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Effects of land use on wild bee functional diversity

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Effects of land use on wild bee functional diversity

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THESIS

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ABSTRACT

EFFECTS OF LAND USE ON WILD BEE FUNCTIONAL DIVERSITY

By

Katherine A. Odanaka

University of New Hampshire, May 2019

Globally, wild bees are facing major declines due to many different factors. Land use is regarded as one of the most damaging of these factors as changes in land use can result in the destruction of critical wild bee habitat and foraging resources. Relative abundance and species richness have been used as standard methods for measuring the health of wild bee communities yet neither abundance nor richness are able to quantify how landscape change affects the traits found in members of the population. Phylogenetic methods are a novel tool that can measure community structure by examining how traits influence population structure. The focus of this thesis is to uncover how differences in land use, from grazing to successional states in forests, influence a number of aspects wild bee diversity and community structure.

Landscape change is one of the main drivers of wild bee declines due to alteration in available nesting and foraging resources. This project analyzed the relative abundance, species richness, and the phylogenetic diversity of six landscapes. We found that grazed areas had significantly lower levels of abundance and richness, but it did not alter the phylogenetic diversity of wild bee communities found at grazed sites. Nesting traits were major drivers of the community composition for wild bees found at grazed sites. Landscapes that exhibited lower management intensities and no grazing supported higher bee abundance and richness due to more available
nesting substrates and increased foraging densities. Lastly, we found numerous indicator species that can be used for environmental monitoring.

Forest margins offer valuable resources for wild bees in the form of additional nesting substrates and valuable forage, yet only early successional states and mosaic forested landscapes may support diverse bee communities. Our study found that canopy cover, a sign of later successional states in forested landscapes, reduces wild bee abundance and richness. Disturbances within forests were favored by wild bees, as these sites offered warmer climates and more nesting and foraging resources. Additionally, bees were found to distribute themselves close to or further away from forest margins based on their nesting traits.

This research revealed that alterations in landscape has major impacts on the composition of wild bee communities. Certain land use types influence specific functional traits and thus have more influence over how wild bee communities comprise themselves. Grazing was found to be a major negative driving force for wild bees while landscapes that contained a more heterogeneous structure supported a more diverse bee community. This thesis emphasizes the need for heterogeneous landscapes due to their importance in providing much needed foraging and nesting resources for wild bee communities and for wild bee conservation.
GENERAL INTRODUCTION

Many flowering plants, including many agriculturally important crops, are dependent on the pollination services provided by unmanaged, wild bees (Winfree, 2010); an estimated one-third of the food we consume comes from bee pollinated plants (Buchmann and Nabhan, 1996). Despite how reliant humans are on wild bees, their abundance and diversity is declining worldwide due to human activities such as changes in land use, climate change, introduced species, and disease (Potts et al., 2010; Vanbergen and Garratt, 2013; Winfree, 2010).

Currently, there has been an increase in public awareness regarding the plight of bees, resulting in governmental policy changes and public willingness to be involved with bee related citizen-science projects and to conserve native habitat and resources for bees (Wilson et al., 2017). Many of these projects include surveys of wild bee populations, and assess various functional traits such as nesting biology or behavior (Biesmeijer et al., 2006; Fiedler et al., 2012; Kratschmer et al., 2019; Quintero et al., 2009; Sjödin et al., 2008). Both nesting biology and bee behavior can influence how the bee community responds to changes in habitat or in management of landscapes, and what favors one species may not necessarily favor another (Bartomeus and Winfree, 2013; Tucker and Rehan, 2018; Williams et al., 2010). By altering the amount of available food and nesting resources, certain groups of bees, such as those that only nest in stems or are specialist feeders, can become extirpated from environments, thus changing the bee community composition of that landscape (Burkle et al., 2013; Mallinger et al., 2016; Potts et al., 2010; Sheffield et al., 2013). Further understanding of wild bee community structure and its response to human mediated landscape change will allow for more informed decisions necessary for wild bee conservation.
Land use as a driver of bee declines

Globally, wild bee populations have been declining due, in major part, to anthropogenic changes to the environment. These impacts can be categorized into broad groups, such as intensified land use, climate change, introduced species, and spread of disease (Goulson et al., 2015, 2008; Kearns et al., 1998; Potts et al., 2010; Vanbergen and Garratt, 2013; Winfree, 2010). Additionally, the reduction of wild bee populations in response to these stressors cannot be attributed to a single cause; rather it is the interplay between these different environmental pressures that are causing wild bee declines worldwide (Goulson et al., 2015, 2008; Vanbergen and Garratt, 2013).

Of the many anthropogenic environmental modifications, land use if one of the most crucial to address. Intensified land use, such as in agriculture, and conversion to urban or agricultural landscapes, is the most widespread cause of habitat destruction and fragmentation, which are important drivers of bee declines (Mallinger et al., 2016; Newbold et al., 2015; Quintero et al., 2009). Agriculture is the number one cause of land conversion and use; as much as 38% of the world’s surface is used for intensive agricultural purposes (Harrison et al., 2017a; M’Gonigle et al., 2015; Williams and Kremen, 2007). Natural habitat is cleared to make way for pastures or new farms, fracturing the natural landscape and reducing important sources of nesting materials and nutrition for pollinators and natural enemies, in addition to creating vast monocultures that cover the landscape. Bees are central-place foragers and are highly dependent on resource availability in the vicinity of their nest (Ferreira et al., 2015; Williams and Kremen, 2007). Furthermore, many bee species, especially those that are rare due to their specialist floral requirements or reduced foraging season and life cycle are especially vulnerable within these landscapes (Burkle et al., 2013; Harrison et al., 2017b; Kremen and M’Gonigle, 2015; Williams et
al., 2010). Studies have shown that heterogeneous landscapes will have greater connectivity between fragmented patches of habitat which increases recolonization of those patches and decreases local extinction risk (Ferreira et al., 2015; Kennedy et al., 2013; Le Féon et al., 2010; Steffan-Dewenter et al., 2002). This stresses the importance of natural or semi-natural remnants within the landscape, or the implementation of restorative areas such as hedgerows, wildflower plantings. Even converting edges of already established crop land can act as refuges for beneficial insects, such as bees, and other arthropods (Decocq et al., 2016; Le Féon et al., 2010; M’Gonigle et al., 2015; Steffan-Dewenter et al., 2002; Williams and Kremen, 2007).

**Using natural areas in agriculture for bees**

Monocultures can provide an immense bounty of resources for native pollinators while in bloom, but quickly turn into resource deserts once the flowering period is over (Vanbergen and Garratt, 2013). Through pollination, native bees provide a free essential service for many agriculturally important crops (Biesmeijer et al., 2006; Williams et al., 2010). However, in areas of vast monocultures where there are little to no natural areas, native bee diversity and abundance is low and pollination declines (Kearns et al., 1998; Williams and Kremen, 2007). Farmers are unable to rely on native bees to assist in pollination, and have a higher dependence on honeybees, which are often expensive to maintain, rent, transport, possibly spreading disease and pests, and are ineffective pollinators for many crop plants (Goulson et al., 2015; Potts et al., 2010). With the rising cost of honeybees, many farmers will need to rely upon the services of native bees to satisfy their pollination needs.
In order to attract and retain native pollinators in agricultural landscapes, it is important to establish or retain habitat that fulfills their nutritional and nesting needs. One of the most commonly suggested methods for attracting pollinators is to establish and protect semi-natural habitat in these areas (Blaauw and Isaacs, 2014a; Carvalheiro et al., 2010; Goulson et al., 2015; Hannon and Sisk, 2009; M’Gonigle et al., 2015; Winfree, 2010). Semi-natural areas, including forest fragments, hedge rows, flower plantings, and crop margins, all provide these essentials for pollinators, thus they are important to retain within the agricultural environment (Billeter et al., 2008; Williams and Kremen, 2007). Solitary wild bee species richness and abundance is known to increase as the proportion of semi-natural habitats increased (Steffan-Dewenter et al., 2002). Previous research has shown that farms that are near forest edges or semi-natural habitat have increased yields from the pollination services of the wild bees that inhabit those environments, as well as increased predation from natural enemies (Decocq et al., 2016; Ricketts, 2004). This shows the importance of conserving native or semi-native habitat within highly intensively managed agricultural land. Furthermore, areas that are free from tilling or that are abandoned provide protected and much needed nesting sites, such as long grass, holes, dead stems, and bare ground (Morandin et al., 2007). Tilling is highly destructive to ground nesting bees, as the mechanical process uproots and destroys any nests located within the agricultural setting or any potential nesting sites, such as the abandoned rodent holes that ground-nesting bumble bee queens use to establish their colony (Williams et al., 2010; Winfree, 2010). Research has shown that emerging spring-time bumblebee queens will not nest in intensively managed agricultural sites even though they will return to forage on mass-blooming crops; rather they will nest in adjacent uncultivated areas due to abundant nesting materials such as long grass and abandoned rodent burrows (Goulson et al., 2008). For non-*Bombus* wild bees, research in intensively managed agricultural landscapes
in the Central Valley of California has shown that production yield will benefit from the presence of semi-natural areas (Morandin and Kremen, 2013). Without any additional support from either hedgerows, flower plantings, or other semi-natural habitat, pollinating insects, like bees and syrphid flies, and their natural enemies are unable to find the resources needed to survive.

Semi-natural areas protect native pollinators from the drift of agricultural chemicals such as pesticides, herbicides, and fungicides, and offer alternative food sources that are free of toxic residues that are associated with intensive agriculture (Billeter et al., 2008). Research has shown that applications of pesticides, herbicides, and fungicides reduce pollinator visitation, abundance and diversity within cropland, either through the direct killing of bees or through residues acquired from sprayed plants and alter the foraging and learned behavior of bumble bees and honey bees (Goulson et al., 2008, 2015; Kearns et al., 1998; Vanbergen & Garratt, 2013). Conversely, in the presence of semi-natural areas within the landscape, like hedgerows and wind breaks, bees and other beneficial insects are protected from toxic agricultural chemical drift (Vaughan et al., 2017).

As agricultural areas continue to expand, more and more semi-natural land is destroyed and fractured, creating small islands of native habitat within vast swaths of farmland. Forests, in particular, have been documented as important supporters of many beneficial arthropods, including pollinators, especially if they are close to agricultural fields (Decocq et al., 2016; Ferreira et al., 2015; Harrison et al., 2017b; Ricketts, 2004; Watson et al., 2011; Winfree et al., 2007). Forests and forest margins are important sources of native bee diversity and abundance as they provide ample food sources when trees and herbaceous plants located in the understory bloom, and nesting materials, such as holes in trees, broken sticks and open bare ground (Aizen and Feinsinger, 1994; Bailey et al., 2014; De Marco and Coelho, 2004; Farwig et al., 2009; Hanula et al., 2015; Joshi et al., 2016; Ricketts, 2004; Taki et al., 2013, 2007). Additionally, research has shown that farms
located near forest edges will have better pollination and yield (Carvalheiro et al., 2010; Mitchell et al., 2014). These farms benefit from bees and other pollinators moving from the forest edge into farmland as they search for pollen and nectar. Further research has shown that as farms move away from forested and other semi-natural landscapes, pollination and yield decrease, thus showing how important semi-natural land is as a resource that will sustain pollinators and enable the valuable ecosystem service they can provide (Carvalheiro et al., 2010; Mitchell et al., 2014).

