2018

No Farm Is An Island: Pollinators And Pollination In Agricultural Landscapes

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Recommended Citation

Nicholson, Charles C., "No Farm Is An Island: Pollinators And Pollination In Agricultural Landscapes" (2018). *Graduate College Dissertations and Theses*. 985.
https://scholarworks.uvm.edu/graddis/985

NO FARM IS AN ISLAND: POLLINATORS AND POLLINATION IN AGRICULTURAL LANDSCAPES

A Dissertation Presented

by

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to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
Specializing in Natural Resources

October, 2018

Defense Date: August 2, 2018
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ABSTRACT

Productive, resilient and sustainable agricultural systems are required to meet the immediate needs of a burgeoning human population, while avoiding ecosystem collapse. Agriculture provides food, fiber, fuels and other products for our current population of 7 billion and is still the major livelihood for 40% of people worldwide. By replacing natural habitat and employing chemical inputs, agriculture also negatively impacts biodiversity and impairs the provision of ecosystem services. This poses a challenge for agriculture as these impacted services are often those required for high yielding and high-quality crop production. Evidence is accumulating that agricultural management can safeguard biodiversity and ecosystem services while maintaining production, but critical questions remain concerning how management actions are shaped by broader landscape pattern and how these actions influence service-providing organisms across space and time.

Through a combination of observational, experimental and modeling approaches, my dissertation examines relationships between management actions, landscape pattern and service-providing organisms using crop pollination by wild bees as a model system. First, I investigate how local management and landscape pattern interact to affect pollination services and the abundance and diversity of native bees in Vermont, USA. I then use two established models of pollinator foraging to investigate whether one popular intervention, enhancing floral resources, improves crop visitation, and whether pollinator traits and landscape pattern influence this effect. Next, I use a national data set of native bee diversity to test whether habitat enhancements increase taxonomic and functional diversity of native bee communities. Finally, I investigate whether resource continuity provided by consecutively blooming crops benefits wild bee communities. These four chapters contribute ecological knowledge of plant-animal interactions in anthropogenic landscapes. My findings also provide land managers with clear information about the effects of landscape conservation and farm management on crop pollinators.

CITATIONS

Material from this dissertation has been published in the following form:

Nicholson, C.C., Koh, I., Richardson, L.L., Beauchemin, A., Ricketts, T.H.. (2017). Farm and landscape factors interact to affect the supply of pollination services. *Agriculture Ecosystems & the Environment 250*, 113–122.

Material from this dissertation has been submitted for publication to *Journal of Applied Ecology* on June, 18, 2018 in the following form:

Nicholson, C.C., Ricketts, T.H., Koh, I., Smith, H.G., Lonsdorf, E., Olsson, O.. Flowering resources distract pollinators from crops: model predictions from landscape simulations. *Journal of Applied Ecology*.

ACKNOWLEDGEMENTS

I am a lucky animal. Science is a social enterprise and I have benefitted from the advice, encouragement, warning, support, and collaboration of farmers, colleagues, friends, and loved ones. A lot of shoulders have helped lift up what is here presented and I would like to express my deepest gratitude to them.

This work would not have been possible without the cooperation of Vermont's berry growers. Helen, Melissa, Paul, Sam, John & Carol, Linda & Al, Adam, Mike, Nora, Pat, Bill, Amanda, Bill, Reggie, Nancy, thank you for letting me study where you farm.

I have had a lot of fun working with many bright and considerate students over four field seasons: Melissa Moldovan, Katie Burns, Paige Carncross, Kristian Moore (2014); Jen Hayes, Rose Watts, Ashlin Treadway (2015); Jen Hayes (redux!), Kristen Switzer, Liana Vitousek, Olivia Honigman (2016); Alex Frayer, Cassidy Motahari, Anna Clayton (2017). Swinging nets and sampling Vermont's creemees has been a joy.

I would like to gratefully acknowledge the support of the National Science Foundation Graduate Research Fellowship Program and Sustainable Agriculture Research and Education (SARE) program of the USDA National Institute of Food and Agriculture.

The community at the Gund continues to be a source of support, inspiration, and most importantly fun. I have enjoyed our conversations both in and out of the Library. You embody "other regarding preferences".

Our lab group has been a guiding force. Alicia Ellis, Jesse Gourevitch, Insu Koh, Steve Posner, Renaivo Rasolofoson, Leif Richardson, Nitin Singh, Laura Sonter, Aaron Schwartz, Keri Bryan Watson, thank you for surrounding me with great role models.

My committee members Alison Brody, Nicholas Gotelli, Jenifer Pontius each provided input, support, and encouragement along the way, for which I am grateful.

My respect for my advisor, Taylor Ricketts, goes far beyond his scientific contributions. He is a great dad, thoughtful leader, ace field biologist, and true mentor. He has contributed immensely to this work through his support and guidance.

I want to express my deep appreciation for a few non-human taxa. To the Apoidea, whom are much than just data, for valuing flowers even more than I do. And to *Coffea arabica and C. canephora*, for stimulation.

A PhD is not always fun. To friends who have helped keep the light on I say: yawp!

My love for the natural world comes from my family. From my Ma, who taught me to read a landscape. From my Da, who taught me to dare to ask. For my Sister, who taught us all to see things a little differently.

I am a human in love. Nina. This couldn't have happened without your balance. I can't wait to marry you.

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CHAPTER 1: INTRODUCTION

1.1 Background, Motivation and Scope

1.1.1 Background

Agriculture is a global driver of ecosystem change and is the Earth's largest biome (Ellis & Ramankutty, 2008). Over the last three centuries pasture and cropland area has increased five-fold to occupy a third of the globe's ice-free land (Ramankutty & Foley, 1999). This impressive global footprint is coupled with intensive practices that have expanded crop and livestock production: per capita cereal output increased by 100 kg per person between 1961 and 2014 (Ramankutty et al., 2018) and domesticated animal biomass is now 14 times greater than all other wild mammals combined (Bar-On, Phillips, & Milo, 2018). These gains in production coincide with extensive species loss (Pimm et al., 2014) and impaired ecosystem service provision (MEA, 2005). Across biomes and taxonomic groups, conversion to pasture and cropland has reduced local species richness by ~20–30% (Newbold et al., 2015). Intensive management practices and shifting human diets (i.e., greater per capita demand for meat and total calories) are the dominant force behind recent biodiversity loss (Bengtsson, Ahnström, & Weibull, 2005; Clark & Tilman, 2017; Foley et al., 2011; Matson, Parton, & Power, 1997). Managing the scale and intensity of agriculture will determine the condition of the ecosystems on which human wellbeing ultimately depends.

Ecosystem services are the functions provided by nature that improve and sustain human life (Daily, 1997). Humans value ecosystems directly for their provisioning services – goods such as food, fiber, fuel and pharmaceuticals acquired from both natural and managed landscapes. Agriculture is a major source of provisioning services, and in turn depends on other supporting (e.g., genetic diversity) and regulating services (e.g., soil retention, biological control, pollination). Regulating services such as seed dispersal, pest control, and pollination are supplied by mobile organisms that forage across habitat boundaries (Lundberg & Moberg, 2003). The flow of these services to people depends on the distribution and movement of energy, matter and other organisms (including humans) between areas of natural and anthropogenic land cover (Mitchell et al., 2015; Sonter et al., 2017). Although these services are delivered locally, understanding the flow of these services requires considering broader landscape structure (i.e., the composition and configuration of habitat patches) and the life history traits of mobile organisms providing them (Fahrig et al., 2011; Kremen et al., 2007). There is an enduring need to explore, through models and field experimentation, how land use change and agricultural management across spatiotemporal scales influences mobile organisms and the services they provide.

Pollination is an important ecosystem service provided by mobile organisms. In addition to supporting reproductive success for 88% of angiosperms (c. 308,000 species; Ollerton et al., 2011), bees, birds, bats and other animals visit and transfer pollen between flowers of crop species. Over two-thirds of global food production comes from crops dependent on animal-mediated pollination (Klein et al., 2007), including many fruits and seeds that provide nutrients essential to a balanced human diet (Eilers, Kremen, Greenleaf, Garber, & Klein, 2011) and in global regions where access to these nutrients is needed most (Ellis, Myers, & Ricketts, 2015). The demand for pollinator dependent crops is increasing, and the last five decades have seen the production of these crops surge by >300% (Aizen & Harder, 2009), accounting for most of the 30% expansion of global agricultural land over this period (Aizen, Garibaldi, Cunningham, & Klein, 2008; Garibaldi, Aizen, Klein, Cunningham, & Harder, 2011).

While agriculture is becoming increasingly dependent on pollination, pollinators are declining. An estimated 16% of vertebrate pollinators are threatened with extinction (Aslan, Zavaleta, Tershy, & Croll, 2013), and although no such listing exists for insects, regional and national assessments indicate high levels of threat, particularly for butterflies and bees (Bommarco, Lundin, Smith, & Rundlof, 2012; Van Dyck, Van Strien, Maes, & Van Swaay, 2009). Although many taxa are important for pollination (Rader et al., 2016; Ratto et al., 2018), bees are the dominant pollinator for most pollinator-dependent crops. Bees are experiencing range shifts (Kerr et al., 2015), altered physiology (Miller-Struttmann et al., 2015; Renauld, Hutchinson, Loeb, Poveda, & Connelly, 2016) and disrupted phenologies (Bartomeus et al., 2011; Høye et al., 2013; Kudo & Ida, 2013). Local and global extinctions of bees have occurred (Cameron et al., 2011; Cox & Elmqvist, 2000; Ollerton et al., 2014). In North America two species were recently listed as threatened, *Bombus terricola* and *Bombus affinis*, with the latter species critically endangered. More generally, a long term, on-going decline of bees has been established, with observed negative trends in abundance (Bommarco et al., 2012; Cameron et al., 2011), species diversity (Bartomeus et al., 2013; Biesmeijer et al., 2006; Martins, Gonçalves, & Melo, 2013), and shifts in community composition (Burkle, Marlin, & Knight, 2013; Carvalheiro et al., 2013). These declines can impair wild plant reproductive success over time (Pauw & Hawkins, 2011) and reconfigure plant-pollinator networks (Brosi & Briggs, 2013; Petanidou et al., 2008), thereby shifting the trajectory of co-evolution (Guimarães, Jordano, & Thompson, 2011).

Threats affecting both managed and wild bees are also alarming given their important role in our food systems. For some crops, wild bees are more effective than managed bees at transferring pollen on a per visit basis (Benjamin, Reilly, & Winfree, 2014; Park, Raguso, Losey, & Danforth, 2016) and can boost yields even when managed bees are present (Garibaldi et al., 2011; Gibbs et al., 2016). Interactions between wild bees and managed bees can increase crop visitation (Greenleaf & Kremen, 2006). Diverse wild bee communities also stabilize crop production by buffering against intra and inter-annual climate variability (Brittain, Kremen, & Klein, 2013; Rader et al., 2013). For these reasons, management actions that safeguard wild bees are increasingly considered in crop management plans (Garibaldi et al., 2014; Isaacs et al., 2017).

1.2.1 Motivation

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) recently assessed the status and trends of pollinators and pollination services globally (Potts et al., 2016a, 2016b). Alongside climate change, disease, invasive species and pesticides, this consortium identified land use change and management intensity as major stressors on the abundance, diversity and health of wild and managed pollinators. Potential responses to these stressors range from relatively large-scale and long-term transformative responses (e.g., changing societies’ relationship with nature) to more immediate and straightforward responses that reduce or avoid risks (e.g., maintaining pollinator habitat adjacent to crops). My dissertation focuses on the latter, and specifically examines approaches that mitigate land use change and management driven hazards to pollinators, and associated risks to human well-being.

In a recent summary of the years-long IPBES assessment, Potts et al. (2016b) identify three key approaches for safeguarding pollinators and pollination: ecological infrastructure, ecological intensification, and diversified farming (Figure 1). My dissertation directly addresses all three. The first approach, ecological infrastructure, targets land conservation towards small patches of semi-natural habitat distributed throughout agricultural landscapes (Öckinger & Smith, 2007). Protecting natural habitat in agricultural systems is known to benefit the abundance and diversity of pollinators (Kennedy et al., 2013). Ecological intensification aims to reduce reliance on agro-chemicals and other conventional inputs through the management of ecosystem services such as biocontrol, nutrient cycling and pollination (Bommarco, Kleijn, & Potts, 2013). Actions specific to wild bees include improving the availability of floral resources by establishing flower-rich field margins (i.e., habitat enhancements). The final approach, diversified farming, aims to foster beneficial biotic interactions through diversified cultivation techniques. Crop diversity is one such technique that can broaden the spatiotemporal distribution of resources both between and among years (Fahrig et al., 2011; Josefsson, Berg, Hiron, Pärt, & Eggers, 2017; Palmu, Ekroos, Hanson, Smith, & Hedlund, 2014). While not exhaustive, these three approaches offer promising strategies to mitigate the threats placed on pollinators by habitat degradation and conventional agriculture.

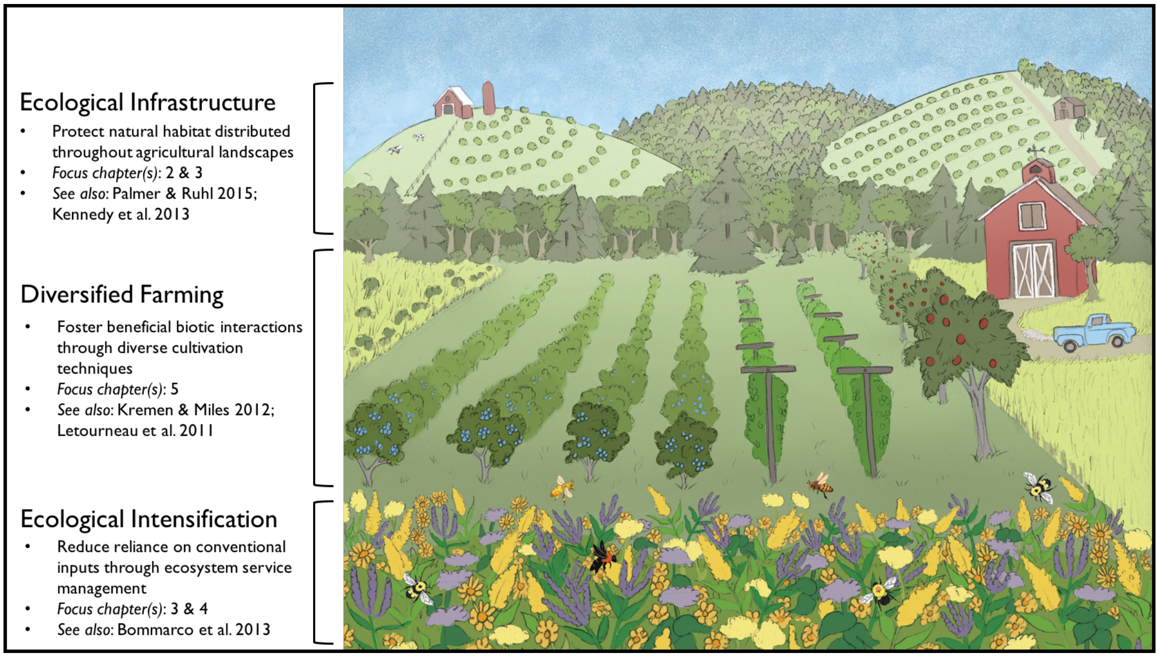

*Figure 1***.** Approaches to safeguard pollinators and pollination in agricultural ecosystems. Achieving sustainable, productive agriculture and conserving pollinator biodiversity will require three complementary approaches: (1) investing in ecological infrastructure by creating or protecting patches of (semi-)natural habitat throughout landscapes; (2) supporting diversified farming systems; and (3) ecological intensification (Potts 2016a, 2016b). Illustration by L. Vitousek.

The outcomes of these management approaches are driven by processes across spatial scales. Landscape moderation theory predicts that the effectiveness of local management, whether conventionally intense or not, depends on the quality and pattern of the surrounding landscape (Dunning, Danielson, & Pulliam, 1992; Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). Specifically, farm-scale interventions should be more effective in simple landscapes (i.e., agricultural land dominates and semi-natural habitats are isolated) than in complex landscapes (i.e., semi-natural area is abundant and connected) (Concepción et al., 2012; Tscharntke et al., 2012). This is because complex landscapes with abundant natural areas can support on-farm populations through continuous colonization (Bianchi, Booij, & Tscharnke, 2006). Complex landscapes can also moderate the impact of management by providing abundant forage and nesting opportunities, or by offering refuge from pesticide hazard (Kremen et al., 2007). Safeguarding pollinators and pollination services requires conservation at multiple spatial scales. No farm is an island and actions made locally can be reinforced by landscape planning at broader spatial scales, but critical questions remain concerning how management actions are shaped by broader landscape pattern and how these actions influence service-providing organisms across space and time.

1.3.1 Research Scope

This dissertation is organized in "paper format," with four distinct chapters each written for publication in peer-reviewed journals. In these four manuscripts, I address each of the three approaches proposed to safeguard farmland pollinators: ecological infrastructure, ecological intensification, and diversified farming. In doing so, I provide further evidence that agriculture is not anathema to conservation; that sustainable, productive farmlands can be commensurate with pollinator diversity. Collectively, these manuscripts combine observational, experimental, and modeling methods. Along the way, I strive to root findings in foundational ecological theory, while simultaneously providing information relevant to farmers and conservation scientists.

In Chapter 2 I introduce my primary study system: specialty crops grown in the spatially heterogeneous working landscape of Vermont, USA. In this context, I explore multi-scale interactions between farm management and landscape pattern. This work elaborates on a theoretical foundation of landscape ecology and my dissertation, that of landscape moderation. I use field data to show that landscapes with variable levels of ecological infrastructure (i.e., amount of natural area) moderate the impact of farms that vary in management intensiveness. I highlight the importance of interacting local and landscape drivers on patterns of wild bee biodiversity and pollination services.

Chapter 3 focuses on a popular form of ecological intensification: establishing flower-rich field margins. These ‘habitat enhancements’ hold promise, but their impacts on pollinator populations and crop pollination remain unclear. Exploring these impacts through field experimentation is challenging, but spatial models can help to develop our predictive understanding of land use change and pollination services. This chapter accomplishes two objectives: validating established pollination service models using field data and applying these models using real landscapes and simulated enhancements. My results identify the conditions under which habitat enhancements are most likely to increase pollination services.

In Chapter 4 I continue to explore the effects of habitat enhancements, focusing on their biodiversity conservation potential. Whether actions such as habitat enhancements, meant to sustain ecosystem services, also protect biodiversity broadly has been called into question, in part because services often only require a few functionally dominant species. This chapter uses biodiversity data collected from a multi-region experiment to test whether establishing pollinator habitat in agriculture increases the functional and taxonomic diversity of wild bee communities.

In Chapter 5 I expand our Vermont study system to observe wild bee communities found on farms with different levels of crop diversity. Broadly, my aim is to explore the ecological dynamics of diversified farming. Specifically, I focus on the response of pollinators at individual, population and community levels to resource continuity provided by consecutively blooming perennial crops. This work demonstrates that crop diversity may benefit pollinators by altering the spatiotemporal distribution of flowering resources.

I conclude my dissertation with a brief synthesis, pointing out not only the intellectual merit of the work, but also its broader impacts and future directions for a society that increasingly expects agriculture to feed ourselves and foster other organisms.

CHAPTER 2: FARM AND LANDSCAPE FACTORS INTERACT TO AFFECT THE SUPPLY OF POLLINATION SERVICES

2.1 Abstract

Farms can harbor substantial biodiversity, which in turn sustains the supply of ecosystem services. The effectiveness of farm management to enhance biodiversity, however, may be modified by land cover in the surrounding landscape beyond a farmer's direct control. We examined how landscape pattern and farm management affect the abundance and diversity of native bees visiting highbush blueberry in Vermont, USA. We quantified landscape pattern at multiple scales and created an agricultural intensity index that represents farm management practices such as pesticide use, mowed and grain crop area. We observed native bee visitation to assess the supply of pollination service provided to blueberry growers. Across 15 farms, 84 wild bee species were observed visiting highbush blueberry, almost a third of bee species recorded in Vermont. Visitation rate, abundance and species richness increased with the amount of natural area surrounding farms. Less intensively managed farms had higher levels of bee visitation, abundance and a more diverse bee community. Bee communities and the pollination services they provide are influenced by interactions between local management and landscape pattern. In particular, intensive farm management appears to compound the negative effects of landscape simplification. To support native pollinators on their farms, growers should consider farming approaches in the context of the broader landscape.

2.2 Introduction

Animal-mediated pollination is an important ecosystem service that regulates crop production and quality (Kennedy et al., 2013; Klatt et al., 2014). Pollinator-dependent crops contribute significantly to the global supply of micronutrients (Chaplin-Kramer et al., 2014; Ellis, Myers, & Ricketts, 2015) and are critical to agricultural economies (Klein et al., 2007). Reliance on pollinators is particularly evident in smallholder agriculture, which are susceptible to yield gaps when pollinator densities are low (Garibaldi et al., 2016).

As the demand for agricultural pollination services surges (Aizen & Harder, 2009; Koh et al., 2016), wild pollinator visitation is expected to safeguard against yield limitations (Garibaldi et al., 2013). Although European honeybees *Apis mellifera* L. are frequently employed as crop pollinators, hive failure is increasingly common and managed populations of this pollinator have declined in recent decades (Lee et al., 2015; Neumann & Carreck, 2010). Native bee communities can complement the activity of honey bees and ensure adequate pollination for many economically important crops (Benjamin, Reilly, & Winfree, 2014; Klein, 2009; Kremen, Williams, & Thorp, 2002). In many cases, native bees are more efficient pollinators because they visit a greater number of flowers per unit time and transfer more pollen per visit. For example, when compared to honeybees pollinating blueberry, native bees have greater visitation rates and deposit more pollen per flower visit (Javorek, Mackenzie, & Vander Kloet, 2002). Diverse native bee communities are also active over a range of climate (Rader, Reilly, Bartomeus, &

Winfree, 2013) and temporal scales (Bartomeus et al., 2011), and therefore provide insurance against single species loss (Winfree, Williams, Dushoff, & Kremen, 2007).

Agriculture disrupts native bee populations at multiple scales through drivers such as habitat degradation, farm management, pathogens and climate change (Goulson & Hughes, 2015; Potts et al., 2010). At broader scales, altered landscape pattern (i.e., changes in the composition and/or configuration of habitat patches) restricts the temporal and spatial distribution of foraging, nesting and overwintering sites (Kremen et al., 2007). Research into landscape pattern effects on pollinators has focused on the importance of habitat composition (i.e., the number and abundance of habitat patches), and to a lesser extent habitat configuration (i.e., the spatial arrangement of habitat patches) (Kennedy et al., 2013). As central place foragers, the amount and proximity of resource patches affects native bee populations and regulates ecosystem service supply, with crop visitation rates declining steeply as farms become more isolated from natural habitats (Ricketts et al., 2008). Changes in landscape pattern can also alter landscape-wide bee species pools, with clear benefits to crop pollination for farms situated in areas with greater extent and proximity of natural habitat (Garibaldi et al., 2011).

At local scales, differences in management can influence the delivery of pollination services to crops. Intensive practices that focus on a few crop species and their specific requirements often leads to input-intensive agriculture (e.g., fertilizer input, pesticide application, habitat simplification and decreased crop diversity) (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). Less-intensive management practices, such as organic farming or increasing crop-non-crop heterogeneity, can improve pollinator abundance and richness (Boreux, Klein, Kruess, Steffan-Dewenter, & Thies, 2013; Kennedy et al., 2013; Kremen & Miles, 2012). Management practices can impact bee communities that translate into differences in pollination services provided to crops. For example, canola seed set was on average three to six times lower on conventional and herbicide-resistant fields than in organic fields, and this reduced seed set was strongly correlated with reduced abundance of native pollinators (Morandin & Winston, 2005).

Theoretical and empirical work shows that landscape pattern and farm management often interact to influence biodiversity (Batáry, Báldi, Kleijn, & Tscharntke, 2011; Carvell et al., 2011; Concepción et al., 2012). The intermediate landscape-complexity hypothesis predicts that less-intensive farm management will have the greatest positive effect on farmland biodiversity in simple landscapes, but less so for farms in spatially complex regions, because these farms already have abundant and diverse species pools (Tscharntke et al., 2005, 2012). This pattern holds for many taxa: landscape pattern can determine how strongly farm management affects the diversity of bees (Holzschuh, Steffan-Dewenter, Kleijn, & Tscharntke, 2007), butterflies (Rundlöf, Bengtsson, & Smith, 2008) and spiders (Schmidt, Roschewitz, Thies, & Tscharntke, 2005). Recent meta-analyses have found that agri-environment practices had the greatest effect on the species richness of multiple taxa (e.g., plants, birds, herbivores, pollinators) in landscapes with low levels of intact natural area (Batáry et al., 2011; Lichtenberg et al., 2017).

The effects of management decisions on biodiversity are clearly context-dependent, but few studies have investigated the resulting effects on ecosystem services (ES). As the biophysical and social conditions by which people obtain benefits from ecosystems, these services can be quantified in terms of supply and benefit. Evaluating ES supply typically involves measuring the presence of species, ecosystems, or ecological processes that contribute to human livelihoods, whereas evaluating ES benefit also involves demand for services, as determined by social and economic factors (Mitchell et al., 2015; Villamagna, Angermeier, & Bennett, 2013). For example, crop pollination can be measured as bee visits to crop flowers (supply) or as changes in the value of crop production (benefit) (Ricketts et al., 2016). Ecosystem service supply and benefit are often related; for pollination, increased visitation is known to be associated with improved production across crops and growing regions (Garibaldi et al., 2013).

Here we use crop pollination to examine how landscape pattern interacts with farm management to affect biodiversity and the supply of an ecosystem service. We focus on wild, native bees visiting highbush blueberry (*Vaccinium corymbosum* L.) because pollination is critical to fruit production for this crop (Dogterom et al., 2000; Isaacs & Kirk, 2010). We predict that native bee biodiversity and ecosystem service supply would be affected by both farm management and habitat composition and configuration, and that these factors interact, such that less-intensive management practices would have the greatest effect in simple landscapes. Rather than classify farms into simple binary categories (e.g., organic vs. conventional), we use an agricultural intensity index to better capture realistic gradients of management strategies. We use this index, combined with landscape data and observations of native bee pollination, to explore the following questions: (i) Do native bee communities respond to differences in landscape composition and configuration, and does this alter the supply of pollination services? (ii) Does farm management influence native bee communities and associated pollination services? (iii) Is the effect of farm management on bee communities and derived pollination services dependent on landscape pattern?

2.3. Methods

2.3.1 Study System

The Champlain Valley, Vermont, USA (44.45° N, 73.09° W) is an important agricultural region due to rich alluvial soils and a growing period extended by a nearby lake. Land cover in the region is spatially heterogeneous; residential exurban areas and small-scale agriculture are interspersed with second-growth forests dominated by maple (*Acer* spp.), birch (*Betula* spp.) and beech (*Fagus grandifolia*). Agriculture in the region is a mix of pastureland and grain production, along with smaller fruit and vegetable farms. Our study system consists of 15 highbush blueberry farms. None of these farms import honeybee hives for pollination, although a few (N = 3) have hives for honey production. Blueberry acreage on these farms ranges from <0.5 ha to 3.6 ha with a median field size of 1.1 hectares.

2.3.2 Agricultural Intensity Index

We quantified differences in farm management by creating an agricultural intensity index that included measures of pesticide use, mowed area and grain crop area. To quantify pesticide use across farms, we adapted the environmental impact quotient

(Kovach, Petzoldt, Degni, & Tette, 1992) to develop a pesticide use index based on known impacts to bees. Pesticide use indices have been used with multiple arthropod taxa (Dormann et al., 2007) and this approach is well documented for native bees (Park et al., 2015). We obtained pesticide identity and use information directly from farmers for each managed crop, and if precise application rates were unknown we used the regionally suggested rates for each reported crop (New England Small Fruit Management Guide 2015-2016). We follow Park et al. (2015) by summing across all pesticides (fungicides, herbicides and insecticides) the product of the pesticide's (i) bee impact quotient (BIQ = pesticide toxicity ratings times the half-life on plant surfaces) (Kovach et al., 1992; Morse, 1989), (ii) percentage active ingredient in material sprayed and (iii) maximum application rate (quantity per acre of a given crop) (see Table A.2 for a list of pesticides recorded in this study). This provides a farm level index that is derived from a crop-specific, per-area calculation of the effects of a farm's pesticide application on bees, and thereby accounts for differences in crop area between farms. We provide measures in terms of acres, because it is the unit relevant to participating land managers. We further captured differences in agricultural intensity by quantifying the extent of grain crops (corn and soy) and mowed areas on and adjacent to study farms. These forms of land use are frequently disturbed, thereby limiting nesting sites, and offer little in terms of floral resources (Nicholson et al., unpublished data). Moreover, landscape-scale assessments report declines in native bee abundance associated with the conversion of natural habitats to row crops (Koh et al., 2016). We calculated the areal coverage of these two land uses within 300 m of each farm's blueberry crop because this scale encompasses the crop area of observed farms.

Rather than arbitrarily weight management variables based on perceived impact to bee populations, we scaled each variable from 0 to 1 and reduced these continuous variables through principle components analysis (PCA). We use the first principle component score (45% of the overall variation), scaled from 0 to 1, as our agricultural intensity index (AII) (Figure A.1**)**. While PCAs are useful for emphasizing variation and eliminating collinearity between dimensions, the resulting scores are unit-less and their biological relevance becomes abstract. We therefore compared AIIs between farms that self-reported as organic or conventional to ground truth our index. We found that our intensity index is associated with, albeit marginally, whether a farm is organic practicing (Figure A.2**;** F= 3.72, *P* = 0.08).

2.3.3 Landscape Classification

We used the 2011 National Land Cover Dataset (NLCD 2011) to quantify landscape composition and configuration within radii of 1000 m and 2000 m centered on each blueberry field. All fields in this study are at least 1 km apart. To determine landscape composition surrounding each farm, for each radius, we quantified the proportion of natural area, here defined as the combined area of wetlands, grasslands, shrub and scrublands, mixed forests, deciduous forest and evergreen forest. We also calculated landscape diversity (Shannon Index) using all land cover types for each radius for each farm as another landscape composition measurement. To obtain statistical measures of spatial configuration we used FRAGSTATS 3.4 (McGarigal & Cushman, 2002) to calculate edge density and mean patch size across all land cover types.

2.3.4 Pollinator Observations

We sampled bees on farms over three summers (2013-2015). Although we visited the majority of farms each year (N = 11), two farms were sampled for a single year and two farms were sampled during two consecutive years (2014-2015). In each year, we visited each farm at least three times during the bloom period (May to June) to observe bee visitation, abundance and diversity. To standardize pollinator activity observations, we sampled between 09:30 and 14:00 h, under favorable conditions (clear to hazy skies, temperature above 15°C, and wind speeds less than 3 m/s).

During each farm visit, we randomly selected two observation bushes at two sites: one site at the blueberry crop edge ("edge sites") and another 50 m from the edge ("interior sites"). To assess farm level pollinator visitation rate and abundance, we performed 10-minute observations at each bush (total of 40 minutes of observation per visit per farm). Observers established a 1-m^3 area and recorded all pollinators making legitimate visits to flowers, here defined as an insect landing on a flower and collecting resources from it. For each 10-minute period, we recorded the number of individuals visiting blueberry flowers to quantify abundance and the number of flowers visited by each individual to quantify visitation rate. During observations, we assigned flower visitors to eight morphospecies groups: *honey bee, Bombus queens, Bombus workers, big black bee, slender black bee, tiny black bee, green bee,* and *other bee*.

Following each observation period, we sampled pollinator diversity via 10-minute aerial netting along one 20-bush transect at each site. Data collectors walked at an even pace collecting flower-visiting bees by hand net, stopping time to process specimens. Within each year, data collectors were rotated among farms and at sites within farms. Transect walks provided bee species richness data, while observations measured bee abundance and the potential supply of pollination services.

2.3.5 Specimen Identification and Richness Estimation

We identified all collected specimens to species using published and online guides (see Supporting Information for identification references). We assigned specimens collected during transect walks to morphospecies groups to illustrate the species composition of each group (Figure 1; Table A.3).

We use our specimen data to estimate species richness as an index of per farm bee diversity using rarefaction methods (Colwell et al., 2012). This approach is recommended because it corrects for bias due to sampling effort and species' rarity by estimating and adding the number of undetected species (Colwell, Chang, & Chang, 2004). We calculated asymptotic species richness estimators using an incidence-based rarefaction method with the iNEXT software (Chao, Chiu, & Jost, 2014; Hsieh, Ma, & Chao, 2016). We constructed bootstrapped 95% confidence intervals and standard errors for estimated species richness of all farms (Figure A.3).

2.3.6 Weather and Other Covariates

During each farm visit, we collected data on abiotic covariates including time of observation, temperature, average wind speed and relative humidity. Crop features may also influence bee activity. To account for difference in floral resource availability among farms we recorded the phenological stage of blueberry bloom on a 0-3 scale depending on the relative proportion of senescent flowers. We also assessed the abundance of other flowering plants within a 10 m radius around the observation point. To account for differences in potential bee nesting sites among farms we recorded the proportion of bare ground beneath crop rows, as well as inter-row vegetative state (e.g., tall grass, mowed grass or bare ground).

We found no relationship between native bee visitation rate, abundance or diversity and measured covariates that varied within sites by date (time, temperature, wind speed, blueberry flower density, weed flower density) in single least squares regression ($P > 0.05$). Within the sampled fields, native bee visitation rate did not differ between field edge and interior sites ($F= 0.11$, $P = 0.74$), so we averaged bee activity data for each farm within each year.

2.3.7 Statistical Analysis

We used linear mixed effects models to analyze the effect of landscape composition and configuration, farm management and their interaction on average native bee visitation rate, abundance and diversity. We included year as a random effect in all models. For each main model, we constructed a null model with all fixed effects variables removed and compared AIC values between the two models. As a goodness-of-fit measure we calculated a log likelihood ratio test between fitted and null models (McFadden, 1974).

Pollinators are known to differ in their efficiency in depositing pollen (Ne'eman et al., 2010). To test whether different pollination efficiencies affect our results, we follow Isaacs and Kirk (2010) and scale morphospecies visits according to their reported average per visit pollen deposition for blueberry (Benjamin et al., 2014; Javorek et al., 2002) (Table A.1). We then calculate total per farm pollen deposition as the sum of expected pollen grains deposited across native morphospecies (i.e., excluding *Apis*) within each year. Our most active morphospecies groups were also effective at transferring pollen (Figure 1; Figure A.4; Table A.1), as such visitation rate and total pollen deposition are strongly correlated ($r^2 = 0.87$, $P < 0.001$) and for simplicity we report results for only visitation rate.

For predicting species richness we took into account the uncertainty associated with each farm's asymptotic richness estimation. We used the same model structure as above but with a weighted regression in which richness slope estimates are weighted by the inverse of their standard error. This variance is a function of sample coverage and this technique further accounts for differences in sampling effort among the farms (Pelini et al., 2014). To better understand the importance of the specific land cover classes that compose our natural area classification, we used the same model structure as above to relate visitation, abundance and estimated species richness with each land cover class separately.

We tested the effects of farm management by modeling visitation, abundance, and estimated species richness using linear mixed effects models with the AII as a fixed effect and year as a random effect. To examine the interaction between landscape pattern and farm management we first identified the most explanatory scale by regressing all response variables against the proportion of natural areas at both scales. We compared the resulting r^2 values, and used the scale with the highest r^2 value in all subsequent analyses (Holland, Bert, & Fahrig, 2004). Critically, we tested for collinearity between our AII and proportion natural area before testing for significant interactions between them. We found that agricultural intensity and proportion natural area were not related ($|r| = 0.40$, $P = 0.144$). In addition, to avoid the potential problem of multicollinearity between main effects and interaction terms, we mean centered main predictor variables, which has been suggested as a solution of reducing multicollinearity without altering regression slopes or hypothesis tests (Jaccard, Wan, & Turrisi,1990; Quinn & Keough, 2002). We log-transformed all response variables to meet assumptions of normality and homoscedasticity and performed all statistical analyses in R v.3.2.2 (R Development core Team 2015) using packages 'lme4', 'lmerTest' and 'MuMin'.

2.4 Results

2.4.1 Blueberry-Visiting Bee Community

From 1,831 collected specimens we identified 84 bee species belonging to 14 genera (Figure 1) that were actively visiting blueberry fields during bloom. The most species rich genera were *Andrena* (28 species), *Lasioglossum* (22 species) and *Bombus* (10 species). The four most common species (*B. impatiens*, *B. bimaculatus*, *A. vicina* and *A. carlini*) accounted for 55% of collected specimens (Figure 1). We focused collection on native species, so we omit a few collected specimens of two non-native species (*Apis mellifera* and *Osmia cornifrons*) from diversity analyses. Sample-based extrapolation of specimen data provided asymptotic richness estimators for each farm for each year (range: 4.13 ± 0.44 – 131.00 ± 118.62 [range estimate ± standard error]). Estimated species richness was strongly correlated with observed species richness across farms (Pearson's r = 0.77, n = 39, $P < 0.001$).

From 118 observation hours we recorded 15,270 floral visits by 3,262 individual native bees. Disaggregating by morphospecies and using our specimen records to understand the species composition of each group, we observed 9,252 flower visits by *Bombus* queens (10 species inclusive), 1,285 by *Bombus* workers (5 spp.), 2,783 by *big black bees* (10 spp.), 1,155 by *slender black bees* (27 spp.), 480 by *tiny black bees* (27 spp.), 162 by *green bees* (6 spp.) and 153 by *other bees* (8 spp.) (Figure 1 & Table A.3). With 1,444 visits, honeybees made up a relatively small proportion of visits (9%). Native bee visitation rate (21.60 ± 1.07 flower visits per 10-minute sample) and abundance (4.61 ± 0.19 individuals per 10-minute sample) were much greater than honeybee visitation rate (2.04 ± 1.10) and abundance (0.62 ± 0.07) (visitation: d.f. = 74, t = 10.56, $P < 0.001$; abundance: d.f. = 74, t = 10.19, $P < 0.0001$).

2.4.2 Landscape Pattern

We found that native bee communities responded consistently to landscape pattern at the larger spatial scale (Figure 2 & Table A.4), and bee visitation rate ($r^2 = 0.51$, $P < 0.001$), abundance ($r^2 = 0.55$, $P < 0.001$) and estimated species richness ($r^2 = 0.31$, $P < 0.001$) increased with the proportion of natural area at this scale. Landscape diversity had no effect on visitation rates or abundance at either scale, but estimated species richness was positively related to landscape diversity at the larger scale (Table

A.4; 1000 m: $r^2 = 0.02$, P = 0.365; 2000 m: $r^2 = 0.14$, $P = 0.016$). When examining natural land cover classes individually, we consistently found that visitation rate, abundance and species richness are positively related to deciduous and mixed forest types at both scales, whereas the direction and significance of other land cover classes varied (Figure A.5). Landscape configuration variables (edge density and average patch area) were not significantly related to bee visitation rate, abundance or estimated species richness (Table A.5). Based on a high degree of explained variance, the proportion natural area at the 2000 m scale was used for all remaining analyses.

2.4.3 Farm Management

Native bee visitation ($r^2 = 0.19$, P = 0.004), abundance ($r^2 = 0.16$, P = 0.011) and species richness ($r^2 = 0.14$, P = 0.018) declined with increasing agricultural intensity (Figure 3 & Table A.6).

2.4.4 Landscape Moderated Effects of Farm Management

We found a significant interaction between our AII and proportion natural area on visitation rate (7.44 ± 2.29 (interaction slope estimate ± standard error), t = 3.25, $P = 0.002$), native bee abundance (3.42 ± 1.51, t = 2.26, $P = 0.030$) and estimated species richness (6.166 ± 2.15, t = 2.86, $P = 0.007$) (Table A.7). We did not find collinearity between the centered variables and their interactions in multiple linear regression models (all $|r| < 0.5$). We visualize this interaction as a surface of predicted visitation, abundance and richness values bounded by a convex hull containing all observed combinations of proportion natural area and AII (Figure 4). We did not find a significant interaction between farm management and landscape diversity or the two configuration measures, edge density and average patch size (Table A.8).

2.5 Discussion

At least 84 species of wild bees visit highbush blueberry flowers on Vermont farms, representing almost a third of the state's recorded bee fauna (J. Ascher, unpublished data). Bee diversity, abundance and visitation were higher on farms where less intensive practices were employed, and were positively correlated with proportion of natural area in the surrounding landscape. Moreover, farm management and landscape pattern interact such that the negative effects of intensive agriculture on native bee communities are compounded by landscape simplification.

2.5.1 Landscape Effects on Native Bee Communities

We found that landscape composition had a significant effect on native bee communities and derived pollination services, whereas landscape configuration did not. Landscapes with more natural area support robust bee populations because these areas provide access to floral resources, as well as nesting substrates and materials (Williams & Kremen, 2007). Previous studies of bees have found that the amount of natural area surrounding focal sites supports abundant and stable of pollinator communities (Cusser, Neff, & Jha, 2016; Garibaldi et al., 2011; Kremen et al., 2002). We also found that the diversity of native bees is positively related to landscape heterogeneity at large spatial scales. Habitat diversity provides variety in forage and nesting sites and wild bees have been shown to prefer patches surrounded by a multiple habitat types (Hirsch, Pfaff, & Wolters, 2003). Our results bolster the evidence for a predictive relationship between the extent of natural areas and the supply of pollination services (Garibaldi et al., 2011, and references therein).

Aggregating land cover classes is common practice (Greenleaf & Kremen, 2006; Holzschuh, Dudenhöffer, & Tscharntke, 2012; Klein et al., 2012), yet specific classes can influence native bee communities differently. For instance, we found that the coverage of mixed or deciduous forests is a strong predictor of native bee visitation and diversity (Fig. A.5), because these areas offer abundant nesting substrates (Kremen et al., 2007; Watson, Wolf, & Ascher, 2011). While summarizing land cover illustrates how large-scale landscape patterns influence native bee communities, identifying specific land cover classes can help managers understand what aspects of their landscapes support pollinator populations.

