
<td>Historical</td>
<td>Contemporary</td>
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<td>1</td>
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† Found to be in decline in Northeast U.S. by Bartomeus et al. 2013 (note: this study used a subset of UNHC bee specimens)

* Associated with nesting habit, but did not construct nest
Figure 1. The historical New Hampshire plant-pollinator interaction bipartite network showing the 112 unique interactions and their contemporary (1988-2016) presence or absence. Black lines (7/112; 6%) represent interactions that were maintained from the historical period through the present; red lines (35/112; 31%) represent interactions that were lost due to bee or plant species extirpations or declines; blue lines (70/112; 63%) represent interactions lost due to mismatch.
Figure 2. The historical (1891-1987) New Hampshire plant-pollinator interaction bipartite network for declining wild bee species and the contemporary (1988-2016) presence or absence of these interactions. Yellow lines represent interactions that were maintained from the historical period through the present and red lines represent interactions that were lost.
GENERAL CONCLUSIONS

Widespread wild bee declines have been documented globally (Bartomeus et al. 2013; Burkle et al. 2013; Goulson et al. 2015), yet the drivers of these concerning declines and species losses remain unclear. Based on the research that does exist, it appears increasingly unlikely that there is a simple cause. Climate change, chemical pesticides, competition for resources, and land use intensification all have been identified as stressors on wild bee populations and likely coalesce to create novel and multifaceted challenges (Kearns et al. 1998; vanBergen 2013; Woodcock et al. 2017). Although these factors have been identified as likely causes of bee declines, there remain wide gaps in knowledge surrounding the health and stability of wild bee communities. The individual species that comprise the regional wild bee community of northeastern North America are understudied and overshadowed by agriculturally and publicly popular bees such as the European honey bee (*Apis mellifera*) and bumble bees (*Bombus* spp.). To address and mediate these conservation challenges, it is critical that we have inclusive baseline information on individual wild bee species and their unique ecologies. Looking historically to identify long-term patterns enables us to detect community and species-level changes and illustrates fluctuations in network stability over time scales that are often obscured due to lack of long-term data. This study uses a rare long-term dataset of wild bee museum specimens from the University of New Hampshire Insect Collections (UNHC) to track species-level changes and plant-pollinator network interactions over 125 years, broken down into a historical (1891-1986) and contemporary (1987-2016) sampling period.

Based on the findings from the first chapter of this study, the contemporary wild bee community in New Hampshire comprises 16 declining species, 18 increasing species, and 86
species that experienced no significant change based on relative abundance comparisons between the historical and contemporary period. The life history and ecological characteristics of each species that experienced a significant decrease or increase were used to explain potential causes of change. These changes could not be explained by guild affiliations or particular life history traits, yet range shifts correlated closely tied with declines, with over half of the decreasing species experiencing a significant change in latitude or elevation. Corresponding with warming temperatures, these range shifts were primarily northern and upward, signaling that declining species may now be experiencing greater competition in their former ranges. A core aim of this study was to provide baseline documentation of the regional biodiversity in New Hampshire that can serve as a reference for further research. Although the diversity of wild bees is often eclipsed by focal managed species such as *Apis mellifera*, and certain species of *Bombus*, *Megachile*, and *Osmia* due to the agricultural pollination services they provide (Cane 2001), many species found to be in decline in this study are important pollinators of major crops (Adamson et al. 2012). The lack of unification through taxonomic association or behavioral characteristics that explain decline further signals the importance of species-level analysis and continued monitoring of the wild bee community in New Hampshire to track future status changes of vulnerable species identified in this study. Future work should give additional focus to landscape changes, habitat loss, and agricultural management techniques.

The second chapter of this study revealed a notable loss of interactions in the wild bee plant-pollinator network of New Hampshire between the historical and contemporary periods. The introduction and consequent expansion of exotic bee species resulted in dramatic increases of exotic species interactions in the contemporary network. Only four exotic bee interactions were present in the historical network compared with 114 in the contemporary network. Shifting
focus to the native ranges of the floral plant hosts revealed a similarly striking increase: the exotic flora of the historical network was involved in 10% of interactions, increasing to 40% in the contemporary network. These parallel increases in exotic bee fauna and flora are corroborated by findings that exotic bee species prefer exotic flora (Goulson 2003; Hanley & Goulson 2003; Macivor et al. 2014). Similarly, local parallel declines between functionally connected plants and pollinators were detected in Britain and the Netherlands (Biesmeijer et al. 2006). Many of the wild bee species that were identified in Chapter 1 to be declining experienced a decrease in diet breadth. Additionally, the rare and endangered network plant species were historically pollinated by some declining bee species and a majority did not have any interactions recorded later than 1981. The overall bee and plant species of critical importance to the network changed almost entirely, indicating an ecological shift that bears important consideration given the potential for extinction cascades as a result of biodiversity loss (Dirzo et al. 2014). The information accompanying the historical specimens of this database did not allow for a complete phenological analysis, though potential phenological mismatch between bee species and floral hosts should be investigated in future studies as previous studies have shown that changes in phenology, particularly in spring, contribute to network instability (Bartomeus et al. 2013; Burkle et al. 2013).

The findings of this study highlight long-term compositional shifts in species that comprise the wild bee community of New Hampshire in addition to the network changes of floral plant species visited by these wild bee species. Future regional monitoring will be critical to understanding the complex environmental and anthropogenic factors that drive and affect changes in the stability of these ecological communities.
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Figure S1. Rarefaction curves illustrating the species richness of the New Hampshire wild bee community sampled during historical (1891-1987) and contemporary (1988-2016) periods.
**Figure S2.** Relative abundance of wild bee genera (proportion within family) comparing a historical sample (1891-1987, light blue) and contemporary sample (1988-2016, dark blue) of the New Hampshire wild bee community.

* declining genus, p<0.05

** increasing genus, p<0.05