Succession is a natural process in which plants and animals colonize an area over time (Lincoln et al., 1982). Succession has two forms; primary and secondary succession with the main difference being that primary succession occurs in an area that has never been inhabited, such as newly formed volcanic islands (Lincoln et al., 1982). Secondary succession occurs after a disturbance, such as fire or when a tree falls in a forest, creating an opening in the canopy. Habitats are considered to be in early succession will be characterized by open ground, which caters to ground-nesting bees, and abundant herbaceous flowering plants (Swanson et al., 2011). Later states of succession, which are characterized by mature or old growth and closed canopies, are less favorable to certain bees, especially those that nest in bare ground or are smaller and need more sunlight to warm their bodies (Hanula et al., 2015; Taki et al., 2007). It is estimated that within temperate forests, much like the ones found in New England, the early stages of succession will have a high diversity of flora and fauna (Taki et al., 2013). Previous studies have shown that this early stage of forest succession is important for solitary native bees because it provides a more open environment that is reminiscent to grassland-like habitats that will have more floral resources (Hanula et al., 2015; Roberts et al., 2017; Taki et al., 2013). As forests continue through succession and develop into closed canopy systems, solitary native bee abundance and diversity decrease while social bees tend to favor these conditions (Hanula et al., 2015; Taki et al., 2013). Habitats
that are able to maintain an early successional state will have a larger diversity and abundance of native bees (Potts et al., 2003). Earlier successional states in different habitats can be maintained through various means such as fire or animal grazing, and bees living in these habitats are often well-adapted to surviving in these environments (Noy-Meir, 1995; Sjödin et al., 2008; Vulliamy et al., 2006). Both fire and ungulate grazing have been occurring in many areas around the globe, creating and shaping the different environments so that they may support plants and animal species that are resistant or thrive in the presence of these pressures (Noy-Meir, 1995). One example is the American central plains, where plants have evolved with the pressures of grazing brought on by the presence of bison and wildfires created by lightning strikes (Noss et al., 2015). Additionally, there are habitats that evolved in the presence of regular wildfire, such as areas in Israel that have high bee diversity in large areas that are intensely grazed by cattle (Noy-Meir, 1995; Vulliamy et al., 2006). In both of these examples, regular occurrences of wildfire or grazing has maintained the early successional environments and often, the plants have responded favorably by producing more leaves or flowers, which in turn assists bees as they forage for nectar and pollen (Vulliamy et al., 2006). While there are benefits from both fire and grazing, there are also various negative consequences as well. For fire, negative consequences include nest destruction, either through high temperatures that overheat the developing larvae and pupae of ground-nesting bees or total destruction of the nests of stem and wood nesting bees (Cane and Neff, 2011). Destruction of all nests leads to the loss of the next generation, which then affects future downstream populations of bees. Additionally, the loss of forage material to fire affects the ability of bees to provision nests in the short-term, but communities of both flowering plants and bees are quick to recover (Cane & Neff, 2011; Potts et al., 2003).
**Effects of grazing and importance of silvopasture**

Animal grazing has been a constant in many areas of the US. Bison grazing pressure has shaped the flora and fauna of the American prairie (Noy-Meir, 1995), while the grazing of pigs within the southern longleaf pine forests caused delayed growth and regeneration of dilapidated stretches of longleaf pine (Frost, 2006). There are pros and cons to animal grazing and how it affects native bee abundance and diversity. Many of the consequences of grazing mirror those presented by fire, such as removal of nesting and food resources and destruction of nests and adults (Kearns et al., 1998; Noy-Meir, 1995). In areas where there are introductions of grazing animals, previous research has shown that grazing reduces native bee diversity and abundance through the removal of important floral resources (Kearns et al., 1998; Xie et al., 2008). This is especially a problem in areas of intensive grazing, where the animals are not rotated through different pastures and the plant community has little to no recovery time. Furthermore, in areas of intensive grazing, preferences of certain plant species can alter plant community composition by allowing unfavorable plants to grow in abundance, thus affecting the native bee community. If plants preferred by bees for pollen and nectar are reduced because of grazing by animals, the native bee community will in turn be affected as well. Additional problems arising from animal grazing are soil compaction, which makes it difficult for soil-nesting bees to excavate their nests, and the direct trampling and therefore mortality of nests and adult bees (Kearns et al., 1998; Sugden, 1985).

There are also positive impacts of grazing on landscapes. Previous research has shown that grazing by cattle can actually increase both abundance and diversity by keeping an environment in a constant state of early succession (Vulliamy et al., 2006). As cattle graze, they open up patches of bare soil that allow for good nesting resources for bees as well as control vegetative growth (Kimoto et al., 2012b). Cattle grazing in grasslands can lead to higher plant species richness and
diversity (Noy-Meir, 1995). Moreover, in areas where plants have a long history of grazing pressure, many of the native forbs are especially adapted to grazing and will thrive in the presence of ungulates (Noy-Meir, 1995). Although some native plants may increase their flower output in the presence of grazing, and thus appear to be thriving, those plants still had reduced seed set (Mayer, 2004). Bees in these areas are also well-adapted to grazing pressure and will respond positively to grazing with increases in both abundance and species diversity (Vulliamy et al., 2006).

In these types of environments, if the grazing pressure is reduced or removed entirely, plants and bees may respond negatively, with reduced abundances and diversity (Vulliamy et al., 2006).

**Phylogenetic methods**

In the past decade, there has been a new synthesis to combine the insights of phylogeny and functional traits to inform community ecology. The use of phylogenetic information as a novel tool can help evaluate the health of a community’s structure as recent work has indicated that landscapes with higher phylogenetic diversity can support higher ecosystem functioning (Cadotte et al., 2017; Grab et al., 2019; Srivastava et al., 2012). This is due to the fact that ecosystem functioning is tied to species richness, thus the diversity of species within that ecosystem (Grab et al., 2019). Phylogenies created for ecosystems of interest portray not only species richness but also the evolutionary history of those species inhabiting that environment. Thus, the more phylogenetically rich the species composition of an environment is, the higher the ecosystem functioning is for that environment. Phylogenetic methods can additionally be used to indicate if various functional traits that are present within communities are evolutionarily conserved. By calculating the strength of the phylogenetic signal for traits of interest, we can deduce if traits will
be passed down through evolutionary history. Previous research has indicated that traits possessing a relatively strong phylogenetic signal are those that pertain to set life history traits, such as body size (Cachera and Le Loc, 2017), while those traits that are known to be more plastic in nature, such as behavior, will have weaker signals (Blomberg et al., 2003; Cachera and Le Loc, 2017).

Nesting biology and behavior in bees are functional traits that have been shown to be conserved, yet previous studies have not examined the phylogenetic signal of these traits. However, it is assumed on the basis of extensive phylogenetic data that these traits are conserved within the different families and genera (Grundel et al., 2010; Ricketts et al., 2008; Williams et al., 2010). Additionally, floral preference, or lecty, is another functional trait in bees that dictates their foraging behavior. Most bees are polylectic, or generalists, and will visit many different flower species in order to collect pollen and nectar. The remaining species are considered oligolectic and specialize on specific plant genera or species. This specificity causes major behavioral and physiological modifications such as longer limbs in oil collecting bees or specialized hairs for pollen transport (Michener, 2007).

**Research objectives**

This research aims to provide further understanding of how different aspects of the wild bee community respond to anthropogenic changes in land use and composition. Chapter 1 focuses on wild bee functional and phylogenetic diversity in order to assess how land use and management intensity alter wild bee community composition. Assessment of all aspects of community structure analyzed indicate strong impacts of land use pressure and relatively low impacts of management intensity. Chapter 2 assesses the role of forest margins as influencers of wild bee communities.
when bees are grouped by their functional traits. Landscape features heavily influenced overall bee community make up, but distance from forest edge may also influence community structure. Lastly, is a short conclusion which summarizes the overall findings found by this research as well as the potential impacts and future directions.
CHAPTER I

Impact indicators: effects of land use management on wild bee functional diversity

INTRODUCTION

Worldwide populations of wild bees are declining as a result of human-mediated environmental change. The population changes observed in wild bee communities cannot be attributed to a single cause, but rather it is the interaction of many different environmental stressors such as climate change, spread of disease, and intensified land usage (Goulson et al., 2015, 2008; Vanbergen and Garratt, 2013). Of the different pressures exerted on to wild bee populations, increased land use is considered to be one of the most important drivers of change within the wild bee community (Brown et al., 2016). Intensified land use includes anthropogenic activities such as the conversion of natural habitat to urban or agricultural landscapes that causes the destruction of valuable bee habitat and food resources (Newbold et al., 2015; Quintero et al., 2009). Land use is also responsible in shaping how bee communities respond to environmental changes, including the loss or gain of species (Harrison et al., 2017a, 2017b; Newbold et al., 2015).

Agriculture covers an estimated 38% of the world’s surface, and within the US alone an estimated 614 million acres are dedicated specifically to pasture and rangeland for cattle grazing (Harrison et al., 2017a; Kremen and M’Gonigle, 2015; Nickerson and Borchers, 2012; Williams and Kremen, 2007). Conventional agriculture often includes applications of pesticides and other agrochemicals and converts heterogeneous landscapes to those that are dominated by monoculture, all of which negatively affect wild bee diversity (Goulson et al., 2015, 2008; Kearns et al., 1998;
Mallinger et al., 2015; Quintero et al., 2009; Vanbergen and Garratt, 2013). Conversely, previous studies have shown that organic agriculture can bolster wild bee diversity. Organic farming emphasizes floral and crop diversity together with reduced usage of pesticides and other agrochemicals (Tscharntke et al., 2005; Winfree et al., 2007). Furthermore, increasing awareness of wild bee decline has led to a public push for the retention of semi-natural areas within or around agricultural land, as well as the establishment of restorative areas on reclaimed farmland (Billeter et al., 2008; Williams and Kremen, 2007). These conservation areas that are found within conventional farms include wild flower plantings, hedge rows, and even crop margins that act as significant refuges for pollinators, such as bees, and other beneficial insects (Decocq et al., 2016; Kremen & M’Gonigle, 2015; Le Féon et al., 2010; Steffan-Dewenter et al., 2002).

Ungulate grazing has been shaping environments in many areas around the globe (Noy-Meir, 1995), and can have both negative and positive impacts on environments and wild bee communities. Negative impacts on bee populations include the removal of nesting and food resources as well as the destruction of nests and adults (Kearns et al., 1998; Noy-Meir, 1995). Additionally, the introduction of grazing animals has shown to reduce bee diversity and abundance, especially in areas of overgrazing, where the plant community has little to no recovery time (Kearns et al., 1998; Xie et al., 2008). Further problems arising from animal grazing include soil compaction, which makes it difficult for soil nesting bees to excavate their nests, and the direct trampling and mortality of nests and adult bees (Kearns et al., 1998; Sugden, 1985). Grazing may also have positive impacts on landscapes, and previous research has shown that grazing by cattle can increase both abundance and diversity of other species, including wild bees, by keeping an environment in a constant state of moderate disturbance (Vulliamy et al., 2006). As cattle graze, they open up patches of bare soil that are suitable nesting sites for bees while additionally
controlling for vegetative growth (Kimoto et al., 2012b). Noy-Meir (1995) found that cattle grazing in Mediterranean grasslands led to higher plant species richness and diversity. Additionally in the same region, Vulliamy et al. (2006) found that the wild bee community responded favorably to the higher plant richness and diversity that resulted from grazing. Their results indicate that wild bee diversity is linked to that of their floral food source and that changes in floral diversity, like those caused by grazing, would lead to changes in wild bee communities.