Beyond landscape composition, the effects of habitat alteration are often the result of landscape configuration: the size, juxtaposition and orientation of landscape elements. Our analyses of configuration metrics did not reveal any significant relationship between native bee communities and average patch size or edge density. Our results suggest that bees are not responding to edge density at the landscape level, and patchy landscapes with more habitat edges do not factor significantly into predicting bee activity or diversity.

2.5.2 Farm Management Effects on Native Bee Communities

Few studies have assessed differences in ecosystem service between farms that vary in management intensity, and the evidence for effects of management actions on pollination services is wanting (Kremen & Miles, 2012; Winqvist, Ahnstrom, &

Bengtsson, 2012). We quantified the supply of pollination services and found that farm management had a significant effect on both the biodiversity of native bees and flower visitation rate. Our agricultural intensity index is useful because it characterizes farm management as a continuous gradient and allows for a more quantitative examination of management intensity (Mas & Dietsch, 2003). Constricting farms to binary categories (e.g., organic vs. conventional) has been criticized (Puech et al., 2014), and composite indices can provide a convenient single measure of agricultural intensity and better characterize local management heterogeneity (Hendrickx et al., 2007; Herzog et al., 2006; Le Féon et al., 2010). Although our measures of pesticide use were farm and crop-specific, we recognize that other management practices likely vary between crops. Additionally, our intensity index provides only a static, early-season snapshot of a farm's management, when in fact management intensity is likely to vary across a growing season as new crops emerge and different practices employed. Future development of continuous management gradients could benefit from considering a suite of crop-specific processes and tracking changes in management intensity over time.

The beneficial effects of less intensive farming for pollinating insects arise from reduced agrochemical use and increased area of resource rich ruderal habitats. Pesticide application directly affects native bees via lethal exposure to insecticides or fungicides (Johnson, 2015) or indirectly by herbicides altering local habitat quality. Less intensive farming practices lead to greater plant diversity in and around farmland habitats (Roschewitz, Gabriel, Tscharntke, & Thies 2005; Winqvist et al., 2011) and these local floral resources can support larger, more diverse local native pollinator populations

(Krauss, Steffan-Dewenter, Muller, & Tscharntke, 2005). Farm management differences can also impact community structure: higher floral abundance and diversity on less intensive farms are linked to larger bee populations, but also larger and more robust insect-flower interaction networks (Power & Stout, 2011). Yet, several studies have found an absence of biodiversity benefits from less intensive farming (Clough, Kruess, Kleijn, & Tscharntke, 2005; Ekroos, Piha, & Tiainen, 2008; Purtauf et al., 2005). These contrasting effects of farm management may be due in part to the crucial mediating role of landscape pattern in determining biodiversity and ecosystem service (Bengtsson, Ahnström, & Weibull, 2005).

2.5.3 Landscape Moderated Effects of Farm Management on Bee Communities

Farm management and landscape composition combined to influence on-farm native bee diversity and ecosystem service supply. Bee communities on more intensive farms in areas with little natural area are less abundant and diverse compared to areas with abundant natural areas. The capacity of natural areas within the broader landscape to buffer the negative effects of farm management may be attributed to more abundant resources or refuge from pesticide exposure. Natural areas provide greater forage and nesting opportunities, allowing for greater population sizes and more diverse species assemblages. In our system, deciduous forest coverage is a strong predictor of native bee communities (Figure A.5), resources found in this habitat type are important for early spring pollinators such as those that frequent blueberry (Watson et al., 2011). These same natural areas may also provide refuge from pesticide exposure, an effect of landscape pattern that has been observed for the natural enemies of agricultural pests (Landis, Wratten, & Gurr, 2000).

Previous studies have shown interacting effects of farm management and landscape pattern on biodiversity of bees and other taxa (Dormann et al., 2007; Holzschuh et al., 2007; Roschewitz et al., 2005), but few studies demonstrate a similar interacting pattern for resulting ecosystem services. While theory predicts that biodiversity will be linked to ecosystem service supply (Cardinale et al., 2012), the evidence for this link is conditional on spatial scale and ecosystem service measurement approaches (Ricketts et al., 2016). We show that differences in the supply of an important agricultural ES, crop pollination, depend on the combined effect of landscape composition and farm management.

Our measure of pollination supply (i.e. bee visits flower^{-1} time^{-1}), is used frequently (Carvalheiro, Seymour, Veldtman, & Nicolson 2010; Klein et al., 2012; Nielsen, Reitan, Rinvoll, & Brysting, 2017; Winfree et al., 2008) but does not capture actual pollen deposition on stigmas or plant reproductive success. Pollinators can differ in the amount of pollen they transfer in a single visit (Cane & Schiffhauer, 2003), and sonicating taxa in particular are expected to pollinate blueberry effectively. In our case, the morphospecies group with the highest visitation rates (*Bombus* spp.) is also known to be an effective pollen vector in blueberry (Benjamin et al., 2014; Javorek et al., 2002; Scott, Ginsberg, & Alm, 2016) (Figure A.4, Table A.3), reinforcing their important role in this system. Compared to other blueberry systems (Blaauw & Isaacs, 2014; Isaacs & Kirk, 2010), Vermont blueberries are pollinated predominantly by a wild community of bees. This allows for clearer interpretation of their ecological role, but we also recognize that our findings may not hold for systems dominated by managed pollinators.

Similar research in California almond orchards has demonstrated that organic management increased pollinator visitation rate, but flower visitation was only enhanced by organic farming when orchards were surrounded by at least 10% natural habitat (Klein et al., 2012). Here we show that the negative effects of intensive management are strongest in landscapes with <50% natural area (Figure 4). Interestingly, as the amount of natural area increases, visitation, abundance and species richness continue to increase, despite agricultural intensity. A similar effect was observed in New York apple orchards: predicted bee abundance and richness were highest where the proportion of natural areas was greatest and pesticide use was most intense (Park et al., 2015). In landscapes with expansive natural areas, levels of organism immigration will be high (Bianchi, Booij, & Tscharntke, 2006; Ricketts et al., 2008) and the effects of farm management may be crowded out by increased immigration and dispersal success (Hanski, 2011; Pickett & Thompson, 1978; Tscharntke et al., 2005). A corollary of this effect, is that extensive natural areas can buffer the effect of local disturbances, including more intensive agriculture, through landscape compensation (Tscharntke et al., 2005).

Our results provide support for the intermediate landscape-complexity hypothesis (Tscharntke et al., 2012), which predicts that the effects of less intensive management will be strongest in structurally simple (1-20% natural habitat) rather than in cleared (<1% non-crop habitat) or complex (>30% natural habitat) agricultural landscapes. Yet, according to this categorization, our sites are predominately situated in ‘complex’ landscapes, and the proportion of natural habitat at the 2 km scale (range: 29-86%) is high compared to other study systems: 8-60% (Winfree et al., 2008), 0-62% (Kremen et al., 2004), 1-28% (Steffan-Dewenter et al., 2002). These simple categories of landscape complexity have two limitations. First, they were derived from studies in central Europe, and may not hold for other biomes or regions. Second, they do not emphasize the analogous nature of this dynamic across a range of landscape complexity, albeit with varying magnitude in response. Intermediate landscape complexity is relative and our results provide evidence that the response of pollinator communities to landscape pattern, given differing levels of agricultural intensity, is a continuous relationship even at the upper bounds of landscape complexity.

2.6 Conclusions

Conservation planning requires action at multiple spatial scales. Our results suggest that management actions taken at the farm scale can be reinforced by landscape planning at broader spatial scales. In landscapes with extensive natural area, bee biodiversity and pollination service levels are high irrespective of agricultural intensity, and under these conditions preservation of natural areas is a priority. Conversely, in landscapes with less natural area, we can expect that local farm management, such as organic practices, could benefit biodiversity and ecosystem service. Our results demonstrate the ecological tradeoffs inherent when farm management is context dependent and bolster calls for cross-scale landscape design in agroecosystems (Landis, 2017). We do not quantify the realized benefit (e.g., improved yield) or costs of supporting pollinator populations in agriculture. The cost to farmers of converting to less intensive farming practices, or the opportunity costs of not intensifying, will vary depending on farm size, climate, soil characteristics and crop types. Future research should strive to integrate ecological and economic tradeoffs of landscape-dependent farm management. The challenge of ensuring food security, while simultaneously sustaining populations of service-providing organisms, will necessarily combine landscape planning and farm management.

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2.8 Figures

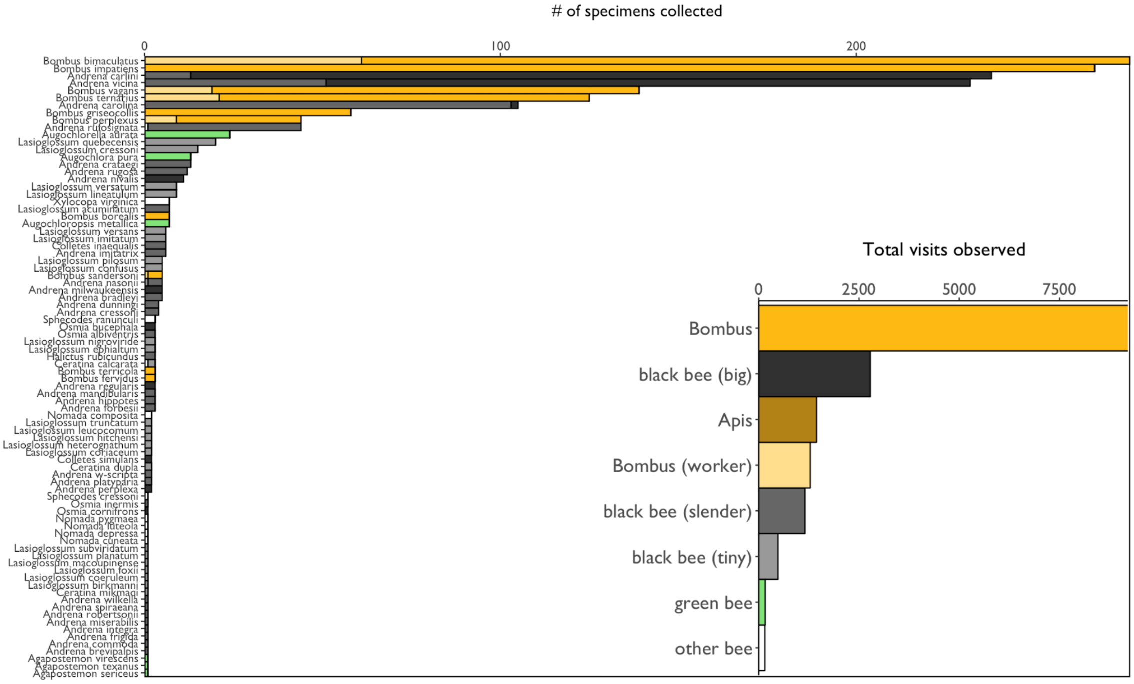

Figure 2.1. Rank-abundance plot for species collected. Inset depicts the total floral visits of eight morphospecies observed. To provide information on the species composition of morphospecies groups, the rank abundance plot is color coded according to inset. Some species belong to more than one morphospecies due to caste and sex morphological differences. Non-native species are omitted from the rank abundance plot (see Table A.3 for more information).

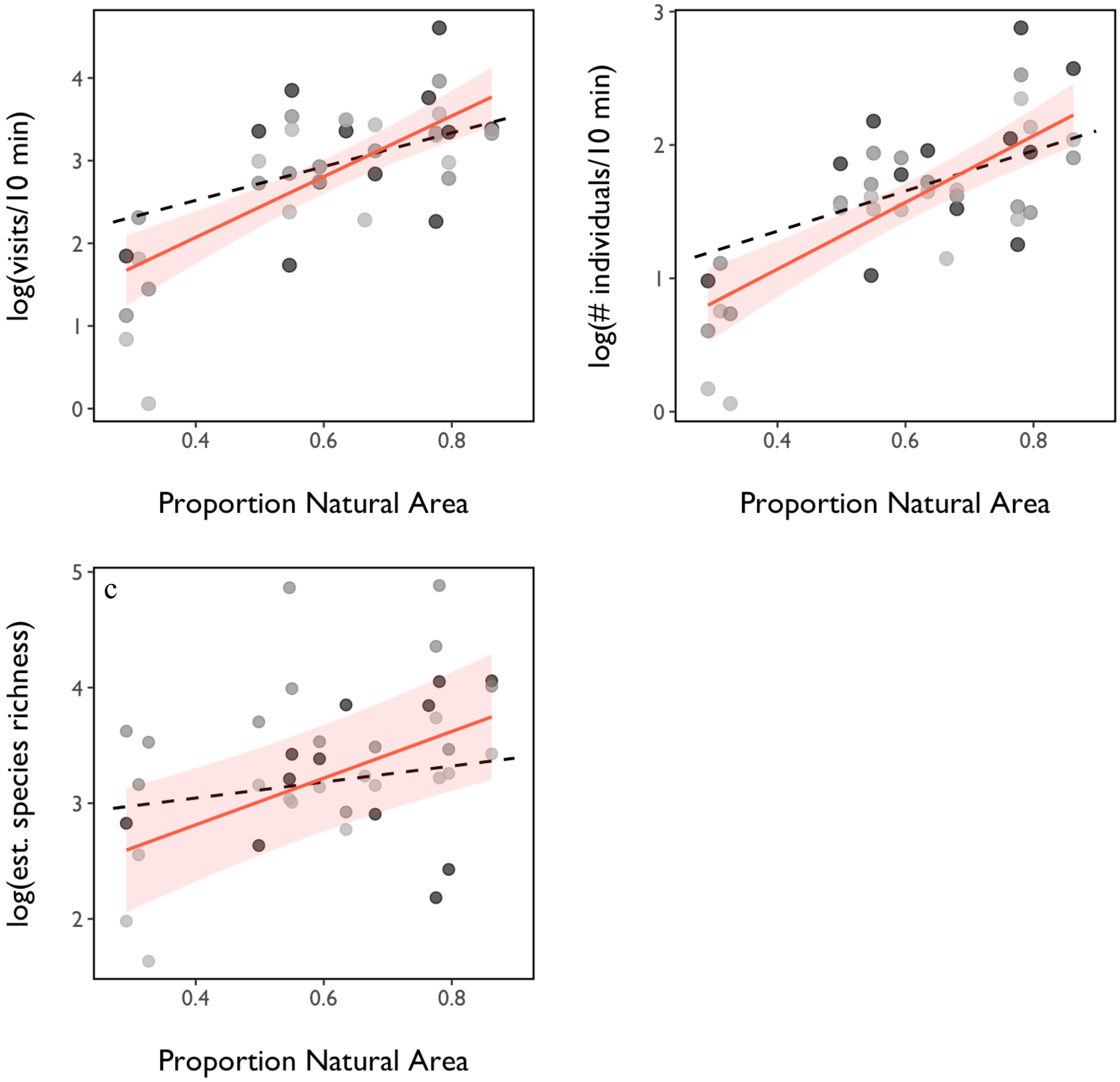

Figure 2.2. Effect of proportion natural area on native bee (a) visitation rate (b) abundance and (c) species richness. Points and model fit with 95% confidence intervals for the amount of natural area at the 2000 m scale shown for each of three sampling years (red line and shading). Model fit (black dashed line) for 1000m scale is also depicted (points not shown). Results are from mixed effects models with year as a random effect.

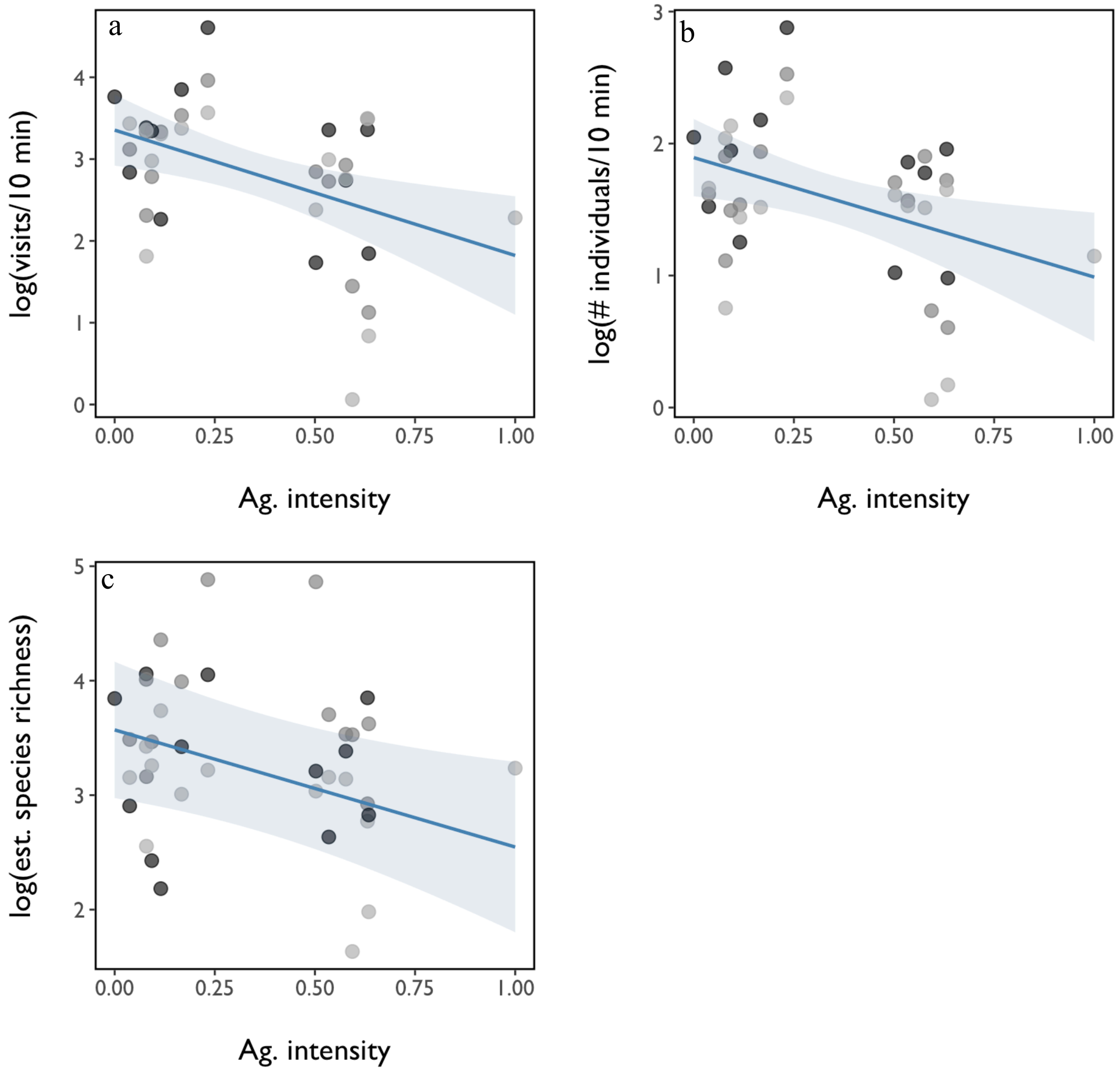

Figure 2.3. Effect of agricultural intensity on native bee (a) visitation rate (b) abundance and (c) species richness. Points and model fit with 95% confidence intervals shown for each of three sampling years (blue line and shading). Results are from mixed effects models with year as a random effect.

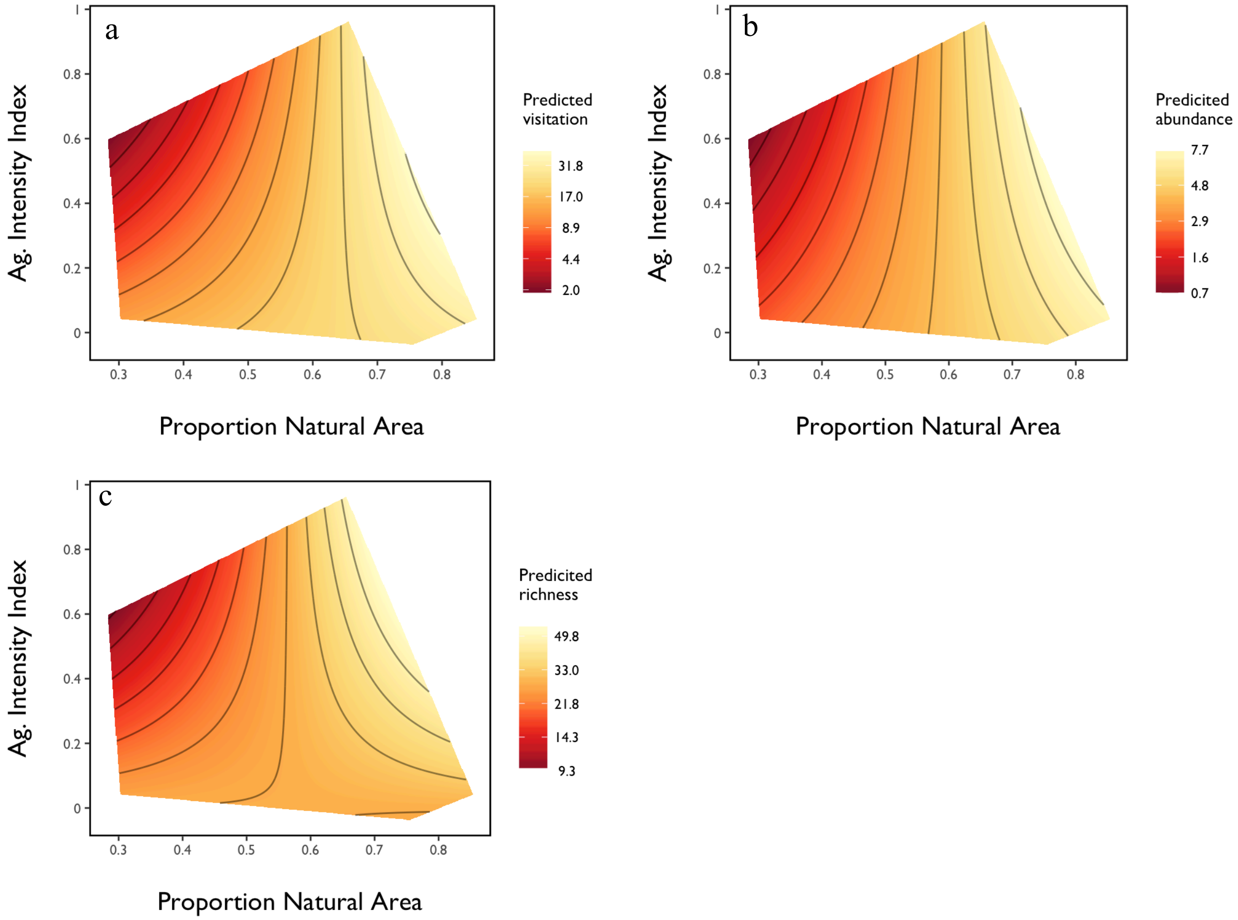

Figure 2.4. Response of native bee (a) visitation, (b) abundance and (c) estimated species richness to the interaction of agricultural intensity and the amount of natural area within 2000 m of farm sites. Data are fitted values derived from final mixed effects models and log-transformed. Contour lines indicates areas of similarity. The convex hull delimits the sample space to the range of parameter combinations assessed in our study.

2.9 Appendix – Supplementary Tables and Figures

Table A.1 Average pollen deposition (pollen grains with pollen tubes per stigma) from studies of bees visiting blueberry.

Morphospecies group	Mean Pollen deposition	Reference	Species observed in studies
Apis	11.7	Javorek et al., 2002	*Apis mellifera*
Bombus	41.1	Javorek et al., 2002; Benjamin et al., 2014	*Bombus bimaculatus, B. griseocollis, B. impatiens, B. perplexus, B. ternarius , B. terricola , B. vagans*
Worker Bombus	34.3	Javorek et al., 2002	*B. ternarius, B. terricola*
Big Black	27.4	Javorek et al., 2002; Benjamin et al., 2014	*Andrena vicina, A. carlini, Colletes inaequalis, C. thoracicus, C. validus*
Slender black	24.8	Javorek et al., 2002; Benjamin et al., 2014	*Andrena banksi, A. barbara, A. bradeyi, A. carolina, A. cressonii, A. fenningeri, A. ilicis, A. imitatrix, A. mandibularis, A. morrisonella, A. screpteropsis*
Tiny Black	17.6	Benjamin et al., 2014	*Ceratina calcarata, Halictus rubicundus, H. confusus, Lasioglossum acuminatum, L. coeruleum, L. fuscipenne, L. leucocomum, L. oblongum, L. pilosum, L. versatum, L. weemsi, L. zephyrum*
green	17.6	Benjamin et al., 2014	*Augochlora pura, Augochlorella aurata*

Table A.2 List of insecticides (I), herbicide (H), and fungicides (F) applied across farms. Pesticide application rate ranges are for the entire study and derived from suggested application rates from extension documents and pesticide labels. The bee impact quotient (BIQ) is a relative impact score based on honey bee toxicity and plant surface half-life of a pesticide (Morse 1989, Kovach et al. 1992, Park et al. 2015). The toxicity of adjuvants and penetrants on bees is largely unknown and are not included in index calculations and are not shown.

Classification	Active ingredient	Trade name(s)	Min rate (lb or L/A)	Max rate (lb or L/A)	BIQ
I	bifenthrin	Brigade	0.189	0.946	28.5
I	carbaryl	Carbaryl, Sevin XLR	4.170	4.170	15
I	imidacloprid	Prey 1.6	0.088	0.240	28.5
I	malathion	Malathion	1.421	1.705	15
I	methomyl	Lannate	0.500	1.000	15
I	permethrin	Permethrin	0.059	0.118	15
I	phosmet	Imidan	1.300	1.300	28.5
I	pyrethrin	pyganic	0.133	0.532	28.5
I	spinetoram	Delegate	0.088	0.177	18.81
H	clethodim	Intensity	0.177	0.240	9
H	glyphosphate	Roundup	1.136	5.682	9
H	metribuzin	Metribusin	1.300	2.600	9
H	Paraquat dichloride	Gramaxone	1.137	2.273	6.3
H	pendimethalin	Prowl	5.450	5.450	9
H	terbacil	Sinbar	0.060	0.177	9
F	captan	Captec, Captan	0.852	1.136	3
F	copper hydroxide	Kocide	0.750	1.750	9.3
F	copper oxychloride & copper hydroxide	Badge	1.137	2.273	9.3
F	copper sulfate	Cuprofix Ultra40	2.000	4.000	9.3
F	fenhexamid	Elevate	1.500	1.500	3
F	metiram	Polyram	3.000	4.500	9.3
F	Phosphoric acid	Rampart	1.136	3.409	3
F	pyraclostrobin & boscalid	Pristine	0.550	0.680	9.3
F	thiophanate-methyl	Topsin-M	0.240	0.240	9.3
F	triforine	Funginex	1.700	3.000	9.3

Table A.3 Species list of collected bees and corresponding morphospecies groups. During bush observation bees were assigned to species groups on the wing. Collected specimens were identified to species and morphospecies. Totals given for 'observed' and 'collected are for morphospecies groups. Whether a species has been reported to sonicate, along with referencing literature, is provided (see Sonication References for complete citations).

Morphospecies	Species collected	Individuals observed	Individuals netted	Known to sonicate	Reference
Bombus		1474	997		
	Bombus bimaculatus Cresson			x	Macior 1964; Larson & Barrett 1999
	Bombus borealis Kirby				
	Bombus fervidus Fabricius				
	Bombus griseocollis DeGeer			x	Macior 1964; Cane & Payne 1988
	Bombus impatiens Cresson			x	Macior 1964; Cane & Payne 1988; Sampson 1993
	Bombus perplexus Cresson			x	Sampson 1993
	Bombus sandersoni Franklin				
	Bombus ternarius Cockerell			x	Heinrich 1976; Sampson 1993; Larson & Barrett 1999
	Bombus terricola Kirby			x	Sampson 1993; Batra 1993; Larson & Barrett 1999
	Bombus vagans Smith			x	Macior 1964; Sampson 1993; Wilson & Stine 1996; Richardson & Irwin 2015
Black bee (big)		879	435		

			Andrena carlini Cockerell	x	Sampson 1993
			Andrena carolina Viereck	x	Sampson 1993
			Andrena milwaukeensis Graenicher		
			Andrena nivalis Smith	x	Sampson 1993
			Andrena perplexa Smith		
			Andrena regularis Malloch		
			Andrena vicina Smith	x	Sampson 1993
			Colletes simulans Cresson	x	Bowers 1975; Buchmann 1983
			Osmia bucephala Cresson		
			Osmia cornifrons Radoszkowski		
Black bee (slender)	487	299			
			Andrena bradleyi Viereck	x	Sampson 1993; Rogers et al. 2014
			Andrena brevipalpis Cockerell ♂		
			Andrena carlini Cockerell ♂	x	Sampson 1993
			Andrena carolina Viereck ♂	x	Sampson 1993
			Andrena commoda Smith		
			Andrena crataegi Robertson ♂		
			Andrena cressonii Robertson		
			Andrena dunningi Cockerell ♂		
			Andrena forbesii Robertson ♂	x	Sampson 1993
			Andrena frigida Smith		
			Andrena hippotes Robertson ♂		
			Andrena imitatrix Cresson ♂		
			Andrena integra Smith		
			Andrena mandibularis Robertson		
			Andrena miserabilis Cresson		
			Andrena nasonii Robertson		
			Andrena platyparia Robertson ♂		
			Andrena robertsonii Dalla Torre		
			Andrena rufosignata Cockerell	x	Sampson 1993

	Andrena rugosa Robertson				
	Andrena spiraeana Robertson				
	Andrena vicina Smith ♂				
	Andrena w-scripta Viereck				
	Andrena wilkella Kirby				
	Colletes inaequalis Say				
	Osmia albiventris Cresson				
	Osmia inermis Zetterstedt ♂				
Black bee (tiny)		305	103		
	Andrena nasonii Robertson ♂				
	Ceratina calcarata Robertson ♂				
	Ceratina dupla Say				
	Ceratina mikmaqi Rehan & Sheffield				
	Lasioglossum acuminatum (McGinley)				
	Lasioglossum birkmanni (Crawford)				
	Lasioglossum coeruleum (Robertson)				
	Lasioglossum coriaceum (Smith)				
	Lasioglossum cressonii (Robertson)				
	Lasioglossum ephialtum Gibbs				
	Lasioglossum foxii (Robertson)				
	Lasioglossum heterognathum (Mitchell)				
	Lasioglossum hitchensi Gibbs				
	Lasioglossum imitatum (Smith)				
	Lasioglossum leucocomum (Lovell)				
	Lasioglossum lineatulum (Crawford)				
	Lasioglossum macoupinense (Robertson)				
	Lasioglossum nigroviride (Graenicher)				
	Lasioglossum pilosum (Smith)			x	Larson & Barrett 1999
	Lasioglossum planatum (Lovell)				
	Lasioglossum quebecense (Crawford)				
	Lasioglossum subviridatum (Cockerell)				

	Lasioglossum truncatum (Robertson)				
	Lasioglossum versans (Lovell)				
	Lasioglossum versatum (Robertson)				
	Halictus confusus Smith				
	Halictus rubicundus Christ			x	Sampson 1993
Green Bee		78	47		
	Agapostemon sericeus Forster			x	Roberts 1969
	Agapostemon texanus Cresson			x	Roberts 1969
	Agapostemon virescens Fabricius				
	Augochlora pura Say			x	Pereira et al. 2011; Sigrist & Sazima 2015
	Augochlorella aurata Smith			x	Bowers 1975; Buchmann 1983; Buchmann 1985
	Augochloropsis metallica Fabricius			x	Bowers 1975; Cane et al. 1985; Solís-Montero et al. 2015
Other		39	19		
	Nomada composita Mitchell				
	Nomada cuneata Robertson ♂				
	Nomada depressa Cresson ♂				
	Nomada luteola Olivier				
	Nomada pygmaea Cresson				
	Sphecodes cressonii Robertson				
	Sphecodes ranunculi Robertson ♂				
	Xylocopa virginica Linnaeus			x	Buchmann 1985; Cane et al. 1985

♂ specimens for which a record of a male specimen exists

Table A.4 Model coefficients at two spatial scales for the *proportion natural area* and (a) visitation rate, (b) abundance and (c) estimated species richness, as well as *landscape diversity* and (d) visitation rate, (e) abundance and (f) estimated species richness.

	Estimate	Std. Error	*t*	*P*	Estimate	Std. Error	*t*	*P*
	2000 m				1000 m			
(a) *Visitation Rate*								
(Intercept)	0.603	0.364	1.655		1.703	0.346	4.929	
Proportion natural area	3.673	0.575	6.389	P < 0.0001	2.042	0.579	3.527	0.001
(b) *Abundance*								
(Intercept)	0.069	0.230	0.301		0.750	0.218	3.438	
Proportion natural area	2.499	0.360	6.944	P < 0.0001	1.508	0.366	4.124	P < 0.001
(c) *Est. Spp. Richness*								
(Intercept)	1.652	0.360	4.589		2.415	0.382	6.316	
Proportion natural area	2.018	0.490	4.116	P < 0.0001	0.691	0.504	1.371	0.176
(d) *Visitation Rate*								
(Intercept)	2.221	0.914	2.431		2.740	0.782	3.502	
Landscape diversity	0.349	0.511	0.683	0.496	0.060	0.472	0.127	0.899
(e) *Abundance*								
(Intercept)	1.323	0.602	2.197		1.516	0.514	2.949	
Landscape diversity	0.151	0.336	0.449	0.656	0.046	0.309	0.147	0.884
(f) *Est. Spp. Richness*								
(Intercept)	0.980	0.765	1.281		2.216	0.697	3.182	
Landscape diversity	1.055	0.421	2.505	0.016	0.366	0.402	0.911	0.365

Table A.5 Model coefficients at two spatial scales for *edge density* and (a) visitation rate, (b) abundance and (c) estimated species richness, as well as *patch area* and (d) visitation rate, (e) abundance and (f) estimated species richness.

	Estimate	Std. Error	*t*	*P*	Estimate	Std. Error	*t*	*P*
	2000 m				1000 m			
(a) *Visitation Rate*								
(Intercept)	2.748	0.878	3.129		3.315	0.742	4.468	
Edge density	0.001	0.011	0.103	0.918	-0.007	0.010	-0.656	0.513
(b) *Abundance*								
(Intercept)	1.212	0.574	2.111		1.401	0.489	2.863	
Edge density	0.005	0.007	0.667	0.509	0.003	0.007	0.394	0.696
(c) *Est. Spp. Richness*								
(Intercept)	1.586	0.781	2.031		2.986	0.691	4.319	
Edge density	0.017	0.010	1.642	0.107	-0.003	0.009	-0.288	0.774
(d) *Visitation Rate*								
(Intercept)	2.177	0.547	3.983		1.918	0.506	3.792	
Patch area (mean)	0.106	0.085	1.250	0.216	0.180	0.096	1.889	0.065
(e) *Abundance*								
(Intercept)	1.347	0.365	3.689		1.185	0.342	3.468	
Patch area (mean)	0.039	0.056	0.695	0.492	0.080	0.064	1.241	0.223
(f) *Est. Spp. Richness*								
(Intercept)	2.983	0.567	5.260		2.218	0.499	4.444	
Patch area (mean)	-0.028	0.079	-0.362	0.718	0.118	0.086	1.364	0.178

Table A.6 Model coefficients for the relationship between *agricultural intensity* and (a) visitation rate, (b) abundance and (c) estimated species richness.

	Estimate	Std. Error	*t*	*P*
(a) *Visitation Rate*				
(Intercept)	3.354	0.213	15.714	
Agricultural intensity	-1.532	0.501	-3.056	0.004
(b) *Abundance*				
(Intercept)	1.893	0.144	13.151	
Agricultural intensity	-0.905	0.338	-2.676	0.011
(c) *Est. Spp. Richness*				
(Intercept)	3.169	0.294	10.797	
Agricultural intensity	-1.023	0.412	-2.481	0.018

Table A.7 Model coefficients and significance for the interaction between agricultural intensity and proportion natural area at the 2000m scale on native bee (a) visitation rate, (b) abundance and (c) Estimated species richness

	Estimate	Std. Error	*t*	*P*
(a) *Visitation Rate*				
(Intercept)	3.010	0.104	28.996	0.000
Agricultural intensity	-0.287	0.399	-0.718	0.477
Natural area @ 2 km scale	3.592	0.590	6.089	0.000
Interaction	7.441	2.288	3.252	0.002
(b) *Abundance*				
(Intercept)	1.671	0.087	19.210	0.000
Agricultural intensity	0.003	0.264	0.013	0.990
Natural area @ 2 km scale	2.541	0.391	6.505	0.000
Interaction	3.419	1.513	2.259	0.030
(c) *Est. Spp. Richness*				
(Intercept)	3.070	0.204	15.057	0.001
Agricultural intensity	0.214	0.451	0.474	0.639
Natural area @ 2 km scale	1.869	0.581	3.218	0.003
Interaction	6.166	2.153	2.864	0.007

Table A.8 Model coefficients for the interaction between agricultural intensity and *edge density* at the 2000m scale and (a) visitation rate, (b) abundance and (c) estimated species richness, as well as the interaction between agricultural intensity and *patch area* at the 2000m scale and (d) visitation rate, (e) abundance and (f) estimated species richness.

	Estimate	Std. Error	*t*	*P*
(a) ***Visitation Rate***				
(Intercept)	2.874	0.157	18.350	0.000
Agricultural intensity	-2.026	0.587	-3.452	0.001
Edge Density @ 2 km scale	0.022	0.014	1.547	0.130
Edge density × Agricultural intensity	-0.025	0.065	-0.393	0.696
(b) ***Abundance***				
(Intercept)	1.605	0.103	15.582	0.000
Agricultural intensity	-1.301	0.386	-3.370	0.002
Edge Density @ 2 km scale	0.018	0.009	1.908	0.064
Edge density × Agricultural intensity	-0.012	0.043	-0.271	0.788
(c) ***Est. Spp. Richness***				
(Intercept)	2.806	0.231	12.150	0.001
Agricultural intensity	-1.057	0.490	-2.157	0.037
Edge Density @ 2 km scale	0.018	0.012	1.476	0.148
Edge density × Agricultural intensity	0.065	0.051	1.277	0.210
(d) ***Visitation Rate***				
(Intercept)	3.001	0.162	18.576	0.000
Agricultural intensity	-1.822	0.587	-3.104	0.004
Mean patch area @ 2 km scale	-0.071	0.093	-0.766	0.448
Mean patch area × Agricultural intensity	0.697	0.431	1.616	0.114
(e) *Abundance*				
(Intercept)	1.644	0.111	14.841	0.000
Agricultural intensity	-1.154	0.402	-2.867	0.007
Mean patch area @ 2 km scale	-0.067	0.064	-1.057	0.297
Mean patch area × Agricultural intensity	0.236	0.295	0.799	0.429
(f) ***Est. Spp. Richness***				
(Intercept)	2.830	0.269	10.537	0.001
Agricultural intensity	-1.534	0.498	-3.080	0.004
Mean patch area @ 2 km scale	-0.175	0.087	-2.005	0.052
Mean patch area × Agricultural intensity	-0.170	0.397	-0.429	0.671

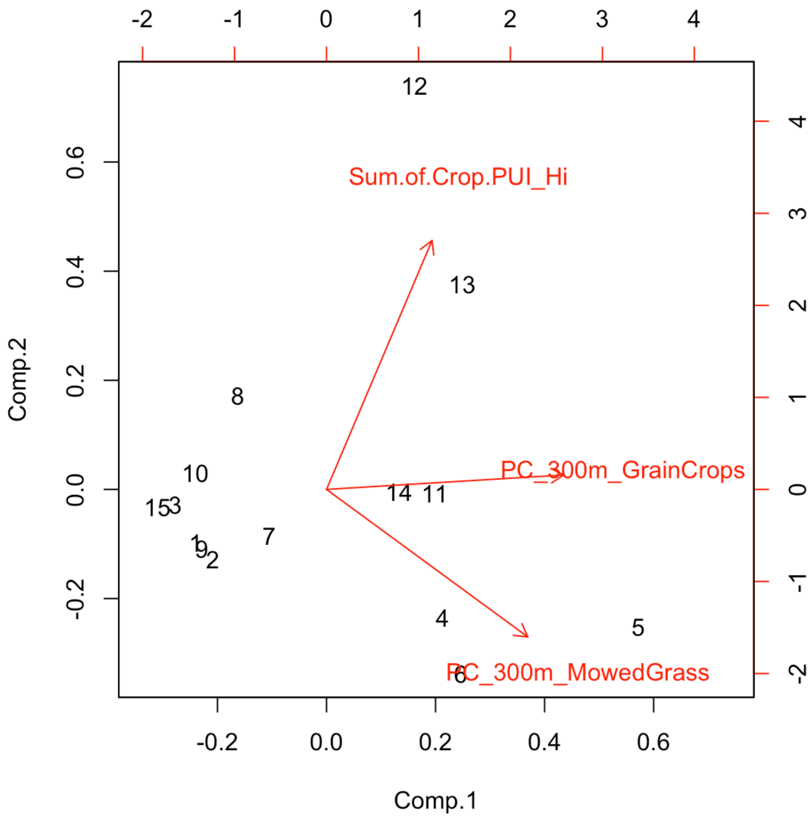

Figure A.1 Biplot of the PCA illustrating the ordination of farms with respect to pesticide use, mowed areas and grain crop area.

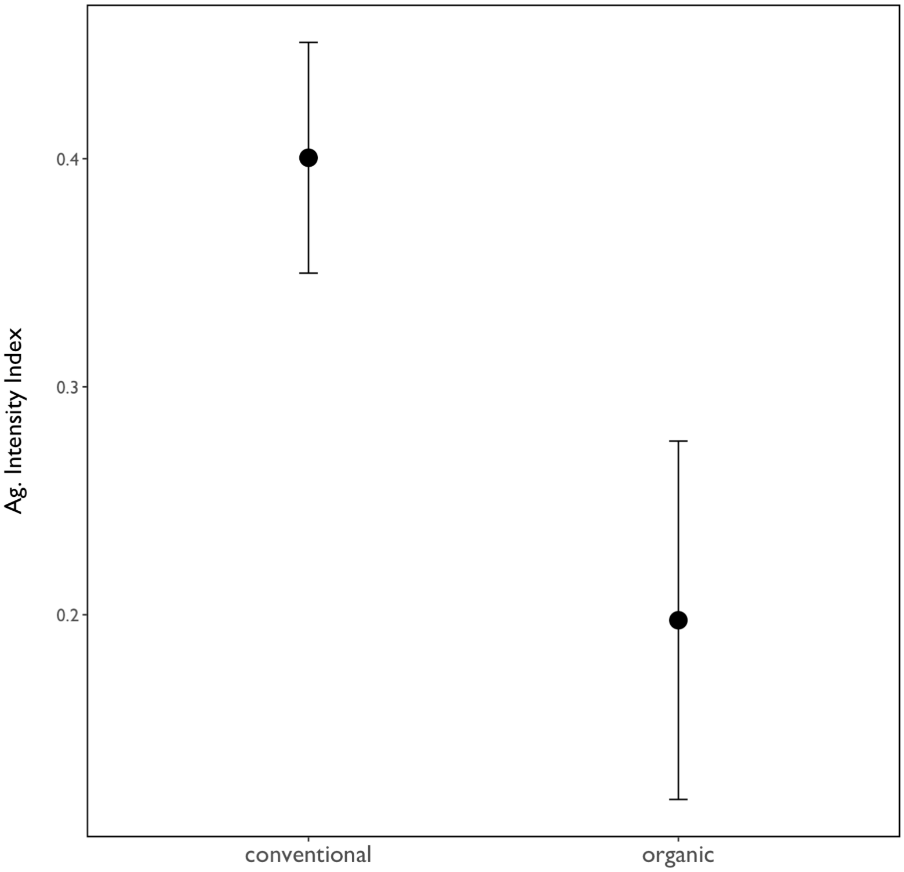

Figure A.2 Mean agricultural intensity index scores for conventional (N=6) and organic practicing farms (N=9) ($F(1, 13) = 3.712$, $p = 0.08$). Agricultural intensity scores log transformed to meet assumption of normality. Error bars represent 1 SEM.

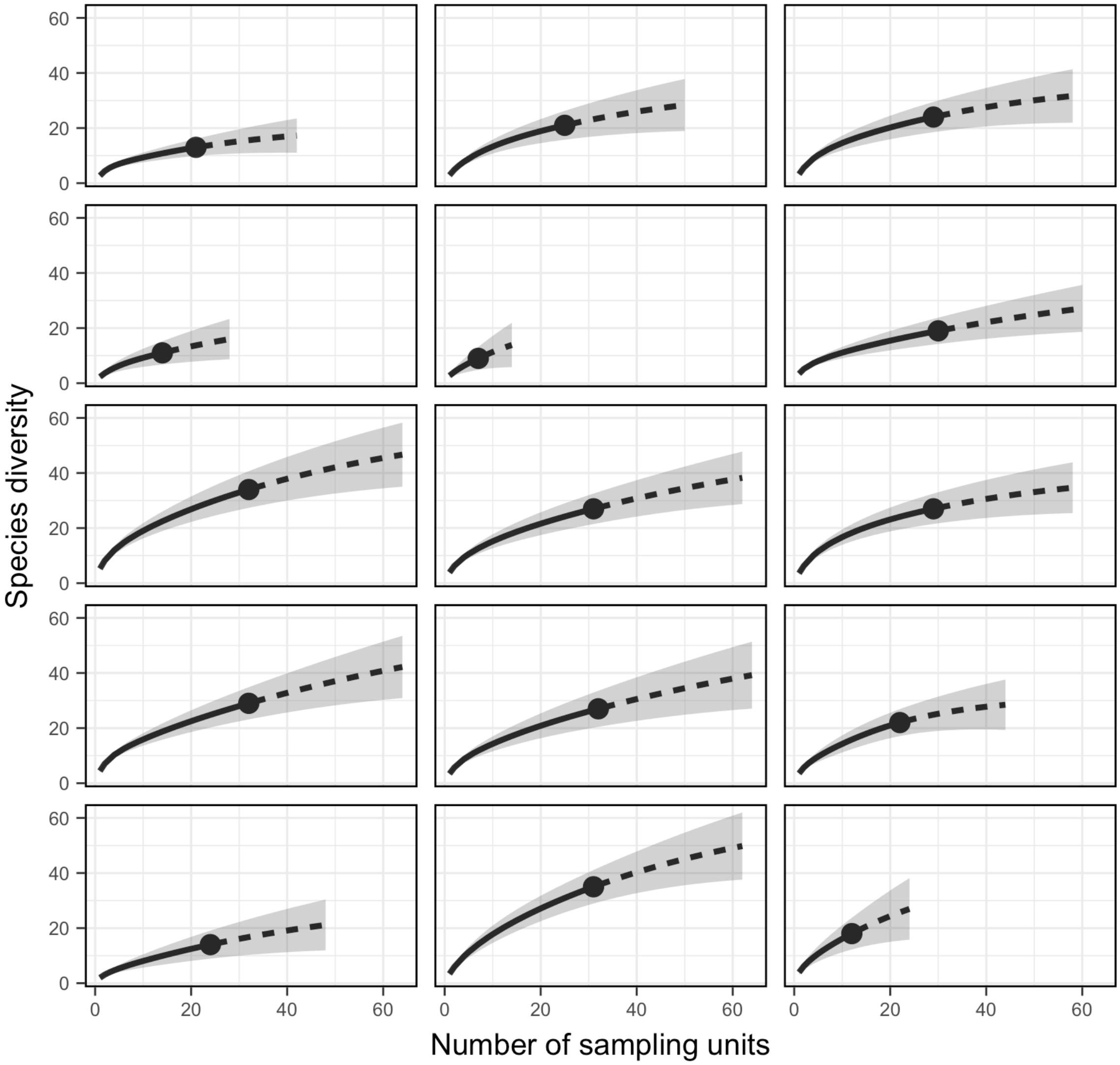

Figure A.3 Incidence-based species richness estimates for each farm. Shaded regions represent 95% bootstrapped confidence intervals for interpolated (solid line) and estimated (dashed line) species richness.

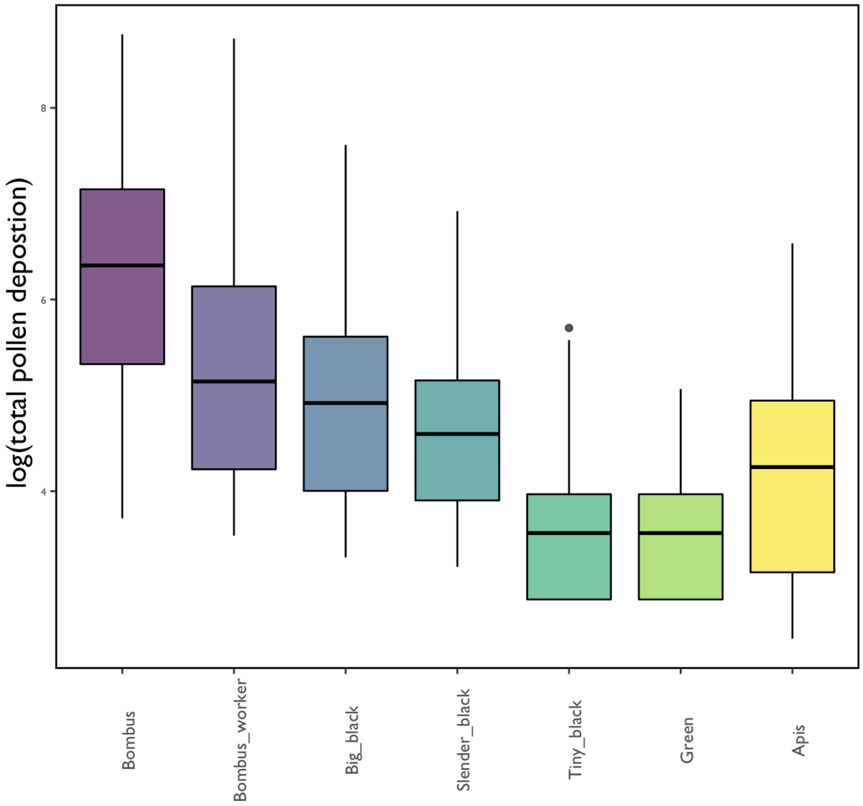

Figure A.4 The expected total pollen deposition for each morphospecies group after scaling visitation rate by reported pollen deposition values (see Table A.1).

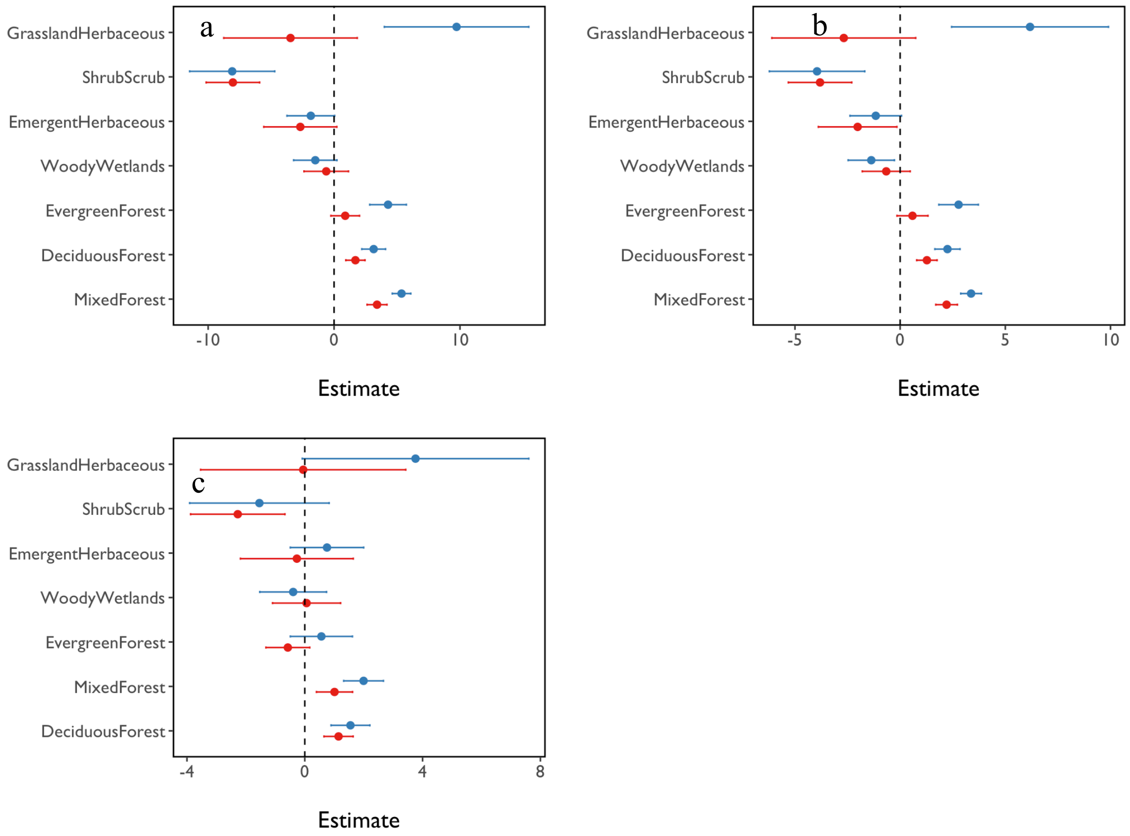

Figure A.5 The effect of individual land use classes at 2000 m (blue) and 1000 m (red) on (a) visitation rate, (b) abundance and (c) estimated species richness. Slope estimates and standard errors are from mixed effects models with the proportion coverage of each land use arcsine transformed and year as a random factor.

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CHAPTER 3: FLOWERING RESOURCES DISTRACT POLLINATORS FROM CROPS: MODEL PREDICTIONS FROM LANDSCAPE SIMULATIONS

3.1 Abstract

Enhancing floral resources is a widely accepted strategy for supporting wild bees and promoting crop pollination. Planning effective enhancements can be informed with pollination service models, but these models should capture the behavioral and spatial dynamics of service-providing organisms. Model predictions, and hence management recommendations, are likely to be sensitive to these dynamics.

We used two established models of pollinator foraging to investigate whether habitat enhancement improves crop visitation; whether this effect is influenced by pollinator traits and landscape pattern; and whether behavioral detail improves model predictions.

The more detailed central place foraging model better predicted variation in bee visitation observed between habitat types, because it included optimized tradeoffs between patch quality and distance. Both models performed well when predicting visitation rates across broader scales.

Using real agricultural landscapes and simulating habitat enhancements, we found that additional floral resources can have diverging effects on predicted crop visitation. When co-flowering resources were added, optimally foraging bees concentrated in enhancements to the detriment of crop pollination. For both models adding nesting resources increased crop visitation. Finally, the marginal effect of enhancements was greater in simple landscapes.

Our model results help to identify the conditions under which habitat enhancements are most likely to increase pollination services. Three design principles emerge: 1) enhancing only flowers can diminish services by distracting pollinators away from crops, 2) providing nesting resources is more likely to increase bee populations and crop visitation, and 3) the benefit of enhancements will be greatest in landscapes that do not already contain abundant habitat.

3.2 Introduction

Reproductive success for 88% of angiosperms depends on pollination by bees, birds, bats and other animals (Ollerton, Winfree, & Tarrant, 2011). Pollinators also provide a critical ecosystem service, with two-thirds of global crops benefitting from animal-mediated pollination (Klein et al., 2007), including many fruits and seeds that provide nutrients essential for balanced human diets (Eilers, Kremen, Greenleaf, Garber, & Klein,2011). Although many taxa contribute to pollination (e.g., Ratto et al., 2018), bees are the most important crop pollinators worldwide. Increasing evidence indicates that wild bees provide pollination services that are equal or greater in value to those provided by managed bees (Garibaldi et al., 2013).

Wild bees are important for food systems and their widespread decline has prompted efforts to conserve populations in agricultural regions (Garibaldi et al., 2014). Strategies to improve wild bees focus on three key resources: floral resources, nesting sites and refugia from hazards such as pesticides or disease (Dicks et al., 2015; Roulston & Goodell, 2011). Of these three resources, floral resources are frequently identified as an important constraint on pollinator persistence in agriculture (Carvell et al., 2006; Potts, Vulliamy, Dafni, Ne ’eman, & Willmer, 2003; Williams, Regetz, & Kremen, 2012). Providing floral resources can improve wild bee reproduction (Carvell, Bourke, Osborne, & Heard, 2015), abundance (Jönsson et al., 2015), species richness (Scheper et al., 2015) and population persistence (M’Gonigle, Ponisio, Cutler, & Kremen, 2015), as well as increase crop pollination (Blaauw & Isaacs, 2014).

Maintaining farm hedgerows or establishing floral strips hold promise, but their impacts on pollinator communities and crop production are varied and unclear (Scheper et al., 2015). The effectiveness of adding pollinator habitat (hence, ‘enhancements’) depends on its size, location, bloom duration and species composition (Haaland, Naisbit, & Bersier, 2011). In particular, the ‘Circe principle’ predicts that pollinator individuals may be attracted to resource-rich patches and remain there (Lander, Bebber, Choy, Harris, & Boshier, 2011), such that enhancements may distract pollinators from the crops themselves (Bartomeus & Winfree, 2011; Morandin & Kremen, 2013). Therefore, even the sign of the effect of enhancements on crop pollination services is uncertain and depends on characteristics of the strips relative to surrounding habitat.

Whether enhancements improve local resources relative to landscape-wide resource availability can impact their effectiveness (Scheper et al., 2015). Conservation actions are more effective in structurally simple landscapes than in structurally complex landscapes (Tscharntke et al., 2005). In structurally complex landscapes enhancement benefits are less pronounced because farmland populations are subsidized by the continuous colonization of species from the surrounding species-rich landscape, whereas in simple landscapes the extent to which enhancements improve habitat conditions is greater (Kleijn et al., 2011). Enhancement strategies should therefore be designed and assessed within the context of landscape pattern (Carvell et al., 2011).

Exploring multiple drivers across spatial scales through field-based experimentation is difficult given the possible range of conditions and interactive effects. Ecosystem service models are one approach to overcome these experimental limitations. These models strive to link land use to altered ecosystem function and then to link these changes in function to the provision of ecosystem services that affect human well-being (Keeler et al., 2012). However, these models have two important limitations. First, they typically provide only static snapshots of current service provision or value (Naidoo et al., 2008). Approaches that instead map the marginal value – the value of a unit change in a landscape (Turner, Pearce, & Bateman, 1994) – are needed because conservation decisions usually involve evaluating the outcome of incremental changes to a landscape (Ricketts & Lonsdorf, 2013). Second, ecosystem service models are typically simple, with many known dynamics excluded for tractability. The consequences of these simplifications are largely unknown because models are seldom compared to each other or validated with field data (Schulp et al., 2014; Seppelt et al., 2011). It is therefore unclear to what degree findings, and hence management recommendations, are sensitive to model design and detail.

Bees are central place foragers (Olsson, Brown, & Helf, 2008; Schoener, 1979) that vary in their flight range (Greenleaf, Williams, Winfree, & Kremen, 2007), yet ecosystem service models for crop-pollinating bees typically include simplifying assumptions regarding dispersal ability and behavior. The model by Lonsdorf et al.

(2009) assumes that bees diffuse out from the nest and use habitats indiscriminately with respect to foraging returns. By contrast, the more recent model by Olsson et al. (2015) assumes that bees optimize habitat use to maximize fitness. These models differ in their treatment of foraging behavior; whether this detail affects agreement between predicted and observed crop visitation remain untested.

Here we use two established models of pollinator foraging to investigate whether habitat enhancement improves crop visitation. Our objectives are to (1) validate and compare these pollination service models, (2) apply the models to test the effects of habitat enhancement on crop visitation, and (3) ask whether effects depend on the species' functional traits and landscape context. We use field observations of bee visitors to compare predictions of both models. We then apply the models to predict the marginal change in visitation following simulated additions of pollinator habitat. We compare predictions from different sizes, resource composition, and for bees with different foraging ranges. Last, we evaluate the degree to which effectiveness of enhancements depends on broader landscape pattern.

3.3 Methods

3.3.1 Models

We use two habitat-use model models: the Lonsdorf et al. model (LEM) (Lonsdorf et al., 2009) and the central place foraging model (CPF) (Olsson & Bolin, 2014). Solitary and social bees are central place foragers that provision brood with resources collected within a home range around a nest (Cresswell, Osborne, & Goulson, 2000). In both models bees require places to nest, and fitness at a nest site depends on the amount and proximity of foraging resources. Therefore, the input data for both models are maps of nesting and foraging suitability. Both models assume that number of bees produced (i.e., fitness) is entirely dependent on nesting quality and floral resources, and that each nesting site (pixel) can only have a single nest. The models produce indices of habitat quality and bee visitation rates from the available nests, and therefore do not include population dynamics or competition.

The difference between the models lies in their treatment of foraging behavior. The LEM predicts that pollinator foraging, and therefore patch visitation, decreases with increasing distance to patches and bees therefore diffuse into the landscape from nest site (Figure 1c, e). The CPF describes optimal patch selection by a pollinator which is determined by distance to a given patch from the nest and the quality of the patch (Figure 1b). Within the CPF framework pollinator travel distances are dynamic with respect to the habitat quality of the entire landscape, such that they will be shorter in areas with more patches of high floral quality. Pollinators therefore concentrate on nearby, high quality patches (Figure 1d). The models' different treatment of foraging behavior results in distinct predictions of the rate that pollinators visit patches. The theory of both models has been previously described, but we present basic necessary theory here (and in the Appendix).

3.3.1.1 Lonsdorf et al. model. The LEM maps relative fitness of pollinators in nests and then models visitation as the distance-weighted average fitness of surrounding nests (Figure 1c). Given maps of floral and nesting quality the model calculates pollinator fitness for every pixel. It assumes that fitness depends on the quality of nest sites and surrounding resource availability, with nearby resources always contributing more than those farther away. Lonsdorf et al. (2009) describe an index of nest fitness, G_i, within nest site i as:

$$G_i = N_i \frac{\sum_{j=1}^{M} F_j e^{-\frac{D_{ij}}{\alpha}}}{\sum_{j=1}^{M} e^{-\frac{D_{ij}}{\alpha}}}$$

where N_i represents the suitability of pixel i for nesting and the fraction represents the distance-weighted average floral quality of the landscape surrounding nest site x. D_{ij} is the Euclidean distance between nest site x and floral site j. The numerator is a distance weighted sum of all floral resources across all M pixels where F_j is the floral quality, scaled from 0 to 1, of site j. The model's single parameter, α, is a distance-decay scalar representing the average distance the bee would travel to forage.

Given this fitness raster, the model employs the same framework to redistribute bees from nest sites into the landscape. With increasing distance from nest sites in all directions the model assumes an exponential decay in visitation. The model produces a relative index (0–1) of pollinator visitation, P_j, as the distance-weighted average fitness of surrounding nests at site j:

$$P_j = \frac{\sum_{j=1}^{M} G_i e^{-\frac{D_{ij}}{\alpha}}}{\sum_{j=1}^{M} e^{-\frac{D_{ij}}{\alpha}}}$$

3.3.1.2 Central place foraging model. In the CPF pollinators maximize their fitness through their habitat choice and visitation is based on a patch's floral quality relative to its distance from a nest. It has two parameters: the maximum travel distance to a patch of infinite quality (τ_{max}) and a coefficient (ω, where $\omega < 0$) that scales patch quality by distance. Olsson et al. (2014) describe a fitness isocline within a quality-distance state space as:

$$\tau = \tau_{\max} + \frac{\omega}{A}$$

where A is the quality of the patch and τ is the maximum travel distance accepted to a patch of that quality. Patches falling below the isocline will have positive marginal fitness contribution and should be used by foragers, whereas patches above it are not visited because foraging costs outweigh gains (Figure 1b). In other words, to maximize fitness a patch of quality A should only be used if it takes less than τ time units to travel there and back from the nest. The fitness of a nest can then be expressed as the sum of the marginal values of the included patches (Olsson et al., 2015). The CPF assumes that visitation is proportional to fitness value of the patches and redistributes a number of bees that is proportional to total fitness of the patch back into the landscape.

The CPF used here is a two parameter approximation to the original CPF (Olsson et al., 2015; Olsson & Bolin, 2014). In the original model ω is a composite parameter that depends on several different life-history parameters (e.g. metabolic rate of flying, predation rate, forager load size). In the current version this parameter has been approximated numerically, while maintaining and the model's dynamics and optimization of behavior. For a full description of this two parameter CPF see Appendix 3.1. The benefit of using this approximated version is that the parameters, $\tau_{\max}$ and ω, which make intuitive sense and can be estimated from field data, can be selected (rather than solved for), and that it is computationally more efficient.

3.3.2. Model Comparison

For ecosystem services provided by organisms, behavioral assumptions may fundamentally change model predictions. However, the models' predictions have yet to be comparatively validated. We therefore first compare how well model predictions fit observed visitation levels across different landscapes. We then use observations of bee visitors in patches of different forage quality to validate and compare predictions of both models.

3.3.2.1 Field observations. To compare model performance between landscapes, we use previously published observational data of highbush blueberry (*Vaccinium corymbosum* L.) visitation at 15 farms (Nicholson et al., 2017). We observed bees during the flowering season of highbush blueberry (May-June) over three summers (2013-2015) in an agricultural region of Vermont, USA. We standardize pollinator activity observations to between 09:30 and 14:00 h, clear to hazy skies, temperature above 15 °C, and wind speeds less than 3 m/s. Within a 1-m^3 area observers recorded all flower-visitors during 10-min observation periods.

To compare model performance within landscapes we observed pollinators in two patch types over two years (2016-2017): open scrub (OS) and blueberry (BLU), respectively representing patches with low and high average floral density. Open scrub patches were present within 300 m of all farms (N = 8) and are characterized as open areas dominated by early successional grasses and forbs. We paired sampling such that pollinator observations at patches occurred synchronously or within one hour of each other. In each 1-m^3 observation plot we recorded the total number of floral units (Rundlöf, Persson, Smith, & Bommarco, 2014).

3.3.2.2 Model parameters. We predict pollinator visitation and fitness across a range of parameter values. The CPF's two parameters (τ_x and ω) determine a bee's maximum foraging distance and the trade-off between energy gains and travel costs, respectively. We present three CPF bee types along a gradient of habitat selection strategies that balance foraging ability and patch acceptability. For example, the bee type with the largest τ_x (2.5 km) has a correspondingly low ω_x value (-17) and thus the minimum patch quality (A) it can use is relatively high (Figure 2). These parameter combinations represent realistic metabolic tradeoffs between flexibility in patch acceptance and foraging distance (Westphal, Steffan-Dewenter, &Tscharntke, 2006). The LEM's parameter (α) determines the average distance in kilometers a bee would fly. We present three LEM bee types with average flight distances ranging from 0.25 to 1.25 km (Figure 2). With these parameters both models investigate bees with similar flight ranges.

3.3.3 Model Application

We simulate habitat enhancement across different strategies of size, location, and resource composition. We then test whether the effect of enhancements on crop visitation is moderated by larger scale landscape quality.

3.3.3.1 Baseline landscapes. We focus on agricultural landscapes in Vermont, USA characterized by heterogeneously distributed pastureland and cultivated farmland combined with intact natural areas, predominately deciduous hardwood forests. For the 15 farms we use the national Crop Data Layer (CDL, NASS 2008) resampled to 9 m resolution to provide maps of surrounding land-cover. Based on similarity in crop characteristics, we reduced 173 agricultural land-use categories to 32 representative crop types and retained 13 non-crop categories. We attribute relative floral and nesting values (ranging from 0-20) to these 45 land-cover types based on expert opinion (see Koh et al. 2016 for full description of methods). These maps provide our baseline data of floral and nesting availability.

3.3.3.2 Landscapes with simulated pollinator habitat. We generated 'enhancement' scenarios by virtually adding a pollinator habitat to each farm landscape. For each farm, we centered habitat enhancements along the opposing longer edges of each crop field. Because focal crop fields vary in size, we developed two size classes of pollinator enhancements that were proportionally equivalent to the focal field. Small enhancements were approximately 18% of focal field size and large enhancements were approximately 36% of focal field size (Figure 1f). Finally, we generated three pollinator habitat resource composition scenarios: patches provide only floral resources (F), only nesting resources (N), or both (F + N). For F scenarios, we reclassified pollinator habitat patches to have a maximum floral value (1.0), while keeping nesting values equal to baseline nesting values. For N scenarios, we did the same for nesting values, while keeping floral values equal to baseline. For F + N scenarios, we set both values to the maximum. This results in 12 possible enhancement scenarios (i.e., two size classes, two sites, and three resource compositions).

3.3.3.3 Landscape quality index. To characterize broader landscape composition, we follow Kennedy et al. (2013) and use an index of landscape quality

(LQI) that is based on pollinator fitness. The LEM and CPF both code land-cover classes in terms of their contributions to pollinator floral and nesting resources – with landscapes containing more high resource quality patches resulting in greater landscape-wide fitness. To calculate LQI, we average fitness values within an area equal to three times α for the LEM and two times τ_x for the CPF. These scales ensured that we measured the landscape available for bees visiting our focal crop pixels. Consistent with Olsson et al. (2015), the models' assessments of landscape quality are strongly correlated (Pearson's $r = 0.93$; Figure S.1).

3.4 Analyses

3.4.1 Model Comparison Analysis

Our aim is to compare both models' predicted visitation with field observations. We compared observed and predicted data for each foraging model with linear mixed-effects regression using the lme4 package in R (v. 3.3.2) (Bates, Mächler, Bolker, & Walker, 2015). For each statistical test, we looked at the main effect of predicted visitation as well as a model prediction by year interaction. We included year and farm as random effects to account for differences in observed visitation values associated with these variables. We analyzed data at the farm by year level and log-transformed [$\ln(x + 1)$] native bee visitation rate (visits/bee/1m^3/10 minutes) to ensure normally distributed residuals.

3.4.2 Model Application Analysis

Our aim is to quantify the marginal change in pollination services to blueberry resulting from pollinator habitat enhancement. We applied the LEM and CPF to both enhanced and baseline maps and calculated the difference in visitation (*V*) across all *i* blueberry pixels:

$$\Delta_{\mathrm{V}} = \sum_{i=1}^{i} V_{i,\ enhanced} - \sum_{i=1}^{i} V_{i,\ baseline}$$

where Δ_V is the change in visitation resulting from the addition of pollinator habitat patches in the landscape. We used these results to determine to what extent enhancement is modified by broader landscape composition and pollinator habitat strategy using mixed effect models. We included fixed effects for pollinator habitat patch size (small or large) and resource composition (N, F, and N + F) and their interaction with each other and landscape quality. We treated the different locations of pollinator habitat as sites, and included them as a random factor nested within farm. We performed backwards model selection eliminating terms based on model AIC. To compare effects across bee foraging ranges, we performed the model selection procedure for each value, but retained the model with most terms. We then analyzed the predicted change in visitation for each bee type with this largest model. We present type II Wald F tests with Kenward–Roger degrees of freedom approximation. We validated all statistical models for normality and homogeneity of variances.

3.5 Results

3.5.1 Model Validation and Comparison

Model predictions diverge considerably when comparing visitation at different patches within landscapes. Our field observations showed that blueberry patches had greater floral density and more native bee visits than open scrub patches (Figure 3; floral density: $F_{1,22}$ = 378.4, $P < 0.0001$; visitation: $F_{1,22}$ = 19.25, $P = 0.0002$). The CPF predictions fit those field observations, whereas the LEM predictions did not (Figure 4). For the LEM, there was a poor fit to observed visitation (Figure 4a; $r^2 = 0.04$; $F_{1,6.007}$ = 1.321; $P = 0.29$). For the CPF, there was a positive fit to observed visitation (Figure 4b; $r^2 = 0.42$; $F_{1,27.64}$ = 25.51; $P < 0.001$). For simplicity, we report results for only the far foraging bees (i.e. $\alpha = 1.25$ and $\tau_x = 2.5$); however, results do not qualitatively differ across parameter values for either model (Table S.1). Comparing model results between landscapes show that both models successfully predicted landscape level visitation (LEM: $R^2 = 0.14$; $F_{1,35.95} = 5.959$; $P = 0.019$; CPF: $R^2 = 0.14$; $F_{1,35.12}$ = 5.885; $P = 0.021$.

3.5.1.1 Effects of enhancement strategy. The marginal effect of habitat enhancements depended on resource composition and patch size (Figure 5). For the LEM, the percent change in visitation was small but always non-negative. Visitation change was highest when patches provided nesting and floral resources (F + N) (Figure 5a). For the CPF, adding only floral (F) resources resulted in non-positive (i.e. decrease or no change) visitation change. Adding only nesting resources (N) caused non-negative visitation change, and when added with floral resources (F + N) could rescue negative pollination change (Figure 5b). These results do not qualitatively differ across bee foraging ranges for either model (Figures S2 & S3).

Enhancement size influenced LEM-predicted visitation, with large patches resulting in greater positive visitation change, regardless of resource composition (Figure 5a). Patch size also influenced CPF-predicted visitation change, but the effect was dependent on resource composition. Specifically, when patches only add floral resources, crop visitation decreases less for small patches (Figure 5b). Conversely, visitation change from adding nesting resources was greater with larger patches.

3.5.1.2 Effects of landscape quality. Landscape quality modified the marginal effect of additional pollinator habitat (Table 1; Figure 6). Because this relationship did not qualitatively differ between patch size (Figure S4), we focus on results from large enhancements. For the LEM, change in visitation decreased with increasing landscape quality (Figure 6a). For the CPF, if pollinator habitat patches added only floral resources (F, dashed line) change in visitation was independent of landscape quality (Figure 6b). If pollinator habitat added nesting resources (N, dotted line) or floral and nesting resources (F + N, solid line), change in visitation decreased with increasing landscape quality; however, this effect depended on bee foraging range.

3.5.1.3 Effects of bee type. The CPF better captures differences in patch quality, we therefore focus on CPF model results when examining bees with different foraging ranges. For short foraging ($\tau_x = 0.5$) and medium foraging bees ($\tau_x = 1.5$), the effect of added pollinator habitat decreased with increasing landscape quality, except when only floral resources were added (Table 1; Figure 7). For the far foraging bee ($\tau_x = 2.5$), there was no significant interaction between resource composition and landscape quality (Table 1).

3.6 Discussion

Our model comparisons reveal that behavioral assumptions result in diverging predictions of pollinator response to local land use change. Our model application shows that the benefits of establishing pollinator habitat depend strongly on enhancement strategy and landscape context. Additional floral resources may concentrate pollinators away from crop patches, while adding nesting resources increases pollination. Taken together, our results demonstrate that (1) accounting for organism behavior matters, (2) promoting crop pollination through habitat enhancement depends on whether floral or nesting resources are added, (3) enhancement effectiveness depends on landscape context, and (4) bees with different foraging strategies vary in their response to habitat enhancements.

Side by side validation of ecosystem service models reveals the conditions under which models do or do not perform well. In this case, we see that accurately capturing foraging behavior matters. Our comparison showed that the central place foraging model, because it accounts for tradeoffs between patch quality and distance, better captured variation in bee visitation between habitat types. Both models can accurately predict the relative abundance of bees at landscape scales. Previous work across multiple regions shows that the LEM captures substantial variance (i.e., >55%) in observed bee abundance among farms (Lonsdorf et al., 2009) and this model is useful for predicting the landscape scale supply of pollination services (Koh et al., 2016). However, a known limitation of the LEM is that it does not perform well in fine-grain heterogeneous landscapes (Kennedy et al., 2013), perhaps because bees do not forage optimally (Olsson et al., 2015). We validate both models with observational data to demonstrate that, while both models predict landscape-scale patterns of abundance, the CPF captures patch differences and therefore excels at predicting visitation change resulting from habitat addition.

The net effect of pollinator habitat enhancement depends critically on what resources that new habitat offers. We consistently saw large differences in crop visitation depending on whether pollinator enhancements added floral or nesting resources. When only flowering resources were added the CPF predicted large negative change in crop visitation because bees were selectively foraging in the enhancement instead of crops. Our simulations provide support for the Circe principle; when presented with a wealth of concurrently flowering resources, pollinators remain in resource rich patches. While numerous studies have demonstrated a conservation benefit of adding flower strips (i.e., increased species richness and greater population abundance), fewer studies have shown a corresponding increase in pollination services to crops (but see Blaauw & Isaacs, 2014; Feltham, Park, Minderman, & Goulson, 2015). Other studies have found little or no effect of habitat enhancement on pollinator communities (Sardiñas, Ponisio, & Kremen, 2016). Jönsson et al. (2015) found that bumblebees were more abundant in sown flower strips than in adjacent habitat, a response that agrees with our simulations.

Adding nesting resources increased crop visitation for both models. Our model results suggest that inconsistent observations from field experiments could be driven by whether or not additional pollinator habitat augmented nesting availability. For the LEM the addition of floral and nesting resources is additive and caused the greatest increase in visitation. We observed the greatest CPF-predicted increase in visitation when pollinator habitat added only nesting resources. Adding nesting resources effectively increases the number of bees that a given landscape is able to support. Pollinator populations are often constrained by the availability of nesting resources (Potts et al., 2005; Steffan-Dewenter & Schiele, 2008) and nest location can be a key determinant of the distribution of pollination in a landscape (Lonsdorf et al., 2009; Sardiñas & Kremen, 2014). In addition to demonstrating unintended consequences of adding floral resources, our simulations highlight the importance of creating nesting habitat for promoting bee populations and crop pollination.

We observed that landscape quality moderated the effect of establishing pollinator habitat. We found the effect of habitat addition tended to be greatest in simple landscapes, lending support to theories of landscape-moderated conservation effectiveness (Kleijn et al., 2011; Tscharntke et al., 2005). The conservation benefits of local management should be highest in structurally simple, rather than in cleared or in complex landscapes. Complex landscapes with abundant natural areas have high levels of immigration (Bianchi, Booij, & Tscharntke, 2006; Ricketts et al., 2008) and offer spatiotemporal stability of resources (Rundlöf et al., 2014; Schellhorn, Gagic, & Bommarco, 2015). Local interventions such as additional habitat may not result in meaningful pollination change in complex landscapes because a mosaic of different habitats already exists and the ‘ecological contrast’ of enhancements is small (Kleijn et al., 2011). For the CPF, we observed the strongest landscape moderation when pollinator habitat enhanced local populations through additional nesting resources. When only floral resources were added, landscape context did not matter. We propose that this difference is because landscape moderation affects population-level processes rather than behavior (Rundlöf & Smith, 2006).

We also observed that bee foraging range influenced how strongly landscape quality moderated the effect of additional pollinator habitat. Specifically, within the CPF framework we did not observe a significant interaction between landscape quality and resource composition for bees with large foraging ranges (i.e. $\tau_x = 2.5$). These results suggest that, because these bees are able to utilize resources across a larger range, they are less responsive to small scale land use change. In the context of wild bee biodiversity conservation, these results indicate that enhancements most impact bees with shorter foraging ranges, which are often locally rare and small bees (Bommarco et al., 2010).

A few caveats deserve mention regarding predictions derived from applying models to real landscapes. First, we analyze changes in visitation that would occur only during the period of crop bloom. Additional floral resources are most likely to benefit pollinators during periods of low availability, within and across years (Häussler et al., 2017; Rundlöf et al., 2014). While we focus on responses of pollinator communities to enhancement at a single point in time, other models have considered temporal dynamics. Häussler et al. (2017) found that in simulated landscapes flower strips resulted in population growth over time. Taken together our results suggest that providing additional floral resources may benefit wild bee populations in the long term, while impacting pollination services by distracting bees during crop bloom. Second, the present versions of the CPF and LEM do not allow for inter- or intra-specific competition. Incorporating competition would permit investigation of how different foraging behaviors may result in species coexistence, and this work is underway (Bolin et al., *in press*). Finally, although we validate both models with observational data, our model application is predictive. It is likely that site specific aspects of farm management or pollinator habitat design would influence how crop pollination might change (Williams & Lonsdorf, 2018). This research is ongoing and field trials are currently investigating the cost-effectiveness of pollinator habitat enhancement for crop pollination (Isaacs et al., 2017).

3.7 Conclusions

Our findings demonstrate that spatially explicit ecosystem service models are useful for predicting the effects of land use change. Determining the marginal value of local land use change, such as pollinator habitat enhancement, requires a model that captures foraging decisions based on patch quality and distance. Our CPF simulations show that if bees forage optimally, then the Circe principle can occur, whereby crop pollinators concentrate in co-flowering enhancements. Pollinator conservation research largely focuses on floral resources, but here we show the importance of providing nesting substrate as well. The effectiveness of pollinator habitat not only depends on resources provided, but larger landscape quality. Enhancing biodiversity and ecosystem services are frequently shaped by land-use interactions across spatial scales, and our results show that pollinator habitat enhancement is no exception. Managing ecosystem services in agriculture is best supported by models that accurately capture the behavior and landscape dynamics of the organisms underpinning service provision.

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3.9 Tables

Table 1 Effects of pollinator habitat enhancement strategy and landscape quality on the marginal change in crop pollination predicted by (a) CPF and (b) LEM for bees with three foraging ranges.

(a) CPF	$\tau_x = 0.5$			$\tau_x = 1.5$			$\tau_x = 2.5$		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
HE Size	10.67	1,143	**0.001**	0.964	1,143	0.328	0.179	1,143	0.673
Resource composition	190.6	2,143	**< 0.001**	141.2	2,143	**< 0.001**	131.7	2,143	**< 0.001**
Landscape quality	3.578	1,13	0.081	2.158	1,13	0.166	0.672	1,13	0.427
HE Size x Rsrsc composition	15.14	2,143	**< 0.001**	11.40	2,143	**< 0.001**	9.365	2,143	**< 0.001**
Landscape quality x Rsrsc composition	15.19	2,143	**< 0.001**	8.188	2,143	**< 0.001**	2.694	2,143	0.071
(b) LEM	$\alpha = 0.25$			$\alpha = 0.75$			$\alpha = 1.25$		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
HE Size	95.45	1,140	**< 0.001**	97.72	1,140	**< 0.001**	101.5	1,140	**< 0.001**
Resource composition	203.5	2,140	**< 0.001**	206.9	2,140	**< 0.001**	215.2	2,140	**< 0.001**
Landscape quality	12.59	1,13	**0.001**	18.82	1,13	**0.001**	23.98	1,13	**< 0.001**
HE Size x Rsrsc composition	18.38	2,140	**< 0.001**	19.49	2,140	**< 0.001**	20.43	2,140	**< 0.001**
HE Size x Landscape quality	16.46	1,140	**< 0.001**	26.05	1,140	**< 0.001**	33.68	1,140	**< 0.001**
Landscape quality x Rsrsc composition	43.62	2,140	**< 0.001**	66.80	2,140	**< 0.001**	83.60	2,140	**< 0.001**
Landscape quality x Rsrsc composition x HE size	3.161	2,140	**0.005**	5.446	2,140	**0.005**	7.181	2,140	**0.001**

3.10 Figures

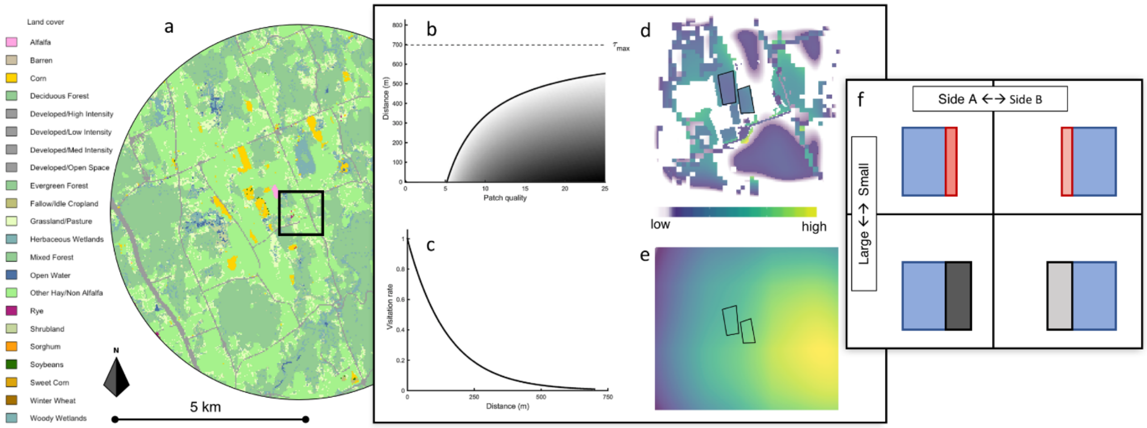


Figure 3.1 Crop pollination modeling. Given (a) land cover information, two pollinator foraging models, (b) the central place foraging model (CPF) and (c) the Lonsdorf et al. model (LEM) make spatially explicit predictions of pollinator visitation (d, e). We simulate the addition of pollinator habitat enhancements (f) next to blueberry fields (blue squares) that vary in patch size (*small*, red; *large*, black) and resource composition (*F*; *F* + *N*; *N*; not depicted).