Phylogenetic and functional diversity should inform each other, yet many studies investigating the relationship between functional and phylogenetic diversity have concluded the opposite (Arnan et al., 2017; Devictor et al., 2010; Losos, 2008; Webb et al., 2002). However, despite these past findings, it has been acknowledged that functional and phylogenetic diversity should be linked if traits are conserved (Webb et al., 2002). Moreover, for wild bees specifically, traits for nesting biology and behavior are conserved, and thus their functional traits and phylogenetic diversity are thought to be linked (Grundel et al., 2010; Ricketts et al., 2008; Williams et al., 2010). Recently there has been a push to integrate the usage of phylogeny and functional traits to inform findings of community ecology. Phylogenetic information provides a novel tool for evaluating community structure. Recent work has determined that communities with higher phylogenetic diversity support higher ecosystem functioning due to maintaining more species diversity (Turley and Brudvig, 2016; Winfree et al., 2018). Furthermore, current research analyzing the phylogenetic diversity of different wild bee populations across landscape types indicates that many of these communities are comprised of closely related species, and thus appear to be phylogenetically clustered (Harmon-Threatt & Ackerly, 2013; Hendrix et al., 2018; Hoiss et al., 2012). Hoiss et al. (2012) determined that the phylogenetic clustering of bee species at higher altitudes was a result of environmental filtering shaping the community, while Hendrix et al.
(2018) found that a lack of flowers was the main cause of wild bee phylogenetic clustering in agricultural landscapes. Additionally, Grab et al. (2019) found that landscapes dominated by agricultural practices lose phylogenetic bee diversity in a nonrandom fashion, with some bee groups being lost more frequently and heavily, generating phylogenetically clustered communities.

Functional diversity and phylogenetic analyses can be used to highlight biological traits, such as nesting biology or social behavior, that make indicator species unique to specific environments. Indicator species are any species that are indicative of specific habitat and environmental conditions (Lincoln et al., 1982). In conservation and environmental management, indicator species of habitats that are of particular interest can be used to monitor and assess overall community stability and the health of specific species of interest (Cáceres, 2013). For example, research by Kerr et al. (2000) determined that easily identified species of butterfly and skipper populations could be used to monitor and assess taxonomically challenging hymenopteran diversity at the landscape scale in endangered oak savanna habitats. Furthermore, indicator species can provide information reflecting environmental status, impacts of environmental change, and predict the diversity of a community as these species have unique features that tie them to their chosen habitat and other species in their environment (Cáceres, 2013). Tscharntke et al. (1998) found that trap-nesting bees and wasps, which are ecologically constrained by their nesting biology, are good indicators of landscape change and habitat quality as changes in their populations will reflect alterations in the availability of stems and cavities in their environment. While wild bees themselves can be indicators of plant diversity in a landscape (Tscharntke et al., 1998), certain bee guilds can be used as accurate monitors of overall bee community health. Sheffield et al. (2013) suggest that cleptoparasitic bees, which are bees that invade the nest of their host in order to lay eggs on premade pollen balls, have the potential to be bioindicators of healthy bee populations due
to their parasitic nature. Parasites, including cleptoparasites, are dependent on the survival and persistence of their host and any changes in host diversity and density will first be seen in the parasites (Sheffield et al., 2013). The use of wild bees as a group and specific bee guilds as bioindicators is a valuable tool to measure how land use and environmental change affects wild bee communities.

Wild bee species respond differently to changes in habitat and floral diversity depending on certain life histories and what favors one species may not necessarily benefit another (Bartomeus et al., 2013; Tucker and Rehan, 2018; Williams et al., 2010). Both meta-analyses and comparative approaches shed light on how bees respond to environmental change by showing differences within and between different guilds over time (Bartomeus et al., 2013; Biesmeijer et al., 2006)(Bartomeus et al., 2013; Biesmeijer et al., 2006). Both Williams et al. (2010) and Bartomeus et al. (2013) found that the wild bee community response to environmental change is largely dependent on biological traits. Although their conclusions were similar, Bartomeus et al. (2013) used historic museum specimens and comparative approaches for northeastern US wild bee communities while Williams et al. (2010) used a meta-analysis approach with more recent studies conducted globally. While informative, the previous meta-analyses encompass large areas and do not consider environments and changes within wild bee communities at a regional scale. The overarching goal of this study was to investigate how land usage affects wild bee community abundance, richness, and phylogenetic composition. We combined data from three years and six land use types in New England to: i) characterize the status of wild bees across management intensity and presence of grazing, and ii) identify indicator species and discuss functional diversity across land use types.
MATERIALS AND METHODS

This study combines bee biomonitoring data from Strafford County, New Hampshire (43.2383° N, 71.0236° W). Wild bee samples were collected every two weeks from the same six landscapes over three years (2015-2017). Three of the landscapes (meadow, organic and conventional) were used for a previous comparison of management practices and yearly effects on wild bee communities (Tucker and Rehan, 2018). Data from the remaining landscapes (clear-cut, silvopasture, pasture) are unpublished and are utilized here to investigate the effects of different forest management practices on wild bee communities. For our analyses, we classified the environments in two different ways: first by management intensity and second by the presence or absence of grazing (Fig. 1). For management intensity, landscapes were classified as either low (meadow, pasture), moderate (organic, silvopasture), or high (conventional, clear-cut). Landscapes were then either classified as un-grazed (meadow, organic, conventional) or grazed (pasture, silvopasture, clear-cut).

Bees were sampled consistently every other week starting in April through to October using a combined method of pan traps and sweep netting (Tucker and Rehan, 2018, 2017). Across all landscapes, three replicate sites were each sampled using 30 pan traps (7 cm diameter, 100mL), colored either blue, white, or yellow, that were filled with soapy water and placed along 100 m transects, alternating between the three colors and with 10m separating each trap. All traps were set before 8AM and were collected the same day at 4PM allowing a total of 8 hours for collection. At the time of collection, contents of each trap were poured through a sieve and any specimens from that transect were placed into a vial containing 70% ethanol. Sweep netting occurred at each site where there were large areas of blooming flowers and was conducted using aerial nets between the hours of 10AM and 2PM on the same day as the pan trapping. The timing of the sweep
collection was 10 thirty second intervals (total of 5 minutes) with 1-minute pauses in between to allow for specimen transfer to vials filled with 70% ethanol and collection information and for bees to return to the flowers after they had been disturbed. Collected bee specimens were prepared following the protocols in Droge (2015) and then pinned and labeled with relevant location information and a QR code. Species identification was done by E. Tucker and K. Odanaka using online keys found on Discover life (http://www.discoverlife.org/) and previously published taxonomic keys (Gibbs, 2011; Gibbs et al., 2013; Mitchell, 1962, 1960; Rehan and Sheffield, 2011; all specimens are stored in the Rehan Lab at UNH).

**Statistical analyses**

All statistical analyses were conducted using R (R Core Team). Negative binomial generalized linear models were used to analyze the effects of grazing presence and management intensity on both wild bee abundance and species richness. Results from the models that were found to be significant were then analyzed further using post hoc Tukey tests. For these models, we grouped the wild bee population by three functional traits: nesting biology (ground or stem), behavior (solitary, social, or cleptoparasitic), and lecty (polylecty, oligolecty, or parasitic) (Table I). Names of traits were used following those in Kratschmer et al. (2019). Additionally, we examined how these traits were impacted by landscape type by conducting a PCA using bee abundance and the six landscapes, then superimposing a calculated community weighted means of each examined trait onto the PCA using the ‘envfit’ function in the vegan R package (Kratschmer et al., 2019). ‘Envfit’ calculates the correlation between species assemblages and its ordination on a PCA as well as the p-values of the inputted traits, selecting only those that are
found to be significant. Community weighted means were calculated using the function CWM in the R package FD (Laliberté et al., 2014).

For our phylogenetic analyses, we used a previously published species level phylogeny consisting of over 1300 wasp and bee species as the basis for our phylogenetic tree (Hedtke, et al., 2013). We modified the original tree by adding any species from our study not already present on the original tree using the function add.species.to.genus in the R package ‘Phytools’ (Revell, 2012). Any species not found in our study was removed from the tree using the drop.tip function within the R package ‘Ape’ (Paradis et al., 2004). The resulting modified tree contained only taxa found in our study representing 239 species from 32 genera spread over five bee families. This tree was then used to calculate the phylogenetic signal of our three traits using Moran’s I and Abouheif’s C_{mean} which measure phylogenetic signal by estimating how closely trait evolution follows Brownian motion (Cachera and Le Loc, 2017). Output values are between -1 and 1 indicating no phylogenetic signal (-1) and total phylogenetic signal (1) (Cachera and Le Loc, 2017).

In order to explore changes within our wild bee phylogenetic diversity we chose two measures of phylogenetic structure that determine if species found within communities are more clustered (closely related) or more even (spread) across our phylogenetic tree. Using our modified phylogenetic tree, we first converted the tree into a distance matrix, which represented the different evolutionary relationships between species, using ‘Ape’. We then used functions in the package ‘Picante’ to evaluate the phylogenetic diversity of each site (Kembel et al., 2010; Paradis et al., 2004). All calculations used abundance weighted data matrices to account for differences in species abundance. We ran a mean pairwise distance (MPD) analysis and a mean nearest taxon distance (MNTD) analysis using the ses.mpd and ses.mntd functions. Both of these functions compare the diversity observed at our sites to a randomly constructed null model. The resulting
phylogenetic differences between the observed and the randomized communities divided by the standard deviation of the null phylogenetic distance are known as standard effect size (SES) values. P-values for both the MPD and the MNTD tests are given as quantiles. Positive SES values and high quantiles indicate that communities are more phylogenetically diverse (evenness), while negative output numbers and low quantiles indicate less phylogenetic diversity (clustering) (Kembel et al., 2010). Both SES values and significant p values (< 0.05) are reported (Kembel et al., 2010). For the pasture landscape and conventional farm, we ran Wilcoxon tests in order to find deficiencies of certain functional traits or specific genera at these sites. Following the phylogenetic diversity analysis, we ran an analysis for indicator species using the package ‘Indicspecies’ (Cáceres and Legendre, 2009). We examined both the specificity, which indicates the predictive ability of a species for a specific environment, and the fidelity, which indicates how abundant a species is given a specific environmental type, of each species (Cáceres and Legendre, 2009) in order to extrapolate which species were unique to management intensity and grazing presence.