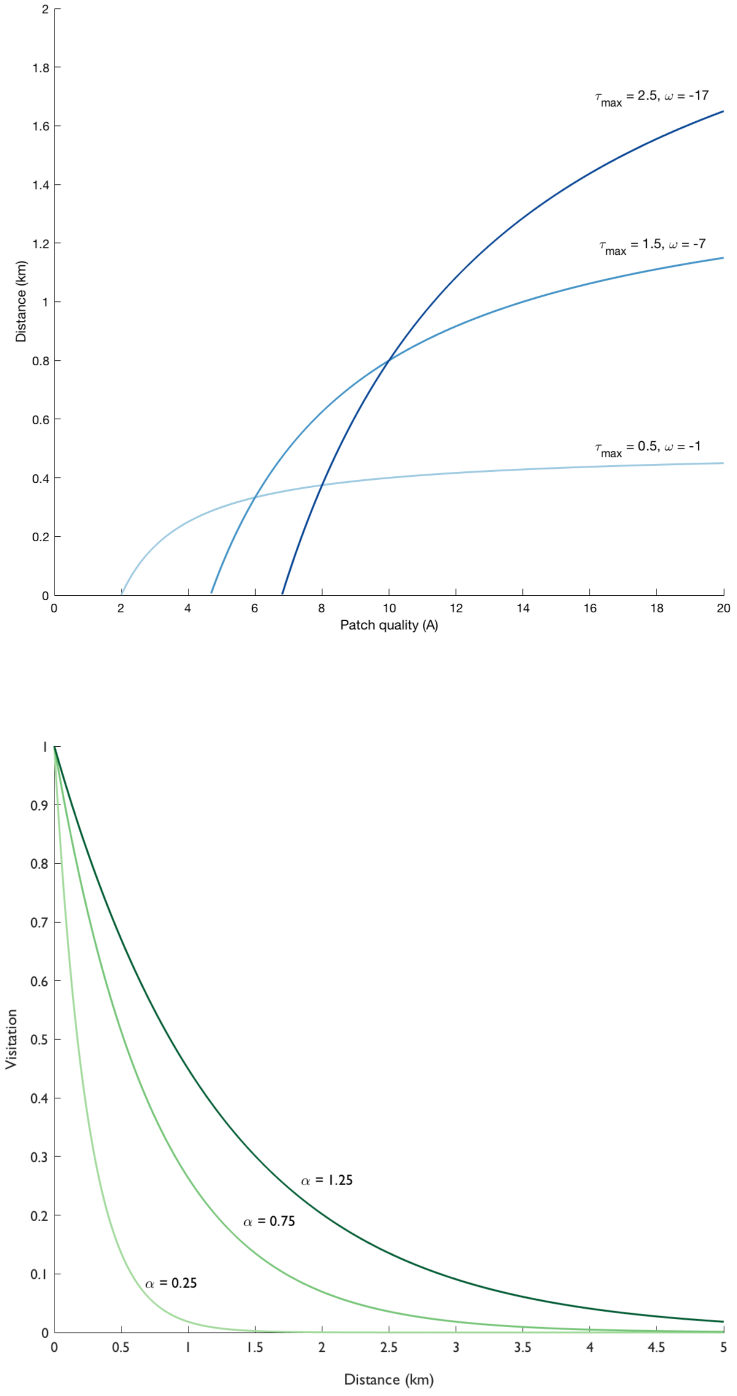


Figure 3.2 Model parameters determining foraging range used in analysis for the (a) LEM and (b) CPF.

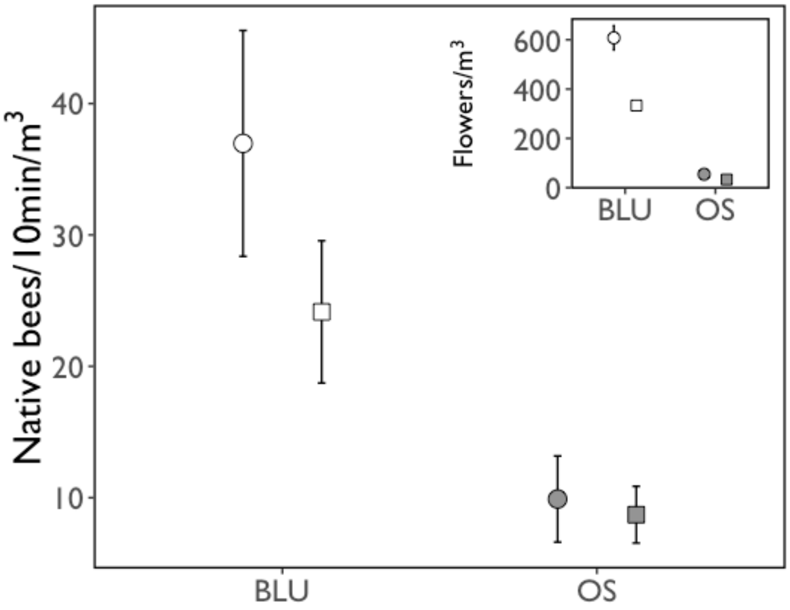


Figure 3.3 Observed native bee visitation rates between blueberry (white) and open scrub (gray) habitat patches for 2016 (circles) and 2017 (squares). Inset depicts floral unit density at the same patches.

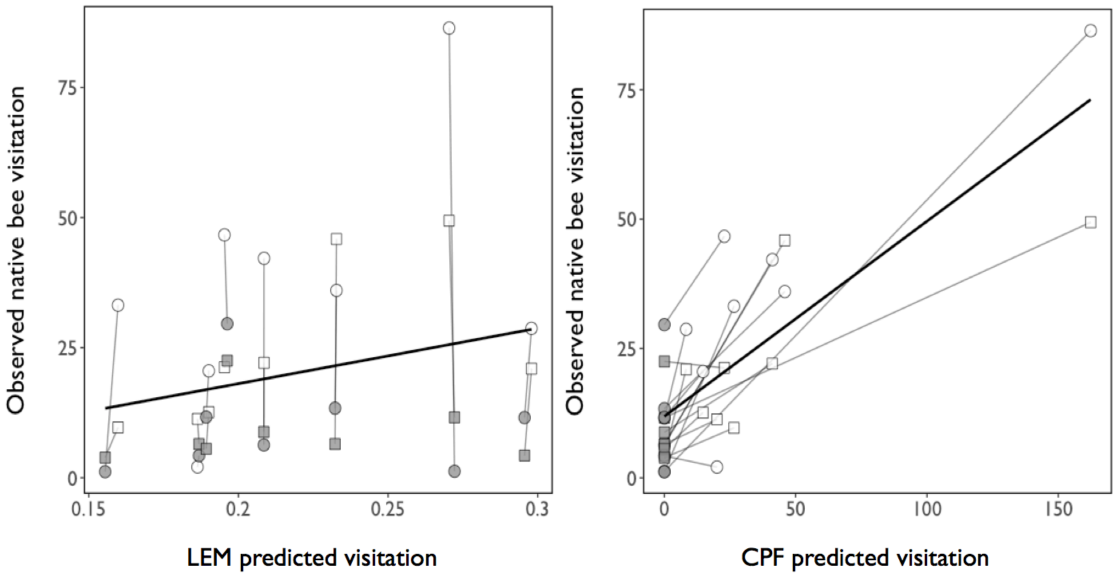


Figure 3.4 Model agreement with field data. Model comparison using predicted and observed visitation rates from LEM (a) and CPF (b). Symbols depict visitation at blueberry (white) and open scrub (gray) habitat patches for 2016 (circles) and 2017 (squares) for bees with large foraging ranges.

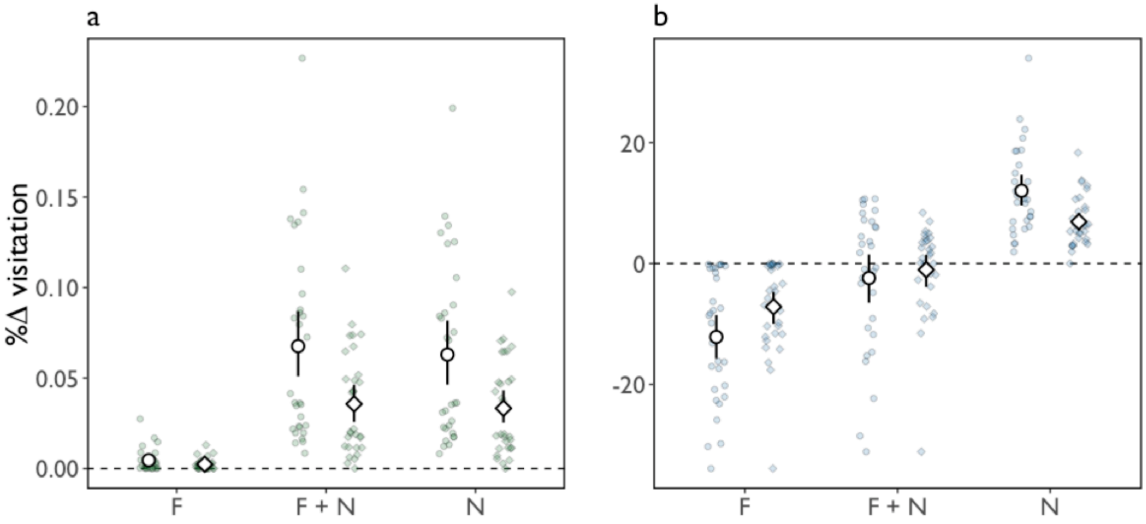


Figure 3.5 *Pollinator habitat enhancement strategy* affects crop visitation. The predicted percent change in crop visitation varies between the LEM (a, green) and CPF (b, blue) both in sign and magnitude. The symbols depict average visitation change (with 95% confidence intervals) resulting from habitat enhancements that differed in size (*large*, circles; *small*, diamonds) and resource composition (*F*, only floral; *F + N*, floral and nesting; *N*, only nesting). Figure depicts model predictions for bees with large foraging ranges ($\alpha = 1.25$ and $\tau_{max} = 2.5$), results for other foraging ranges do not qualitatively differ (see **Figs. S2 & S3**).

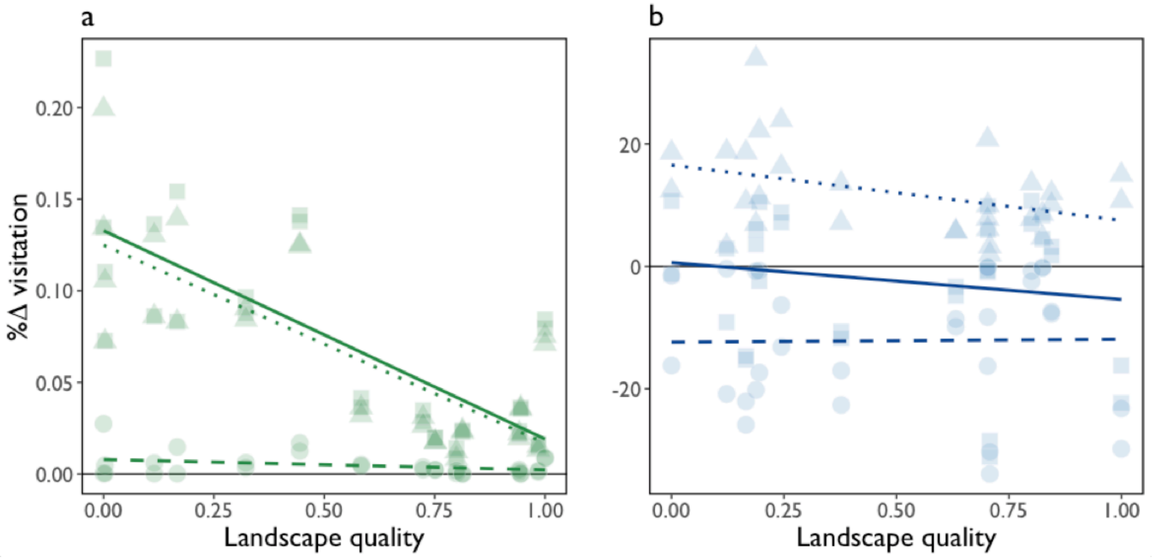


Figure 3.6 Landscape moderates the effect of pollinator habitat enhancement on crop visitation change. The effect of landscape quality (x-axis) and resource composition (*F*, dashed line and circles; *F* + *N*, solid line and squares; *N*, dotted line and diamonds) on crop visitation resulting from pollinator habitat enhancement as predicted by the LEM (α = 1.25; a) and CPF (τ_{max} = 2.5; b).

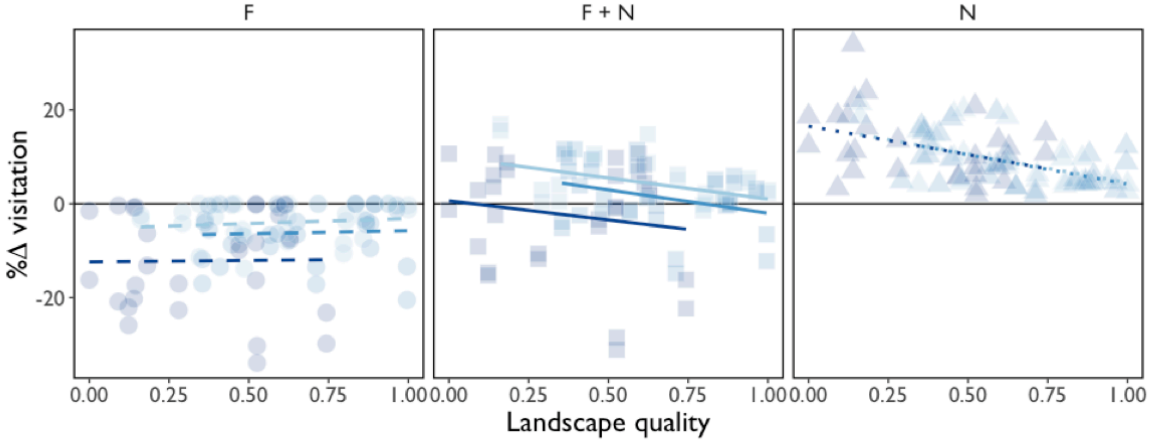
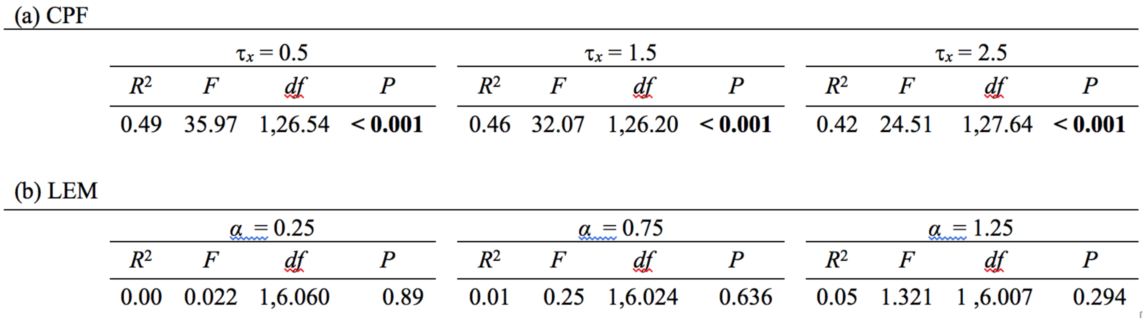


Figure 3.7 Landscape-moderated effect of habitat enhancement depends on bee foraging range. Lines depict the interaction between landscape quality and resource composition predicted by the CPF for bees with increasing foraging range (as in **Fig. 2**: $\tau_{max} = 0.5$, light blue; $\tau_{max} = 1.5$, blue; $\tau_{max} = 2.5$, dark blue.

3.11 Appendix Supplementary Tables and Figures and Model Descriptions

3.11.1 Table and Figures

Table S1 Fit between observed visitation rates and CPF and LEM-predicted visitation values across all parameters values



(a) CPF

$\tau_x = 0.5$				$\tau_x = 1.5$				$\tau_x = 2.5$			
R^2	*F*	*df*	*P*	R^2	*F*	*df*	*P*	R^2	*F*	*df*	*P*
0.49	35.97	1,26.54	**< 0.001**	0.46	32.07	1,26.20	**< 0.001**	0.42	24.51	1,27.64	**< 0.001**

(b) LEM

$\alpha = 0.25$				$\alpha = 0.75$				$\alpha = 1.25$			
R^2	*F*	*df*	*P*	R^2	*F*	*df*	*P*	R^2	*F*	*df*	*P*
0.00	0.022	1,6.060	0.89	0.01	0.25	1,6.024	0.636	0.05	1.321	1 ,6.007	0.294

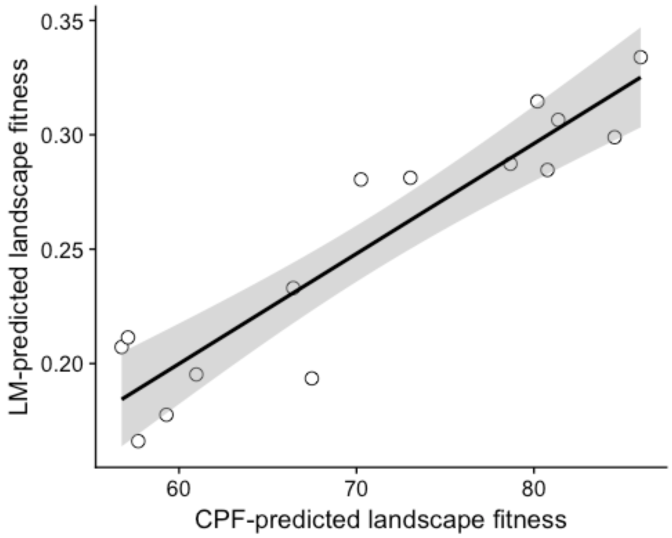


Figure S1 Fit (± SE) between landscape-wide fitness as predicted by both models

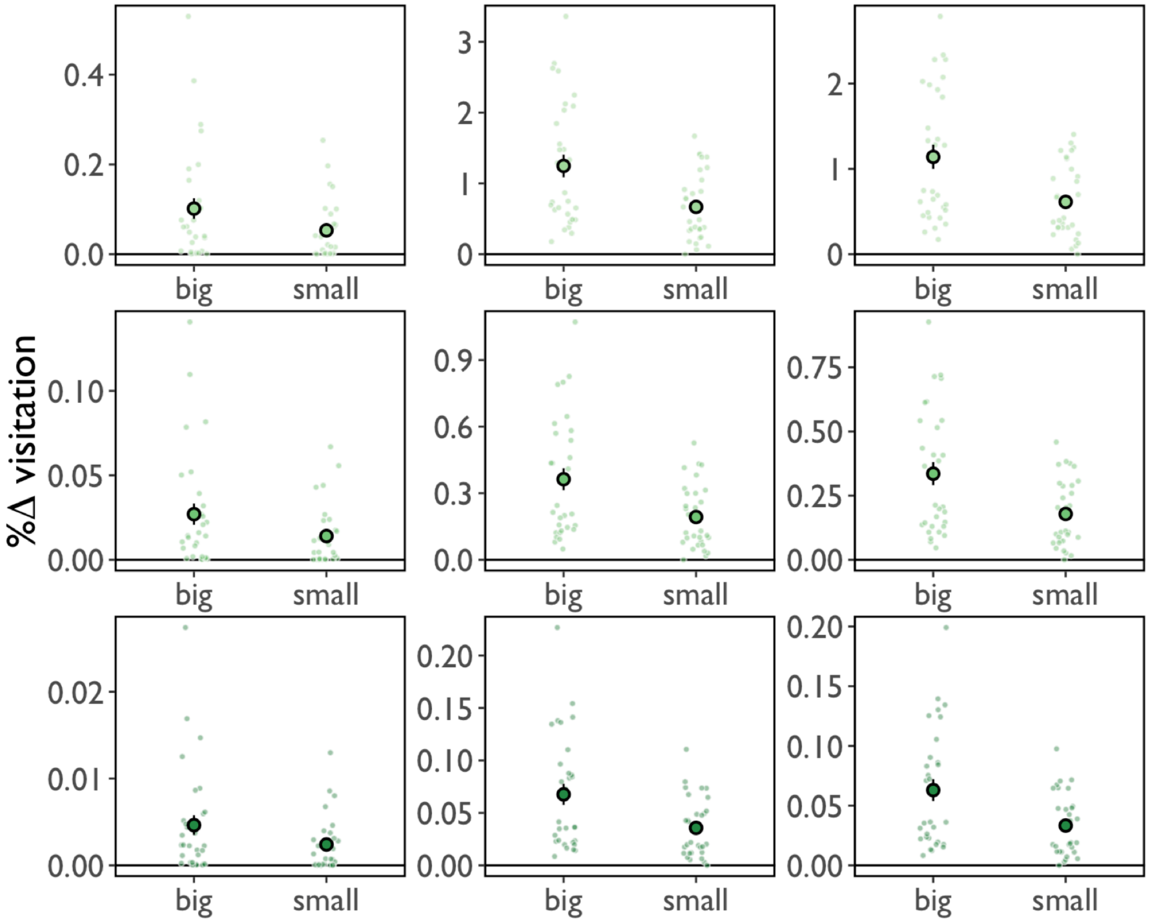


Figure S2 Effect of patch size on LEM-predicted pollination change resulting from the addition of pollinator habitat. Column reflect different resource compositions: floral only, left; floral and nesting, middle; nesting, right. Rows reflect different bee foraging parameters: short foraging, top; medium foraging, middle, far foraging, bottom.

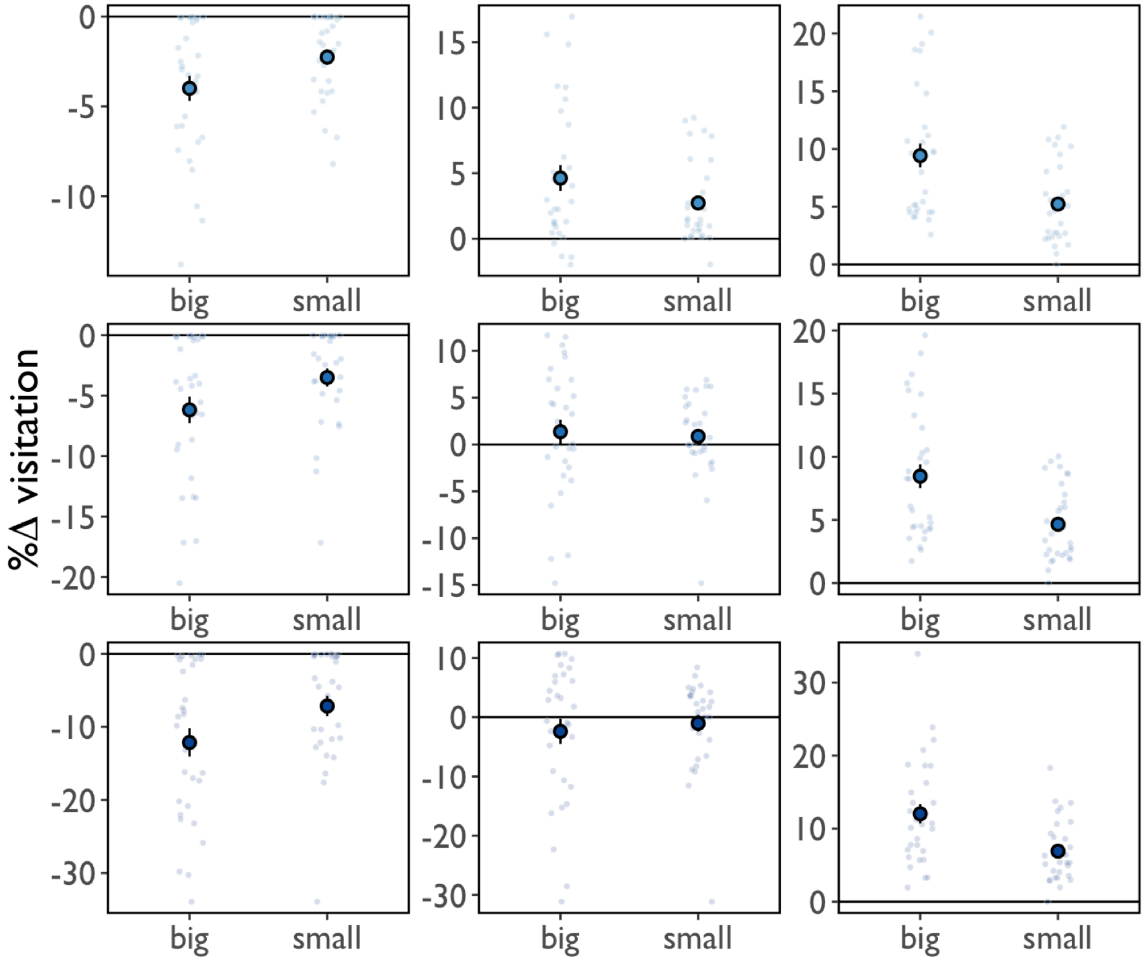


Figure S3 Effect of patch size on CPF-predicted pollination change resulting from the addition of pollinator habitat. Column reflect different resource compositions: floral only, left; floral and nesting, middle; nesting, right. Rows reflect different bee foraging parameters: short foraging, top; medium foraging, middle, far foraging, bottom.

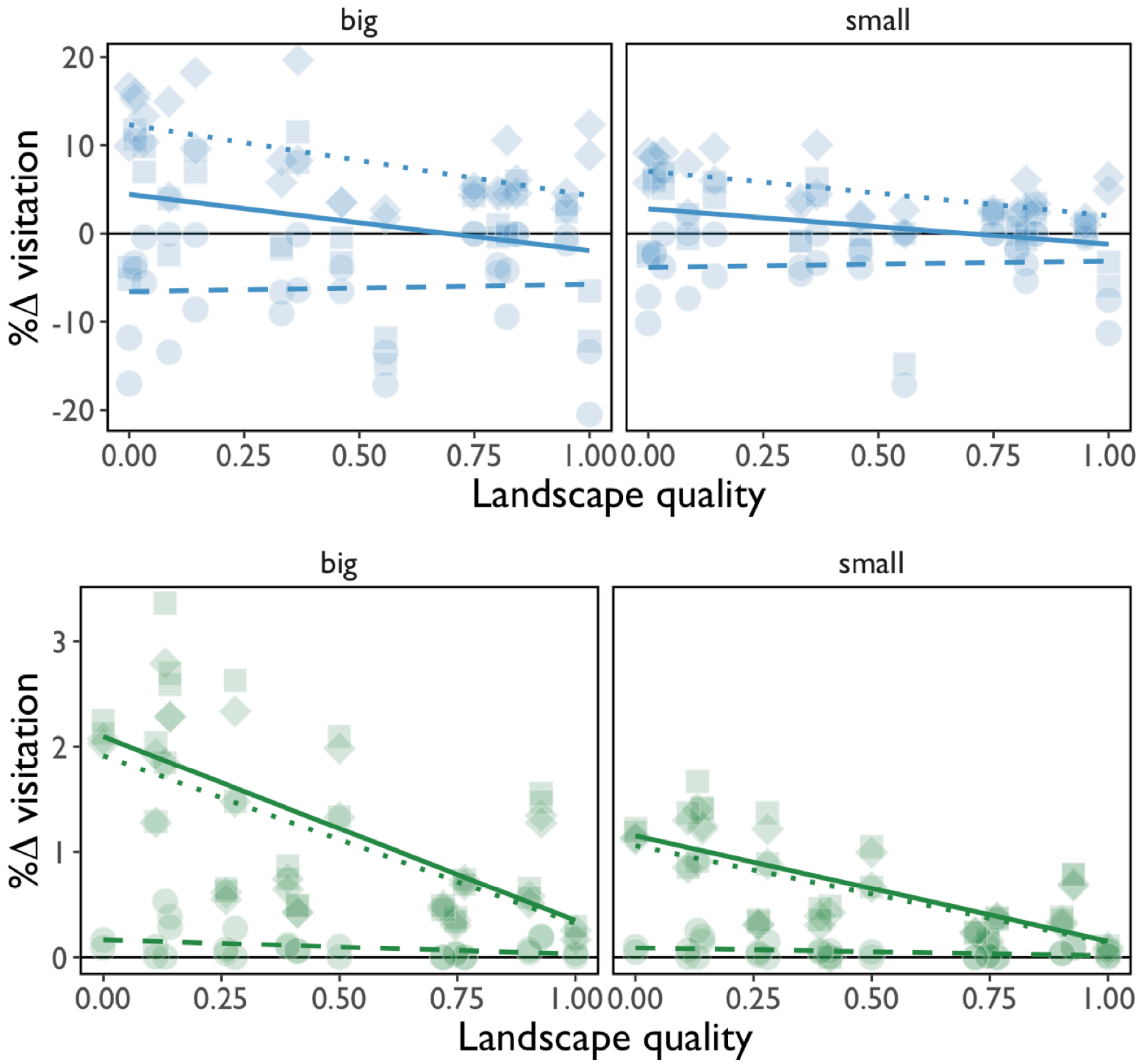


Figure S4 Landscape moderation of pollinator habitat enhancement for both size classes. The effect of landscape quality (x-axis) and resource composition (*F*, dashed line and circles; *F* + *N*, solid line and squares; *N*, dotted line and diamonds) on crop visitation change resulting from the addition of pollinator habitat as predicted by the CPF ($\tau_x = 2.5$; top) and LEM ($\alpha = 1.25$; bottom).

3.11.2 Model Descriptions

Lonsdorf et al. model

The LEM maps relative fitness of pollinators in nests and then models visitation as the distance-weighted average fitness of surrounding nests (**Fig. 1c**). Given maps of floral and nesting quality the model calculates pollinator fitness for every pixel. It assumes that fitness depends on the quality of nest sites and surrounding resource availability, with nearby resources always contributing more than those farther away. Lonsdorf et al. (2009) describe an index of nest fitness, G_i, within nest site *i* as:

$$G_i = N_i \frac{\sum_{j=1}^{M} F_j e^{-\frac{D_{ij}}{\alpha}}}{\sum_{j=1}^{M} e^{-\frac{D_{ij}}{\alpha}}}$$

where N_i represents the suitability of pixel *i* for nesting and the fraction represents the distance-weighted average floral quality of the landscape surrounding nest site x. D_{ij} is the Euclidean distance between nest site *x* and floral site *j*. The numerator is a distance weighted sum of all floral resources across all *M* pixels where F_j is the floral quality, scaled from 0 to 1, of site *j*. The model's single parameter, α, is a distance-decay scalar representing the average distance the bee would travel to forage.

Given this fitness raster, the model employs the same framework to redistribute bees from nest sites into the landscape. With increasing distance from nest sites in all directions the model assumes an exponential decay in visitation. The model produces a relative index (0–1) of pollinator visitation, P_j, as the distance-weighted average fitness of surrounding nests at site j:

$$P_j = \frac{\sum_{j=1}^{M} G_i e^{-\frac{D_{ij}}{\alpha}}}{\sum_{j=1}^{M} e^{-\frac{D_{ij}}{\alpha}}}$$

Central place foraging model

It has previously been shown (Olsson and Bolin 2014, see also Olsson et al. 2015, and Bolin et al. 2018) that the optimal foraging behaviour of a central place forager is to use all habitat patches that are closer to the central place than

$$\tau = \tau^{*}_{m,s} + \frac{\omega_{m,s}}{A} \tag{1}$$

where A is patch quality, $\tau^{*}_{m,s}$ is the maximum travel time individual m of species s would be willing to travel to a patch of infinite quality and $\omega_{m,s}$ is a term <0 that describes the trade-off the individual makes between patch quality and travel time. Both $\tau^{*}_{m,s}$ and $\omega_{m,s}$ are dynamic optimal solutions that maximize fitness, G. Thus, they depend on the

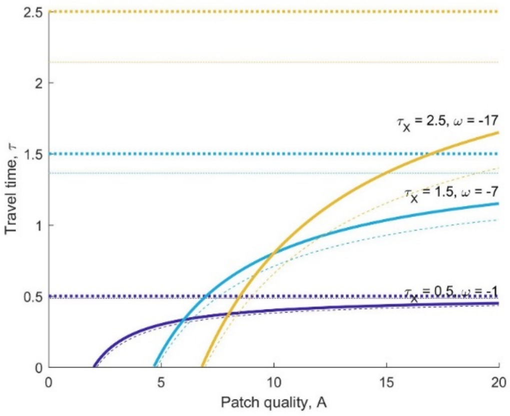


Figure 1. Maximum travel time (τ) to spend for going to a patch of quality A as given by expression 1. The dashed curves are the optimal solutions in particular environments ($\tau^{*}_{m,s}, \omega_{m,s}$), and the solid curves are the maximum capacity of the species, as given by the parameters τ_X, and ω_X. Each color represents one trait combination, i.e. one species

individual's fitness prospects, and therefore the proximity to foraging patches and patch qualities in the environment. They are also determined by several parameters that depend on the species life-history (Table 1). Expression (1) provides a zero-marginal-fitness isocline describing the combination of travel time and patch quality that give no fitness contribution, but those below the curve contribute positively to fitness, and those above would reduce fitness if used (Fig. 1b). In a poor environment this isocline rises higher, which allows the forager to access more patches but at a greater cost. In a rich environment there are many high quality patches near the nest, and thus optimal habitat use is to use those, and avoid going too far-away patches, i.e. a low value of $\tau^*_{m,s}$.

Fitness is defined as the product of long-term survival rate and reproductive value (Olsson and Bolin 2014), which are non-linear functions of travel and foraging times, predation risk and energy intake rate. For any explicit landscape maximum fitness can be calculated, and the optimal choices of $\tau^*_{m,s}$ and $\omega_{m,s}$ can be found (Olsson and Bolin 2014). However, the expressions for these are complex, and computationally expensive. These expressions also include up to 10 parameters, which are related to the species' life history and foraging strategy, which means that describing a species by these parameters is difficult.

Two parameter CPF model with dynamics as in an optimization model

However, here we describe a simplified and approximate solution that is based on the fact that $\tau^*_{m,s}$ has a fixed maximum, with a corresponding minimal value of $\omega_{m,s}$. That is, we can describe the species by their maximum travel distance and trade-off between energy gain and travel time, τ_X and ω_X (we ignore the index s for species to avoid cluttering expressions, but the τ_X and ω_X, as well as all the parameters in Table 1 are species specific). The maximum travel distance an individual of species s would ever travel, τ_X, would thus be to a patch of infinite quality in an environment of quality so low that energy reserves (and hence fitness) were zero (cf. Olsson and Bolin 2014). At that limit the expressions for τ^* and ω are constants, with much simpler expressions and we get:

$$\tau_X = \frac{L}{c(\beta - \alpha)} \tag{2}$$

and

$$\omega_X = \frac{\alpha - 1}{\beta - \alpha} L \ , \tag{3}$$

where the symbols on the right hand side are the species specific values of the parameters described in Table 1. That is, they depend on the metabolic rates and the loading capacity of the forager. The above expressions can be rearranged to:

$$\beta = \frac{L(\alpha - 1)}{\omega_X} + \alpha \tag{4}$$

and

$$c = \frac{\omega}{\tau_X(\alpha - 1)} \ . \tag{5}$$

In the following we assume that loading capacity, L, is constant across species, i.e. we think of similarly sized species, and for simplicity that the metabolic cost of being in the nest, α, is zero. In such cases, any unique combination of τ_X and ω_X will map to a specific combination of c and β. That is, rather than choosing the metabolic rates, which can be difficult to know or measure, we can pick values of maximum travel distance and the trade-off between patch quality and travel distance, which are more intuitive and can be estimated from field data (cf. Olsson and Bolin 2014). It is worth noting, however, that τ_X is the absolute maximum of a species that it would only use in a desperate situation. In most real situations, where fitness is positive, individuals of the species will not travel that far, but use a $\tau^*_{m,s} < \tau_X$.

Similar to Olsson and Bolin (2014), we propose the following measure of habitat suitability in the landscape:

$$S = \sum_{D_i > 0} D_i \tag{6}$$

where

$$D_i = \tau_X + \frac{\omega_X}{A_i} - \tau_i, \tag{7}$$

i.e. S sums the values of all patches below the isocline given by the parameters τ_X and ω_X. Calculating S in itself does not require any optimization, but can be done for any explicit landscape with any combination of the parameters.

Two parameter central place foraging model simulations

The full optimization CPF (Olsson et al. 2015) was run with combinations of c and β that corresponded to combinations of τ_X and ω_X, while keeping the other life-history parameters constant (Table 1). The values of τ_X ranged from 0.5 to 3 km and ω_X from -0.5

to -9. For each such combination 1000 landscapes with 25 m pixel size and patch quality ranging from 0 to 25 were created to produce a wide range of habitat qualities. For each simulation fitness (*G*), optimal $\tau^*_{m,s}$ and $\omega_{m,s}$ and *S* were saved together with the τ_X and ω_X values, and non-linear regression (nls in R) was then used to find functions that described *G*, $\tau^*_{m,s}$ and $\omega_{m,s}$ as functions of τ_X and ω_X. The fit was nearly perfect.

The forager's fitness can thus be described as a function of *S* and τ_X and ω_X:

$$G = a_1\left(1 - e^{-a_2 S^{a_3}}\right) \tag{8}$$

where

$$a_j = k_{\mathrm{j},1} + k_{\mathrm{j},2}\log\tau_X + k_{\mathrm{j},3}\omega_X + k_{\mathrm{j},4}\omega_X\log\tau_X \tag{9}$$

is a general linear function that relates the three parameters in (8) to τ_0 and ω_0. The parameter values to use are:

	$k_{j,1}$	$k_{j,2}$	$k_{j,3}$	$k_{j,4}$
lna_1	5.3456	0.25469	0.062811	-0.038821
a_2	0.028364	0.00052189	0.00068148	-0.00025417
lna_3	-0.60063	-0.42197	-0.037331	0.020081

The optimal maximum travel distance τ^* is another function of the same variables:

$$\tau^*_{m,s} = \tau_X \left(1 - b_1 e^{-b_2 S^{b_3}}\right) \tag{10}$$

where b_1 and b_2 are described by:

$$b_j = m_{\mathrm{j},1} + m_{\mathrm{j},2} \log \tau_X + m_{\mathrm{j},3} \sqrt{-\omega_X} + m_{\mathrm{j},4} \log \tau_X \sqrt{-\omega_X} \tag{11}$$

with values:

	$m_{j,1}$	$m_{j,2}$	$m_{j,3}$	$m_{j,4}$
b_1	0.64254	0.23004	0.0041198	-0.017409
b_2	18.492	-9.7936	-0.15995	1.3360

and b_3=-0.23301-0.019514 b_2.

Finally, the optimal ω^* is:

$$\omega^*_{m,s} = -2 + \frac{2 + \omega_X}{\tau_X} \tau^*_{m,s} \ . \tag{12}$$

Using the above regression functions, it is hence possible to get fitness and the optimal solution of maximum travel distance and trade-off, in any explicit environment for any trait combinations, by using the two parameters τ_X and ω_X, and given values of the other parameters. This method is substantially faster to calculate and therefore preferable to use in large landscapes.

Table 1. Central place foraging model parameters

Parameter	Value	Description
v	1	Flight speed
L	4	Load size the forager may collect
c	variable	Metabolic rate while foraging
μ	0.001	Predation rate while foraging
α	0	Metabolic rate multiplier while in the nest
β	variable	Metabolic rate multiplier of flying
δ	0	Predation rate multiplier while sitting in the nest
ε	2	Predation rate multiplier while flying
x	0.75	Parameter describing diminishing returns of energy
T	250	Length of the breeding season in time units

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CHAPTER 4: POLLINATOR HABITAT ENHANCEMENTS INCREASE TAXONOMIC AND FUNCTIONAL DIVERSITY OF WILD BEE COMMUNITIES ACROSS CROP-REGIONS

4.1 Abstract

Supporting ecosystem services and conserving biodiversity may be compatible goals, but concern exists that actions targeting services advantage common, functionally dominant species. Few studies have examined whether service-providing species and biodiversity respond differently to a given management action. For example, supporting pollination by enhancing floral resources may benefit both dominant crop pollinators and rarer bees of conservation concern, but this remains untested. Here we used a spatially replicated, multiyear experiment to ask whether enhancing floral resources adjacent to crops increase the taxonomic and functional diversity of wild bee communities, while sustaining the provision of ecosystem services by increasing the diversity and abundance of crop pollinators. We sampled bee communities on crops and on enhanced and control field margins in three regions representing major production areas in the US. We found that, compared to control edges and crops, enhanced field margins (1) harbored more abundant and diverse bee communities, (2) had more dissimilar bee communities, and (3) had greater functional diversity. Importantly, however, enhancements did not increase the abundance or diversity of bees on crops, indicating that the provision of pollination services was unchanged by improving pollinator habitat. Taken together, our findings show that actions aimed at promoting crop pollination can benefit broader patterns of biodiversity, underscoring their conservation value, but the benefit of enhancements for

ecosystem services is less clear. Ecosystem service benefits are often context dependent and further experimentation is required to understand the conditions that lead to effective co-management of pollinators and pollination.

4.2 Introduction

Ecosystem services (ES) and biodiversity conservation have been cast as compatible goals based on the implicit assumption that they covary (MEA, 2005). However, evidence that biodiversity and ecosystem services are linked is mixed and the ecological dynamics behind this link remain unclear (Ricketts et al., 2016). While governments and international institutions increasingly adopt ES into conservation planning and decision-making (Bateman et al., 2013; Guerry et al., 2015; Posner, Getz, & Ricketts, 2016), there is concern that ecosystem services are an unsuitable surrogate for biodiversity conservation (Schröter et al., 2014; Vira & Adams, 2009)

Concern around biodiversity and ES co-conservation stems from uncertainty of the underlying mechanisms by which biodiversity drives ecosystem functions (EF) (Cardinale et al., 2012). Mechanisms central to biodiversity-EF theory depend on the functional attributes of communities, the functional dominance of species within a community determines relationships between these ES and species richness (Díaz et al., 2007; Hillebrand, Bennett, & Cadotte, 2008). Although empirical evidence shows that diverse communities optimize resources and can thus be more productive (i.e., niche complementarity, Cardinale et al., 2011; Loreau et al., 2001), ecosystem functioning can also be sustained by a small number of functionally dominant species within a community (i.e., mass ratio (Grime, 1998; Lohbeck et al., 2016). If a few common species, and not species richness, sustain service delivery, then interventions focused on ES may benefit only a subset of total species.

Recent work with pollination has highlighted the potential for decoupled relationships between ES and species richness. Pollination is an important ES for agriculture worldwide (Klein et al., 2007), and diverse bee communities in particular enhance and stabilize yields (Brittain, Kremen, & Klein, 2013; Garibaldi et al., 2011). Although many bee species persist in agricultural landscapes, pollination services can be supplied by a few relatively abundant species (Balvanera, Kremen, & Martinez-Ramos, 2005). If relative contributions of species to ecosystem function are skewed, then a few common, functionally dominant species will drive pollination function differences, while many uncommon and functionally unimportant species drive richness differences (Winfree et al., 2015). This outcome is underscored by results from across crops and bio-geographical regions showing 2% of bee species provide the majority of crop visitation (Kleijn et al., 2015). Moreover, these functionally-dominant species may respond positively to agricultural conservation measures (e.g. organic farming, wildflowers or grass margin strips) (Kleijn et al., 2006). If these actions only benefit functionally dominant species over species richness and diversity, then effective pollination management and pollinator conservation may be incompatible goals (Senapathi et al., 2015).

Few studies have examined whether crop pollinating species and uncommon species respond differently to a given management action and no studies have examined whether efforts that promote one group trade-off conservation of the other (Cariveau &

Winfree, 2015). Pollinator biodiversity and pollination services may have diverging responses. For example, pesticide application can reduce species richness, while pollination levels remain unaffected (Brittain et al., 2010). Conversely, enhancing floral resources may benefit both dominant crop pollinators and uncommon bees, but this remains untested.

Most pollinators, dominant or not, depend on habitat that offers suitable nesting and foraging resources (Kremen et al., 2007). Enhancing local vegetative diversity can improve the abundance and richness of pollinators (Haaland, Naisbit, & Bersier, 2011; Scheper et al., 2015) and can reverse homogenization of pollinator communities in agriculture (Ponisio, M'Gonigle, & Kremen, 2016). Assessing the ecological effects of enhancing pollinator habitat should compare trends between farms with and without enhancements; however, where ecosystem services and biodiversity are assessed is an important design detail. We argue that ecosystem service benefits should be measured where they are realized (i.e., on crops), whereas biodiversity can be measured both on and off crops (Figure 1). Whether enhancements support service provision and biodiversity, therefore, depends on answering the question: do enhancements benefit pollinator communities both on and off crops, in only one location, or in neither location?

We investigate this question with a spatially replicated, multiyear study that established flower rich field margins adjacent to pollinator-dependent crops in four USA agricultural regions. We tested the effect of enhancing pollinator habitat on the taxonomic and functional diversity of wild bee communities. Specifically, we asked: (1) Is there overlap in species pools visiting crop and non-crop areas? (2) Do enhancements increase the diversity of wild bee communities on and off crops? (3) Do enhancements increase functional trait diversity of wild bee communities on and off crops?

4.3 Methods

4.3.1 Study Regions and Experimental Design

We sampled bee diversity in three regions representing major production areas of pollinator-dependent crops in the US: the northern Central Valley of California, Oregon's Willamette valley, and western Michigan (Figure 1). In California, we sampled bees on watermelon (*Citrullus lanatus* Thunb.). Watermelon is monoecious and depends on multiple bee visits to set fruit (Stanghellini, Ambrose, & Schultheis, 2002; Winfree, Williams, Dushoff, & Kremen, 2007) and is visited by > 40 bee species in the Central Valley (Kremen, Williams & Thorp, 2002). In Oregon and Michigan, we sampled bees on highbush blueberry (*Vaccinium corybosum* L.). Blueberry is dependent on native bee pollination because pollen is most effectively removed via sonication (Javorek, Mackenzie, & Vander Kloet, 2002). Previous work found 30 species of bees visiting blueberry in Oregon (Rao, Stephen, & White, 2009) and 167 species in Michigan (Tuell, Ascher, & Isaacs, 2009). In Michigan, we also sampled bees from sour cherry (*Prunus cerasus* L.). Sour cherry is pollinator dependent and 76 wild bees are known floral visitors in this region (Gibbs et al., 2017).

In each crop-region we selected at least ten farms and for half of these seeded an area of land adjacent to crop fields with a diversity of flowering annual and perennial wildflowers (henceforth an 'enhancement edge'). Enhancement edge site preparation varied by region given local management constraints, but largely followed the cultivation methods outlined by Williams et al. (2015). Farms with enhancement edges were paired with farms with unmanaged field margins dominated by grasses (‘control edges’). Bees were sampled both on crop (i.e., crops with and without enhancement edges) and off crop (i.e., enhancement and control edges) during respective bloom periods (Figure 1). Like many previous ecosystem service studies, we focus on the biophysical sources of provision, with wild bee abundance representing the supply pollination services (Ricketts et al., 2016). A full assessment of ES would also quantify realized benefits, but that is beyond the scope of this study.

4.3.1.1 Sample collection. At these four site types (hence, ‘enhancement edges’, ‘control edges’, ‘on crop with’, and ‘on crop without’), we sampled bees via direct aerial netting. On crop collections occurred during crop bloom along transects starting at the crop border and at 25, 50, and 100 m into the crop field. Under amenable weather conditions (>15ºC, low wind speeds, at least partial sun, no precipitation), we walked 40 m transects for 10 minutes netting all wild bees visiting crop flowers. In each crop-region each site was visited three times, except, owing to a brief bloom period of sour cherry, only a single collection day was possible per field in each year, but we sampled bees for a total of 30 minutes to equalize survey effort. Off crop collections occurred following crop bloom at two randomly placed 50 m transects. Under similar weather conditions we walked each transect for 20 minutes. Sites were sampled between three and five times per year depending on the floral phenology of the enhancement edge. Using published keys and reference voucher material, Michigan specimens were identified by JG and TJW and California and Oregon specimens were identified by RT, Robin Jean, and JG. Depending on crop-region, between 2 to 4 non-native bee species were collected (Table S2). These 10 species represent <3% of all individuals and, because we focus on wild native bees, we excluded them from analyses. A total of 215 specimens (<3% of all individuals) could not be identified to species level, for analyses these specimens are retained and given morphospecies identifiers (e.g., *Osmia sp. 1*) unique to each crop-region (Table S1).

4.3.1.2 Wild bee trait data. We compiled information on life history traits known to influence habitat associations for all fully resolved species collected across the crop-regions (Williams et al., 2010). These response traits included body size (measured as the intertegular distance (ITD)) and three categorical traits: dietary specialization (lecty), nesting location, and sociality. For lecty, we recorded bees as oligolectic if females are known to collect pollen from a single family. For sociality and nest location we followed Bartomeus et al. (2013) and scored bees as being solitary, facultatively social or completely social and as nesting in wood, soil, holes, stems or cavities. We compiled these data from published sources (Bartomeus et al., 2013; Cane, Griswold, & Parker, 2007; Forrest et al., 2015; Krombein, 1967; Michener, 2000; Sheffield, Ratti, Packer, & Griswold, 2011) and based on our combined taxonomic expertise. Body size measurements were available for 139 species, for species without ITDs we substituted missing values with the genera specific average body size for each crop region. For social species (e.g., Bombus) we used worker ITDs because this caste is typically more abundant across growing seasons.

4.3.2 Data Analysis

We did not compare communities between crop-regions because our focus is on local drivers rather than large scale biogeographical patterns or evolutionary histories, which likely shape differences between regional species pools. Instead, we focused on differences between site types in terms of taxonomic and functional diversity.

4.3.2.1 Taxonomic diversity. For each site at each farm in each crop region we calculated yearly metrics of both observed (species richness, Shannon diversity) and estimated (chao1) species diversity. We used these diversity metrics as response variables in linear mixed models with site as a fixed effect and farm nested in crop-region and year as separate random effects (Bates, Mächler, Bolker, & Walker, 2015). We report results of pairwise comparisons with a Bonferroni-Holm correction.

We investigated community composition differences between site type using abundance-based Bray-Curtis dissimilarities. We compared community dissimilarity between site types using permutational multivariate analysis of variance (PERMANOVA (Anderson & Walsh, 2013)), with farm as a strata within which to constrain permutations, effectively shuffling bee communities among site types. To understand whether bee communities are dissimilar between specific site types within crop-regions, we performed pairwise comparisons between site type combinations (six total comparison per region, Figure 1). We used nonmetric multidimensional scaling to visualize these differences.

We further compared species composition by assessing associations between individual bee species and site types using indicator species analysis (De Cáceres & Legendre, 2009). We calculated indicator values (IV) for each bee species, which are the product of a species frequency within a site type (fidelity) and the predictive power of the species as indicator of the site type (specificity) (De Cáceres, Legendre, & Moretti, 2010). We tested the statistical significance of these associations with 999 permutations (Dufrêne & Legendre, 1997).

4.3.2.2 Functional diversity. We computed two complementary trait diversity indices (trait richness and trait dispersion) using the ‘FD’ package weighting by abundance and with a Cailliez correction for non-Euclidean distances due to the inclusion of categorical traits (Laliberté & Legendre, 2010; Villéger, Mason, & Mouillot, 2008). We calculate trait richness (FRic) based on total branch lengths of a trait dendrogram (Gagic et al., 2015), which quantifies the extent of trait complementarity among species (Petchey & Gaston, 2006). This index is highly correlated with the other trait richness metrics and allows quantification of communities with low species richness (Garibaldi et al., 2015). We also calculated trait dispersion (FDis) which quantifies the average multivariate distance of every species in trait space from its community centroid (if richness = 1, then FDis = 0) (Laliberté & Legendre, 2010).

We further explored trait composition by calculating the community weighted mean (CWM) of each of our four traits. For categorical traits, CWM represents the proportion of individuals at a site type expressing one of the possible traits (Díaz et al., 2007). For each crop region, we calculated functional diversity and trait composition for the community of bees collected at each site on each farm separately for each year. To determine whether functional diversity and average community weighted trait values differ between sites, we used these metrics as response variables with the same model structure as above with body size log transformed and a logit transformation of proportional CWM values (Warton & Hui, 2011).

4.4 Results

4.4.1 Wild Bees Collected on and off Crops

Across the 4 crop-regions, we collected 7435 specimens representing 223 fully resolved species belonging to 35 genera. The most species-rich genera were *Lasioglossum* (55 species), *Andrena* (42 species), *Melissodes* (16 species), and *Bombus* (15 species). Most species were collected infrequently: 37% of species were observed two or fewer times. Specifically, on enhanced edges 130 species were singletons or doubletons, on control edges: 80 species, on crops with: 63 species and on crops without enhancements: 58 species (Figure S1). The four crop regions differed in the abundance and richness of taxa collected (Figure 2; Table S1). The proportion of total specimens composed of species only collected on crops ranged from 0% (CA) to 42% (MI cherry). Similarly, the proportion of off crop species (i.e. only collected on enhanced and control edges) ranged from 14% (MI cherry) to 61% (OR). The proportion of ubiquitous species (i.e., those collected on all site types) ranged from 8% (OR) to 71% (CA). Across crop-regions, 35 species were collected exclusively on crops and 134 species were collected exclusively off crops (Figure 2).

Indicator species analysis revealed significant associations with enhanced edges for 41 species, control edges for 11 species, on crops with enhancements for 15 species and without for 13 species. Species positively associated with enhancements were taxonomically diverse (Table S3) and included both regionally important crop-pollinating species (e.g., MI blueberry: *Bombus* sp.) and more uncommon species (e.g., MI blueberry: *Melissodes* sp.).

Across crop-regions, abundance, diversity and estimated richness of wild bees collected on enhanced edges were greater compared to communities collected on crops and control edges (Figure 3; Table 1). Species evenness did not differ between site types, except communities collected on crops with enhancements were more even than the enhancements themselves (Figure 3; Table 1). Between crops with and without enhancements the same set of diversity measures did not differ (Figure 3; Table 1). Notably, wild bee abundance on crops, our measure of potential ecosystem service supply, did not differ between treatments. Our focal comparisons, on crop with v. on crop without (Figure 1a, black arrows) and enhanced edge v. control edge (Figure 1b, red arrows) were consistent across crop-regions (Figure S2).

4.4.2 Wild Bee Composition between Site Types

Pairwise comparisons within crop-regions show that communities were consistently dissimilar between site types. Most of this dissimilarity is unsurprising given comparisons are between communities collected at different time periods (Figure 1a, dashed lines). For concurrent comparisons (Figure 1a, black and red arrows), enhanced and controlled edge communities were dissimilar for all crop-regions, except Oregon (enhanced v. control, Table 2, Figure S3). Whereas communities collected on crops were similar to one another (on crop with v. on crop without, Table 2, Figure S3).

4.4.3 Trait Composition Between Site Types

Functional trait richness and dispersion of bee communities was greater on enhanced edges compared to control edges and on crops (Figure 4; Table 3). Bee body sizes were larger off crop, and largest in enhanced edges (Figure 6; Table 4). Enhanced and controlled edges tended to have lower proportions of polylectic species, and polyleges were encountered least often on enhanced edges (Figure 6; Table 4). Bees off crops were less frequently solitary species and nested in cavities (Figure 6; Table 4).

4.5 Discussion

We found that enhancements supported ecologically diverse and distinct communities of wild bees when compared to control edges and crops. Enhanced edges harbored greater taxonomic and functional diversity and we observed greatest community dissimilarity among enhancements sites. These results indicate that restoring floral resources in agriculture can increase diversity locally and support greater β-diversity at landscape scales. Conversely, abundance and diversity of wild bee communities on crops did not differ between enhanced and unenhanced farms within sites. These findings indicate that the community benefits experienced by enhancements are not spilling over to crops. Taken together, our findings show that pollinator habitat enhancements benefit broader patterns of biodiversity, but do not achieve their intended purpose: improving crop pollination services. The ecosystem service benefits from restoring pollinator habitat are often context dependent and further experimentation is required to understand the conditions that benefit both pollinators and pollination.

We observed greater abundance, richness and diversity of wild bees collected on enhanced edges, adding support to a growing body of evidence that small, field-scale habitat restoration can increase farmland biodiversity (Carvell et al., 2007; Schulte et al., 2017; Williams et al., 2015). The strength of the effect of enhancements varied between regions, but was consistently positive. On average enhanced edges supported 44% greater wild bee abundance and 40% greater diversity compared to unmanaged control edges. We found that the evenness of bee communities did not differ between sites, except when comparing enhanced edges and their corresponding on crop communities. This difference is unsurprising because we observed more singletons and doubletons on enhancement edges compared to control edges or crops.

However, between crops with and without enhancements, we did not observe greater abundance, richness and diversity of wild bees. This is surprising given that previous studies have shown that enhanced floral resources adjacent to pollinator-dependent crops often increase crop visitation (Morandin & Kremen, 2013) and support higher crop yields (Blaauw & Isaacs, 2014a). Increased wild bee presence on crops is likely the product of additional nesting and foraging resources (Potts et al., 2005; Roulston & Goodell, 2011). Enhancing floral resources in agriculture can promote the persistence of diverse wild bee communities (Carvell et al., 2017), but it is often assumed these actions will improve crop pollination in kind. The ecosystem service benefits of restoring pollinator habitat are context dependent (Sardiñas, Ponisio, & Kremen, 2016; Scheper et al., 2015) and take time to materialize (Blaauw & Isaacs, 2014b). Whether, and to what degree, enhancements affect the provision of ecosystems services remains unresolved.

We also show that on-farm enhancement of floral resources promotes more heterogeneous bee communities. Community composition was more dissimilar among enhanced edges than among control edges. Therefore, enhanced edges not only harbored more diverse communities, but supported greater landscape levels of β-diversity as well. Anthropogenic land use can alter patterns of β-diversity by homogenizing habitat structure across entire landscapes (McKinney & Lockwood, 1999; Püttker, de Arruda Bueno, Prado, & Pardini, 2015), thereby imposing ecological filters that generate communities similar in species composition (de Castro Solar et al., 2015; Tabarelli, Peres, & Melo, 2012), trait composition (Karp et al., 2012), and evolutionary history (Frishkoff et al., 2014). Similarly, restoration may filter communities and increase β-diversity by creating habitat heterogeneity. For example, restoration of hedgerows increased β-diversity in Californian agricultural landscapes by re-establishing a phenotypically diverse assemblage of wild bees (Ponisio et al., 2016). In this system, only mature hedgerows (established >10 years ago) supported higher community dissimilarity when compared to non-restored controls. Interestingly, in our system we found high levels of community dissimilarity on enhanced edges that had been established for <2 years. The rapid response of bee communities in our system may be explained by findings showing early phase restoration benefits for pollinator communities due to greater colonization and persistence (M'Gonigle et al., 2015). Biotic homogenization of communities is increasingly considered a signature of the

Anthropocene (Magurran et al., 2015), leading to calls for conservation planning to consider drivers of changing β-diversity patterns (Socolar, Gilroy, Kunin, & Edwards, 2016). Like others, we show that floral enhancements help counter biotic homogenization of wild bee communities in agriculture.

In addition to increasing taxonomic diversity and dissimilarity, enhanced edges also supported bee communities with greater functional richness and dissimilarity. Agricultural land use reduces functional diversity of many taxa (Flynn et al., 2009), including wild bees (Forrest et al., 2015). Functional diversity has been linked to reproductive success in wild plant communities (Fontaine, 2006), as well as crop species (Hoehn et al., 2008). Using a similar set of traits and diversity metrics as those applied here, Garibaldi et al. (2013) showed that functional diversity was positively related with fruit set across biogeographical regions for multiple crops. Functional diversity may also stabilize the provision of pollination services (Winfree & Kremen, 2009), because functional groups respond differently in the face of change (i.e., response diversity (Brittain et al., 2013; Cariveau et al., 2013; Elmqvist et al., 2003)) or multiple species share similar traits (i.e., functional redundancy (Blüthgen & Klein, 2011; Naeem, 1998). Although the functional diversity on crops with and without enhanced edges did not differ, enhanced edges may act as pools of functional diversity and contribute to ecosystem resilience.

Enhanced edges differed in the trait composition of their bee communities. Specifically, enhancement bees had larger body sizes, more often nested in stems and cavities, and were less often diet generalists or solitary species. However, trait composition varied largely between crop-regions. For example, more solitary species observed on crops is partly driven by the dominance of this functional group in MI cherry crops. This same group of cherry-visiting solitary species, also tended to have smaller body size when compared to off crop communities. Across crop regions, fewer polylectic species were collected on enhanced edges. Trophic specialization can impact species' sensitivity to land-use change (Newbold et al., 2012; Winfree et al., 2011) and previous work has found that oligolectic bees are less abundant on farms (Forrest et al., 2015).

We have shown that enhancements do not always increase the supply of pollination services, yet a few points deserve mention. First, we do not demonstrate whether this pattern carries through to crop production. Properly determining whether enhancements improve pollination services would require assessing assessing actual changes in crop production. Furthermore, enhancing crop field margins may promote multiple ecosystem services beyond crop pollination (e.g., pest control, soil retention) and their net benefit may only be realized if measured as a net change in production (Lundin, Smith, Rundlöf, & Bommarco, 2013). This work is ongoing, but beyond the scope of the present paper. Second, our results lead to an important point concerning quantifying where biodiversity and ecosystem service benefits occur in landscapes. Ecosystem service benefits should be assessed where they are realized, on crops. Conversely, biodiversity benefits can be measured off crops, and potentially even in the broader landscape. Comparing only biodiversity observed on crops may lead to flawed conclusions about the conservation potential of enhancing habitat in agriculture (Haaland et al 2011).

Agricultural systems vary widely in their ability to support biodiversity (Karp et al., 2012; Kremen & Miles, 2012) and previous work has indicated that farmland conservation may benefit only a subset of total species (Kleijn et al., 2006). Consistent with other findings (Hannon & Sisk, 2009; Jönsson et al., 2015; Morandin & Kremen, 2013), we find that enhancing the availability of floral resources improves wild bee biodiversity broadly. Two primary goals of restoring habitat are to conserve biodiversity and restore ecosystem functions and services (Rey Benayas, Newton, Diaz, & Bullock, 2009). Farms with enhanced floral resources had more taxonomically and functionally diverse and distinct communities of wild bees, therefore actions taken to promote ecosystem services did not preclude biodiversity conservation. In fact, in our study enhancement effects are stronger for biodiversity than their intended conservation objective: crop pollination. These results underscore the potential multiple benefits of habitat restoration in agriculture.

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4.7 Tables

Table 1 Differences in (a) observed Shannon diversity, (b) Chao1 estimated species richness, and (c) observed evenness between combinations of site types.

(a) Abundance

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	-1.16	0.22	-5.23	**< 0.001**
On crop with - enhanced edge	-1.63	0.23	-7.03	**< 0.001**
On crop without - enhanced edge	-1.46	0.23	-6.28	**< 0.001**
On crop with - control edge	-0.48	0.24	-1.99	0.14
On crop without - control edge	-0.30	0.24	-1.26	0.42
On crop without - on crop with	0.17	0.25	0.71	0.48

(b) Diversity

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	-0.56	0.12	-4.56	**< 0.001**
On crop with - enhanced edge	-0.75	0.12	-6.39	**< 0.001**
On crop without - enhanced edge	-0.80	0.13	-6.16	**< 0.001**
On crop with - control edge	-0.19	0.13	-1.41	0.32
On crop without - control edge	-0.23	0.12	-1.90	0.17
On crop without - on crop with	-0.04	0.14	-0.33	0.74

(c) Estimated richness

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	-9.17	1.87	-4.89	**< 0.001**
On crop with - enhanced edge	-12.08	1.87	-6.45	**< 0.001**
On crop without - enhanced edge	-12.14	1.96	-6.18	**< 0.001**
On crop with - control edge	-2.92	2.02	-1.44	0.38
On crop without - control edge	-2.97	1.94	-1.53	0.38
On crop without - on crop with	-0.05	2.08	-0.03	0.98

(d) Evenness

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	0.02	0.02	0.88	0.76
On crop with - enhanced edge	0.07	0.02	3.29	**0.01**
On crop without - enhanced edge	0.04	0.02	1.65	0.40
On crop with - control edge	0.05	0.02	2.36	0.09
On crop without - control edge	0.02	0.02	0.81	0.76
On crop without - on crop with	-0.03	0.02	-1.43	0.46

P-values corrected for multiple comparisons using Holm’s sequential Bonferroni procedure

Table 2 Pairwise differences in community dissimilarity between combinations of site types for each crop-region. *P*-values from PERMANOVAs comparing abundance-cased Bray-Curtis dissimilarities are reported, with corresponding *F* statistics in parentheses.

Community dissimilarity

	MI blu	MI che	OR blu	CA wat
Control edge v. enhanced edge	**(1.93)** **0.01**	**(1.66)** **0.02**	(1.3) 0.12	**(5.99)** **0.01**
On crop with v. on crop without	(1.01) 0.47	(1.26) 0.11	(1.01) 0.51	(0.48) 0.94
Enhanced edge v. on crop with	**(3.61)** **0.01**	**(6.02)** **0.01**	**(2.7)** **0.01**	**(3.88)** **0.01**
Enhanced edge v. on crop without	**(4.43)** **0.01**	**(6.43)** **0.01**	**(3.29)** **0.01**	**(3.08)** **0.01**
Control edge v. on crop with	**(2.76)** **0.01**	**(3.51)** **0.01**	**(1.87)** **0.01**	**(1.47)** **0.04**
Control edge v. on crop without	**(3.51)** **0.01**	**(3.75)** **0.01**	**(2.31)** **0.01**	**(1.5)** **0.02**

Table 3 Differences in (a) functional richness and (b) dispersion between combinations of site types.

(a) Functional richness

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	-0.34	0.06	-5.73	**< 0.001**
On crop with - enhanced edge	-0.51	0.05	-9.98	**< 0.001**
On crop without - enhanced edge	-0.49	0.06	-7.97	**< 0.001**
On crop with - control edge	-0.17	0.06	-2.74	**0.01**
On crop without - control edge	-0.15	0.05	-2.84	**0.01**
On crop without - on crop with	0.02	0.06	0.32	0.75

(b) Functional dispersion

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	-0.08	0.02	-3.99	**< 0.001**
On crop with - enhanced edge	-0.13	0.02	-7.14	**< 0.001**
On crop without - enhanced edge	-0.12	0.02	-5.58	**< 0.001**
On crop with - control edge	-0.05	0.02	-2.36	0.06
On crop without - control edge	-0.04	0.02	-1.93	0.11
On crop without - on crop with	0.01	0.02	0.63	0.53

P-values corrected for multiple comparisons using Holm's sequential Bonferroni procedure

Table 4 Differences in (a) wild bee body size, (b) proportion polylectic, (c) proportion solitary and (d) proportion cavity nesting between combinations of site types.

(a) Body size

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	-0.20	0.07	-3.08	**0.01**
On crop with - enhanced edge	-0.15	0.05	-3.09	**0.01**
On crop without - enhanced edge	-0.05	0.07	-0.72	0.83
On crop with - control edge	0.06	0.07	0.82	0.83
On crop without - control edge	0.16	0.05	3.12	**0.01**
On crop without - on crop with	0.10	0.07	1.40	0.49

(b) Polylecty

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	0.58	0.23	2.56	**0.04**
On crop with - enhanced edge	0.98	0.18	5.54	**< 0.001**
On crop without - enhanced edge	0.90	0.23	3.86	**< 0.001**
On crop with - control edge	0.40	0.24	1.69	0.24
On crop without - control edge	0.32	0.19	1.75	0.24
On crop without - on crop with	-0.08	0.24	-0.33	0.74

(c) Solitary

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	-0.21	0.41	-0.51	1.00
On crop with - enhanced edge	1.08	0.34	3.15	**0.01**
On crop without - enhanced edge	0.94	0.43	2.19	0.09
On crop with - control edge	1.29	0.44	2.95	**0.01**
On crop without - control edge	1.15	0.36	3.23	**0.01**
On crop without - on crop with	-0.14	0.45	-0.31	1.00

(d) Cavity nesting

	estimate	std. error	*z*	*P*
Control edge - enhanced edge	0.58	0.23	2.56	**0.04**
On crop with - enhanced edge	0.98	0.18	5.54	**< 0.001**
On crop without - enhanced edge	0.90	0.23	3.86	**< 0.001**
On crop with - control edge	0.40	0.24	1.69	0.24
On crop without - control edge	0.32	0.19	1.75	0.24
On crop without - on crop with	-0.08	0.24	-0.33	0.74

P-values corrected for multiple comparisons using Holm's sequential Bonferroni procedure

4.8 Figures

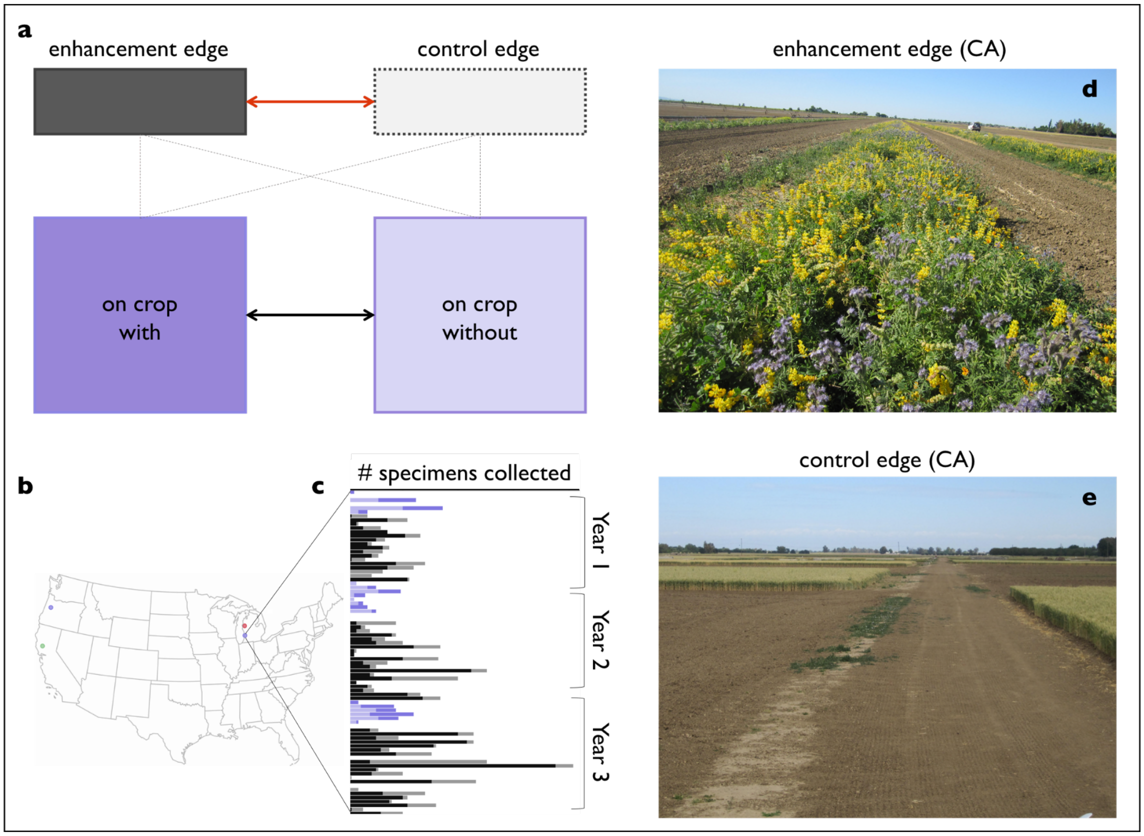

Figure 1 Enhancing pollinator habitat in four USA agricultural regions. Our experimental design (a) consisted of farms with and without pollinator enhancements. Bees were collected both on and off crops at the four site types shown. This effort was replicated in four USA agricultural regions (b; OR blueberry, CA watermelon, MI cherry & MI blueberry) over multiple years (c, e.g. MI blueberry effort where each bar is a sample day). Collections on crops occurred before collections on control and enhanced edges. We therefore emphasize (a, bold arrows) comparisons from concurrent collections, although bee communities could be compared through time (a, dotted lines). Enhancements consisted of diverse wildflower mixes (d) and were paired with unmanaged field margins (e).

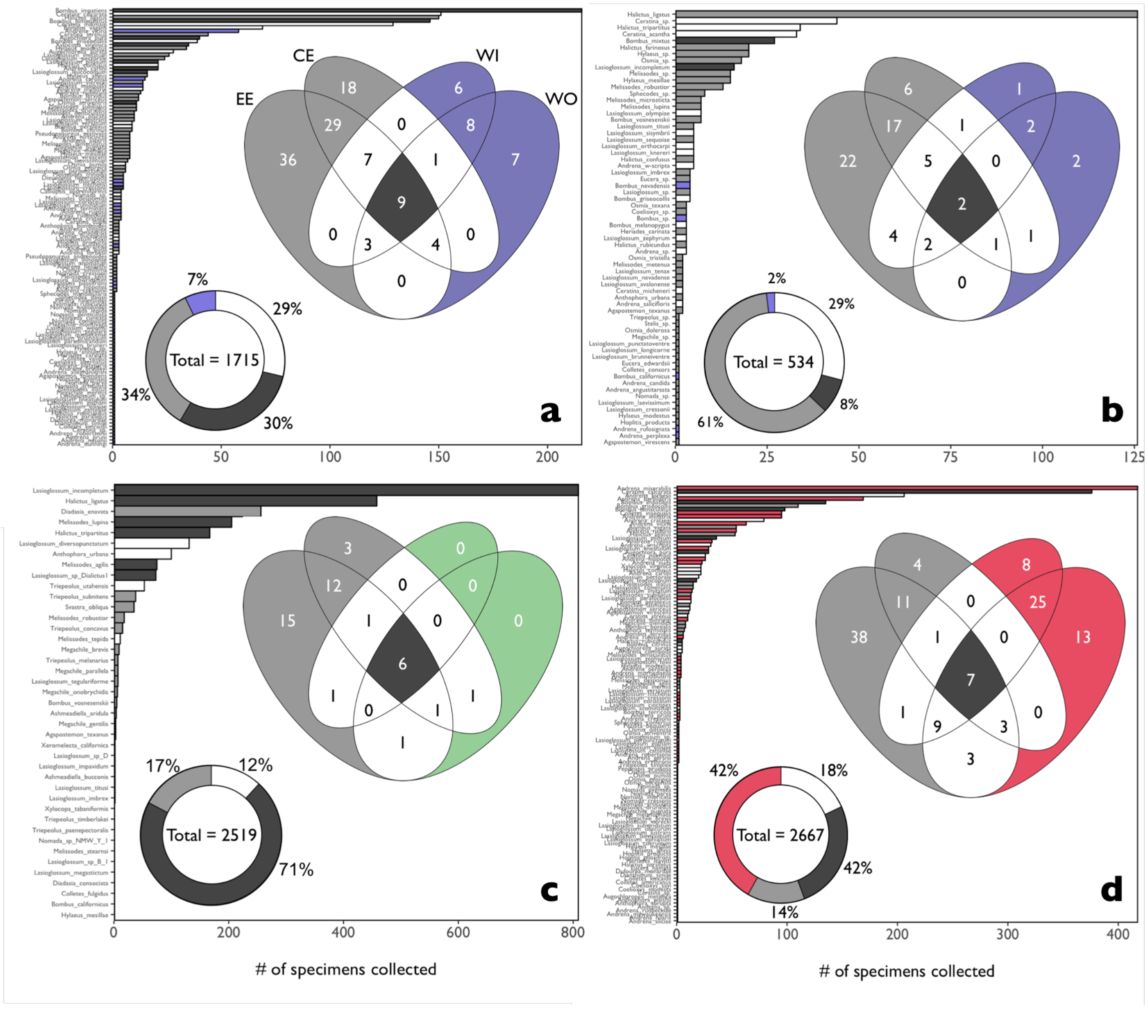

Figure 2 Wild bee rank abundance plots for Michigan blueberry (a), Oregon blueberry (b), California watermelon (c), and Michigan cherry (d). Venn diagrams depict the number of species that were collected on enhanced edges (EE), control edges (CE), on crops with EE (WI) and on crops without EE (WO). Plots are color coded by whether species were collected only on crops (colors), collected only off crops (light gray), collected across combinations of on and off crops locations (white), or collected across all site types (dark gray). Pie charts depict the proportion of total specimens belonging to these classes. Each bar represents a species, for species names and trait information see Table S1.

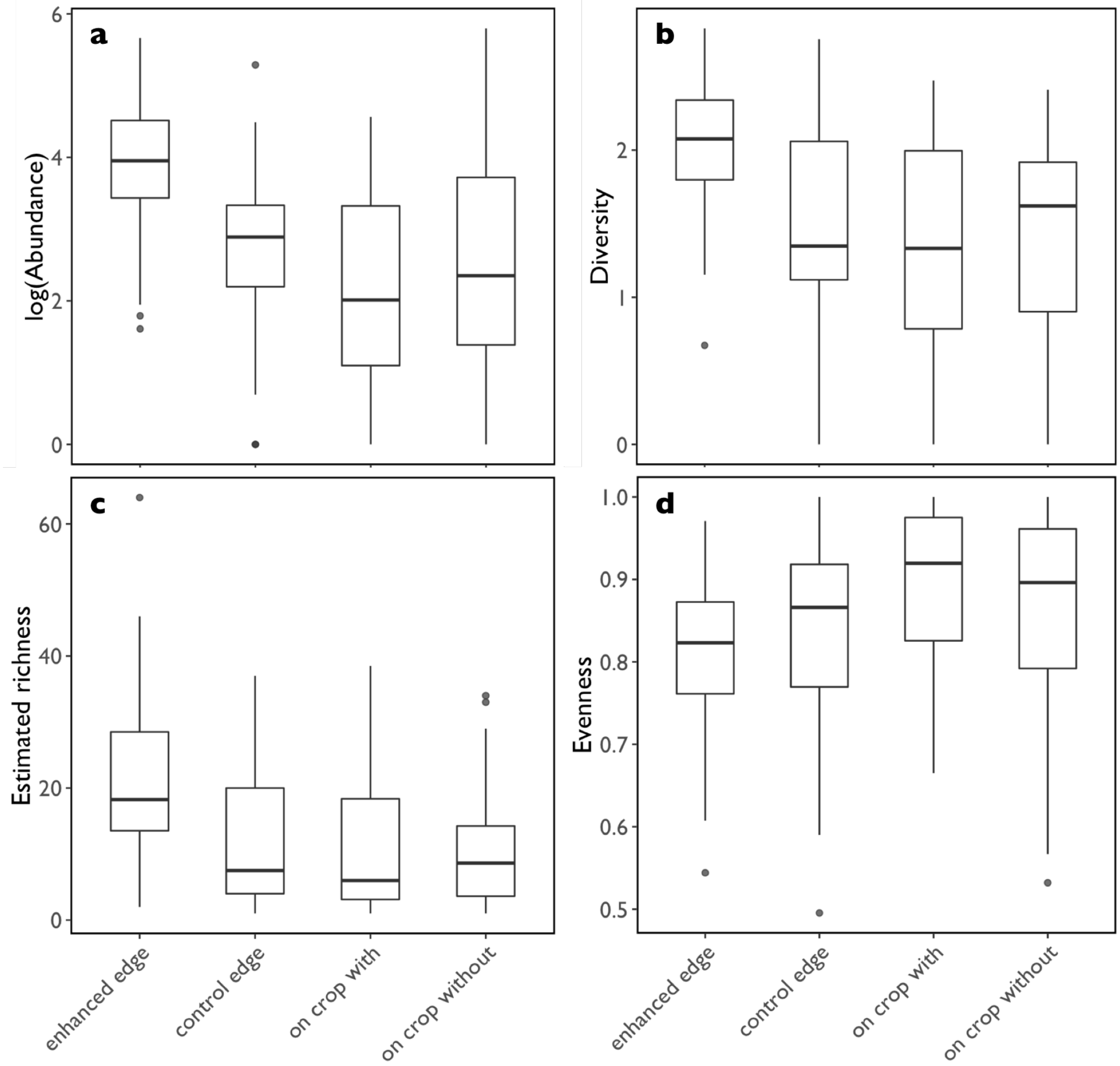

Figure 3 Enhanced edges harbored wild bee communities that were more abundant (a, note log scale) and diverse (b, Shannon diversity) and had greater estimated species richness (c, Chao1 estimator). The evenness of communities did not differ between sites, except between enhanced edges and their crops (d, Pielou's J). For the statistical significance of all comparisons see Table 1.

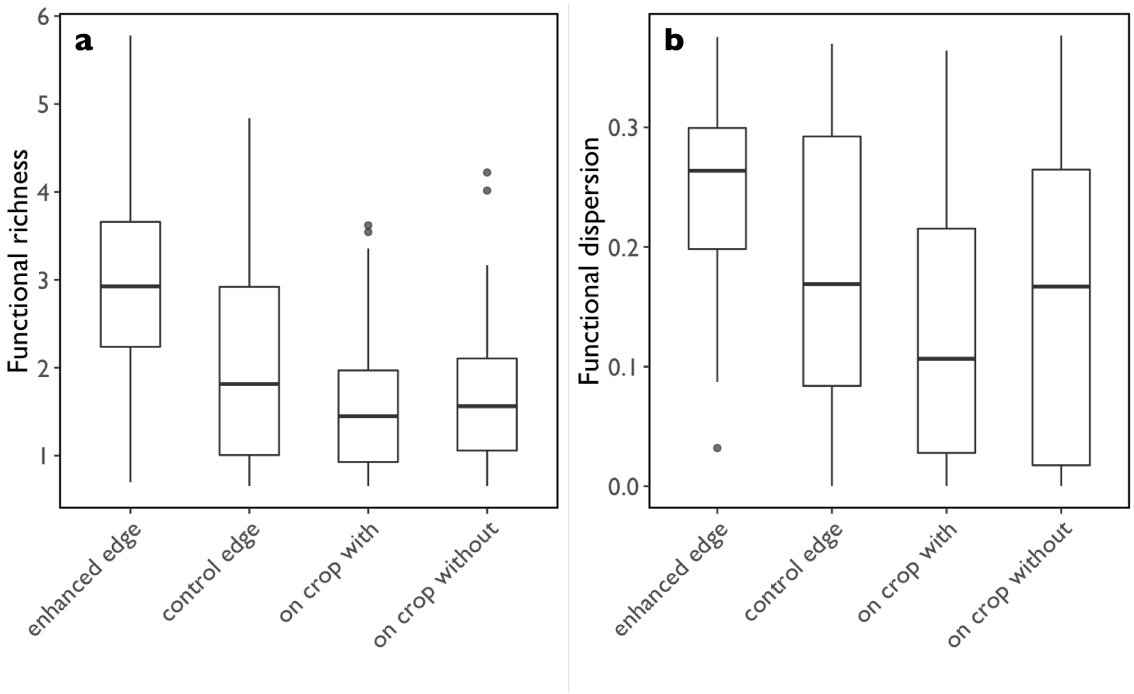

Figure 4 Enhanced edges harbored wild bee communities with greater functional richness (a) and dispersion (b) than control edges or crops communities. Control edges also have greater functional richness than on crop communities. For the statistical significance of all comparisons see Table 1.