RESULTS

A total of 12,074 bee specimens from 236 species and 32 different genera were collected between 2015 and 2017. Un-grazed sites (n = 10,650; n = 231 respectively) had eight-fold more bee abundance and about two times more species richness than grazed sites (n = 1395; n = 109 respectively; Table 2). Overall, while the effect of management intensity on wild bee abundance and richness was not significant (abundance: $X^2 = 2.45$, df = 2, $p = 0.29$; richness: $X^2 = 4.07$, df = 2, $p = <0.13$), the interaction effect of management intensity and grazing pressure on wild bee communities was highly significant (abundance: $X^2 = 3285.72$, df = 2, $p = <0.001$; richness: $X^2 =$
18.85, df = 2, p = < 0.001; Fig 2b). Additionally, un-grazed sites had the greatest wild bee abundance and richness when compared to grazed sites ($X^2 = 7545.24, df = 1, p < 0.001; X^2 = 568.49, df = 1, p = < 0.001; Fig. 2a). No MNTD value was significant for any individual landscape (1.95 ≥ SES ≥ 0.98, 0.95 ≥ p ≥ 0.85; Fig. 3b). When the MPD of individual landscapes were examined, all but the conventional (SES = 1.15, p = 0.09) and the pasture (SES = -0.002, p = 0.452) were significant (SES > 1.5, p > 0.95; Fig. 3a). We then further investigated the community composition of both these landscapes and found that the pasture landscape was depauperate of *Andrena* species ($X^2 = 13.28, df = 5, p = 0.02; Fig. 4). Of the 65 species found at the pasture, only five were in the genus *Andrena*. For conventional farmland, although the results were not significant ($X^2 = 0.42, df = 2, p = 0.80; Fig. 5) we found an overall reduction of stem nesting species in comparison. Furthermore, we observed no cleptoparasitic species at conventional farmland.

**Functional traits**

Our PCA results indicate that presence or absence of grazing explains most of the variation in wild bee abundance at our six sites (Fig. 6). Furthermore, analysis on the community weighted means of our measured functional traits indicated that nesting alone (p = 0.024) was a significant driver of bee assemblages in grazed landscapes. When the wild bee community was grouped by nesting biology, we found no interaction between management intensity and wild bee abundance and richness. Only nesting biology had a significant effect on abundance ($X^2 = 38.76, df = 1, p < 0.001$) and richness ($X^2 = 43.68, df = 1, p < 0.001$). There was also no interaction effect between grazing and nesting biology; however both grazing alone (abundance: $X^2 = 47.47, df = 1, p <$
0.001; richness: $X^2 = 38.76$, df = 1, $p < 0.001$) and nesting biology alone (abundance: $X^2 = 23.11$, df = 1, $p < 0.001$; richness: $X^2 = 52.12$, df = 1, $p < 0.001$) had significant effects on wild bee abundance and richness.

For behavior, there were no interaction effects between management intensity and behavior for abundance ($X^2 = 0.19$, df = 4, $p = 0.99$) nor for richness ($X^2 = 0.62$, df = 4, $p = 0.96$). Like with nesting biology, only behavior was significant (abundance: $X^2 = 81.64$, df = 2, $p < 0.001$; richness: $X^2 = 78.59$, df = 2, $p < 0.001$). When examining grazing and behavior, grazing alone and behavior alone had significant effects on wild bee abundance (grazing: $X^2 = 68.45$, df = 1, $p < 0.001$; behavior: $X^2 = 109.62$, df = 2, $p < 0.001$) and richness (grazing: $X^2 = 42.58$, df = 1, $p < 0.001$; behavior: $X^2 = 113.45$, df = 2, $p < 0.001$). For trait conservatism, we found that nesting biology had the strongest phylogenetic signal ($I = 0.825$, $C_{mean} = 0.826$; Table 3), followed by behavior ($I = 0.766$, $C_{mean} = 0.768$), and finally lecty ($I = 0.721$, $C_{mean} = 0.722$; Table 3); all significant at $p = 0.001$.

**Indicator species**

A total of 17 species were found to be highly significant indicators of un-grazed landscapes, and when investigated further six of these species were found to have both high specificity and fidelity (Table 4). These six species contained three species of *Bombus* (*B. griseocollis* [Degeer, 1773], *B. bimaculatus* [Cresson, 1863], *B. impatiens* [Cresson, 1863]), one *Lasioglossum* (*L. leucozonium* [Schrank, 1781]), one *Hylaeus* (*H. affinis* [Smith, 1853]), and one *Ceratina* (*C. mikmaqi* [Rehan & Sheffield, 2011]). *Bombus griseocollis*, specifically, was found to be the best predictor of un-grazed landscapes. With the exception of *B. bimaculatus* and *H. affinis,*
these species were among the most commonly found and had frequencies greater than 100 individuals captured overall at un-grazed sites. Three species were found to be indicators of different management intensities (Table 4). *Lasioglossum versatum* was indicative of both high and low intensities, *Lasioglossum lineatulum* was an indicator for moderate management only, and *Hylaeus modestus* was indicative of low and moderate intensities. Both nesting biologies (ground and stem) were represented by these three species and all have solitary behavior.

**DISCUSSION**

In this study, we investigated how management intensity and grazing presence shapes different aspects of wild bee communities. We documented how different levels of landscape management and the presence or absence of grazing influences the diversity of wild bee populations. Our data revealed that the interaction between grazing presence and management intensity highly influences wild bee abundance and richness but does not reduce overall phylogenetic diversity. Grazed landscapes are able to sustain their phylogenetic diversity despite low abundance and species richness due to their ability to maintain open ground that is attractive to the phylogenetically diverse group of bees that use this nesting resource. Finally, we determined a set of indicator species for potential bio-monitoring grazed landscapes and different levels of land use management.

**Management intensity and grazing presence**

Our results indicate that management intensity with no grazing presence supports the
most abundant wild bee communities. The large number of bee species and individuals found at un-grazed managed landscapes was most likely due to the accumulation of wild flowers and other plant material in the absence of grazing (Forrest et al., 2015; Tucker & Rehan, 2018). Our findings provide further support for the growing body of literature that indicates the importance of farming practices that maintain heterogeneous landscapes that support wild bees (Forrest et al., 2015; Tscharntke 2005; Tucker & Rehan, 2017, 2018; Winfree, 2010). Landscape heterogeneity has been shown to be favored by wild bees due to its ability to provide enough resources that maintain floral specialists and generalists as well as all nesting guilds (Forrest et al., 2015; Mallinger et al., 2016; Potts et al., 2003b; Steckel et al., 2014; Vulliamy et al., 2006). Of the three un-grazed landscapes, conventional farmland was the only landscape found to have low phylogenetic diversity which was due to a landscape wide reduction in all stem nesting species. Furthermore, because stem nesting cleptoparasitic species, namely those in the genus *Coelioxys*, were absent from conventional farmland, we can infer the total health of the stem nesting community. Intense modifications in behavior, physiology, and dietary limitations underlying the switch to the parasitic lifestyle is unidirectional, ultimately binding the parasite to its host (Litman et al., 2013). If changes occur in host populations, evidence of the negative effects should be reflected in parasitic species. The complete absence of *Coelioxys* implies that the overall stem nesting community is unstable and not healthy enough to support the tertiary trophic level occupied by parasitic life histories (Sheffield et al., 2013). High intensity management homogenizes the landscape by removing excessive vegetation and reducing natural landscapes, all of which provide the nesting resources for stem nesting bees (Williams et al., 2010). Together, the findings from our phylogenetic, abundance, and richness data suggest that moderate management intensity of landscapes is beneficial for wild bee communities.
Wild bee abundance and species richness was significantly negatively impacted by the presence of grazing. We found that grazed landscapes had bee communities that were eight-fold less abundant and about half as rich than un-grazed landscapes. This suggests that grazing intensity is a major driving force in shaping wild bee community composition. Indeed, our results are further supported by our PCA and community weighted means which clearly separated grazed from un-grazed sites. Further, nesting biology was the only trait that was a significant parameter of the PCA. Soil compaction, the destruction and removal of stems and twigs, and the reduction of floral resources are all disturbances bee face due to grazing (Kearns et al., 1998; Noy-Meir, 1995; Sugden, 1985). Bees are obligate floravores and have been found to choose areas based on their floral density (Sjödin, 2007). Intensive grazing not only reduces floral density but also simplifies plant diversity and alters floral composition (Debano, 2006; Kruess & Tscharntke, 2002; Xie et al., 2008). Changes in plant communities can then induce changes in pollinator communities causing shifts in plant-pollinator interactions, such as reducing the number of floral specialists within the community and ultimately weakening important ecological functions (Debano, 2006; Kimoto et al., 2012b; Yoshihara et al., 2008). The low abundance and richness of wild bees found at our grazed sites indicate that the bee community is responding negatively to grazing pressures.

Despite the overall low abundance and richness at the grazed sites, only one grazed landscape (pasture) was found to show less species diversity than what is expected in a randomly generated model in our phylogenetic analysis. We found that the pasture lacked species of *Andrena* and this most likely accounts for the low levels of phylogenetic diversity in this landscape. Members of the genus *Andrena* are important pollinators of early spring blooming plants and contain many floral specialists (Mitchell, 1960a). Of the three grazed landscapes, pasture sites lacked the early floral resources needed to support a diverse population of spring and specialist
Andrena species. Furthermore, all five of the Andrena species (A. carlini, A. commoda, A. cressonii, A. vicina, A. wilkella) found at the pasture site are generalists and have long foraging seasons that extend into middle and late summer. Unlike floral specialists that are tied to a select number of floral species and a specific blooming period, these generalists are able to forage on any available flowers and are unconstrained by specific seasonality. The severe lack of Andrena specifically at the pasture site mirror the findings of Hendrix et al. (2018), who also noted phylogenetic clustering in communities lacking Andrena. In their study, Hendrix et al. (2018) noted that landscapes that were lacking diverse floral resources were also scarce of Andrena species and that this bee genus may be overall more impacted at landscape scales by changes in plant communities. Furthermore, using phylogenetic diversity estimates, Grab et al. (2019) found that species of Andrena are particularly sensitive to changes in land use. Our results support those by Grab et al. (2019) and Hendrix et al. (2018), and further suggest that Andrena, in particular, may be more susceptible to changes in floral communities brought on by grazing pressure.

**Functional traits**

While past studies have found weak relationships between functional and phylogenetic diversity (Arnan et al., 2017; Devictor et al., 2010; Losos, 2008; Webb et al., 2002) it is known that the functional traits for nesting biology and behavior in wild bees is genetically conserved, thus linking together functional trait diversity with phylogenetic relationships (Grundel et al., 2010; Ricketts et al., 2008; Williams et al., 2010). Furthermore, previous research has indicated that conserved traits in closely related species should have detectible phylogenetic signals (Cachera and Le Loc, 2017). We estimated the phylogenetic signals of three different functional
traits that are known to be conserved (nesting biology, behavior, and lecty) using Moran’s I and Abouheif’s $C_{\text{mean}}$ and found relatively strong signals for each trait. This finding provides support that nesting biology, behavior and lecty are most likely genetically coded traits and are thus evolutionarily conserved. The observation that functional traits are evolutionary conserved within functional niches has been found across terrestrial, marine, plant and animal communities (Cachera and Le Loc, 2017; Losos, 2008; Pearman et al., 2008).

**Indicator species**

The presence of indicator species allows for improved future monitoring of how wild bee populations respond to changes occurring in their environments. We found eight indicator species of un-grazed landscapes and an additional three species indicative of landscape management intensity, mainly in low to moderate intensity. These eleven species represent two behavior types (solitary, eusocial), and both types of nesting biology measured in this study (ground, stem). Many common and easily identified species were selected as indicators for un-grazed habitats, including three species of bumble bee. The bumble bee species identified as indicators in this study could be used as a possible conservation tool to assess the effects of grazing animals to pollinator populations. Bumble bees, specifically, are ideal indicators because many species are large bodied and can be identified by non-experts using available guides, making them appealing for use in conservation and restoration. Indicator species can be used to gauge the impact of management and whether alternative practices should be considered.
CONCLUSIONS

Landscape alteration has major impacts on wild bees and understanding how communities respond to disturbance can inform sustainable land use, restoration and conservation practices. We found that grazing presence has the most negative impact on wild bee community abundance and richness, but interestingly little to no impact on landscape phylogenetic diversity, due to their ability to maintain open soil for ground nesting bees. Additionally, we found that landscapes featuring, low to moderately intensive management schemes supported more abundant and species rich wild bee populations. Our data suggest that regional landscapes, if they are able to provide resources that the majority of species can use, are able to maintain their phylogenetic diversity despite low levels of species abundance and richness. Moreover, the finding of common and easily identified wild bee species as indicators facilitates their adoption as an important tool for assessing the status of changing landscapes.

ACKNOWLEDGEMENTS

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### Table 1. Table denoting the examined functional traits used for analysis and how we defined the different types of traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Types</th>
<th>Definition</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nesting</td>
<td>Ground</td>
<td>Nest is excavated in the ground; majority of species</td>
<td>Habitat requirement; impacts the richness and abundance of certain species as well as the overall diversity of the bee community</td>
</tr>
<tr>
<td></td>
<td>Stem</td>
<td>Nest is excavated in pithy stems, wood, pre-made cavities, and dead wood</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Parasitic</td>
<td>Host nest is invaded by bee, who then lays own egg inside</td>
<td>Can be used to indicate and monitor host populations (Hudson et al., 2006; Sheffield et al., 2013)</td>
</tr>
<tr>
<td>Behavior</td>
<td>Solitary</td>
<td>Individual female establishes and provides for offspring alone</td>
<td>Differences in behavior can be linked to longer or shorter seasonal activity (Kratschmer et al., 2019)</td>
</tr>
<tr>
<td></td>
<td>Sub-social</td>
<td>Females may form loose colonies comprised of foundress and daughters</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Eusocial</td>
<td>Establish colonies with divisions of labor</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Parasitic</td>
<td>See above</td>
<td></td>
</tr>
<tr>
<td>Lecty</td>
<td>Polylectic</td>
<td>Females are generalists and forage for pollen on a variety of plant taxa</td>
<td>Visits many different plants to collect nectar and pollen; have no morphological adaptations for pollen collection</td>
</tr>
<tr>
<td></td>
<td>Oligolectic</td>
<td>Females are pollen specialists and forage for pollen on closely related plant(s)</td>
<td>Have specific morphological adaptations for pollen collection; tied to their host plant(s)</td>
</tr>
<tr>
<td></td>
<td>Parasitic</td>
<td>Females do not intentionally collect pollen</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. The values for relative species abundance and richness as well as the standard effect sizes for mean nearest taxon distance and mean pairwise distance for each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Grazing presence</th>
<th>Management intensity</th>
<th>Abundance total</th>
<th>Richness total</th>
<th>Mean nearest taxon distance</th>
<th>Mean pairwise distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clear-cut</td>
<td>Yes</td>
<td>High</td>
<td>545</td>
<td>70</td>
<td>1.55</td>
<td>2.022</td>
</tr>
<tr>
<td>Pasture</td>
<td>Yes</td>
<td>Low</td>
<td>520</td>
<td>65</td>
<td>0.43</td>
<td>-0.12</td>
</tr>
<tr>
<td>Silvopasture</td>
<td>Yes</td>
<td>Moderate</td>
<td>330</td>
<td>67</td>
<td>1.05</td>
<td>1.92</td>
</tr>
<tr>
<td>Conventional</td>
<td>No</td>
<td>High</td>
<td>2882</td>
<td>132</td>
<td>1.58</td>
<td>1.07</td>
</tr>
<tr>
<td>Meadow</td>
<td>No</td>
<td>Low</td>
<td>2800</td>
<td>155</td>
<td>1.17</td>
<td>1.54</td>
</tr>
<tr>
<td>Organic</td>
<td>No</td>
<td>Moderate</td>
<td>4968</td>
<td>179</td>
<td>1.72</td>
<td>1.93</td>
</tr>
</tbody>
</table>
Table 3. Results from the phylogenetic signal tests on the combined set of the traits and the individual subcomponents using both Moran’s I and Abouheif’s $C_{\text{mean}}$.

<table>
<thead>
<tr>
<th>Model</th>
<th>Moran’s I</th>
<th>Abouheif’s $C_{\text{mean}}$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phylogeny – all traits</td>
<td>0.347</td>
<td>0.350</td>
<td>$= 0.001$</td>
</tr>
<tr>
<td>Phylogeny – nesting</td>
<td>0.825</td>
<td>0.826</td>
<td>$= 0.001$</td>
</tr>
<tr>
<td>Phylogeny – behavior</td>
<td>0.766</td>
<td>0.768</td>
<td>$= 0.001$</td>
</tr>
<tr>
<td>Phylogeny – lecty</td>
<td>0.721</td>
<td>0.722</td>
<td>$= 0.001$</td>
</tr>
</tbody>
</table>
Table 4. Table denoting the eleven indicator species for un-grazed landscapes and management intensity. These species were selected as indicators due their high specificity for marked landscapes or management intensity and abundant nature within those environments. Multiple “X”s denote species that are found in both.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Nesting biology</th>
<th>Behavior</th>
<th>Un-grazed landscapes</th>
<th>Low intensity</th>
<th>Moderate intensity</th>
<th>High intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Apidae</strong></td>
<td><em>Bombus bimaculatus</em></td>
<td>Ground</td>
<td>Social</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Bombus griseocolis</em></td>
<td>Ground</td>
<td>Social</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Bombus impatiens</em></td>
<td>Ground</td>
<td>Social</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Ceratina mikmaqi</em></td>
<td>Stem</td>
<td>Solitary</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Colletidae</strong></td>
<td><em>Hylaeus affinis</em></td>
<td>Stem</td>
<td>Solitary</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Hylaeus modestus</em></td>
<td>Stem</td>
<td>Solitary</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Halictidae</strong></td>
<td><em>Halictus rubicundus</em></td>
<td>Ground</td>
<td>Social</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lasioglossum hitchensi</em></td>
<td>Ground</td>
<td>Social</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lasioglossum leucozonium</em></td>
<td>Ground</td>
<td>Solitary</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lasioglossum lineatulum</em></td>
<td>Ground</td>
<td>Social</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lasioglossum versatum</em></td>
<td>Ground</td>
<td>Social</td>
<td>x</td>
<td></td>
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Fig. 1. The organization of landscapes by presence or absence of grazing and increasing magnitude of management intensity.
**Fig. 2.** Effects of grazing pressure (a) and management intensity (b); a) Both wild bee abundance and species richness were affected negatively by the presence of grazing; b) Wild bee abundance was significantly affected by moderate management intensity; however, species richness was only significant between moderate and high management intensity.
Fig. 3. a) Phylogenetic results for Mean Nearest Taxon Distance (MNTD) indicate that sites have expected levels of species groupings. b) Mean Pairwise Distance (MPD) analysis indicate that all landscapes except pasture and conventional farmland (denoted by asterisks) exhibited more diversity than expected from a null model.
Fig. 4. The species richness of *Andrena* for grazed landscapes. Pasture sites are depauperate in *Andrena* species compared to other grazed landscapes.
Fig. 5. The observed richness of only stem nesting species found at the three un-grazed landscapes.

There are no cleptoparasitic stem nesting species, genus *Coelioxys*, in conventional farmland sites.
Fig. 6. PCA showing communities of wild bees in six different landscape types and separated by year. Nesting was the only trait found to be significantly correlated with the parameters of the PCA.
CHAPTER II:

Wild bee distribution near forested landscapes is dependent on land use

INTRODUCTION

Within the past 10 years our collective knowledge regarding the biology, behavior, and evolutionary history of wild bees has expanded exponentially. Despite previous studies, we still know very little regarding the habitat requirements of wild bees and their interactions with surrounding landscapes. Human mediated environmental change is now a constant process and modifications in land use, especially agricultural expansion, are among the most damaging to wild bee communities as former habitat and nesting resources are converted to pastureland and ever expanding agriculture (Harrison et al., 2017; M’Gonigle et al., 2015; Mallinger et al., 2016; Newbold et al., 2015; Quintero et al., 2009; Williams & Kremen, 2007). As central-place foragers, bees are highly dependent on the availability of resources near their nest, and without access to acceptable forage or nesting sites risk extirpation from these environments (Ferreira et al., 2013; Greenleaf et al., 2007; Williams & Kremen, 2007).

Drastic alterations to environments, especially land designated for agricultural use, can have differing impacts on wild bee communities. Studies relating to how bee populations respond to these changes reveal differing results. Some research results indicate that certain landscape modifications can cause positive changes in bee communities, like use of organic practices and low intensity management (Bengtsson et al., 2005; Morandin & Winston, 2005; Power & Stout, 2011; Tucker & Rehan, 2018). Other studies demonstrate the negative impacts of human land use
on bee populations (Kremen et al., 2002; Potts et al., 2010; Senapathi et al., 2015; Williams & Kremen, 2007). These contrasting reactions by different populations could be an indication that wild bee communities are responding to landscape level changes in local resources, including nesting substrate and forage availability, brought on by anthropogenic changes to the environment (Winfree et al., 2011). Previous studies in agricultural, forest and rangeland settings have provided some insight of how bees respond to human mediated environmental change (Blaauw and Isaacs, 2014b; Carvalheiro et al., 2010; Farwig et al., 2009; Garibaldi et al., 2013; Kimoto et al., 2012b; Noy-Meir, 1995; Quintero et al., 2009; Senapathi et al., 2015; Winfree et al., 2007). This information in turn can then be used to inform decisions for wild bee conservation in these areas.

Forests provide many important ecosystem services, including providing a source of beneficial arthropods that disperse into surrounding areas (Decocq et al., 2016). Prior research has indicated that farms located close to forest margins have increased pollination and yield as they benefit from the movement of bees and other pollinators from the forest environment to the farms in search of foraging resources (Carvalheiro et al., 2010; Mitchell et al., 2014). The effect of forests and other seminatural areas exporting these critical pollination services has been shown in both tropical (Ferreira et al., 2015; Ricketts, 2004) and temperate regions (Bailey et al., 2014; Schüepp et al., 2013; Watson et al., 2011). Furthermore, studies have shown that as distance away from forest margins increases, pollination and yield on farms decrease, demonstrating the importance of forest margins near agricultural landscapes (Carvalheiro et al., 2010; Chacoff & Aizen, 2006; De Marco & Coelho, 2004; Mitchell et al., 2014). Additionally, forested environments provide ample resources that bees may not find in agriculturally intensive areas. This includes spring foraging sources, such as understory flowers and herbaceous plants, as well as nesting habitats in tree cavities and dead broken sticks and in bare ground (Aizen & Feinsinger, 1994; Bailey et al.,
2014; De Marco & Coelho, 2004; Farwig et al., 2009; Hanula, et al., 2015; Joshi et al., 2016; Taki et al., 2013; Taki et al., 2007; Winfree et al., 2007).