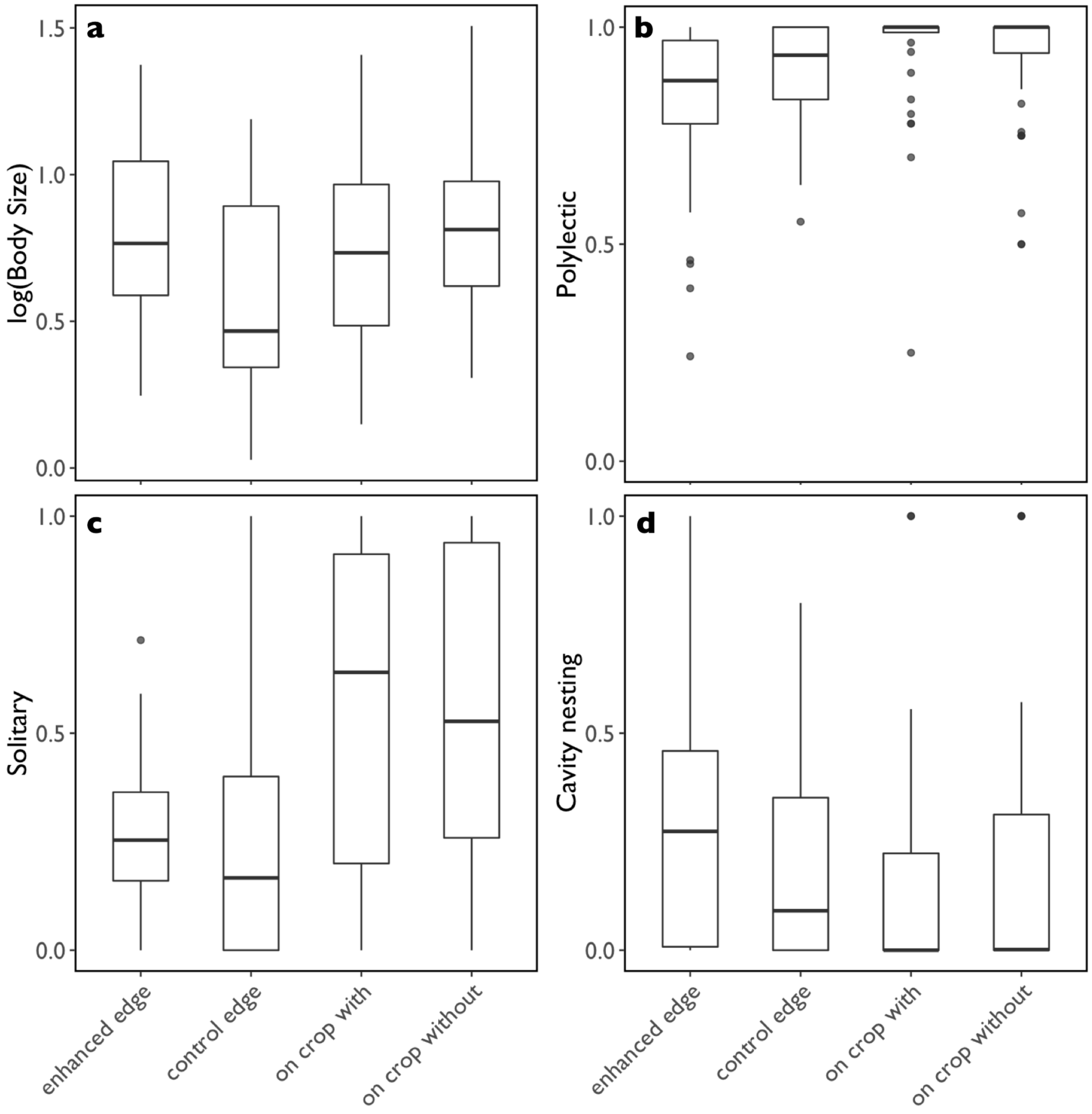

Figure 5 Community weighted mean (CWM) values for 4 traits. Body size (a) is the average intertegular distance across species at a site weighted by abundance. For the categorical traits polylecty (b), sociality (c), and nesting location (d) CWM values are the proportion of bees with a given trait collected at a site. For the statistical significance of all comparison see Table 4.

4.9 Appendix – Supplementary Tables and Figures

Table S1 Species collected from across 4 crop-regions at enhancement edges (EE), control edges (CE), on crops with EE (WI), and on crops without EE (WO). Abundance column (abd) reports specimen totals collected across site types. For fully resolved species the following functional traits are reported: diet specialization (lec), sociality (soc), nest location (nst), and body size (ITD).

	Species	Family	EE	CE	WI	WO	abd	lec	soc	nst	ITD
Michigan blueberry											
	Agapostemon sericeus	Halictidae	1	1	0	0	12	poly	fac	soil	1.90
	Agapostemon splendens	Halictidae	1	0	0	0	1	poly	fac	soil	2.38
	Agapostemon virescens	Halictidae	1	1	0	0	8	poly	fac	soil	2.16
	Andrena alleghaniensis	Andrenidae	1	0	0	0	1	poly	sol	soil	2.32
	Andrena asteris	Andrenidae	1	1	0	0	8	oligo	sol	soil	2.90
	Andrena bradleyi	Andrenidae	0	0	0	1	1	oligo	sol	soil	2.03
	Andrena canadensis	Andrenidae	1	1	0	0	3	oligo	sol	soil	1.98
	Andrena carlini	Andrenidae	1	1	1	1	21	poly	sol	soil	2.70
	Andrena carolina	Andrenidae	0	0	1	1	15	oligo	sol	soil	1.70
	Andrena crataegi	Andrenidae	1	1	0	0	4	poly	sol	soil	2.20
	Andrena cressonii	Andrenidae	1	1	0	0	2	poly	sol	soil	1.75
	Andrena dunningi	Andrenidae	0	0	1	0	1	poly	sol	soil	2.44
	Andrena forbesii	Andrenidae	1	1	1	0	3	poly	sol	soil	2.10
	Andrena helianthi	Andrenidae	1	0	0	0	2	oligo	sol	soil	2.16
	Andrena hippotes	Andrenidae	0	0	1	1	2	poly	sol	soil	2.00
	Andrena hirticincta	Andrenidae	1	1	0	0	8	oligo	sol	soil	2.91
	Andrena imitatrix	Andrenidae	1	0	1	1	14	poly	sol	soil	1.90
	Andrena nasonii	Andrenidae	1	0	0	0	1	poly	sol	soil	1.80

Andrena nubecula	Andrenidae	1	1	0	0	13	oligo	sol	soil	1.84
Andrena nuda	Andrenidae	0	1	0	0	3	poly	sol	soil	2.19
Andrena perplexa	Andrenidae	0	0	1	0	3	poly	sol	soil	2.39
Andrena placata	Andrenidae	1	1	0	0	10	oligo	sol	soil	2.50
Andrena platyparia	Andrenidae	0	0	0	1	1	oligo	sol	soil	2.19
Andrena pruni	Andrenidae	0	0	1	0	1	poly	sol	soil	2.30
Andrena robertsonii	Andrenidae	0	1	0	0	1	poly	sol	soil	1.78
Andrena rudbeckiae	Andrenidae	1	0	0	0	4	oligo	sol	soil	2.16
Andrena rugosa	Andrenidae	0	0	1	1	4	poly	sol	soil	2.30
Andrena simplex	Andrenidae	1	1	0	0	3	oligo	sol	soil	2.34
Andrena vicina	Andrenidae	0	0	1	1	58	poly	sol	soil	2.48
Anthophora bomboides	Apidae	1	0	0	0	3	poly	sol	soil	3.37
Anthophora terminalis	Apidae	1	0	0	0	4	poly	sol	wood	3.76
Augochlora pura	Halictidae	1	1	1	1	40	poly	sol	wood	1.60
Augochlorella aurata	Halictidae	1	1	0	1	28	poly	soc	soil	1.53
Bombus bimaculatus	Apidae	1	1	1	1	146	poly	soc	cavity	3.74
Bombus citrinus	Apidae	1	1	0	0	9	poly	sol	cavity	4.09
Bombus fervidus	Apidae	1	1	0	0	12	poly	soc	cavity	3.63
Bombus griseocollis	Apidae	1	0	1	1	39	poly	soc	cavity	4.34
Bombus impatiens	Apidae	1	1	1	1	216	poly	soc	cavity	4.51
Bombus perplexus	Apidae	1	1	1	0	9	poly	soc	cavity	3.67
Bombus vagans	Apidae	1	1	0	1	69	poly	soc	cavity	3.12
Calliopsis andreniformis	Andrenidae	0	1	0	0	4	poly	sol	soil	1.24
Ceratina calcarata	Apidae	1	1	1	0	151	poly	fac	stem	1.27
Ceratina dupla	Apidae	1	1	0	0	3	poly	fac	cavity	1.17
Ceratina mikmaqi	Apidae	1	1	1	0	129	poly	fac	cavity	1.27
Ceratina sp.	Apidae	1	0	0	0	1	NA	NA	NA	NA
Ceratina strenua	Apidae	1	1	0	0	44	poly	fac	stem	0.93
Coelioxys alternatus	Megachilidae	1	0	0	0	1	para	par	soil	2.53

Colletes inaequalis	Colletidae	0	0	1	1	14	poly	sol	soil	2.86
Colletes kincaidii	Colletidae	1	0	0	0	1	poly	sol	soil	2.63
Colletes thoracicus	Colletidae	0	0	1	1	5	poly	sol	soil	3.19
Colletes validus	Colletidae	0	0	0	1	1	poly	sol	soil	2.90
Dianthidium simile	Megachilidae	1	0	0	0	1	oligo	sol	soil	NA
Dieunomia heteropoda	Halictidae	1	0	0	0	5	oligo	sol	soil	NA
Dufourea monardae	Halictidae	1	0	0	0	1	oligo	sol	soil	NA
Halictus confusus	Halictidae	1	1	1	0	21	poly	fac	soil	1.40
Halictus ligatus	Halictidae	1	1	0	0	150	poly	soc	soil	1.82
Halictus parallelus	Halictidae	0	1	0	0	1	poly	soc	soil	2.55
Halictus rubicundus	Halictidae	0	1	0	0	1	poly	fac	soil	1.75
Heriades carinata	Megachilidae	1	0	0	0	1	poly	sol	cavity	NA
Hoplitis pilosifrons	Megachilidae	1	0	0	0	2	poly	sol	stem	1.55
Hoplitis producta	Megachilidae	0	1	0	0	3	poly	sol	stem	1.24
Hylaeus affinis	Colletidae	1	1	0	0	16	poly	sol	hole	1.30
Hylaeus annulatus	Colletidae	0	1	0	0	1	poly	sol	cavity	1.10
Hylaeus mesillae	Colletidae	1	1	0	0	8	poly	sol	hole	0.98
Hylaeus modestus	Colletidae	1	1	0	0	34	poly	sol	hole	1.03
Hylaeus sp.	Colletidae	1	0	0	0	1	NA	NA	NA	NA
Lasioglossum acuminatum	Halictidae	0	0	1	1	4	poly	fac	soil	1.92
Lasioglossum anomalum	Halictidae	1	0	0	0	2	poly	soc	soil	1.04
Lasioglossum bruneri	Halictidae	0	1	0	0	1	poly	soc	soil	1.45
Lasioglossum cattellae	Halictidae	1	0	0	0	1	poly	soc	soil	1.36
Lasioglossum coriaceum	Halictidae	1	1	0	1	4	poly	fac	soil	1.95
Lasioglossum cressonii	Halictidae	1	1	1	1	5	poly	soc	wood	1.18
Lasioglossum ellisiae	Halictidae	1	0	0	0	1	poly	soc	soil	1.36
Lasioglossum foxii	Halictidae	0	1	1	1	3	poly	sol	soil	1.43

Lasioglossum gotham	Halictidae	0	0	0	1	1	poly	sol	soil	1.36
Lasioglossum hitchensi	Halictidae	0	0	1	1	5	poly	soc	soil	1.36
Lasioglossum illinoense	Halictidae	0	1	0	0	2	poly	soc	soil	1.36
Lasioglossum imitatum	Halictidae	1	1	0	0	26	poly	soc	soil	0.82
Lasioglossum laevissimum	Halictidae	1	1	0	0	7	poly	soc	soil	1.36
Lasioglossum leucocomum	Halictidae	1	1	1	1	16	poly	soc	soil	1.29
Lasioglossum lineatulum	Halictidae	1	0	0	0	1	poly	soc	soil	1.29
Lasioglossum lustrans	Halictidae	1	1	0	0	10	oligo	sol	soil	1.36
Lasioglossum paradmirandum	Halictidae	0	1	0	0	1	poly	soc	soil	1.36
Lasioglossum pectorale	Halictidae	1	1	0	0	24	poly	sol	soil	1.45
Lasioglossum perpunctatum	Halictidae	1	1	0	0	6	poly	soc	soil	1.20
Lasioglossum pilosum	Halictidae	1	1	1	1	21	poly	soc	soil	1.21
Lasioglossum pruinosum	Halictidae	0	1	0	0	1	poly	soc	soil	1.36
Lasioglossum quebecense	Halictidae	0	0	1	0	1	poly	sol	soil	1.63
Lasioglossum sp.	Halictidae	0	0	1	0	1	NA	NA	NA	NA
Lasioglossum subviridatum	Halictidae	0	0	1	0	2	poly	soc	wood	1.20
Lasioglossum tegulare	Halictidae	0	0	0	1	1	poly	soc	soil	0.93
Lasioglossum versatum	Halictidae	1	1	0	1	9	poly	soc	soil	1.35
Lasioglossum vierecki	Halictidae	1	0	0	0	14	poly	sol	soil	0.86
Lasioglossum weemsi	Halictidae	1	0	0	0	1	poly	soc	soil	1.13
Megachile inermis	Megachilidae	0	1	0	0	1	poly	sol	hole	4.28
Megachile mendica	Megachilidae	1	1	0	0	8	poly	sol	hole	3.06
Megachile montivaga	Megachilidae	1	0	0	0	1	poly	sol	cavity	2.68
Megachile pugnata	Megachilidae	1	0	0	0	8	oligo	sol	hole	3.53
Melissodes agilis	Apidae	1	0	0	0	2	oligo	sol	soil	2.33
Melissodes bimaculatus	Apidae	1	0	0	0	8	poly	sol	soil	2.33
Melissodes denticulatus	Apidae	1	1	0	0	10	oligo	sol	soil	2.33

Melissodes desponsus	Apidae	1	0	0	0	4	oligo	sol	soil	2.33
Melissodes druriellus	Apidae	1	0	0	0	11	oligo	sol	soil	2.33
Melissodes illatus	Apidae	1	0	0	0	1	oligo	sol	soil	2.33
Melissodes subillatus	Apidae	1	1	0	0	11	oligo	sol	soil	2.33
Melissodes trinodis	Apidae	1	0	0	0	5	oligo	sol	soil	2.33
Nomada articulata	Apidae	1	0	0	0	1	para	par	soil	1.53
Nomada composita	Apidae	0	0	0	1	1	para	par	soil	1.77
Nomada cressonii	Apidae	0	1	0	0	2	para	par	soil	1.74
Nomada cuneata	Apidae	0	1	0	0	1	para	par	soil	1.77
Nomada denticulata	Apidae	0	0	0	1	1	para	par	soil	1.95
Nomada lepida	Apidae	0	1	0	0	1	para	par	soil	1.77
Nomada luteoloides	Apidae	0	1	0	0	1	para	par	soil	1.82
Nomada parva	Apidae	0	1	0	0	1	para	par	soil	1.77
Nomada pygmaea	Apidae	0	1	0	0	1	para	par	soil	1.46
Nomada rubicunda	Apidae	1	0	0	0	1	para	par	soil	1.77
Nomada sp.	Apidae	1	1	1	0	4	NA	NA	NA	NA
Osmia atriventris	Megachilidae	1	1	1	1	11	poly	sol	hole	1.92
Osmia bucephala	Megachilidae	1	0	1	1	3	poly	sol	hole	3.54
Osmia georgica	Megachilidae	1	1	0	0	6	oligo	sol	cavity	2.36
Osmia pumila	Megachilidae	1	1	1	0	6	poly	sol	hole	1.61
Osmia simillima	Megachilidae	1	1	0	0	2	poly	sol	cavity	2.36
Perdita halictoides	Andrenidae	1	0	0	0	1	oligo	sol	soil	NA
Pseudopanurgus aestivalis	Andrenidae	1	0	0	0	8	oligo	sol	soil	1.59
Pseudopanurgus andrenoides	Andrenidae	1	1	0	0	2	oligo	sol	soil	1.59
Sphecodes davisii	Halictidae	1	0	0	0	1	para	par	soil	1.55
Sphecodes mandibularis	Halictidae	1	0	0	0	1	para	par	soil	1.52
Xylocopa virginica	Apidae	1	1	1	1	35	poly	fac	wood	6.07

Michigan cherry											
	Agapostemon sericeus	Halictidae	1	0	1	1	12	poly	fac	soil	1.90
	Agapostemon virescens	Halictidae	1	0	0	0	11	poly	fac	soil	2.16
	Andrena aliciae	Andrenidae	1	0	0	0	1	oligo	sol	soil	2.16
	Andrena barbilabris	Andrenidae	0	0	1	1	169	poly	sol	soil	2.03
	Andrena carlini	Andrenidae	1	0	1	1	22	poly	sol	soil	2.70
	Andrena commoda	Andrenidae	1	0	0	1	5	poly	sol	soil	2.20
	Andrena crataegi	Andrenidae	1	0	1	1	79	poly	sol	soil	2.20
	Andrena cressonii	Andrenidae	0	0	1	1	3	poly	sol	soil	1.75
	Andrena dunningi	Andrenidae	0	0	1	1	10	poly	sol	soil	2.44
	Andrena erythronii	Andrenidae	0	0	1	1	2	oligo	sol	soil	2.30
	Andrena forbesii	Andrenidae	1	0	1	1	206	poly	sol	soil	2.10
	Andrena geranii	Andrenidae	0	0	0	1	2	poly	sol	soil	2.38
	Andrena hilaris	Andrenidae	1	0	0	0	1	poly	sol	soil	2.16
	Andrena hippotes	Andrenidae	0	0	1	1	26	poly	sol	soil	2.00
	Andrena imitatrix	Andrenidae	0	0	1	1	95	poly	sol	soil	1.90
	Andrena mandibularis	Andrenidae	0	0	1	0	4	poly	sol	soil	2.18
	Andrena milwaukeensis	Andrenidae	0	0	0	1	1	poly	sol	soil	2.29
	Andrena miserabilis	Andrenidae	0	0	1	1	418	poly	sol	soil	1.70
	Andrena morrisonella	Andrenidae	0	0	1	1	4	poly	sol	soil	1.90
	Andrena nasonii	Andrenidae	0	0	1	1	54	poly	sol	soil	1.80
	Andrena nuda	Andrenidae	0	0	1	1	23	poly	sol	soil	2.19
	Andrena perplexa	Andrenidae	0	0	1	1	4	poly	sol	soil	2.39
	Andrena pruni	Andrenidae	0	0	1	1	3	poly	sol	soil	2.30
	Andrena robertsonii	Andrenidae	0	0	0	1	2	poly	sol	soil	1.78
	Andrena rudbeckiae	Andrenidae	1	0	0	0	1	oligo	sol	soil	2.16
	Andrena rufosignata	Andrenidae	0	0	1	1	6	poly	sol	soil	2.57
	Andrena rugosa	Andrenidae	0	0	1	1	32	poly	sol	soil	2.30

Andrena sp.	Andrenidae	0	0	1	0	1	NA	NA	NA	NA
Andrena vicina	Andrenidae	0	0	1	1	63	poly	sol	soil	2.48
Andrena w-scripta	Andrenidae	1	0	1	1	31	poly	sol	soil	1.70
Anthophora abrupta	Apidae	1	0	0	0	1	poly	sol	NA	3.37
Anthophora terminalis	Apidae	1	1	0	0	7	poly	sol	wood	3.76
Anthophora walshii	Apidae	1	0	0	0	1	poly	sol	soil	3.37
Augochlora pura	Halictidae	1	1	1	1	29	poly	sol	wood	1.60
Augochlorella aurata	Halictidae	1	1	1	0	5	poly	soc	soil	1.53
Augochloropsis metallica	Halictidae	1	0	0	0	1	poly	sol	soil	1.91
Bombus bimaculatus	Apidae	1	1	1	1	98	poly	soc	cavity	3.74
Bombus borealis	Apidae	1	1	0	0	8	poly	soc	cavity	4.73
Bombus citrinus	Apidae	1	0	0	0	5	poly	sol	cavity	4.09
Bombus fervidus	Apidae	1	1	0	0	6	poly	soc	cavity	3.63
Bombus griseocollis	Apidae	1	1	0	0	110	poly	soc	cavity	4.34
Bombus impatiens	Apidae	1	1	1	1	135	poly	soc	cavity	4.51
Bombus perplexus	Apidae	1	0	0	1	13	poly	soc	cavity	3.67
Bombus terricola	Apidae	1	0	0	0	3	poly	soc	cavity	3.19
Bombus vagans	Apidae	1	1	0	0	54	poly	soc	cavity	3.12
Ceratina calcarata	Apidae	1	1	1	1	376	poly	fac	stem	1.27
Ceratina mikmaqi	Apidae	1	1	0	1	26	poly	fac	cavity	1.27
Ceratina sp.	Apidae	1	0	0	0	1	NA	NA	NA	NA
Ceratina strenua	Apidae	1	1	0	1	10	poly	fac	stem	0.93
Coelioxys modesta	Megachilidae	1	0	0	0	1	para	par	hole	2.43
Coelioxys sayi	Megachilidae	1	0	0	0	1	para	par	hole	2.63
Colletes americanus	Colletidae	0	1	0	0	1	poly	sol	soil	2.81
Colletes inaequalis	Colletidae	0	0	1	1	95	poly	sol	soil	2.86
Colletes kincaidii	Colletidae	1	0	0	0	1	poly	sol	soil	2.63
Dianthidium simile	Megachilidae	1	0	0	0	1	oligo	sol	soil	NA

Dufourea monardae	Halictidae	1	0	0	0	1	oligo	sol	soil	NA
Eucera hamata	Apidae	1	0	0	0	1	poly	sol	soil	NA
Halictus confusus	Halictidae	1	0	1	1	22	poly	fac	soil	1.40
Halictus ligatus	Halictidae	1	1	0	0	53	poly	soc	soil	1.82
Halictus parallelus	Halictidae	1	0	0	0	1	poly	soc	soil	2.55
Halictus rubicundus	Halictidae	1	1	1	1	5	poly	fac	soil	1.75
Heriades leavitti	Megachilidae	0	1	0	0	1	poly	sol	cavity	NA
Hoplitis pilosifrons	Megachilidae	1	0	0	0	1	poly	sol	stem	1.55
Hoplitis producta	Megachilidae	1	0	0	0	1	poly	sol	stem	1.24
Hylaeus affinis	Colletidae	1	0	0	0	1	poly	sol	hole	1.30
Hylaeus mesillae	Colletidae	1	0	0	0	1	poly	sol	hole	0.98
Hylaeus modestus	Colletidae	1	1	0	0	4	poly	sol	hole	1.03
Lasioglossum acuminatum	Halictidae	1	0	1	1	3	poly	fac	soil	1.92
Lasioglossum cattellae	Halictidae	0	0	1	1	2	poly	soc	soil	1.36
Lasioglossum cinctipes	Halictidae	0	0	1	1	3	poly	soc	soil	2.00
Lasioglossum coeruleum	Halictidae	0	0	1	0	1	poly	soc	wood	1.35
Lasioglossum coriaceum	Halictidae	0	0	1	0	3	poly	fac	soil	1.95
Lasioglossum cressonii	Halictidae	0	0	1	1	3	poly	soc	wood	1.18
Lasioglossum ellisiae	Halictidae	0	0	0	1	2	poly	soc	soil	1.36
Lasioglossum ephialtum	Halictidae	0	0	0	1	1	poly	soc	soil	1.26
Lasioglossum foxii	Halictidae	0	0	0	1	4	poly	sol	soil	1.43
Lasioglossum gotham	Halictidae	0	0	1	1	2	poly	sol	soil	1.36
Lasioglossum hitchensi	Halictidae	0	0	0	1	3	poly	soc	soil	1.36
Lasioglossum imitatum	Halictidae	0	0	1	1	14	poly	soc	soil	0.82
Lasioglossum laevissimum	Halictidae	0	0	0	1	1	poly	soc	soil	1.36
Lasioglossum leucocomum	Halictidae	1	1	1	1	18	poly	soc	soil	1.29
Lasioglossum lineatulum	Halictidae	0	0	1	1	29	poly	soc	soil	1.29

Lasioglossum lustrans	Halictidae	0	1	0	0	1	oligo	sol	soil	1.36
Lasioglossum obscurum	Halictidae	0	0	0	1	1	poly	soc	soil	1.31
Lasioglossum paraforbesii	Halictidae	0	0	1	1	13	poly	sol	soil	1.36
Lasioglossum pectorale	Halictidae	1	1	0	1	20	poly	sol	soil	1.45
Lasioglossum perpunctatum	Halictidae	1	0	0	1	2	poly	soc	soil	1.20
Lasioglossum pilosum	Halictidae	1	1	1	1	36	poly	soc	soil	1.21
Lasioglossum sp.	Halictidae	0	0	1	0	2	NA	NA	NA	NA
Lasioglossum subviridatum	Halictidae	0	0	1	0	1	poly	soc	wood	1.20
Lasioglossum versatum	Halictidae	1	0	1	1	3	poly	soc	soil	1.35
Lasioglossum vierecki	Halictidae	1	0	0	0	1	poly	sol	soil	0.86
Lasioglossum zephyrum	Halictidae	0	0	1	1	4	poly	soc	soil	1.44
Megachile brevis	Megachilidae	1	0	0	0	1	poly	sol	hole	2.61
Megachile inermis	Megachilidae	1	1	0	0	3	poly	sol	hole	4.28
Megachile latimanus	Megachilidae	1	1	0	0	12	poly	sol	soil	4.06
Megachile melanophaea	Megachilidae	1	0	0	0	1	poly	sol	soil	3.89
Megachile mendica	Megachilidae	1	1	0	0	8	poly	sol	hole	3.06
Megachile pugnata	Megachilidae	1	0	0	0	1	oligo	sol	hole	3.53
Melissodes agilis	Apidae	1	0	0	0	3	oligo	sol	soil	2.33
Melissodes bimaculatus	Apidae	1	0	0	0	4	poly	sol	soil	2.33
Melissodes communis	Apidae	1	0	0	0	15	poly	sol	soil	2.33
Melissodes desponsus	Apidae	1	0	0	0	3	oligo	sol	soil	2.33
Melissodes druriellus	Apidae	1	0	0	0	1	oligo	sol	soil	2.33
Melissodes illatus	Apidae	1	1	0	0	15	oligo	sol	soil	2.33
Melissodes subillatus	Apidae	1	0	0	0	13	oligo	sol	soil	2.33
Nomada articulata	Apidae	1	0	0	0	1	para	par	soil	1.53
Nomada cressonii	Apidae	0	0	1	0	1	para	par	soil	1.74
Nomada imbricata	Apidae	0	0	0	1	1	para	par	soil	2.15

	Nomada parva	Apidae	0	0	0	1	1	para	par	soil	1.77
	Nomada pygmaea	Apidae	0	0	0	1	1	para	par	soil	1.46
	Nomada sp.	Apidae	0	0	0	1	1	NA	NA	NA	NA
	Osmia atriventris	Megachilidae	0	0	1	1	2	poly	sol	hole	1.92
	Osmia bucephala	Megachilidae	1	0	0	0	1	poly	sol	hole	3.54
	Osmia distincta	Megachilidae	1	0	0	0	2	oligo	sol	cavity	2.36
	Osmia georgica	Megachilidae	1	0	0	0	1	oligo	sol	cavity	2.36
	Osmia pumila	Megachilidae	0	0	1	0	1	poly	sol	hole	1.61
	Osmia simillima	Megachilidae	0	1	0	0	1	poly	sol	cavity	2.36
	Peponapis pruinosa	Apidae	1	0	0	0	1	oligo	sol	soil	3.71
	Perdita bequaerti	Andrenidae	1	0	0	0	2	oligo	sol	soil	NA
	Sphecodes confertus	Halictidae	1	0	1	0	2	para	par	soil	1.48
	Triepeolus simplex	Apidae	1	0	0	0	1	para	par	soil	NA
	Xylocopa virginica	Apidae	1	0	1	1	22	poly	fac	wood	6.07
Oregon blueberry											
	Agapostemon texanus	Halictidae	1	0	0	0	2	poly	fac	soil	1.87
	Agapostemon virescens	Halictidae	1	0	0	0	1	poly	fac	soil	2.16
	Andrena angustitarsata	Andrenidae	1	0	0	0	1	poly	sol	soil	1.80
	Andrena candida	Andrenidae	1	0	0	0	1	poly	sol	soil	1.65
	Andrena perplexa	Andrenidae	0	0	0	1	1	poly	sol	soil	2.39
	Andrena rufosignata	Andrenidae	0	0	0	1	1	poly	sol	soil	2.57
	Andrena salicifloris	Andrenidae	1	0	1	0	2	poly	sol	soil	2.16
	Andrena sp.	Andrenidae	1	0	1	0	3	NA	NA	NA	NA
	Andrena w-scripta	Andrenidae	1	0	1	0	5	poly	sol	soil	1.70
	Anthophora urbana	Apidae	1	0	0	0	2	poly	sol	soil	2.98
	Bombus californicus	Apidae	0	0	1	0	1	poly	soc	cavity	3.61
	Bombus griseocollis	Apidae	1	1	1	0	4	poly	soc	cavity	4.34

Bombus melanopygus	Apidae	1	0	1	0	3	poly	soc	cavity	3.86
Bombus mixtus	Apidae	1	1	1	1	27	poly	soc	cavity	3.84
Bombus nevadensis	Apidae	0	0	1	1	4	poly	soc	cavity	3.84
Bombus sp.	Apidae	0	0	1	1	3	NA	NA	NA	NA
Bombus vosnesenskii	Apidae	1	1	0	0	7	poly	soc	soil	3.55
Ceratina acantha	Apidae	1	1	1	0	33	poly	sol	stem	1.15
Ceratina micheneri	Apidae	0	1	1	0	2	poly	sol	stem	1.16
Ceratina sp.	Apidae	1	1	0	1	44	NA	NA	NA	NA
Coelioxys sp.	Megachilidae	1	1	0	0	3	NA	NA	NA	NA
Colletes consors	Colletidae	1	0	0	0	1	poly	sol	soil	2.88
Eucera edwardsii	Apidae	0	1	0	0	1	poly	sol	soil	NA
Eucera sp.	Apidae	1	0	0	0	4	NA	NA	NA	NA
Halictus confusus	Halictidae	1	1	0	0	5	poly	fac	soil	1.40
Halictus farinosus	Halictidae	1	1	0	0	20	poly	soc	soil	2.13
Halictus ligatus	Halictidae	1	1	0	0	126	poly	soc	soil	1.82
Halictus rubicundus	Halictidae	1	0	0	0	3	poly	fac	soil	1.75
Halictus tripartitus	Halictidae	1	1	1	0	34	poly	soc	soil	1.20
Heriades carinata	Megachilidae	1	1	0	0	3	poly	sol	cavity	NA
Hoplitis producta	Megachilidae	1	0	0	0	1	poly	sol	stem	1.24
Hylaeus mesillae	Colletidae	1	1	0	0	15	poly	sol	hole	0.98
Hylaeus modestus	Colletidae	0	1	0	0	1	poly	sol	hole	1.03
Hylaeus sp.	Colletidae	1	1	0	0	20	NA	NA	NA	NA
Lasioglossum avalonense	Halictidae	1	0	0	0	2	poly	soc	soil	1.36
Lasioglossum brunneiventre	Halictidae	1	0	0	0	1	poly	soc	soil	1.36
Lasioglossum cressonii	Halictidae	0	1	0	0	1	poly	soc	wood	1.18
Lasioglossum imbrex	Halictidae	1	0	0	0	4	poly	soc	soil	1.36
Lasioglossum incompletum	Halictidae	1	1	1	1	16	poly	soc	soil	1.36
Lasioglossum knereri	Halictidae	1	1	1	0	5	poly	soc	soil	1.36

	Lasioglossum laevissimum	Halictidae	1	0	0	0	1	poly	soc	soil	1.36
	Lasioglossum longicorne	Halictidae	1	0	0	0	1	poly	soc	soil	1.36
	Lasioglossum nevadense	Halictidae	1	0	0	0	2	poly	soc	soil	1.36
	Lasioglossum olympiae	Halictidae	1	0	1	1	7	poly	sol	soil	1.36
	Lasioglossum orthocarpi	Halictidae	1	0	1	1	5	poly	soc	soil	1.36
	Lasioglossum punctatoventre	Halictidae	1	0	0	0	1	poly	soc	soil	1.36
	Lasioglossum sequoiae	Halictidae	0	1	0	0	5	poly	sol	soil	1.36
	Lasioglossum sisymbrii	Halictidae	1	1	1	0	5	poly	sol	soil	1.36
	Lasioglossum sp.	Halictidae	1	1	0	0	4	NA	NA	NA	NA
	Lasioglossum tenax	Halictidae	1	0	0	0	2	poly	sol	soil	1.36
	Lasioglossum titusi	Halictidae	1	1	0	0	5	poly	sol	soil	1.93
	Lasioglossum zephyrum	Halictidae	0	1	0	1	3	poly	soc	soil	1.44
	Megachile sp.	Megachilidae	0	1	0	0	1	NA	NA	NA	NA
	Melissodes lupina	Apidae	1	1	0	0	7	oligo	sol	soil	2.20
	Melissodes metenua	Apidae	1	0	0	0	2	NA	sol	soil	2.33
	Melissodes microsticta	Apidae	1	1	0	0	7	oligo	sol	soil	2.33
	Melissodes robustior	Apidae	1	1	0	0	13	oligo	sol	soil	2.88
	Melissodes sp.	Apidae	1	1	0	0	15	NA	NA	NA	NA
	Nomada sp.	Apidae	1	0	0	0	1	NA	NA	NA	NA
	Osmia dolerosa	Megachilidae	1	0	0	0	1	poly	sol	wood	2.36
	Osmia sp.	Megachilidae	1	1	0	0	18	NA	NA	NA	NA
	Osmia texana	Megachilidae	1	1	0	0	3	oligo	sol	soil	2.30
	Osmia tristella	Megachilidae	1	0	0	0	2	poly	sol	stem	2.30
	Sphecodes sp.	Halictidae	1	1	0	0	8	NA	NA	NA	NA
	Stelis sp.	Megachilidae	0	1	0	0	1	NA	NA	NA	NA
	Triepeolus sp.	Apidae	1	0	0	0	1	NA	NA	NA	NA
California watermelon											

Agapostemon texanus	Halictidae	1	1	0	0	3	poly	fac	soil	1.87
Anthophora urbana	Apidae	1	0	0	1	100	poly	sol	soil	2.98
Ashmeadiella aridula	Megachilidae	1	1	0	0	4	poly	sol	cavity	1.25
Ashmeadiella bucconis	Megachilidae	1	0	0	0	2	poly	sol	cavity	1.25
Bombus californicus	Apidae	1	0	0	0	1	poly	soc	cavity	3.61
Bombus vosnesenskii	Apidae	1	0	0	0	5	poly	soc	soil	3.55
Colletes fulgidus	Colletidae	0	1	0	0	1	oligo	sol	soil	2.88
Diadasia consociata	Apidae	1	0	0	0	1	oligo	sol	soil	1.85
Diadasia enavata	Apidae	1	1	0	0	256	oligo	sol	soil	2.74
Halictus ligatus	Halictidae	1	1	1	1	458	poly	soc	soil	1.82
Halictus tripartitus	Halictidae	1	1	1	1	167	poly	soc	soil	1.20
Hylaeus mesillae	Colletidae	0	1	0	0	1	poly	sol	hole	0.98
Lasioglossum diversopunctatum	Halictidae	1	1	0	1	131	NA	NA	soil	1.36
Lasioglossum imbrex	Halictidae	0	1	0	1	2	poly	soc	soil	1.36
Lasioglossum impavidum	Halictidae	1	0	0	0	2	NA	NA	soil	1.36
Lasioglossum incompletum	Halictidae	1	1	1	1	810	poly	soc	soil	1.36
Lasioglossum megastictum	Halictidae	1	0	0	0	1	NA	NA	soil	1.36
Lasioglossum sp B 1	Halictidae	1	0	0	0	1	NA	NA	NA	NA
Lasioglossum sp D	Halictidae	1	1	0	0	2	NA	soc	soil	1.36
Lasioglossum sp Dialictus1	Halictidae	1	1	1	1	73	NA	NA	NA	NA
Lasioglossum tegulariforme	Halictidae	1	1	0	0	7	NA	soc	soil	1.36
Lasioglossum titusi	Halictidae	1	1	0	0	2	poly	sol	soil	1.93
Megachile brevis	Megachilidae	1	1	0	0	9	poly	sol	hole	2.61
Megachile gentilis	Megachilidae	1	0	0	0	3	poly	sol	cavity	2.63
Megachile onobrychidis	Megachilidae	1	0	0	0	6	poly	sol	cavity	2.58
Megachile parallela	Megachilidae	1	1	0	0	7	poly	sol	soil	3.27
Melissodes agilis	Apidae	1	1	1	1	75	oligo	sol	soil	2.33

Melissodes lupina	Apidae	1	1	1	1	205	oligo	sol	soil	2.20
Melissodes robustior	Apidae	1	1	0	0	18	oligo	sol	soil	2.88
Melissodes stearnsi	Apidae	1	0	0	0	1	oligo	sol	soil	2.04
Melissodes tepida	Apidae	1	0	1	0	11	poly	sol	soil	2.21
Nomada sp NMW Y1	Apidae	1	0	0	0	1	NA	NA	NA	NA
Svastra obliqua	Apidae	1	1	0	0	35	NA	sol	soil	3.67
Triepeolus concavus	Apidae	1	1	0	0	15	para	par	soil	NA
Triepeolus melanarius	Apidae	1	0	0	0	7	para	par	soil	NA
Triepeolus paenepectoralis	Apidae	0	1	0	0	1	para	par	soil	NA
Triepeolus subnitens	Apidae	1	1	0	0	38	para	par	soil	NA
Triepeolus timberlakei	Apidae	1	0	0	0	1	para	par	soil	NA
Triepeolus utahensis	Apidae	1	1	1	0	53	para	par	soil	NA
Xeromelecta californica	Apidae	1	0	0	0	2	para	par	soil	2.15
Xylocopa tabaniformis	Apidae	1	0	0	0	1	poly	sol	stem	5.84

Table S2 Total number (Abd) of non-native species collected from across 4 crop-regions regions at enhanced edges (EE), control edges (CE), on crops with EE (WI), and on crops without EE (WO).

	Non-native species	EE	CE	W/	W/0	Abd
Michigan blueberry						
	Andrena wilkella	1	1	0	0	27
	Anthidium oblongatum	1	1	0	0	4
	Lasioglossum leucozonium	1	1	0	0	75
	Megachile rotundata	1	1	0	0	3
					Total abundance	109
Michigan cherry						
	Andrena wilkella	1	1	0	0	12
	Lasioglossum leucozonium	1	1	0	0	27
	Megachile rotundata	1	0	0	0	1
	Osmia cornifrons	0	0	1	1	18
					Total abundance	58
Oregon blueberry						
	Hylaeus punctatus	1	0	0	0	2
	Lasioglossum zonulum	1	1	1	0	5
					Total abundance	7
California watermelon						
	Ceratina dallatorreana	1	1	1	0	9
	Hylaeus leptocephalus	0	1	0	1	1
	Megachile apicalis	1	1	0	0	10
					Total abundance	11

Table S3 Indicator values (IV) for species sampled across the four site types.