Although forests remain an important source of wild bees, not all forested environments are able to support abundant and diverse bee communities. Mature forests or forests that are in later stages of succession, are less favorable to bees due to cooler temperature resulting from lack of sunlight and reduced foraging resources (Hanula et al., 2015; Taki et al., 2007). In comparison, forests that are younger or in earlier stages of succession are preferred by bees, as there is greater abundance of herbaceous plants, open ground, and overall warmer temperatures (Swanson et al., 2011). Previous studies have shown that these early stage forests, which emulate the grassland habitats favorable for bees, are critical for the survival of solitary native bee populations, as they provide essential floral resources and nesting habitat (Hanula et al., 2015; Roberts et al., 2017; Taki et al., 2013). As forests continue to age and mature, conditions within the forest become less favorable to solitary bee communities and their numbers and diversity decrease, whereas bumble bees specifically, tend to favor mature forests, and will increase in diversity and abundance (Hanula et al., 2015; Taki et al., 2013). Forests that are able to maintain states of early succession, through various means such as fires, grazing, or management will often have a more diverse and abundant native bee population (Potts et al., 2003a).

Thinning and gap creation are common means of forest management and restoration practice used to promote tree health by reducing competition and stand density. Gap creation involves the entire removal of dense stands of trees in order to create an open patch within a mature stand, while thinning reduces stand density without removal of all the trees in one area. Both forestry practices have been proven to positively benefit pollinators in forests where either gap creation or thinning has taken place (Hanula et al., 2016). Gap creation and thinning create spaces
of open and disturbed ground that is preferred by ground nesting bees to establish nests. Additionally, gaps created within the canopy cover allow for increased amounts of sunlight in the understory which not only aids in the recovery of the herbaceous undergrowth that provides forage for wild bees, but also increases microhabitat temperature to levels that are within the suitable range for bee biology (Hanula et al., 2016; Taki et al., 2013).

Rangeland and pasture systems are widespread globally and are important agricultural systems that support diverse and abundant wild bee populations (Kimoto et al., 2012a). The impact of livestock grazing has been previously found to be detrimental to the survivorship of wild bees as grazing alters plant composition and structure, removes valuable nesting and foraging resources, and causes direct bee mortality by trampling (Kimoto et al., 2012b; Sugden, 1985). Yet other studies indicate that grazing in pastures promotes healthy wild bee populations, with prior studies indicating increases of abundance and richness under grazing pressure (Kimoto et al., 2012b; Noy-Meir, 1995; Vulliamy et al., 2006). Based on the varying results of previous research, whether or not grazing has positive or negative effects on wild bee community structure and population density appears to be dependent on various factors such as shared evolutionary history, the species of grazing animal, the intensity and duration of the grazing period, and the current structure of the bee community (Kimoto et al., 2012b). These uncertainties make it difficult to assess the potential of using pasture systems as a means of wild bee conservation.

There are ways to incorporate land management practices so that grazing pressure has minimal effect on the environment. One such practice is silvopasture, in which trees and livestock are managed together in a mutually beneficial way such that consequences of overgrazing is reduced and a continuous forage is present (Clason and Robinson, 2000). Trees are used to provide shade and protection while grazing animals are able to forage in the understory on forbs to prevent
over-grazing (Klopfenstein et al., 1997). Since the practice of silvopasture encourages the thinning of dense stands of trees and the growth of an herbaceous understory comprising beneficial and often bee friendly plants, it can be hypothesized that this environment will have a positive effect on native bee diversity and abundance. Native bees prefer gap openings in forested areas where sunlight is able to reach the understory, allowing for the growth of flowering plants and forbs in addition to open ground. Much of this type of forested area occurs where there is disturbance, such as tree falls, fires, or where patches of trees are thinned (Hanula et al., 2015; Roberts et al., 2017). The establishment of silvopasture in heavily forested areas, like those found in eastern North America, allows for a similar environment with open space and a healthy understory. In addition, silvopasture returns the environment to an early state of succession through grazing, which is thought to favor a high abundance and diversity of native bees (Roberts et al., 2017). While silvopasture is not a new agricultural practice, the implications for wild bees remains unknown and research is needed to determine if this would be a suitable means for increasing pollinator habitat and function as a sustainable land use practice.

Wild bee populations continue to decline while knowledge of their habitat requirements remain poorly documented, resulting in a need for an understanding of how landscapes influence and shape bee communities (Blaauw and Isaacs, 2014b; Garibaldi et al., 2013; Kerr et al., 2015; Winfree, 2010). Insight into landscape effects and habitat requirements can inform different agricultural management schemes that can double as a means of wild bee conservation. Here we 1) investigate the effects of landscape type and distance from forest margin on wild bee abundance and richness, 2) identify how biological traits create landscape specificity for wild bee species, and 3) describe the wild bee community across New England forest systems for the first time.
MATERIALS AND METHODS

Study sites and sampling

This study was conducted in Strafford County, New Hampshire (43.2383° N, 71.0236° W). Collection locations were in and around mixed eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) forest. Wild bees were sampled every two weeks starting the first week in May through the end of September 2017. Four landscapes were surveyed including: closed canopy forest sites, clear-cut sites where trees had been completely removed, silvopasture sites where selected trees were removed to allow 30% canopy cover for cattle to graze between the remaining trees, and pasture sites adjacent to forests. The creation of both the clear-cut and the silvopasture sites occurred in 2015. Each site was approximately one hectare in area. Pastures were mowed monthly. Ten cows were released at each of the pasture, silvopasture, and clear-cut sites biweekly (alternating weeks to bee collection). Each site contained three 120m transects located at either 10, 20, or 30 meters from forest edges.

We collected bees using colored pan traps that were either blue, white, or yellow following standard procedure (Tucker and Rehan, 2018, 2016). We placed twelve pan traps (7 cm diameter, 100mL) along each 120m transect allowing for 10m between each cup and filled each one with soapy water. Traps were deployed before 8 AM and were collected the same day after 4 PM, allowing for a total of 8 hours collection. When emptying pan traps, contents of each trap were poured through a sieve and any collected specimens were placed in a vial containing 70% ethanol and a collection tag.
**Bee identification**

Following the protocols in Droeg (2015) we washed the bee specimens and dried them with a hair drier. Once dry, specimens were then pinned, labeled with relevant location information and a unique QR code, and identified to species using online keys found on Discover Life (http://www.discoverlife.org/) as well as previously published taxonomic keys (Gibbs, 2011; Gibbs, et al., 2013; Mitchell, 1960, 1962; Rehan and Sheffield 2011; all specimens are housed in the Rehan Lab at UNH).

**Statistical analyses**

All statistical analyses were conducted using R ver. (3.5.2) (R Core Team). To analyze the effects of forest distance and landscape on wild bee abundance and richness, we used generalized linear mixed models with negative binomial distribution (Zuur et al., 2007). Both collection month and distance were used as random effect variables in our models. Fixed variables included site, distance from the forest edge, behavior type, and nesting biology. Analyses of deviance using type II Wald chi square tests were then conducted on our models in order to test for overall significance of treatments; followed by post hoc Tukey tests. For behavior type, bees were categorized as either: social, solitary or cleptoparasitic; and for nesting biology: ground or stem nesters. Bees that were classified as preferring only cavities or alternating between stems and cavities were grouped into the stems category. For behavior, those bees exhibiting communal behavior were grouped into the solitary category (Ascher et al., 2014; Matteson et al., 2008; Selfridge et al., 2017).
RESULTS

A total of 297 bees, representing 63 species and 18 genera were collected. Clear-cut sites maintained the highest total wild bee abundance (mean ± SD; n = 114 ± 14.5), followed by silvopasture (n = 89 ± 13.0), then pasture (n = 82 ± 14.3), and forest (n = 12 ± 2.7) sites. When landscapes were examined individually, clear-cut, silvopasture, and pasture sites all had significantly higher bee abundance than forested sites ($X^2 = 33.85$, df = 3, $p = <0.001$).

Species abundance differed significantly among landscapes and distances from the forest edge ($X^2 = 543.85$, df = 6, $p = <0.001$; Fig. 1a). Post hoc tests for site level differences in species abundance indicate that the clear-cut ($z = 3.321$; $p = 0.005$), silvopasture ($z = 5.021$; $p < 0.001$), and pasture ($z = 4.481$; $p < 0.001$) sites are all significantly different from the forest sites but are not different from each other. Additional post hoc tests for distance indicate that there are significant differences in species abundance between 20 m and 30 m ($z = -22.39$; $p < 0.001$) as well as between 10 m and 30 m ($z = -19.46$; $p < 0.001$). When examined alone, the effects of distance on bee abundance was not significant ($X^2 = 0.524$, df = 2, $p = 0.77$). At 10 m from the forest margin, pasture sites had an observed greater bee abundance than both clear-cut and silvopasture sites, but this was not significant. At 20 m, abundance of bees in pasture sites remain constant while silvopasture sites had a slight but non-significant decline. At 30 m the only observed increase in abundance was at clear-cut sites; there was a slight but not significant decline in bee abundance with the distance from forest margins in pasture sites (Fig. 1a). Bee abundance in silvopasture sites also increased at 30 m from forest edges, reaching about the same number of individuals found in 10 m transects.
Bee species richness differed significantly among landscapes ($X^2 = 30.8$, df = 3, p < 0.001), but not by distance ($X^2 = 0.05$, df = 2, p = 0.975). Like abundance, post hoc tests indicated that clear-cut (z = 5.470; p < 0.001), silvopasture (z = 4.230; p < 0.001), and pasture (z = 4.498; p < 0.001) sites were all significantly different from forest sites, but there was no difference between among the former three landscapes. Similar to abundance estimates, clear-cut sites had the highest overall species richness (n = 38 ±5.3), pasture and silvopasture sites maintained equal amounts of species richness (pasture: n = 32 ±6.4; silvopasture: n = 32 ±13.0), while forest sites had the least species richness (n = 9 ±1.9). Species richness significantly varied among landscapes by distance ($X^2 = 456.47$ df = 6, p = <0.001; Fig. 1b). Interaction effects between landscape and distance indicates that pasture sites maintain the highest species richness at 10 m from forest edges. Silvopasture and clear-cut sites comprise similar species richness and forest sites remains far below the other three landscapes. At the 20 m distance, clear-cut sites increased in species richness, surpassing both silvopasture and pasture landscapes, both of which had slight decreases in species richness. At distances farthest from the forest edge, both clear-cut and silvopasture sites had their respective greatest species richness, while pasture landscapes had consistently declining species richness with distance from forest margins.

**Bee behavior**

The interaction of landscape and behavior on wild bee abundance was slightly significant ($X^2 = 15.44$, df = 6, p = 0.02). Additionally, both landscape ($X^2 = 24.23$, df = 3, p <0.001; Fig.2a) and behavior ($X^2 = 92.13$, df = 2, p < 0.001) were significant when examined separately. Post hoc tests indicate significant differences between cleptoparasitic and solitary behavior (z = 5.15; p
<0.001) as well as kleptoparasitic and social behavior \( (z = 4.82; p < 0.001) \). No kleptoparasites were found at forest sites. Overall, solitary bees were most abundant \( (n = 164 \pm 26.8) \), followed by social bees \( (n = 122 \pm 18.1) \), then kleptoparasites \( (n = 11 \pm 2.3) \). Individuals from solitary species were most common in pasture sites \( (n = 62 \pm 12.5) \) and least common in forested sites \( (n = 7 \pm 2.1) \). The number of solitary individuals collected was second and third highest in the clear-cut and silvopasture sites respectively \( \text{clear-cut: } n = 58 \pm 7.4; \text{silvopasture: } n = 37 \pm 6.5 \). Social bees were most common in clear-cut sites \( (n = 51 \pm 8.5) \) and least common in forest sites \( (n = 5 \pm 0.7) \). Silvopasture sites had more social individuals \( (n = 49 \pm 8.2) \) than pasture sites \( (n = 17 \pm 5.4) \). Kleptoparasitic individuals were most frequent in clear-cut sites \( (n = 5 \pm 1) \). Kleptoparasitic bees were equally collected within pasture and silvopasture sites \( (n = 3 \pm 0.9) \) and no kleptoparasites were found in forested sites.

The effect of species behavior on overall richness was significant \( (X^2 = 60.4; df = 2, p < 0.001) \). Total richness among behavioral categories indicated that solitary bees were the most species rich \( (n = 32 \pm 6.4) \). Species richness of kleptoparasitic bees was almost as high as social species \( (n = 11 \pm 2.3 \text{ and } n = 20 \pm 4.1 \text{ respectively}) \). Across four different landscapes, solitary bees were most diverse in clear-cut sites \( (n = 21 \pm 3.7) \) with far fewer species collected in forested sites \( (n = 5 \pm 1.6) \). Pasture sites were the second highest in solitary bee richness \( (n = 21 \pm 4.7) \) and this was followed by silvopasture sites \( (n = 15 \pm 1.8) \). Social bee richness was highest in silvopasture sites \( (n = 14 \pm 2.3) \), followed by clear-cut \( (n = 12 \pm 2.5) \), then pasture \( (n = 8 \pm 1.9) \), and fewest in forested sites \( (n = 4 \pm 0.4) \). Clear-cut sites had the most kleptoparasite species \( (n = 5 \pm 0.45) \). Pasture and silvopasture sites each had \( (n = 3 \pm 0.4) \) species, and forest sites had no observed kleptoparasites.
Nesting biology

Overall, ground nesters were more abundant \((n = 202 \pm 28.5)\) than stem nesters \((n = 95 \pm 16.1; \chi^2 = 27.88; df = 1; p = <0.001)\). Landscape effects were also found to be significant \((\chi^2 = 27.11; df = 3; p < 0.001; \text{Fig. 3a})\). Ground \((n = 76 \pm 10.3)\) and stem \((n = 38 \pm 5.5)\) nesting individuals were most abundant in clear-cut sites. Abundance of ground and stem nesters \((n = 59 \pm 8.61, n = 30 \pm 5.0 \text{ respectively})\) were second highest in silvopasture sites. Ground nesters \((n = 58 \pm 9.4)\) comprised 71% of the bees captured at pasture sites and the remaining 29% stem nesters \((n = 24 \pm 5.4)\). Three quarters (75%) of the individuals collected from forest sites were ground nesters \((n = 9 \pm 1.5)\) and the remaining 25% stem nesters \((n = 3 \pm 1.3)\). There was a significant interaction between nesting biology and distance to forest margins \((\chi^2 = 10.18; df = 2; p < 0.006; \text{Fig 4a})\). Ground nesting bee abundance increased from 10 to 20 m and remained constant at 30 m. For stem nesters, bee abundance was highest at 10 m and significantly lower at 20 m. At 30 m, stem nesting bee abundance is significantly higher than abundance at 20 m, but also lower than bee abundance at 10 m.

Species richness varied significantly between nesting biology categories \((\chi^2 = 27.34, df = 1, p = <0.001)\). Overall, ground nesting bees had higher species richness than stem nesters \((n = 45 \pm 6.8 \text{ and } n = 19 \pm 4.9 \text{ respectively}; \chi^2 = 27.34, df = 1, p = <0.001)\). Ground nesters were most species rich within clear-cut sites \((n = 28 \pm 4.2)\), followed by pasture and silvopasture sites \((n = 23 \pm 4.2, n = 21 \pm 2.5 \text{ respectively})\). Forest sites had the least ground nesting species richness \((n = 7 \pm 1.4)\). Species richness of stem nesting bees was highest in both clear-cut and silvopasture sites (clear-cut: \(n = 10 \pm 2.3\); silvopasture: \(n = 11 \pm 1.2\)). Pasture sites contained the third highest \((n = 9 \pm 2.44)\) and forested sites had the least number of species \((n = 2 \pm 0.9)\). Interactions between distance and nesting preference were significant \((\chi^2 = 6.64, df = 2, p = 0.04; \text{Fig. 4b})\). Ground
nesting bees initially increased in species richness from 10 to 20 m and remained consistently high at 30 m away from forest margins. Stem nesters had a significant difference in species richness at 20 m from forest margins ($z = -3.164; p = 0.002$).

**Landscape and distance specificity**

Three species were collected in all four landscapes: *Agapostemon virescens*, *Calliopsis andreniformis*, and *Lasioglossum coriaceum*. Conversely, each landscape was found to have species not collected in the other sites. In total, 34 of the 63 (54%) bee species collected in this study were present in only one of four landscapes (Table 1). Clear-cut and pasture sites both contained the highest number of site-specific species ($n = 11$). Clear-cut sites contained the most halictid species, the only species of *Augochlora* (*A. pura*), and *Anthidium* (*A. oblongatum*) found in this study. Pasture sites contained the most species of the family Megachilidae captured in one site ($n = 4$). Included in these four species were the only species of *Hoplistis* (*H. spoliata*), the only *Megachile* (*M. companulae*, *M. latimanus*), and one *Osmia* (*O. albiventris*) species. Furthermore, the only *Melissodes* (*M. druriellus*) was found at a pasture site.

Although forested and silvopasture sites both are comprised of mixed forest, they did not have any similarities in community composition or number of site-specific species. Only two species were found only in forest sites: *Andrena nigrihirta* and *Lasioglossum pilosum*. Silvopasture sites however, contained ten site-specific species, half of which were *Lasioglossum* species, which was the most for any site and includes *L. platyparium*, the only social parasitic species of this genus collected in this study. Silvopasture sites also contained the most landscape specific *Osmia* ($n = 2$) species: *O. atriventris* and *O. collinsiae*. 
Each distance was also found to have specific bee species. Of 63 bee species, 33 (52%) were only found at certain distances from the forest margin (Table 2). Most of the distance specific species were found 30 m from forest margins (n = 15) and the least were found closest to forest margins at 10 m transects (n = 7). Of the total distance specific bees, 81% were found to be ground nesters (n = 27) and six species, all in the genus *Lasioglossum*, were found to be social. Half of all distance specific species were members of the family Halictidae and of those 18 species, nine occurred solely 30 m from forest margins. These include the only *Augochlora* species (*A. pura*) and the only *Agapostemon* species (*A. sericeus*) found solely at 30 m from forest margins. In total, 12 of the 18 (67%) species from the family Halictidae were from the genus *Lasioglossum*. Half of those *Lasioglossum* species (n = 6) were collected 20 m from forest margins and those species comprised 46% of the total specific species to that distance. Additionally, the only *Anthidium* species (*A. manacatum*) found in this study was captured at 20 m from a forest margin. Although transects 10 m from the forest margin contained the least specific species these include the lone specimens of *Hoplitis* (*H. spoliata*) and *Melissodes* (*M. druriellus*).

**DISCUSSION**

This study investigated the effects of landscape and distance from forest margins on wild bee communities. Here we determined site specificity among wild bees as a product of set traits such as species behavior and nesting biology. We document the effects of landscapes including forest, clear-cut, silvopasture, and pasture on bee populations. Our study reveals that wild bees in forested environments are affected by distance from forest margins and by nesting habitat. At the landscape scale, we found bees assorted by their behavior and nesting biology while nesting
biology alone revealed different niches at 10 versus 20 and 30m from forest margins. Findings from our study further support the need for heterogeneous landscape composition to support diverse wild bee communities.

**Landscape effects**

Wild bee behavior and nesting biology was significantly associated with landscape composition. We found that landscapes containing little to no canopy cover supported the most abundant and rich bee communities in comparison to forest sites dominated by dense stands of trees. Our results are consistent with previous findings that indicate that wild bees prefer open landscapes over those that are completely forested (Hanula et al., 2015; Roberts et al., 2017). There is a known negative relationship between forest cover and wild bee abundance and richness (Winfree et al., 2007), and evidence from our study supports this relationship. We found that forested sites maintained the lowest abundance and richness of any sites. Dense forests lack many of the resources important for bee habitat, such as nesting substrate, suitable sunlight, and consistent forage (Hanula et al., 2016, 2015; Swanson et al., 2011). This is especially critical once the spring blooming period has ended and trees begin to produce leaves which block sunlight from reaching the understory and prohibit the growth of additional forage (Schüepp et al., 2013; Taki et al., 2007). Moreover, foraging by bees and other hymenopterans is reduced in the presence of shade and thus cooler temperatures (Herrera, 1995; McKinney & Goodell, 2010; Polatto et al., 2014). The majority of wild bees found in forest sites were solitary ground nesters and were located close to forest margins. This observation provides evidence further supporting the notion that solitary bees will build their nests at forest edges where there is less canopy shade and more open
ground (Klein et al., 2003). Additionally, our results bolster those found by Winfree et al. (2007), who concluded that forested sites support fewer species due to lack of adequate floral and nesting resources. Of 34 species recorded specific to one landscape, only two were exclusive to forested sites, representing only ~6% of the total landscape specific species found in our study.

The pasture, clear-cut, and silvopasture landscapes all represent different stages of deforestation allowing for insight into how wild bee populations respond to disturbance. Previous research has shown that bees respond favorably to disturbance in forested environments and will be found consistently in greater numbers where disturbance has occurred (Fiedler et al., 2012; Hanula & Horn, 2011; Hudson et al., 2013). The most disturbed of our landscapes studied were clear-cut sites, which maintained the highest bee community abundance and species richness in this study. Moreover, because disturbance reverts sections of forest back to early stage succession, our clear-cut sites are able to generate an abundance of essential foraging and nesting resources, which are essential for attracting and retaining populations of solitary bees (Roberts et al., 2017; Taki et al., 2013). Furthermore, Murray et al. (2012) found that local factors impact wild bee community composition and that these factors are related to higher species diversity. The availability of nesting resources is considered a localized environmental factor (Murray et al., 2012) and this can explain the highly taxon and habitat specific differences in the wild bee communities found between our silvopasture and pasture landscapes. Both silvopasture and pasture sites had nearly equal richness and abundance of wild bees, but each landscape provided habitat to different species based on nesting biology and behavior. Where the pasture contained more bare ground and thus catered more towards solitary ground nesting bees, the silvopasture, which lacked exposed soil, housed more stem nesting bees and more species exhibiting social behavior.
Distance

Our results indicate that the overall distribution of wild bees across different distances near forest margins is determined by nesting biology and the availability of specific nesting resources. Bailey et al. (2014) found that distance from the forest margin was one of the most important factors in explaining variance in wild bee communities. We found that distance from forest margins explained differences in bee abundance and richness only when the community was grouped by nesting guild. Stem nesting bees were mostly found at 10 m, while ground nesting species were much more common at 20 and 30 m from forest margins. These variances were likely due to the location of appropriate nesting substrate, as stems and twigs were most abundantly located closest to forest margins, while exposed bare ground increased as distance from forests increased. Furthermore, our results support research by Cane et al. (2006) and Potts et al. (2005, 2003b), who suggest that the availability of nesting resources exert enough pressure to shape bee communities based on their specific nesting guilds.