	Species	Enhanced edge	Control edge	On crop with	On crop without	IV	*P*
Michigan blueberry							
	Agapostemon sericeus	**1**	**1**	0	0	0.35	0.031
	Andrena asteris	**1**	0	0	0	0.39	0.026
	Andrena carlini	0	0	**1**	0	0.36	0.029
	Andrena carolina	0	0	**1**	**1**	0.42	0.006
	Andrena perplexa	0	0	**1**	0	0.40	0.049
	Andrena vicina	0	0	**1**	**1**	0.42	0.006
	Augochlorella aurata	**1**	**1**	0	0	0.33	0.025
	Bombus bimaculatus	**1**	0	0	0	0.40	0.011
	Bombus fervidus	**1**	0	0	0	0.54	0.001
	Bombus impatiens	**1**	**1**	0	0	0.43	0.004
	Bombus vagans	**1**	0	0	0	0.44	0.001
	Ceratina calcarata	**1**	0	0	0	0.65	0.001
	Ceratina mikmaqi	**1**	0	0	0	0.59	0.001
	Ceratina strenua	**1**	0	0	0	0.48	0.002
	Halictus confusus	0	**1**	0	0	0.37	0.016
	Halictus ligatus	**1**	0	0	0	0.52	0.001
	Hylaeus modestus	**1**	**1**	0	0	0.45	0.002
	Lasioglossum imitatum	0	**1**	0	0	0.34	0.041
	Lasioglossum lustrans	0	**1**	0	0	0.51	0.004
	Lasioglossum pectorale	**1**	**1**	0	0	0.51	0.001
	Lasioglossum versatum	0	**1**	0	0	0.36	0.049
	Lasioglossum vierecki	**1**	0	0	0	0.39	0.004
	Megachile pugnata	**1**	0	0	0	0.46	0.001
	Melissodes bimaculatus	**1**	0	0	0	0.50	0.001
	Melissodes druriellus	**1**	0	0	0	0.47	0.001
Michigan cherry							
	Agapostemon virescens	**1**	0	0	0	0.51	0.001
	Andrena barbilabris	0	0	**1**	**1**	0.54	0.001
	Andrena carlini	0	0	**1**	**1**	0.45	0.009
	Andrena dunningi	0	0	**1**	**1**	0.39	0.03

	Andrena forbesii	0	0	**1**	**1**	0.72	0.001
	Andrena hippotes	0	0	0	**1**	0.66	0.001
	Andrena imitatrix	0	0	**1**	**1**	0.50	0.001
	Andrena miserabilis	0	0	**1**	**1**	0.62	0.001
	Andrena nasonii	0	0	0	**1**	0.47	0.004
	Andrena rufosignata	0	0	**1**	0	0.49	0.009
	Andrena rugosa	0	0	**1**	0	0.41	0.02
	Andrena vicina	0	0	**1**	**1**	0.64	0.001
	Andrena w-scripta	0	0	0	**1**	0.39	0.007
	Bombus bimaculatus	**1**	0	0	0	0.59	0.001
	Bombus citrinus	**1**	0	0	0	0.52	0.005
	Bombus griseocollis	**1**	0	0	0	0.60	0.001
	Bombus impatiens	**1**	0	0	0	0.55	0.001
	Bombus perplexus	**1**	0	0	0	0.42	0.014
	Bombus vagans	**1**	**1**	0	0	0.54	0.001
	Colletes inaequalis	0	0	**1**	0	0.52	0.003
	Halictus ligatus	**1**	0	0	0	0.48	0.004
	Lasioglossum foxii	0	0	0	**1**	0.48	0.007
	Lasioglossum paraforbesii	0	0	**1**	0	0.46	0.008
	Lasioglossum pectorale	**1**	0	0	0	0.55	0.001
Oregon blueberry							
	Bombus mixtus	**1**	0	0	0	0.46	0.027
	Halictus farinosus	**1**	0	0	0	0.62	0.002
	Halictus ligatus	**1**	**1**	0	0	0.75	0.001
	Halictus tripartitus	**1**	0	0	0	0.58	0.004
	Hylaeus mesillae	**1**	0	0	0	0.44	0.049
	Lasioglossum incompletum	**1**	0	0	0	0.46	0.034
California watermelon							
	Anthophora urbana	**1**	0	0	0	0.49	0.014
	Diadasia enavata	**1**	0	0	0	0.46	0.026
	Halictus ligatus	**1**	0	0	0	0.46	0.029
	Lasioglossum diversopunctatum	**1**	0	0	0	0.39	0.048
	Lasioglossum incompletum	**1**	0	0	0	0.62	0.001
	Megachile onobrychidis	**1**	0	0	0	0.46	0.028

Melissodes lupina	**1**	0	0	0	0.52	0.003
Melissodes robustior	**1**	0	0	0	0.42	0.046
Triepeolus utahensis	**1**	0	0	0	0.43	0.032

P-values assessed using 999 permutations. Only species significant at $P < 0.05$ are reported

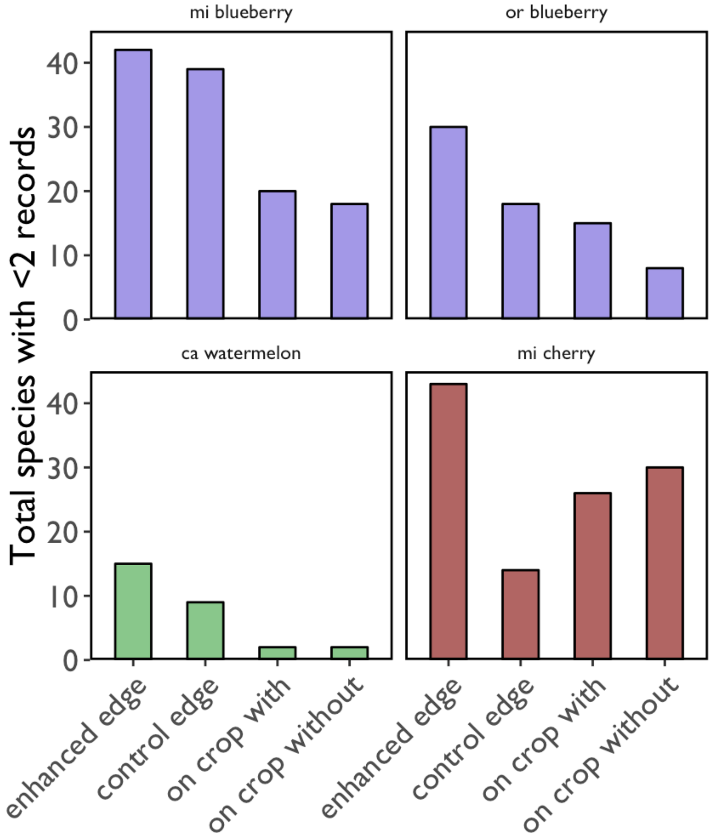

Figure S1 The number of singletons and doubletons collected at each site type for MI blueberry (blue), OR blueberry (blue), CA watermelon (green), and MI cherry (red).

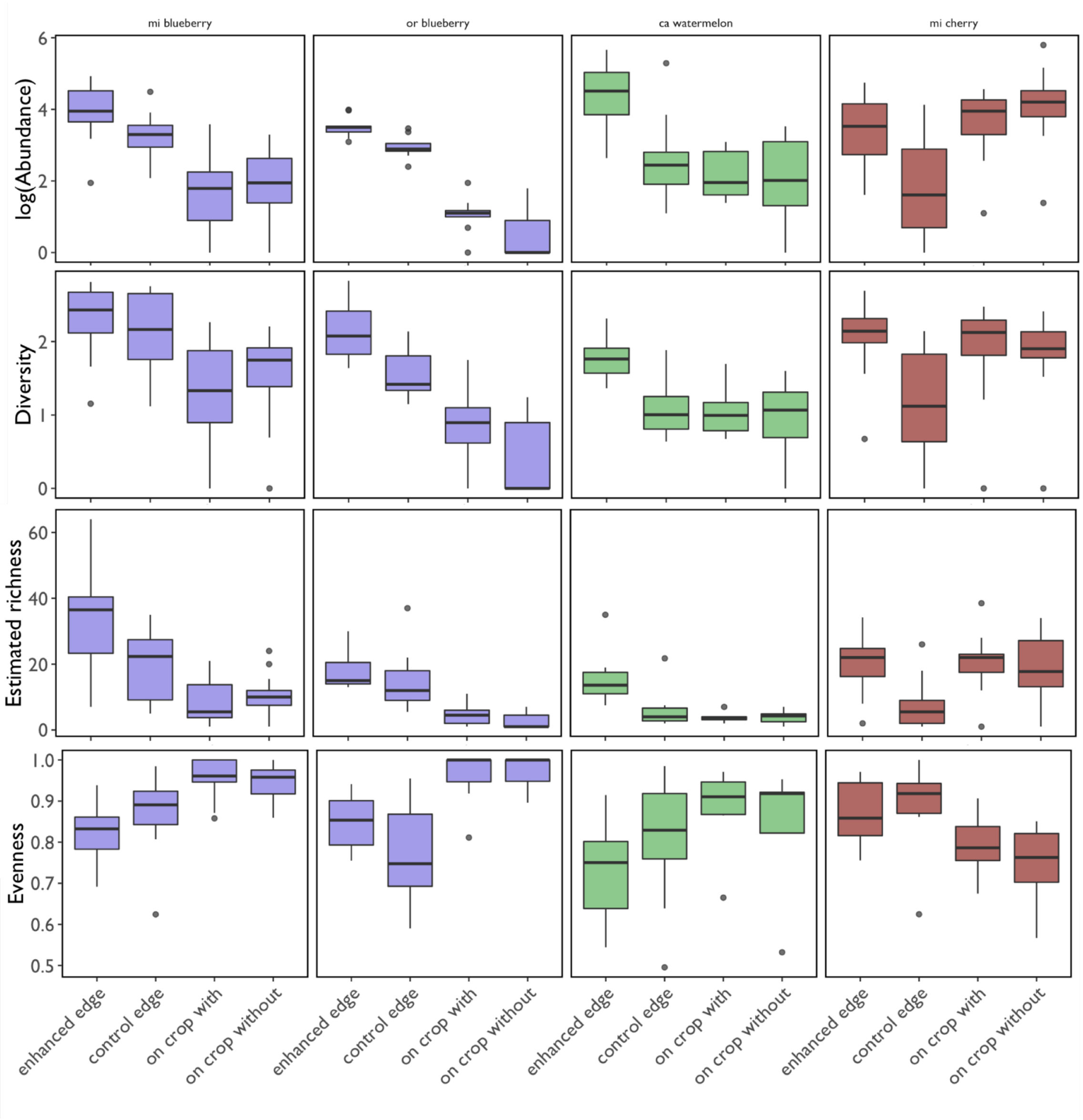

Figure S2 Diversity metrics across crop-regions (from top to bottom): Abundance (note log scale), diversity (Shannon diversity), estimated species richness (Chao1 estimator), and evenness (Pielou's J).

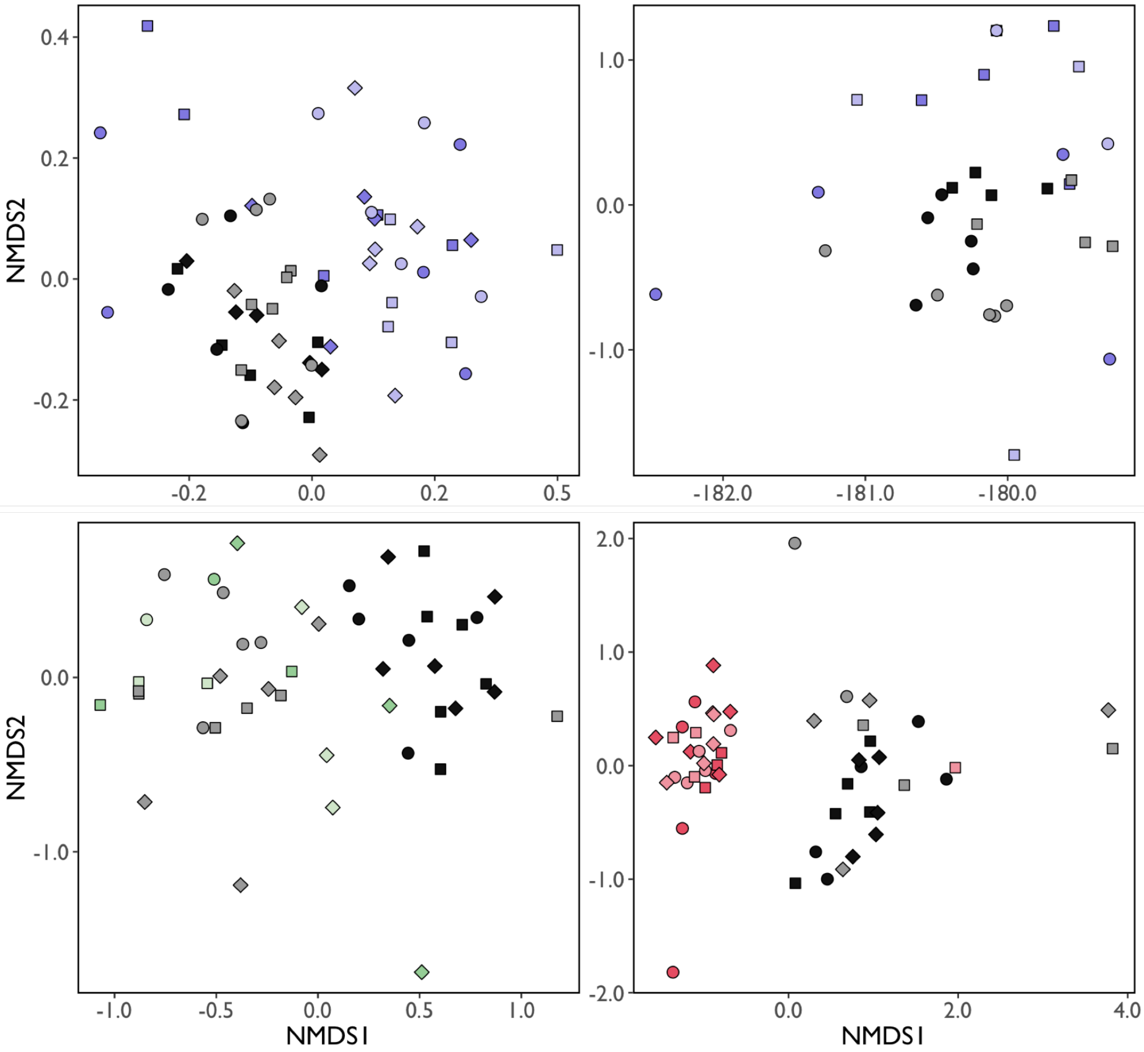

Figure S3 Non-metric multidimensional scaling of study sites for MI blueberry (blue), OR blueberry (blue), CA watermelon (green), and MI cherry (red). Black points are communities collected from enhancements and gray points are from control edges. Dark color points are communities collected on crop with enhancements and light colors from crops without enhancements. Shape correspond to communities collected during the years 2014 (circles), 2015 (squares), and 2016 (diamonds).

CHAPTER 5: CORRIDORS THROUGH TIME: DOES RESOURCE CONTINUITY IMPACT POLLINATOR COMMUNITIES, POPULATIONS AND INDIVIDUALS?

5.1 Abstract

Spatial aspects of connectivity have received considerable attention from both ecologists and conservation biologists, yet temporal connectivity – the linking of habitat patches through time – likely plays an equally important, but largely overlooked role. Different ecosystem properties underpin temporal connectivity, but here we focus on the uninterrupted availability of foraging resources. Resource continuity is expected to be particularly important in highly dynamic landscapes, such as agriculture, but its influence remains untested. We present a framework, grounded in ecological principles of connectivity and metapopulation dynamics, which explains how diversified agriculture, by promoting resource continuity, may support beneficial organisms. We then use a novel natural experiment consisting of farms that either grow blueberry and raspberry crops or raspberry without blueberry. We investigate the response of pollinators to resource continuity at community, population and individual levels using a mix of field sampling and population genetic techniques. We did not observe a strong signal of resource continuity on any of these measures but the effects of resource continuity are expressed most strongly when considering population level impacts. Though far from definitive, our results suggest that agricultural landscapes composed of sequentially flowering crops may bolster local populations through temporal complementarity of flowering resources.

5.2 Introduction

A signature of human activity on the Earth are landscapes fragmented into smaller and more isolated patches (Haddad et al., 2015). These changes to landscape structure negatively affect biodiversity (Fahrig, 2003) and ecosystem functioning (Fischer, Lindenmayer, & Manning, 2006), and consequentially ecosystem services (Mitchell et al., 2015). Increasing landscape connectivity – the extent to which landscape pattern facilitates or impedes movement through a landscape (Taylor, Fahrig, Henein, & Merriam, 1993) – is critical for stemming fragmentation-associated biodiversity loss and is a key aspect of systematic conservation planning (Gilbert-Norton, Wilson, Stevens, & Beard, 2010; Naidoo et al., 2018; Pressey et al., 2007). Connectivity research often focuses on the spatial composition and configuration of static habitat patches (i.e., structural connectivity, Tischendorf & Fahrig, 2000) or the response of organisms to those spatial features (i.e., functional connectivity, Baguette & Van Dyck, 2007).

However, connectivity can be measured through time as well as across space. From an organism's perspective temporally, through variability in the extent, distribution, and quality of habitats over time (Fahrig, 1992). Temporal connectivity dynamics arise when periodic events link habitat patches (e.g., flooding events create hydrological links between unconnected populations within a river network (Fagan, Unmack, Burgess, & Minckley, 2002)) or when the transient occupancy or actions of other organisms induce movement between patches (e.g., mobbing birds increase inter-patch movement when vigilant sentinel species are present, Sieving et al., 2004). However, the influence of connectivity on ecological processes is typically evaluated based on snapshots of landscape pattern (Kindlmann & Burel, 2008; Moilanen & Nieminen, 2002). Although habitat patches can be linked via changes in a landscape over time, these dynamics, and the ecosystem properties underpinning them, are largely overlooked (Kool, Moilansen, & Treml, 2013; Zeigler & Fagan, 2014).

Resource continuity – the uninterrupted availability of foraging, nesting, overwintering, or mating sites (Schellhorn, Gagic, & Bommarco, 2015) – is one ecosystem property that can influence temporal connectivity (Figure 1). Resource availability that is low in frequency, short in duration, but large in magnitude (i.e., resource pulses) drive population trajectories (Holt, 2008; Yang, Bastow, Spence, & Wright, 2008), but if the availability of resources is constricted (i.e., resource bottlenecks), the resulting temporal disconnect can reduce population growth or persistence (Figure 1a). For example, early-season mass-flowering crops temporarily increase pollinator abundance (Holzschuh, Dormann, Tscharntke, & Steffan-Dewenter, 2013; Riedinger et al., 2015; Westphal, Steffan-Dewenter, & Tscharntke, 2003), but reproductive success and inter-annual population growth decline if later season floral resources are lacking (Westphal et al., 2009; Williams et al., 2012). The uninterrupted availability of quality habitat patches within a landscape determines population persistence and ultimately regional biodiversity (Martensen, Saura, & Fortin, 2017; Nordén et al., 2014; Wimberly, 2006).

Understanding how resource continuity affects organisms is especially important in highly dynamic environments, such as agriculture, where management regimes and cultivation techniques cause frequent habitat change (Burel & Baudry, 2005). Diversified agriculture aims to foster beneficial biotic interactions through varied cultivation techniques (Kremen & Miles, 2012) and is a promising agricultural conservation approach (Potts et al., 2016). Crop diversity is often assumed to increase agricultural biodiversity (Bommarco, Kleijn, & Potts, 2013), but the ecological mechanisms driving this increase are not fully explored (but cf. Loreau, Mouquet, & Gonzalez, 2003).

Linking resource continuity to metapopulation theory offers insight into how crop diversity may benefit agricultural biodiversity. Hanski (1999) posited that persistence in dynamic landscapes is influenced by the amount of future habitat available in a focal patch, and by the amount of linked future habitat available in other patches. Resource continuity can lead to local population persistence because temporally connected patches increase metapopulation stability (Figure 1b). Metapopulation models have integrated spatial heterogeneity (habitat patchiness) and temporal dynamics (habitat lifespan) (Dewoody, Feng, & Swihart, 2005; Hanski, 1999; Keymer et al., 2000) and found that populations in highly dynamic landscapes (e.g. environments with unstable resource continuity) tend to have higher extinction risk (Keymer et al., 2000) and lower occupancy (Amarasekare & Possingham, 2001; Hodgson, Moilanen, & Thomas, 2009; Johst et al., 2002) because disturbances alter the amount of habitat available for colonization at a given point in time (Johnson, 2000). However, there are few empirical examples that demonstrate resource continuity effects on communities, populations and individuals, let alone metapopulations.

Here we examine aspects of temporal connectivity and its effect on pollinators. We do not attempt to explore crop diversity impacts on metapopulation dynamics (Figure 1b), but instead focus on an establishing an empirical evidence base for resource continuity (Figure 1a). We focus on pollinators responding to sequentially blooming periods of two perennial crops: summer bearing raspberry (*Rubus idaeus* L.) and highbush blueberry (*Vaccinium corymbosum* L.). We investigate the response of pollinators to this resource continuity at community, population and individual levels. We hypothesize that resource continuity will positively impact pollinator communities, populations and individuals. Specifically, using field observations of bee biodiversity, we ask: do farms with sequentially blooming crops have more abundant and diverse bee communities? We also survey local populations and use population genetics to ask: Does sequential blooming increase the nest density, and average individual size, of an important crop pollinator?

5.3 Methods

5.3.1 Study System

5.3.1.1. Study location. Study farms were located in the Lake Champlain Basin, Vermont, USA (44.45, -73.14). Agriculture in the region is characterized by forage and silage crops for livestock and small farms that provide a local food system with fruits and vegetables. Fruit and vegetable farms in Vermont cover 2755 ha and range in size from 10 to 400 ha, with the majority of farms under 20 ha (USDA 2012 VT census). Berry crops, such as blueberry and raspberry, are an important crop due to their high price point ($7.50 and $13.33/kg, respectively) and access to pick-your-own markets. Like other specialty crops grown in the state, berry farms tend to be small but high yielding, with blueberry and raspberry farms averaging 0.4 and 0.2 ha and yielding 544 and 498 kg/ha, respectively (NASS 2015).

We use a unique natural experiment to investigate the effects of sequential flowering crops on bee communities. Our study system includes farms that either grow both summer-bearing red raspberry and highbush blueberry (purple points, Figure 2a; N = 9), or raspberry without blueberry (red points, Figure 2a; N = 6). Farms with both crops offer greater resource continuity than farms with only raspberry. We examine pollinators between farms with or without resource continuity and between crops for the subset of farms with both blueberry and raspberry.

To confirm that blueberry patches were a dominant floral resource and that treatments did not differ in landscape-wide floral abundance, we conducted vegetation surveys of the surrounding landscape for each of our farms prior to raspberry blooming in 2016. We surveyed flowering plant diversity and abundance in specific habitat types including: flowering crops, orchards, blueberry, mowed grass, pasture, open scrub, shrub, deciduous woods, coniferous woods, and hedgerows. Before visiting farms, we randomly generated a sampling point in each habitat type using ArcGIS (9.1). At each sampling point we established a 20 m transect and recorded all flowering forbs occurring within 2 m. The abundance of flowers for each species was quantified on a logarithmic scale. Between the treatment groups, there was no difference in terms of landscape-wide floral abundance ($t = -0.207$, $P > 0.05$).

5.3.1.2. Study species. Highbush blueberry (*V. corymbosum*) has inflorescences of 5-10 mm long urceolate flowers with poricidal anthers and in Vermont blooms from early May until early June (Figure 2b). Although blueberry floral morphology may limit visitation by some pollinator groups (Courcelles, Button, & Elle, 2013), blueberry provides an important early season resource because of its high density of flowers that remain open for multiple days and offer visitors c. 1-3 µl of sucrose rich nectar (Dedej, 2004; Starast et al., 2014) and pollen that is high in protein (Pernal & Currie, 2001). In the Eastern US numerous native bee species have been documented visiting *V. corymbosum* (Benjamin & Winfree, 2014; Nicholson et al., 2017; Tuell, Ascher, & Isaacs, 2009). Unlike honeybees, many of these bees exhibit sonicating behavior that boosts blueberry pollen removal (Cardinal, Buchmann, & Russell, 2018). Native bees are therefore efficient pollinators due to their high levels of pollen receipt and typically high levels of flower visitation (Benjamin, Reilly, & Winfree, 2014; Dogterom, Winston, & Mukai, 2000; Javorek, Mackenzie, & Vander Kloet, 2002). With increasing visitation, blueberry can increase fruit set, berry size and uniformity, and ripening time (Blaauw & Isaacs, 2014; Button & Elle, 2014).

Summer bearing raspberry (*R. idaeus*) has racemes of multicarpelled flowers 10 mm across and blooms in late May through June (Figure 2c). Raspberry flowers are easily accessible, offer nutritious pollen (Schmidt, Thoenes, & Levin, 1987) and produce copious amounts of nectar (Free, 1993; Willmer, Bataw, & Hughes, 1994), with wild *R. idaeus* flowers reportedly producing on average 17.53 µl of nectar/day (Whitney, 1984). Little is known about the community of insect visitors on cultivated *R. idaeus* in the

Eastern US; however, studies of wild populations indicate that there could be considerable overlap between blueberry and raspberry (Whitney, 1984). Raspberry fruit are an aggregate fruit composed of druplets and benefit from native pollinator visitation (Cane, 2005; Nielsen, Reitan, Rinvoll, & Brysting, 2017). Although commercial raspberry cultivars are self-compatible (Colbert & De Oliveira, 1990), in the absence of pollinators autopollination will not fertilize innermost pistils resulting in misshapen and underdeveloped fruit (Shanks, 1969; Szklanowska & Wieniarska, 1993). Insect visitation increases druplet number and fruit weight and is necessary for the production of commercial quality fruits (Cane, 2005; Chagnon, Gingras, & Oliveira, 1991; Willmer et al., 1994)

5.3.2 Bee Community

5.3.2.1 Bee abundance. We quantified the abundance and diversity of bees visiting blueberry (N = 9) and raspberry patches (N = 15) over two summers (2016-2017). We visited the majority of farms each year (N = 14), but two farms were sampled for a single year. In each year, we visited patches at least 3 times during bloom. We standardized pollinator activity observations of both crops by sampling between 09:30 and 15:00 h, during favorable conditions (clear to hazy skies, temperature above 15°C, and wind speeds less than 3 m/s).

We stratified observations for both raspberry and blueberry by randomly selecting plants at two sites within each patch. We performed three 10-minute observations at each plant (total of 60 minutes of observation per farm visit). Within each year, data collectors were rotated among farms and at sites within farms. To quantify abundance observers established a 1 m^3 area at each observation plant and recorded the number of flower-visiting individuals entering the observation area. During abundance observations, we assigned flower visitors to nine morphospecies groups: *Apis, Bombus, orange Bombus, big black bee, slender black bee, tiny black bee, green bee,* and *other bee*. Following observations, we recorded the number of flowers to assess the total floral resources available.

5.3.2.2 Bee diversity. Following observations, we sampled bee diversity via 10-minute aerial netting along one 20 m transect at each site (total of 20 minutes of specimen collection per visit per farm). Specimens were stifled in ethyl acetate, mounted and identified to species using published and online guides.

We used our specimen data to estimate species bee diversity using rarefaction methods (Colwell et al., 2012). We focused our diversity analysis on resolved native species, we therefore removed non-native and unidentified specimens: *Andrena wilkella* (<0.01% of 2,489 collected specimens), *Osmia cornifrons* (<0.01%) and unidentified (0.02%). We computed incidence-based rarefaction and extrapolation sampling curves for the three most widely used members of the Hill number family (species richness, Shannon diversity and Simpson diversity) with the iNEXT software (Chao, Chiu, & Jost, 2014; Hsieh, Ma, & Chao, 2016). We constructed bootstrapped 95% confidence intervals and standard errors for estimated diversity of all farms. For analyses, we use estimated Simpson's diversity because of its intuitive interpretation in terms of probability and because it is correlated with the other diversity metrics.

To test for differences in community composition between crops (blueberry vs. raspberry) and treatment (with and without blueberry), we used PERMANOVA on a Bray-Curtis distance matrix with log(x + 1) abundance data between farms using the 'vegan' package in R (Oksanen et al., 2013) with crop type or treatment and year as fixed effects, and farm as a random effect. To visualize patterns in species composition, we used NMDS and ordinated the yearly community at each crop type. We also conducted indicator species analyses (Dufrêne & Legendre, 1997) to explore which bees are significantly associated with particular crops or treatments using the 'indicspecies' package in R (De Cáceres, Legendre, & Moretti, 2010). Using log(x + 1) abundance data combined across all crop or treatment and time periods, we calculated indicator values, with significance determined using 999 permutations. We assessed each bee species' preference for crops and treatments by calculating point-biserial correlation coefficients (r_{pb}) for each species, these values compare the species' abundance within a group to its abundance within all other groups (De Cáceres & Legendre, 2009; De Cáceres et al., 2010).

5.3.3. Bumblebee Population Size

Detecting wild bee nests *in situ* is a challenge (O 'connor, Park, & Goulson, 2012) and point-counts are therefore misleading estimates of population size (Crone & Williams, 2016). Population genetics provide a useful and commonly used estimate of nesting density based on sibship reconstruction (Carvell, Bourke, Osborne, & Heard, 2015; Redhead et al., 2016; Wood, Holland, Hughes, & Goulson, 2015). Measures of colony numbers derived from molecular genetic methods are particularly useful for eusocial species, such as *Bombus,* where the majority of individuals are not reproductive (Geib, Strange, & Galen, 2015).

5.3.3.1 Bombus sample collection. We collected *Bombus impatiens* Cresson workers at the end of July and early August 2016. *Bombus impatiens* is an abundant native bumblebee and important crop pollinator in Vermont (Nicholson et al., 2017). Commercial *B. impatiens* colonies were not in use at any farm. From the center of each farm, we searched for *B. impatiens* workers in an area of a circle with radius 300 m collecting specimens until either a minimum of 130 individuals were obtained or 6 hrs elapsed. We caught workers while foraging on flowers and stored collected specimens immediately in 100% ethanol for DNA extraction. After visually checking the species' identity and sex we attempted to remove all males and non-target bumblebees. We were able to collect the minimum number of workers from all but two farms (86 and 67 specimens obtained after 6 hrs). From these collected specimens we randomly selected 120 from each farms for DNA extraction and amplification.

5.3.3.2 Bombus genotyping. DNA was extracted from forelegs of specimens using a modified Chelex® (Bio-Rad, Hercules, CA, USA) protocol (Lozier, Strange, Stewart, & Cameron, 2011; Strange, Knoblett, & Griswold, 2009; Walsh, Metzger, & Higuchi, 1991) and was stored at -20°C until PCR amplification. We genotyped samples in a multiplex reaction at 10 polymorphic microsatellite loci (*B96*, *B124*, *BL11*, *BL15*, *BT10*, *BT28*, *BT30*, *BTERN01*, *BTMS0062*, *BTMS0081*) (Estoup et al., 1995, 1996; Strange et al., 2009). PCRs were 10 µL in volume and contained 2 µL of template DNA, 1.4 mM MgCl2, 0.6 mM of each dNTP, 0.4 U of Taq polymerase, and <0.2 µM of four primers (forward primers labelled with VIC, NED, FAM and PET dyes, Applied Biosystems®). Samples were denatured at 95 °C for 3:30 min, followed by 31 cycles of 95 °C for 30 s, 55 °C annealing for 75 s and 72 °C for 45 s; followed by a final extension step at 72 °C for 15 min. We visualized PCR products on an ABI 3730xl capillary DNA sequencers at the Utah State University Center for Integrated BioSystems using an internal size standard (GeneScan LIZ 500, Applied Biosystems®). We scored fragment sizes using Geneious® version 10.0.

We reprocessed 10% of individuals because they failed to express fully at all loci. We removed *BL15* because this locus did not amplify well, leaving nine loci for analysis. We then retained samples only if data were available from a minimum of six microsatellites. We checked for null alleles and deviations from Hardy-Weinberg equilibrium using the R package ‘PopGenReport’ (Adamack & Gruber, 2014). After reprocessing samples and cleaning data, genotyping success was high (96% of 1790 individuals retained), yielding 113 samples on average per farm, not including the two sites with < 130 samples (64 and 82 individuals were analyzed).

5.3.3.3 Bombus colony assignment. Based on individual’s multi-locus genotypes we estimated the number of nests at each site using maximum likelihood sibship reconstruction in COLONY version 2.0 (Carvell et al., 2012; Lepais et al., 2010; Wang, 2004). We carried out a medium run with full-likelihood precision and a conservative genotyping error rate of 5% based on our results of regenotyping 10% of randomly selected individuals and scoring errors. We assumed a monogamous mating system for males and females, therefore allowing the assignment of full-siblings. To ensure convergence of results in the sibship reconstructions, each site was analyzed three times, each with a different random number seed, and we took the average number of unique nest groups. To account for variation in number of individuals collected, we divided the number of COLONY-estimated nest groups per farm by the number of successfully genotyped individuals, yielding a proportion of unique nests.

5.3.3.4 Morphometric measurements. We measured body size for each of the 1790 specimens used for DNA extraction. We used calipers (Mitutoyo® 500-196-30**)** and an Olympus SZ61 scope to measure the inter-tegular distance (ITD) to the nearest 0.01 mm. This measure scales allometrically with body mass (Cane, 1987) and is frequently used to characterize differences in body size (Forrest, Thorp, Kremen, & Williams, 2015; Greenleaf, Williams, Winfree, & Kremen, 2007).

5.3.4 Statistical Analysis

There is an order of magnitude difference in average flower density between blueberry and raspberry; we therefore z-score transform floral density values to make them comparable. We used nearest neighbor non-parametric local regression (‘loess‘, span = 0.6) to fit smoothed lines with z-score transformed raspberry and blueberry floral density, as well as native bee abundance. We also subset our dataset to those observations occurring on farms with blueberry and raspberry to investigate if there are any crop-dependent differences in morphospecies abundance. For each morphospecies we use linear mixed effects models with crop type as a fixed effect and farm as a random effect. Using a similar model structure, we also tested whether the abundance of a given morphospecies visiting blueberry predicted its abundance on raspberry.

To assess the influences of flower density on observed native bee abundance we used generalized linear mixed-effects models (GLMMs) with a Poisson error distribution. Rather than average abundance at a given observation level (e.g., farm), we used our full dataset of visitation counts with flower density and year as fixed effects and farm, date and site as nested random effects. To assess whether farms with resource continuity (i.e., raspberry farms with blueberry) had more abundant native bee communities we again used GLMMs with blueberry presence or absence and year as a fixed effect and the same random effect structure as above.

To assess the effect of resource continuity on native bee diversity we took into account the uncertainty associated with each farm's Simpson diversity estimation. We used linear models with a weighted regression in which diversity estimates are weighted by the inverse of their standard error. This technique further accounts for differences in sampling effort among the farms because variance is a function of sampling effort (Pelini et al., 2014). We also used linear models to assess whether resource continuity influenced the proportion of detected unique nests. Finally, we used linear mixed effects models to investigate if *B. impatiens* worker body size was influenced by the presence or absence of blueberry.

For the GLMMs we evaluated the statistical significance of each predictor variables using Wald chi-square tests. For the linear models we used type II F-tests and if models had mixed effects we estimated degrees of freedom with Kenward-Roger approximation (Kenward & Roger, 1997). Based on graphical analysis (i.e., residuals vs. predicted values), all models satisfied underlying statistical assumptions, including linearity and homogeneity of variances. We performed all statistical analyses in R version 3.3.2 (R Development core Team 2016) using packages ‘car’ (Fox and Weisberg, 2011), ‘lme4’ (Bates et al., 2015), and ‘lmerTest’ (Kuznetsova, Brockhoff, & Christensen, 2015).

5.4 Results

5.4.1 Floral Resources

Floral resources were consistent for farms that planted both crops (Figure 3). We observed greater floral density on blueberry bushes (average number of flowers/m^3 ± SD = 428.4 ± 324.7) than raspberry (56.1 ± 41.7).

5.4.2 Bee Abundance

For both crops, we observed increasing abundance with greater floral density (blueberry: $z = 7.3$, $P < 0.001$; raspberry $z = 4.4$, $P < 0.001$) (Figure 4). For some morphospecies we observed crop-dependent differences in abundance (Figure 5). We observed more *Bombus* queens on blueberry ($F_{1,22.6} = 17.7$; $P < 0.001$) and on raspberry we observed more honeybees ($F_{1,22.8} = 71.8$; $P < 0.001$), *Bombus* workers ($F_{1,22.8} = 19.4$; $P < 0.001$), tiny black ($F_{1,23.2} = 3.6$; $P = 0.07$), and slender black bees ($F_{1,22.8} = 7.8$; $P = 0.01$) (Figure 5). The average abundance of some morphospecies observed visiting raspberry was positively related to abundance visiting blueberry, albeit sometimes marginally (Figure S1; honeybees: d.f. = 7.1, $t = 2.6$, $P = 0.03$; *Bombus*: d.f. = 12.8, $t = 1.9$, $P = 0.08$; big black bees: d.f. = 13, $t = 2.8$, $P = 0.01$).

5.4.3 Bee Diversity

From 708 specimens collected in blueberry patches, we identified 60 bee species belonging to 11 genera. The most species-rich genera were *Andrena* (19 species), *Bombus* (9 species), and *Lasioglossum* (19 species). The five most common species (*B. impatiens*, *B. bimaculatus*, *A. carlini, A. vicina*, and *B. ternarius*) accounted for 51% of collected specimens (Figure 6). Across the larger system of raspberry patches, we collected 1713 specimens comprising 96 species belonging to 17 genera. The same genera were the most species rich on raspberry (29, 10 and 25 species, respectively) and the five most frequently collected species were (*Ceratina calcarata, B. bimaculatus B. impatiens, C. mikmaqi* and *A. vicina*), accounting for 34% of collected specimens. Many species were common to both blueberry and raspberry (average farm level Jaccard similarity = 0.25 ± 0.07; Figure 6a). Species assemblages between blueberry and raspberry crops were significantly different ($F_{1,42} = 8.9$; $P < 0.001$), but raspberry species assemblages observed on farms with and without blueberry were not different ($F_{1,25} = 1.2$; $P > 0.05$) (Figure 6b). In both cases, species assemblages were different between years (between crops: $F_{1,42} = 2.8$; $P = 0.004$; between treatments: $F_{1,25} = 2.4$; $P = 0.002$). Particular species were significantly associated with either blueberry and raspberry (Table 1). Not surprisingly, the blueberry specialist *Andrena bradleyi* was associated with blueberry, and many stem-nesting genera (e.g. *Ceratina*, *Hoplitis*, *Hylaeus*) were associated with raspberry. Between treatments, a single species was associated with raspberry farms without blueberry, *Augochloropsis metallica* ($r_{pb} = 0.66$, $P = 0.048$).

5.4.4 Community and Population Response to Resource Continuity

Sequential blooming of blueberry and raspberry did not consistently affect pollinator communities, populations and individuals. Native bee abundance (Figure 7a, $\chi^2 = 1.9$, $P > 0.05$) was not significantly different between raspberry farms with or without blueberry. Native bee diversity was not significantly different between raspberry farms with or without blueberry (Figure 7b, $F_{1,25} = 0.4$; $P > 0.05$). Subsetting specimen data to only those species observed on both crops did not change these findings ($F_{1,25} = 1.2$; $P > 0.05$).

Bumblebee colony density was marginally greater on farms that had blueberry (Figure 7c; $F_{1,12} = 3.551$; $P = 0.08$). All farms contained sister pairs of *B.* impatiens workers. From the distribution of resampled colonies per site, we found the average estimated number of nests per site was 76 ± 2.8. Normalizing by the number of individuals collected per site we found on average 70% of workers belonged to colonies with a single representative. There was substantial variation in the intertegular distance of *B. impatiens* workers (Figure S3) but individual size did not differ significantly between treatments (Figure 7d, $F_{1,11.99} = 2.658$; $P > 0.05$).

5.5 Discussion

Resource continuity has the potential to shape population growth and community composition by altering the temporal distribution of resources. We present some of the first empirical evidence testing resource continuity effects on wild bees resulting from sequentially blooming crops. We found that diversified farm systems had continuously available floral resources. Bees did not respond significantly to this resource continuity.

We found marginal effects of resource continuity when considering bumblebee colony density (*P* = 0.08). Though far from definitive, our results suggest that agricultural landscapes composed of sequentially flowering crops do not bolster pollinator populations through temporal complementarity of flowering resources.

5.5.1 Pollinator Population Response to Resource Continuity

We found that *Bombus* colony density was on average greater in landscapes with continuous resources. Research using population genetics shows that colony density changes between spring and summer, and that nest survival between these periods is positively influenced by the availability of local floral resources (Goulson et al., 2010). Other work shows that floral resource availability improves inter-annual survival of bumblebee colonies, with a greater survival of family lineages in landscapes with a greater proportion of spring floral resources (Carvell et al., 2017). The enhanced colony density we observed is likely the result of more queens persisting in landscapes with resource continuity because floral resource availability improved colony survival. In temperate regions, spring is a period in the life cycle of bumblebees when colonies are particularly sensitive to resource limitation (Heinrich, 2004; Suzuki, Kawaguchi, & Toquenaga, 2007). Blueberry patches provide queens with early season pollen and nectar, and in our landscapes had the highest floral density. Mass flowering crop presence is known to increase the density of bumblebees on later blooming crops (Riedinger et al., 2014), but sustained population growth resulting from this resource pulse occurs only if resources are continuously available (Holzschuh et al., 2016).

The effects of resource availability might be expressed physiologically as well. In bees and other Hymenoptera individual size is the product of maternal investment, and progeny size at maturity is often correlated with amount of food provisioned to offspring (Bosch, 2008). Adult bee body size is known to vary with resource availability (Radmacher & Strohm, 2010; Renauld et al., 2016); however, we did not find an effect of resource continuity on the average size of bumblebee workers. Bumblebees are known to have large intraspecific size variation; workers exhibit an almost 10-fold mass difference within species and even within single nests (Goulson et al., 2002). This size variation may be adaptive (Peat, Tucker, & Goulson, 2005), because variably-sized foragers visit flower types appropriate to their morphology, minimizing intra-colony competition and improving foraging efficiency as a whole. If size variation is under selection, it follows that detecting a physiological response to environmental conditions will be challenging without more rigorous experimentation.

5.5.2 Pollinator Community Response to Resource Continuity

We did not observe a greater abundance or diversity of bees in landscapes with resource continuity. If resource continuity leads to metapopulation stability by temporally connecting patches and reducing local extinction rate (Kuussaari et al., 2009), we expected to find a more diverse fauna of bees on raspberry farms with previously blooming blueberry patches. Instead we found that species assemblages were similar between treatments. Community dissimilarity between crops may be due to differences in bee life history and phenology or the biology of the crops themselves acting as an environmental filter. For both blueberry and raspberry, the majority of observed diversity is composed of solitary, small bodied species. Many of these species (e.g., *Andrena*, *Lassioglossum*) have short lifecycles, and our indicator species analysis shows that these species have the strongest association with different crops. Bee phenology is also likely driving dissimilarity, are active during bloom of each crop. This is corroborated by our morphospecies observations, with groups such as slender black bees (predominantly *Andrena* spp. and *Lassioglossum* spp.) showing significant differences in abundance between crops. Cultivation aspects of both crops may underpin community differences. Raspberry pruning management exposes the pithy center of old canes, an ideal nesting substrate, and many genera unique to raspberry are stem nesting species (e.g. *Ceratina*, *Hoplitis*, *Hylaeus*). Floral differences between the crops may drive community dissimilarity as well. Blueberry floral morphology is known to limit visitation (Courcelles et al., 2013), and honeybees are notably less abundant blueberry visitors, presumably because blueberry pollen is inaccessible to honeybees because they cannot sonicate anthers. Raspberry flowers on the other hand offer copious, easily accessible nectar and pollen, and local bee communities might respond strongly to the availability of these resources.

If biological aspects of bees (e.g., differences in life history or phenology) or crops (differences in resources offered) are shaping communities, it is unsurprising that we did not observe a response to resource continuity in terms of diversity. If we subset our specimen data to only those species observed on both crops, we still do not see a difference in community composition. These findings suggest that when looking for effects of resource continuity limiting the scope of research to more generalist species with life cycles that span the duration of the resource period (e.g., *Bombus*) will be fruitful. Responses to resource continuity by short-lived or specialist species will likely be absent or hard to detect.