The effect of distance from forest margins on wild bee communities is a topic of increasing interest, especially in regards to agriculture; yet very few of these distance studies detail changes in specific bee species as distance from forest margins increase (Bailey et al., 2014; Chacoff and Aizen, 2006; Joshi et al., 2016; Taki et al., 2007). Many of these studies are in agriculture settings and show overall declines in species richness and floral visitation rates as distance increases (Carvalheiro et al., 2010; Klein et al., 2003; Kohler et al., 2008; Schüepp et al., 2013). Unlike earlier distance studies, whose maximum distance from the forest edge was 100 m or more (Bailey et al., 2014; Joshi et al., 2016; Taki et al., 2007; Watson et al., 2011), the spatial scale of our project was much narrower, focusing on 10 to 30 m. This reduced scale allows us to detect finer nuances in the distribution of wild bees across shorter distances and examine how species composition...
changes as distance increases. We found that over half of recorded bee species were distance specific and that distance specificity is a product of bee nesting biology. As distance from the forest edge increases, ground nesting species increase. This conclusion further corroborates previous research indicating that nesting resources are able to shape bee communities (Cane et al., 2006; Potts et al., 2005), but our result suggest this might occur at a much finer scale. Unlike nesting biology, we did not detect clear distance specificity among behavioral categories. A total of six social species were found at one specific distance, all found in the genus *Lasioglossum*. Prior research that differentiates between the bee behavior classes in distance analyses focus mainly on honey bees or bumble bees or both as social representatives (Bailey et al., 2014; Joshi et al., 2016). Consequently, little is currently known regarding the responses of social species outside of the Apidae to distances from forest margins. Future studies documenting all species are needed, especially to gain insights into the habitat requirements of the greatly understudied social halictids and the wide range of speciose solitary bees.

**Landscape specificity**

Each landscape in our study contained species not found at other landscapes (Table 1). Our results corroborate previous findings regarding the importance of heterogeneous landscapes for diverse wild bee populations in larger ecosystems, especially agroecosystems where homogeneous landscapes are common (Mallinger et al., 2016; Steckel et al., 2014; Tucker and Rehan, 2018). Both Tucker and Rehan (2018) and Svensson et al. (2000) found that landscape specificity affects species within genera differently and our results mirror those findings. This effect can best be seen in the genus *Lasioglossum*, the most species rich genus captured in our study. Of the 21 captured
species, 10 were specific to one landscape, and five of these were found in exclusively in silvopasture sites. Of the remaining five species, two each were found only in the clear-cut and pasture while one species was found only in forested sites. As indicated by our data, loss of heterogeneous landscapes may extirpate those species that are found in those habitats, thus reducing wild bee diversity and community resilience to environmental change. The implementation of wildflower plantings, hedgerows and increasing seminatural habitats within homogeneous landscapes provides a way to generate the heterogeneous environment that may provide the refuge for those bees that are landscape specific (Decocq et al., 2016; Kremen & M’Gonigle, 2015; Le Fèon et al., 2010; Steffan-Dewenter et al., 2002; Williams & Kremen, 2007).

CONCLUSIONS

It is critical to understand how habitat requirements influence wild bee distribution within landscapes so that decisions regarding conservation will have the most positive impact. We found that overall wild bee abundance and richness in forested landscapes was influenced by the amount of canopy cover present. Sites that maintained higher bee abundance and richness had less canopy and abundant bare ground. Our data further indicates that wild bee conservation practices and current means of forest management could be complimentary. Both aim to reduce tree density in forested areas, while opening the canopy and raising understory temperatures, which benefit both wild bee communities and understory plants (Hanula et al. 2015; Hudson et al. 2013; Taki et al. 2013, 2007). Moreover, reduction of tree density, through managed burns or manual thinning, exposes more ground, allowing for usage by ground nesting bees (Hanula et al. 2015, 2016).
Furthermore, our data suggests that maintaining heterogenous landscapes aids in promoting wild bee diversity especially in areas that are prone to lacking diversity, such as agricultural land use.

ACKNOWLEDGEMENTS

We thank Jacob Withee, Wyatt Shell, Molly Jacobson, Stephanie Gardner, Erika Tucker, and Minna Mathiasson (University of New Hampshire) for their help with fieldwork and specimen processing. Special thanks to Ryan Courtright and Nick Warren for all their help in regards to our field sites. Funding from the University of New Hampshire, the New Hampshire Agricultural Experiment Station and the USDA National Institute of Food and Agriculture Hatch Project 1004515 supported this research.
### Table 1. Species specific to the four different landscapes examined in this study. Species include five bee families (bold) and 11 genera.

Nesting biology indicated with: * = ground nesting, and Δ = stem/cavity nesting species. Social behavior indicated in parentheses with: (sol) = solitary, (soc) = social, and (par) = cleptoparasitic species.

<table>
<thead>
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<th>Pasture</th>
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<tr>
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<td>Andrena vicina * (sol)</td>
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<td>Nomada pygmaea * (par)</td>
<td>Melissodes druriellus * (sol)</td>
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<td>Nomada sayi * (par)</td>
<td>Nomada articulata * (par)</td>
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<td>Hylaeus affinis Δ (sol)</td>
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<td>Lasioglossum oblongum * (soc)</td>
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<td>Lasioglossum platyparium * (par)</td>
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<td>Osmia distincta Δ (sol)</td>
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Table 2. Species specific to distances from forest edge. Species include five bee families (bold) and 11 genera. Nesting biology indicated with: * = ground nesting, and Δ = stem/cavity nesting species. Social behavior indicated in parentheses with: (sol) = solitary, (soc) = social, and (par) = cleptoparasitic species.

<table>
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<td>Nomada cressonii * (par)</td>
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Fig. 1 Effects of the interaction of landscape type and increasing distance from forest margins. A) Wild bee abundance is significantly affected by landscape and forest margin distance. B) Species richness is also significantly influenced by landscape and distance.
Fig. 2 Wild bee species (a) abundance and (b) richness varies significantly among landscapes and behavioral classes. Forest sites had the lowest diversity and abundance of wild bees, and lacked cleptoparasites. Across all remaining landscapes, cleptoparasites were present but significantly lower in richness and abundance than both solitary and social species.
Fig. 3 Species (a) abundance and (b) richness of wild bees across landscapes by nesting biology.

Ground nesting bees were consistently dominant to stem nesting species across all landscapes.
Fig. 4 Species abundance (a) and richness (b) compared across distance measures from forest margins. Ground nesting species were more abundant and diverse at distances further from forest margins. Stem nesting species were most abundant closest to forest margins.
GENERAL CONCLUSIONS

Wild bees are declining world-wide due to anthropogenic alteration of the environment, including climate change, the introduction of alien species and pathogens, and intensive land use and modification (Bartomeus et al., 2013; Goulson et al., 2015; Vanbergen and Garratt, 2013). Numerous global studies have documented the impact of agricultural practices on wild bee diversity (Blaauw and Isaacs, 2014b; Grab et al., 2019; Kremen et al., 2002; Senapathi et al., 2015; Steffan-Dewenter and Westphal, 2008; Tucker and Rehan, 2018), however gaps still exist in understanding how certain landscape features, such as grazing presence and the presence of forest margins, influence community structure. The most widely used metric for measuring wild bee communities are relative abundance and species richness, however neither provide complete insight to community structure. For the past decade, phylogenetic methods have been used as a novel tool in assessing community make up in ecological studies, yet are rarely utilized for wild bee community assessment. The first half of this study combines phylogenetic and traditional measures to analyze how wild bee communities respond to changes in their environment due to land use and management intensity. The second half of this study uses traditional methods to document how successional states within forests and distances from forest edges influence wild bee community structure.

Findings from the first chapter of this study revealed that community abundance and richness of wild bees is most negatively affected by grazing presence, however, the phylogenetic structure of the community remains relatively intact. Grazing corresponds to reduced floral densities and destruction of various nesting resources that would cause lower amounts of abundance and richness (Kearns et al., 1998; Noy-Meir, 1995; Xie et al., 2008) and our data shows a distinct reduction in wild bee species based on the presence of grazing. Furthermore, our data
suggests that grazed landscapes, despite their low levels of species richness and abundance, are able to maintain their phylogenetic diversity in comparison to other regional habitats, indicating that changes in phylogenetic diversity may be influenced by other environmental conditions. Previous studies have stressed the importance of landscape heterogeneity as these environments are able to provide ample sources of foraging and nesting resources (Forrest et al., 2015; Steckel et al., 2014; Tucker and Rehan, 2018). Wild bee populations in our study that were more abundant and species rich were supported by landscapes exhibiting moderate to low management schemes as these landscapes maintained diverse resources that could be utilized by all nesting biologies and behavioral guilds. The findings from our phylogenetic, abundance, and richness data bolster the idea that heterogeneous landscapes coupled with low to moderate management is beneficial for wild bee populations. Future work should incorporate phylogenetic methods with other traditional ecological methods for documenting changes in wild bee communities for similar studies in other regions, and could also be employed on a broader range of New Hampshire systems, such as within alpine and addition farm and forested environments.

Understanding the influence of habitat requirements on wild bee distribution is critical when discerning which conservation strategies will have the most positive impact. Forested areas are known to facilitate the movement of bees to adjacent landscapes (Bailey et al., 2014; Decocq et al., 2016; Mitchell et al., 2014; Ricketts, 2004) and that forests in earlier stages of succession are preferred by wild bees (Hanula et al., 2015; Taki et al., 2013). Indeed, canopy cover, which is an indication of forest succession, was found to influence wild bee diversity in forested sites. Sites with less canopy cover and more bare ground were able to support bee populations that were both more abundant and species rich which further supports the known negative relationship between forest cover and wild bee diversity (Winfree et al., 2007). Sites with high disturbance also
maintained diverse and abundant wild bee communities due to the reversion of the sites to an earlier successional stage which increases levels of available nesting and foraging resources (Roberts et al., 2017). Current methods of forest restoration, which involve reducing tree density as well as opening the canopy and raising the temperature of the understory (Hanula et al., 2015; Hudson et al., 2013; Taki et al., 2013), are complementary to those used for wild bee conservation. Findings from this thesis also highlight the need for maintaining heterogeneous landscapes especially in areas that are lacking floral diversity, such as those used for conventional agriculture. Since each of the landscapes used supported different species assemblages, any loss of heterogeneous environments could result in possible extirpation of the uncommon specific species found at those sites. Implementing hedgerows, wildflower plantings, and the amount of seminatural habitats within environments, can increase the amount of nesting and foraging resources that are provided by heterogeneous landscapes (Kremen and M’Gonigle, 2015; Steffan-Dewenter et al., 2002; Williams and Kremen, 2007) which help promote wild bee diversity in areas of intensive land use. Future work should be aimed at further solidifying the habitat specificity of wild bee species in and around forested landscapes as this information will provide valuable input for conservation strategies used in these environments.

To make conservation decisions that have the most positive impact, understanding how wild bee populations respond to changes in landscape is critical. Results from this study emphasize the impacts of land use and highlight how disturbance and successional states in forested environments influence wild bee community structure. These results contribute to our collective knowledge of wild bee communities and allow for more informed decision making when implementing conservation strategies.
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APPENDIX A: CHAPTER I SUPPLEMENTARY MATERIAL

Figure S1. Phylogenetic tree used for mean pairwise distance and mean nearest taxon distance.
**APPENDIX B: CHAPTER II SUPPLEMENTARY MATERIAL**

**Supplement Table 1.** All species of wild bee captured in this study. Both their nesting biology (ground or stem) and their behavior (solitary, social, cleptoparasitic) have been listed.

<table>
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<th>Family</th>
<th>Species</th>
<th>Nesting biology</th>
<th>Behavior</th>
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<tbody>
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