5.5.3 Implications for Agricultural Landscapes

Many ecosystem services (e.g., pollination, biocontrol) are dependent on mobile organisms with resource needs that often extend beyond periods of focal crop productivity (Schellhorn et al., 2015b; Vasseur et al., 2013). Resource continuity may support service providing organisms, but is an undervalued aspect of agroecological management. Diversified farming is a way to achieve resource continuity. We present a framework, grounded in ecological principles of connectivity and metapopulation dynamics, which explain how crop diversity, by promoting resource continuity, may support beneficial organisms. Meta-analysis show that diversification schemes (e.g., intercropping, push-pull agriculture and inclusion of flowering plants) improve pest control in crops (Letourneau et al., 2011) with studies typically invoking mechanisms based on niche differentiation (i.e., enemies hypothesis (Root, 1973)). Here we argue that in addition to spatially-focused concepts such as landscape complementarity (Dunning, Danielson, & Pulliam, 1992; Fahrig et al., 2011), temporal resource complementarity is a mechanism that can explain the beneficial effects of crop diversity on mobile organisms.

However, few studies have examined crop diversity effects for other beneficial organisms, such as pollinators. Bommarco et al. (2013) identify crop diversification as an ecological intensification management option with known beneficial effects for soil formation, weed suppression and pest control, yet with ‘likely but unproven’ positive impacts on pollination. Different habitats within diverse landscapes can provide pollinators with floral resources across space and time (Mallinger, Gibbs, & Gratton, 2016), however, whether resource complementarity can result from crop diversity is still largely unknown. Our study addresses this gap by providing preliminary evidence of the beneficial effects of resource continuity resulting from diversified agriculture.

5.6 Conclusions

Resource continuity may support local population persistence and temporally connect patches in agricultural landscapes, thereby increasing metapopulation stability and decreasing local extinction. Here we show that landscapes with resource continuity had marginally larger nesting densities of an important crop pollinator, *Bombus impatiens*. We did not find that resource continuity improved the abundance or diversity of visitors to crop flowers, probably due to differences in the community composition of common visitors between crops. Resource continuity did not have individual physiological effects either. More research should test for effects of resource continuity by focusing on generalist species with life cycles that match the resource duration. Moreover, studies examining how movement patterns change over time in landscapes with variably continuous resources will provide critical evidence connecting spatial and temporal connectivity. Crop diversification is an important agroecological approach, and may increase pollinator populations by promoting continuous resource availability. Supporting populations of beneficial organisms requires understanding not only where, but when species interact with the landscape.

AKNOWLEDGEMENTS

CCN was supported by the National Science Foundation Graduate Research Fellowship program and the Sustainable Agriculture Research and Education (SARE) program of the USDA National Institute of Food and Agriculture [Grants DGE-1451866 and GNE16-129]. We thank Anna Clayton, Alex Frayer, Jen Hayes, Olivia Honigman, Cassidy Motahari, and Kristen Switzer and others for data collection. We thank Joyce Knoblett, Jamie Strange and Amber Tripodi at the USDA-ARS Pollinating Insects Research Unit for supplying space and expertise for the population genetic work. We thank Jason Gibbs and Tom Woods for identifying bee specimens. We also thank Xin Jing, Mathew Mitchell, Leif Richardson, and Aaron Schwartz for their input on manuscript drafts.

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5.8 Tables

Table 1 Indicator values for bee species sampled across different crops

Species	Crop	r_{pb}	P
Bombus griseocollis	blueberry	0.83	0.001
Andrena carolina	blueberry	0.71	0.004
Lasioglossum versatum	blueberry	0.65	0.002
Xylocopa virginica	blueberry	0.62	0.004
Lasioglossum lineatulum	blueberry	0.55	0.020
Andrena bradleyi	blueberry	0.47	0.044
Ceratina calcarata	raspberry	0.83	0.001
Ceratina mikmaqi	raspberry	0.75	0.001
Andrena crataegi	raspberry	0.69	0.002
Lasioglossum coriaceum	raspberry	0.69	0.001
Hylaeus modestus	raspberry	0.67	0.002
Andrena rugosa	raspberry	0.58	0.008
Agapostemon sericeus	raspberry	0.58	0.022
Andrena commoda	raspberry	0.58	0.007
Andrena milwaukeensis	raspberry	0.57	0.045

Hylaeus mesillae	raspberry	0.57	0.008
Lasioglossum cressonii	raspberry	0.57	0.026
Ceratina dupla	raspberry	0.55	0.025
Andrena cressonii	raspberry	0.54	0.025
Andrena hippotes	raspberry	0.54	0.033
Augochloropsis metallica	raspberry	0.54	0.024
Hylaeus affinis	raspberry	0.51	0.016
Hoplitis producta	raspberry	0.48	0.030

Point-biserial correlation coefficients (r_{pb}) for all bee species were determined for each crop, with P values assessed using 999 permutations. Species significant at $P < 0.05$ are reported

5.9 Figures

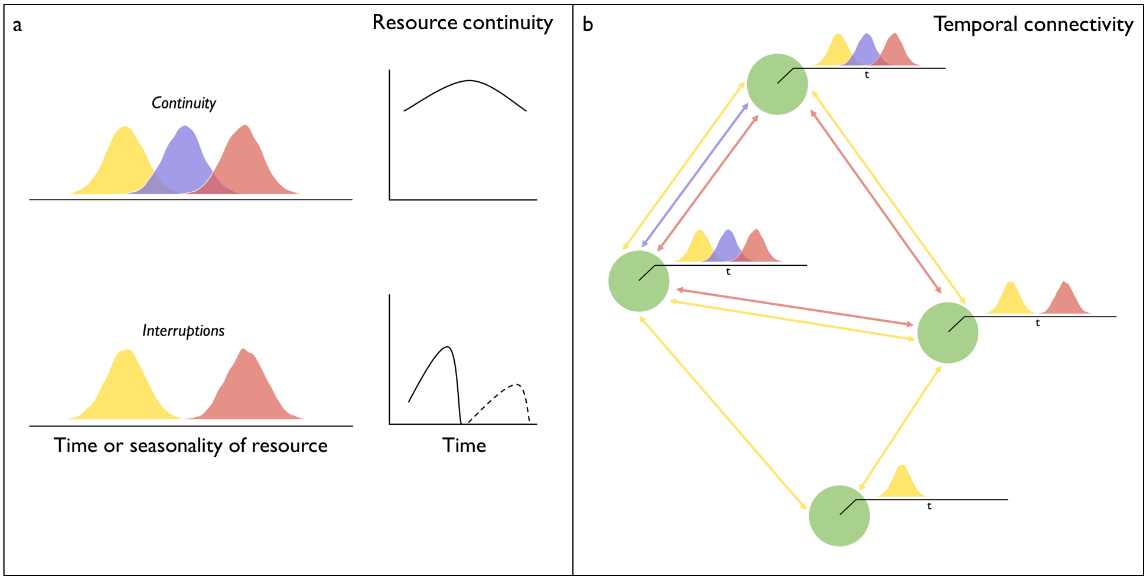

Figure 1 The dynamics of resource continuity (**a**) and temporal connectivity (**b**). The availability of different resources (colors) can change over time and directly impact local communities (a, after Schellhorn et al. 2015). Resource continuity occurs when resources are available through the entire time period (a, top). Corresponding population densities (a, top right) are sustained at high and relatively constant levels. Resource interruptions limit population densities (a, bottom). Resource continuity can affect temporal connectivity (**b**) by changing patch quality over time, thus altering how organisms will move between patches at any given period. For example, during the first resource availability period (yellow) all patches (green circles) are connected. However, where resource discontinuities occur connectivity between patches changes.

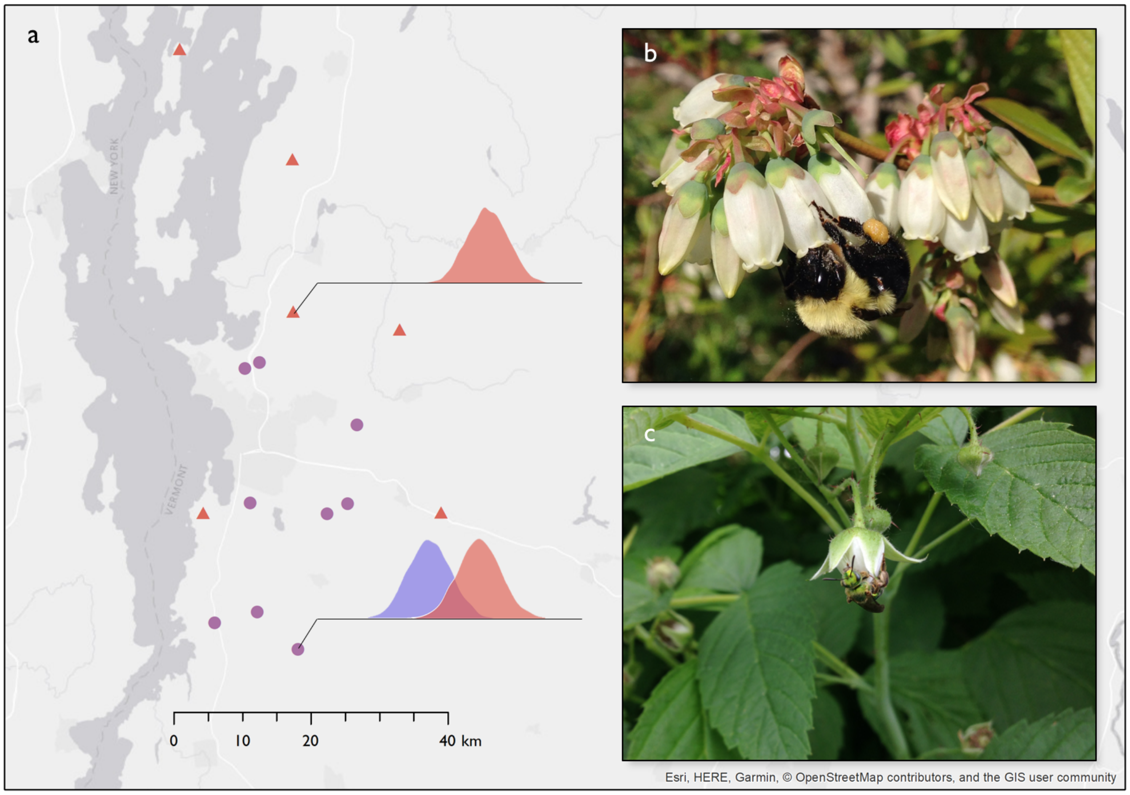

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Figure 2 Map of study area (**a**) depicting the locations of farms with resource continuity (blueberry and raspberry; purple circles) and farms without resource continuity (only raspberry, red triangles) in the Champlain Valley, Vermont, USA. A native bumblebee (*Bombus impatiens*) visiting highbush blueberry flowers (**b**) and a native sweat bee (*Agapostemon sericeus*) visiting a summer bearing raspberry flower (**c**).

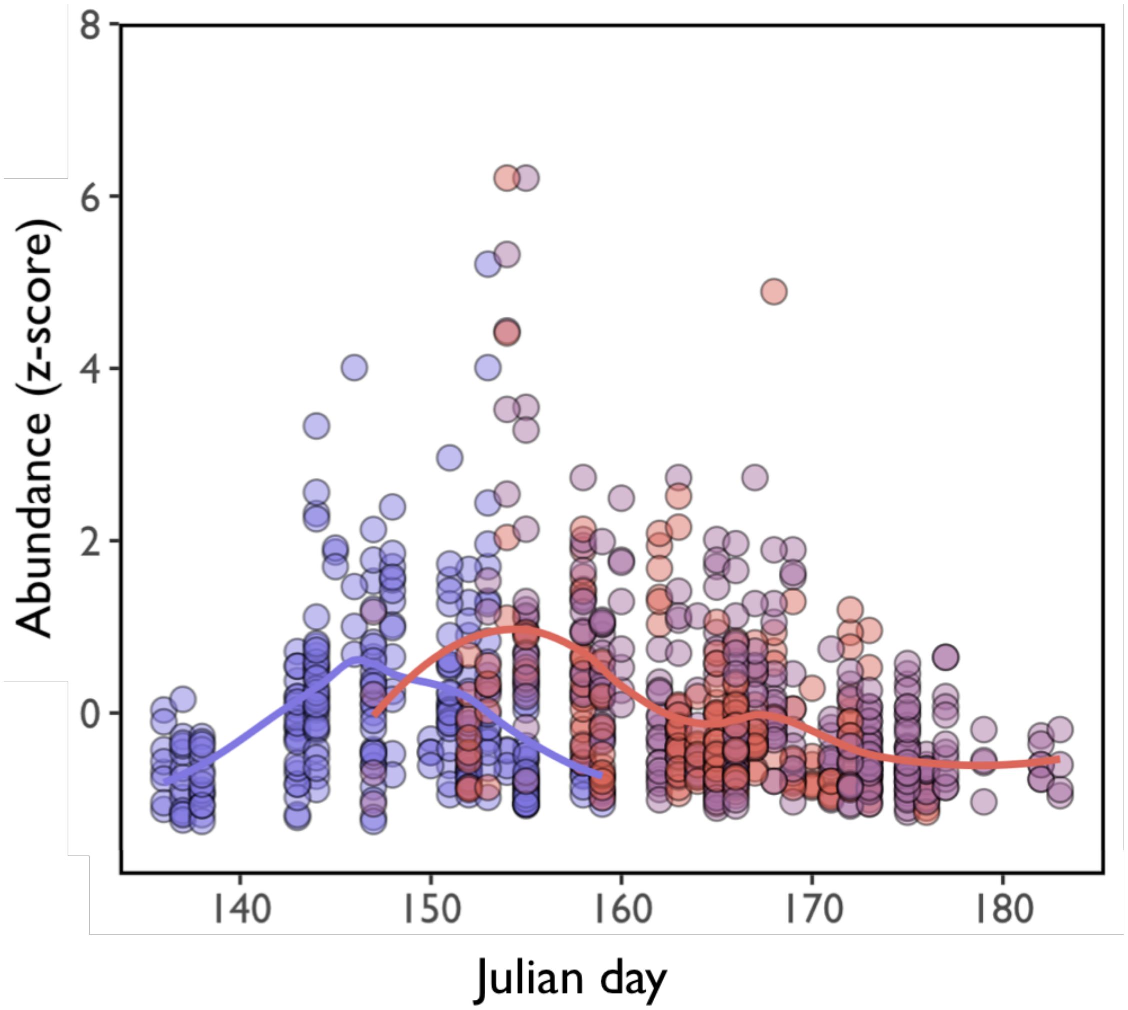

Figure 3 Time series of crop flowering periods. Abundance of flowers for blueberry (blue) and raspberry (red and purple) are z-score transformed for each crop. Smoothed lines are fit through loess regression.

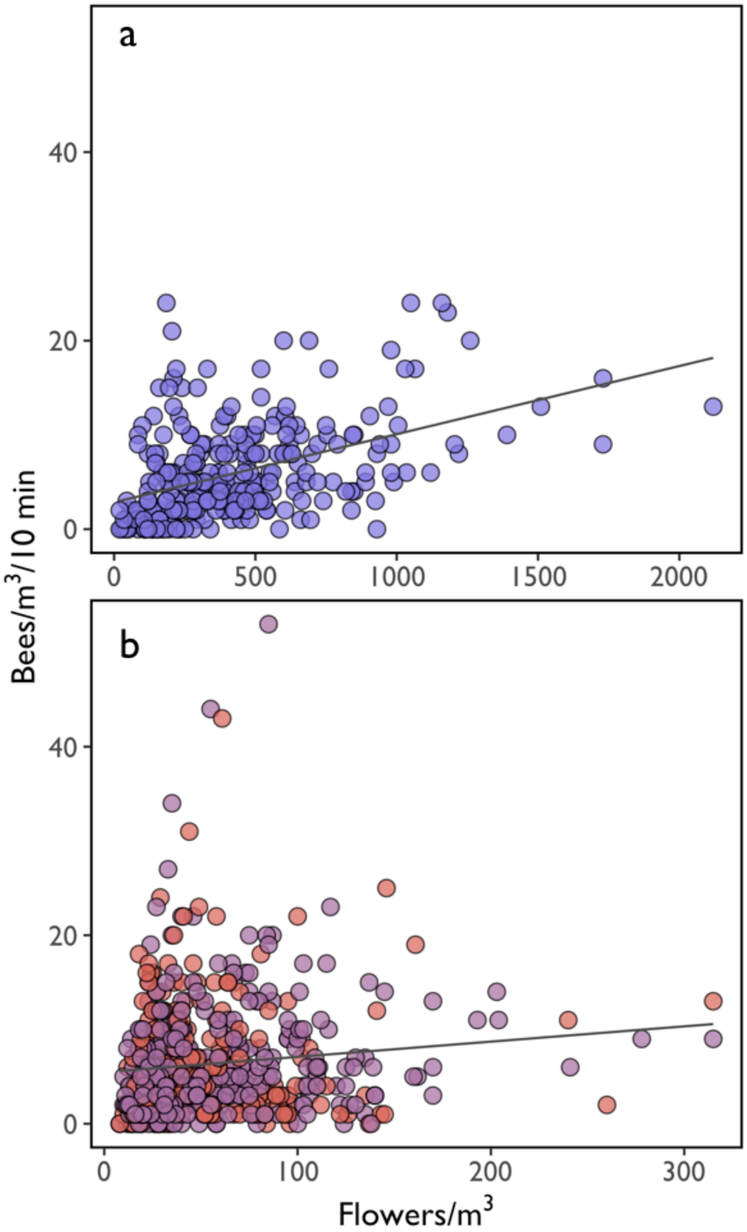

Figure 4 Native bee abundance is positively related with flower density for both blueberry (**a**, blue circles, $P < 0.001$) and raspberry (**b**, red and purple circles, $P < 0.001$).

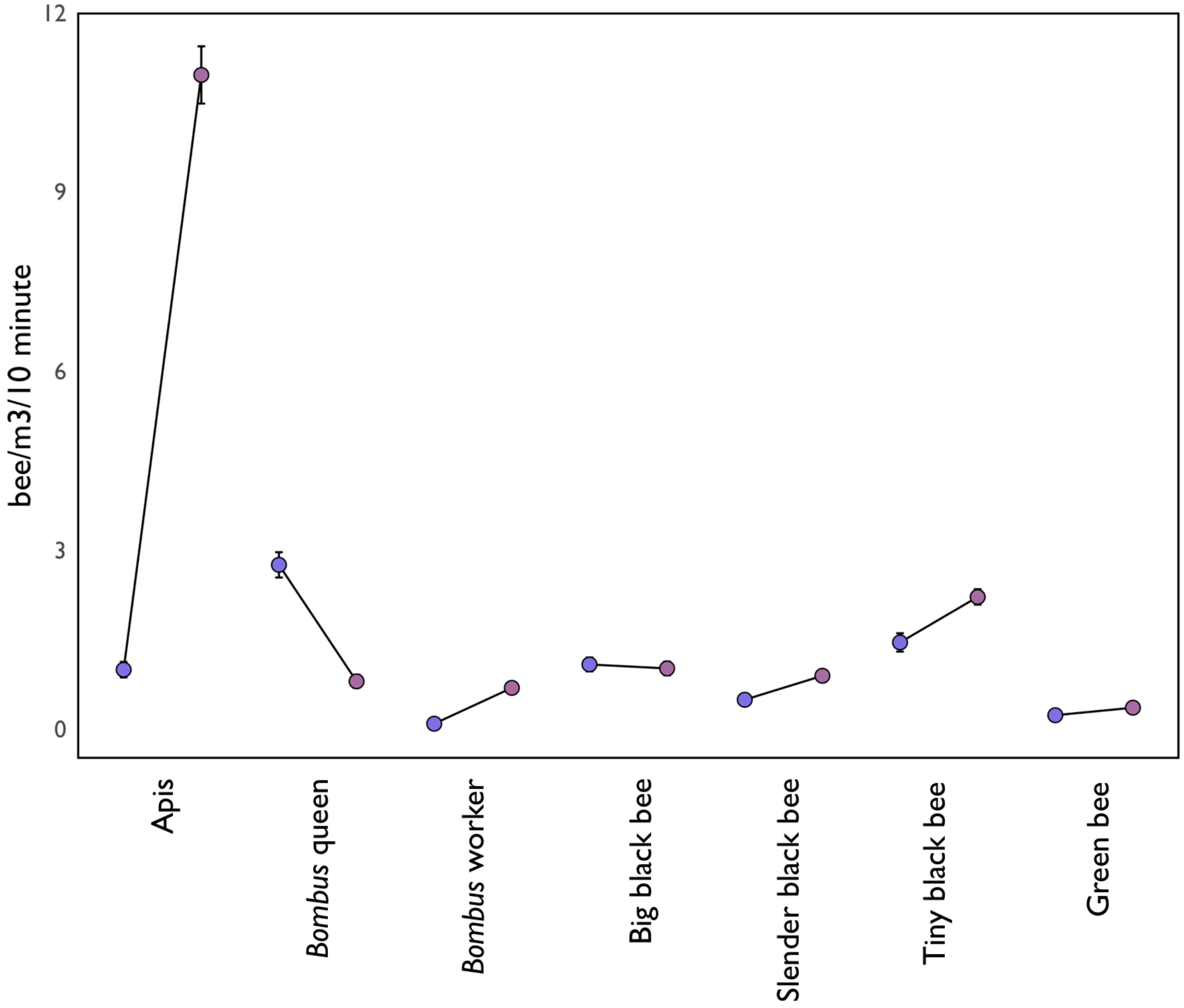

Figure 5 Differences in abundance for morphospecies classes observed visiting blueberry patches (blue) and raspberry patches with blueberry (purple). Points depict average ± SEM. Error bars for many morphospecies are obscured by the data points themselves.

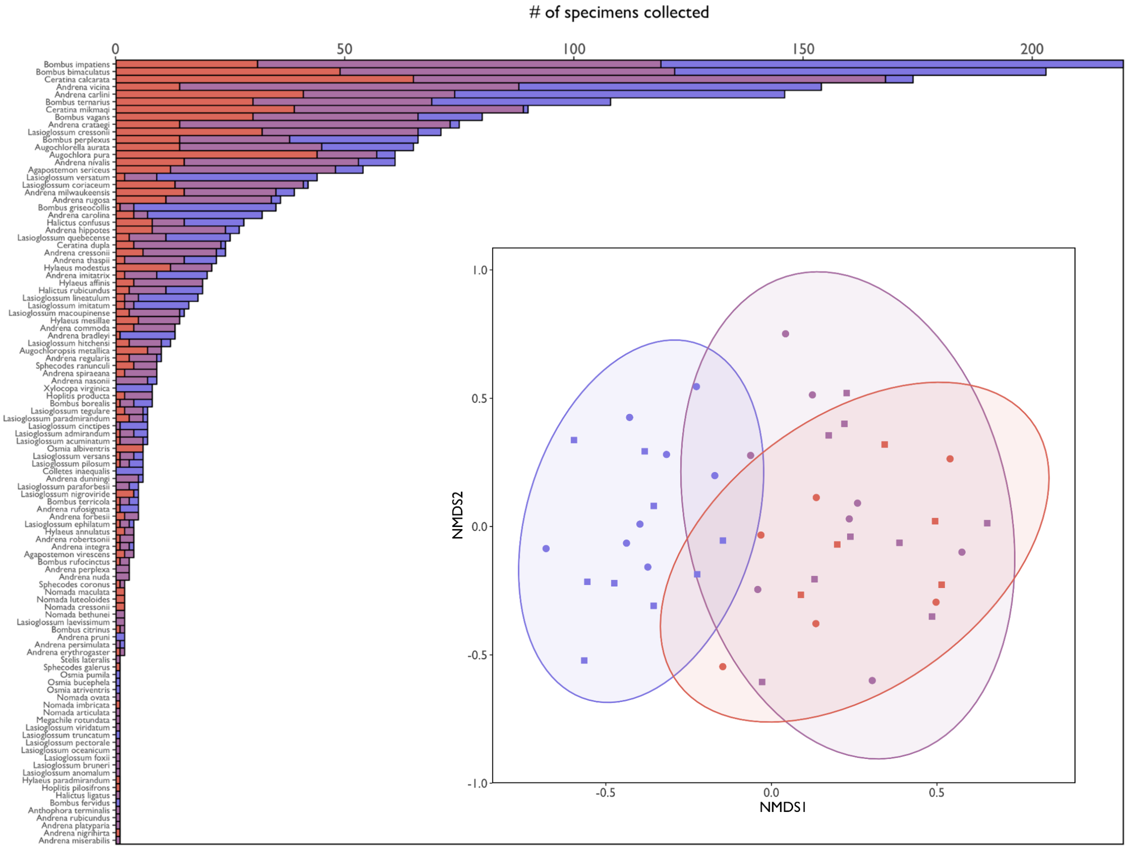

Figure 6 Rank abundance of collected specimens on three crop types: blueberry patches (blue), raspberry patches with blueberry (purple) and raspberry patches without blueberry (red). Non-metric multidimensional scaling of the crop types (inset) based on species abundances (Bray–Curtis dissimilarities). Farms are shaded according to crop type and shaped according to year (2016, circles; 2017, squares).

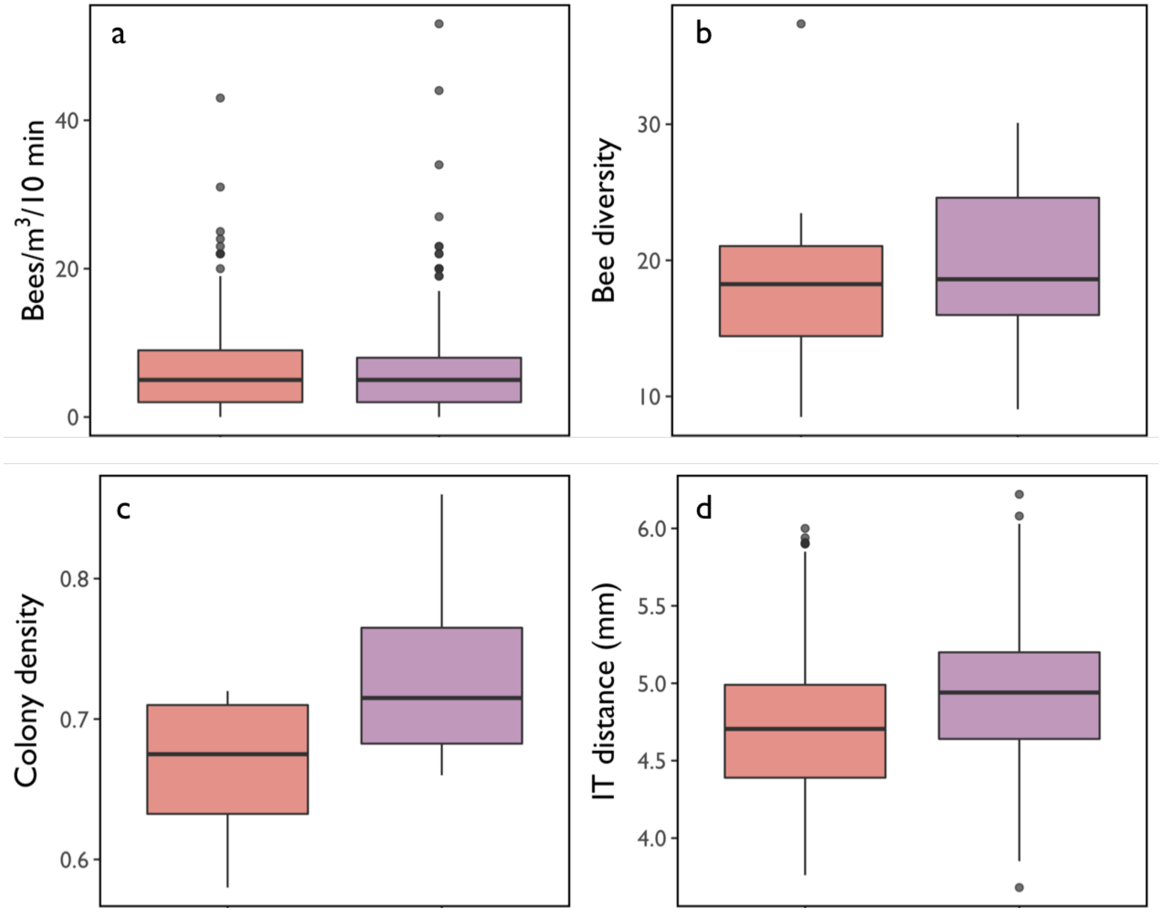

Figure 7 The effect of resource continuity on pollinator individuals, populations, and communities. Boxplots represent raspberry farms without blueberry (red) and with blueberry (purple). The abundance of native bees (**a**), Simpson diversity (**b**), or *B. impatiens* worker size (**d**) was not statistically different. Proportional estimated density of *B. impatiens* colonies (**c**) was marginally higher when resources were continuously available.

5.10 Supplementary Figures

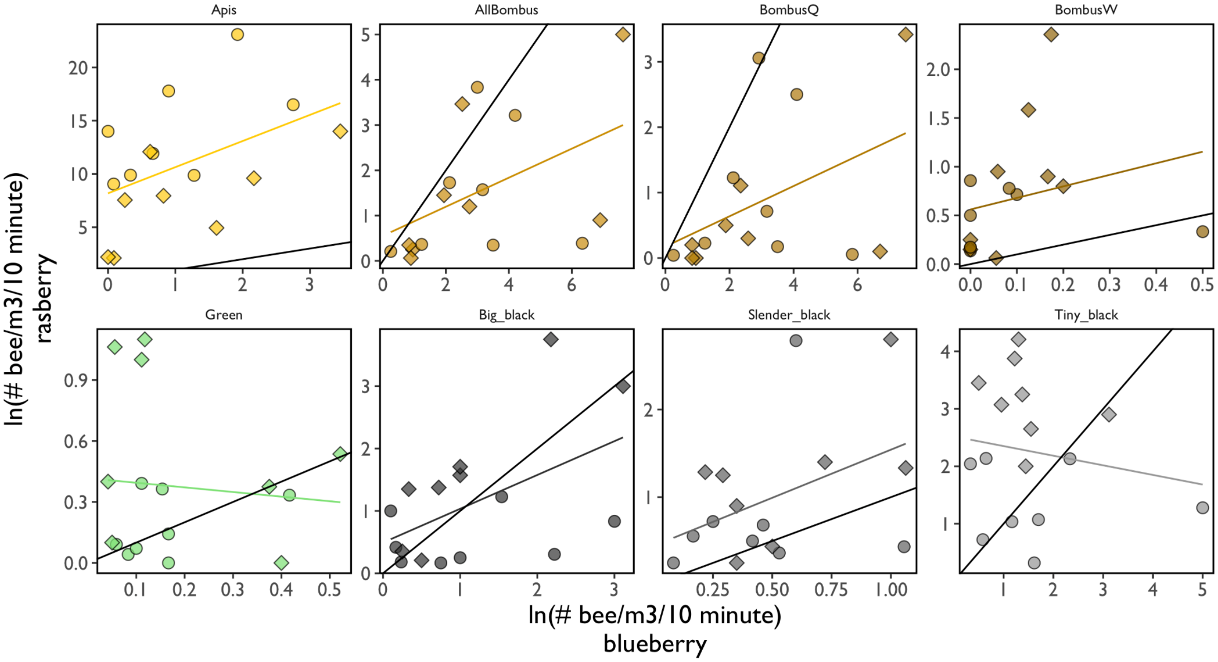

Figure 1 Relationships between abundance of different morphospecies observed on blueberry and raspberry for the subset of farms that had both crops. Shapes are shaded according to morphospecies and shaped according to year (circles: 2016, diamonds: 2017). Thick lines are linear fits. Thin solid line is the 1:1 line.

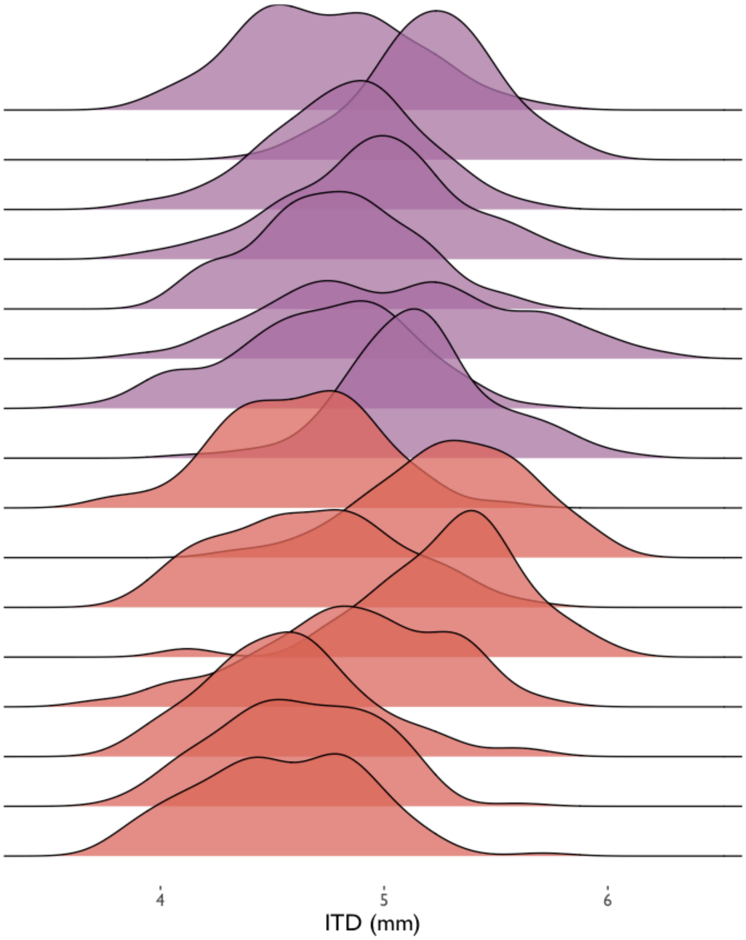

Figure 2 Distributions of *Bombus impatiens* worker body size as measured by intertegular distance (ITD) from individuals sampled on raspberry farms with blueberry (purple) and farms without blueberry (red).

CHAPTER SIX: CONCLUSIONS

Over the past decade we have made significant progress towards understanding how land use change affects the provision of ecosystem services, however critical gaps in our knowledge remain. Consensus is still lacking about the effects of specific management approaches on pollinator diversity, population dynamics and pollination services and there is an enduring need for scientific understanding of the interaction between management and land use change. Research to this end will help develop effective practices that support multifunctional landscapes. To fill these gaps, both theoretical and empirical approaches are necessary to predict and describe biodiversity patterns and ecosystem services provision as landscapes continue to change.

As a first step toward filling these gaps, I investigated how pollinator communities respond to the interaction between ecological infrastructure (i.e., amount of semi-natural area) and management intensity. I found that farm management and landscape pattern interact such that the negative effects of intensive agriculture on native bee communities are compounded by landscape simplification. While other research has shown that landscape pattern moderates how management impacts farmland biodiversity, Chapter 2 presents novel evidence of this effect on the provision of ecosystem services. Additionally, previous work with landscape-management interactions has typically categorized agricultural practice as binary (i.e., conventional vs. organic), whereas I developed a gradient of management intensity. In terms of practical significance, I found that landscapes with extensive natural area had greater wild bee diversity and pollination service supply, irrespective of agricultural intensity. Under these conditions, we should prioritize the maintenance of current levels of ecological infrastructure by protecting natural areas. Conversely, in landscapes with less natural area, I found that local farm management could safeguard biodiversity and ecosystem service under low intensity management. This work represents a consequential step for improving the measurement of agricultural management and understanding how ecological infrastructure moderates management impacts to regulate patterns of both biodiversity and ecosystem services.

In my third chapter I focused on an increasingly popular ecological intensification approach to safeguard pollinators in agriculture landscapes: establishing diverse wildflower plantings adjacent to crop fields. Enhancing pollinator habitat in agriculture holds promise, but moving past notions of ‘if we plant it, they will come’ requires management informed by tools sensitive to the behavioral and landscape dynamics of the organisms underpinning ecosystem services. In part, our incomplete understanding of how landscape pattern links with ecosystem services is due to the difficulty in gathering data about these variables at landscape scales; I overcome this using multiple pollination service models. This chapter accomplishes two objectives: 1) validating two established pollination service models using field data and 2) applying these models using real landscapes and simulated habitat enhancements. Model validation revealed that an optimal foraging model best predicted bee visitation across habitat types. Model application showed that the benefits of establishing pollinator habitat depend strongly on enhancement strategy and landscape context. Side-by-side comparisons of ecosystem service models are rare, and this chapter deepens our awareness of the conditions under which habitat enhancements are most likely to increase pollination services. From a practitioner’s perspective three enhancement design principles emerge: 1) enhancing only flowers can diminish services by distracting pollinators away from crops, 2) providing nesting resources is more likely to increase bee populations and crop visitation, and 3) the ecosystem service benefit of enhancements will be greatest in landscapes that do not already contain abundant habitat.

In these two chapters I show that landscape pattern moderates the effect of management on ecosystem services; in my fourth chapter I continue to explore how habitat enhancements influence pollinator communities, but I focus on whether biodiversity and ecosystem services have diverging responses to this specific management intervention. There is concern that actions aimed to promote ecosystem services may benefit only a subset of total species. I address this concern with a spatially replicated, multiyear habitat enhancement experiment across four US crop-regions. I found that, when compared to unmanaged controls, enhancements had greater taxonomic and functional diversity, and there was greater difference in community composition between enhancement sites. Conversely, we did not observe increased wild bee abundance on crops with enhancements, indicating that there was no benefit of enhancements for the supply of ecosystem services. Taken together, these findings show that actions aimed at promoting crop pollination can promote biodiversity and are a useful conservation tool. However, the benefit of enhancements for ecosystem services is less clear. A lack of an ecosystem service benefit may be explained by linking our modeling results with these empirical results. The enhancement experiment improved the availability of floral resources, whereas our model results demonstrate strong increases in crop visitation only when nesting resources are added. Further field work should investigate whether improving nesting resources directly increases pollinator populations and whether this drives a corresponding increase in pollination services.

Conserving ecological infrastructure at landscape scales and introducing sustainable agricultural practices have costs associated with them, both in terms of implementation and forgone opportunity. Diversified farming may provide a pathway to sustainability without compromising productivity. In my final chapter I explored whether agriculture can support pollinator communities through the floral resources provided by crops themselves. The two novel contributions of this work are 1) a conceptual framework based in theories of landscape connectivity and metapopulation dynamics that describe how crop diversity may benefit pollinator communities by providing resource continuity and 2) an empirical test of resource continuity effects on wild bee communities. We do not observe a strong signal of resource continuity on individuals, populations or communities of wild bees, although the effects of resource continuity are expressed most strongly when considering bumblebee colony density. Crop diversification is an important agroecological approach that may buffer against interrupted resource dynamics by promoting continuous resource availability, but further research is needed.

FUTURE DIRECTIONS

The Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES) has identified land use change and agricultural management as primary drivers of the status and trends of pollinators and pollination (Potts et al. 2016). This dissertation addresses many important gaps in our knowledge of these drivers and their influence on pollinators, from colonies of specific service providers in Vermont to communities of wild bees across US crop-growing regions. Nonetheless, many important lines of questioning remain around how land use and management, either in isolation or interactively, impact pollinators and pollination. Although far from comprehensive, I summarize a few here.

First, enhancing spatial and temporal connectivity at landscape scales may enhance the movement of pollinators, but its role in maintaining plant and pollinator populations remains unclear. In Chapter 2 I describe the importance of landscapes with extensive natural area coverage. In Chapter 5 I present a conceptual framework for how continuously flowering habitat patches could increase landscape connectivity. Future research could examine how both plant reproduction and pollinator populations respond to landscapes that vary along separate axes of spatial and temporal connectivity. This work will require overcoming technological hurdles of tracking pollen and pollinator movement, but understanding these dispersal dynamics could be an emerging frontier in pollination ecology.

Second, the net effects of ecological intensification are unknown and this complicates farmer decision-making around adopting sustainable practices. Future research will need to combine tradeoffs between higher yields via improved ecosystem services and opportunity costs such as lower productivity due to less intensive management. In Chapters 3 and 4, I have shown that enhancements do not always increase the supply of pollination services, yet whether this carries through to crop production is unclear. Enhancing crop field margins may promote multiple ecosystem services (e.g., pest control, soil retention) and their net benefit may only be realized if measured via a change in production. The net benefits of establishing enhancements should be balanced with their implementation and maintenance costs, as well as the cost of forgone yield if arable land is taken out of production. Complete accounting of multiple ecosystem services is a dauntingly complex research program, but a necessary one if ecological intensification aims to be a science-based approach for making agricultural production align with biodiversity protection.

Finally, the impact of land use and management practices, as well as the effectiveness of approaches to safeguard pollinators and pollination, will be influenced by climate change. Climate change has the potential to disrupt pollination phenologies, thereby rewiring interaction networks and altering both plant and pollinator persistence. Climate change also has the potential to shift pollinator ranges and growing regions for both wild and crop plants. Adaptive responses to climate change include increasing crop diversity and regional farm diversity, as well as targeted habitat conservation, management or restoration. In other words, many of the approaches for safeguarding pollinators and pollination today may also help buffer against the risks and hazards associated with climate change. However, the effectiveness of adaptation efforts at securing pollination under climate change is untested. Understanding potential disruptions and effective adaptation strategies is a crucial direction for future research.

SYNTHESIS

This dissertation demonstrates that landscape pattern and farm management have important effects on wild bee communities and the provision of pollination services. Support for this framework comes from a variety of sources, including observational studies (Chapter 2), experimental studies (Chapters 4 and 5), and modeling exercises (Chapter 3). No farm is an island, in the sense that actions taken locally are influenced by events and processes across mosaic agricultural landscapes. I have shown that specific conservation approaches such as enhancing floral resources can benefit pollinators, but the impact of such approaches on pollination and yield is less clear. Other approaches, such as crop diversification, require more research. I have also shown that landscape pattern provides the ecological context that determines the outcome of these local management approaches. Greater appreciation of and research into the multi-scale effects of landscape pattern on biodiversity and ecosystem service provision will support transitioning towards multi-functional agricultural landscapes that are productive, resilient and sustainable.

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