**Evaluating the effects of soil tillage on ground nesting**

**bees in the southeastern United States**

by

Anthony Cuminale

A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
December 9, 2023

Keywords: Native bee, Ground nesting, Tillage, Pollinator, Agroecosystems

Approved by

Geoffrey Williams, Committee Chair, Associate Professor, Department of Entomology and Plant Pathology, Auburn University

Anthony Abbate, Assistant Professor, Department of Entomology and Plant Pathology, Auburn University

Josh Campbell, Faculty, Department of Entomology and Plant Pathology, Auburn University, Northern Plains Agricultural Research Laboratory, USDA-ARS

Audrey Gamble, Associate Professor, Department of Crop, Soil and Environmental Sciences, Auburn University

# Abstract

Pollination by native bees is an economically and ecologically valuable service, necessary in both agricultural and natural landscapes. The majority of bee species nest below ground, an aspect of their biology that raises questions concerning how common farming practices – such as soil tillage affects their abundance and diversity. Tillage methods are broadly categorized as belonging to either a conventional or conservation regime. Conservation tillage is associated with lower intensities of soil disturbance compared to conventional tillage, as well as requiring the buildup of soil surface residues.

In this work, I investigated the effects of tillage on ground nesting bees by intensively sampling with soil emergence traps among four treatment groups: (1) Conventional tillage, (2) Conservation tillage, (3) Reduced tillage, and (4) Field edge. Soil emergence traps were deployed weekly from March-October 2021, and again from March-November 2022. Results from emergence trap collections detected no significant differences among the tillage treatments; however, we observed significantly higher incidence, abundance, and diversity of bee assemblages in the Field Edge treatment compared to all tillage treatments. Our results suggest that bee nesting is depreciated in cultivated fields regardless of tillage type. Implications from this work applies to conservation efforts aimed at mitigating the loss of native bee biodiversity, as well as producers looking to increase the contribution of native bees in agricultural landscapes.

## Acknowledgements

I would like to thank the natural world for constantly provoking my curiosity and providing me with immense experiences of discovery, peace, and healing. I only hope that I can reciprocate these gifts one day through my work. I would also like to thank my family, friends, and colleagues that have supported, inspired, and mentored me throughout the years.

# Table of Contents

# List of Figures

# Chapter 1
# Literature Review

## 1.1 Introduction

Society is supported by ecological processes occurring as a result of interactions between organisms and their environments (De Bello et al., 2010). The decomposition of organic matter, regulation of pest species, and pollination of agricultural crops are examples of services provided by populations of beneficial insect species (Nichols et al., 2008; Porto et al., 2020; Brock et al., 2021). The quality of human life is improved by animal mediated pollination of nutritional and medicinal plants (Garibaldi et al., 2022). As much as 75 % of global food crops benefit from animal mediated pollination, and 35% are dependent upon the phenomena (Klein et al., 2006). The importance of pollinators in agricultural systems is not surprising considering that nearly 83% of all flowering plant species depend on, or benefit from insect mediated pollination (Ollerton et al., 2011). Insects share a deep evolutionary history with ecological processes and organisms (Grimaldi, 2010). It is concerning that declines in both insect diversity and abundance have been observed globally (Sánchez-Bayo and Wyckhuys, 2019; Wagner et al., 2021).

Mounting evidence of declines in bee communities have been documented across the globe (Biesmeijer et al., 2006; Cameron et al., 2011; Bogusch et al., 2020). In North America, declines in bee abundance and diversity is of serious concern. A 2017 review of the statuses of the North American and Hawaiian bee fauna determined that as much as 24% of native bee species are imperiled, and 52% of the remaining species are in decline (Kopec and Burd, 2017). A major driver implicated in these declines has been attributed to the loss of habitat, caused by the expansion of urbanization and agricultural production (Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019). The 2012 Economic Research Service reported that land cover classified as urban areas accumulated to nearly 27 million hectares in the US (Bigelow and Borchers, 2017).

Significantly larger expanses of land are devoted to agricultural production; in the US over 160 million hectares of crop land were cultivated in 2017 (2017 Census of Agriculture, 2019). The total amount of cropland acreage is expected to expand and intensify in the future as a result of increased global demand for goods (Lark et al., 2020).

Solutions to negate the negative effects that modern agriculture imposes on beneficial insect populations, especially bees, include the use of wildflower strips within or adjacent to crop fields to increase the abundance of pollen and nectar resources available for bee communities to forage (Campbell et al., 2017; Klatt et al., 2020). The amount of food resources available is undeniably an important limiting factor for any population, and much emphasis has been placed on amending floral resources to support bee communities. However, there are gaps in our understanding of ground bee nesting biology (Antoine and Forrest, 2021) that may be acting to limit our ability to  promote bee nesting activity. For example, few investigations have sought to understand the effects of common farming practices such as soil tillage, or cover cropping on bee communities inhabiting agroecosystems. Increasing our knowledge and understanding of how management practices affect the abundance, diversity, and distribution of ground nesting bees is well warranted in order to conserve native bee communities.

## 1.2 Native Bees

### 1.2.1 Evolution

The first insects likely appeared between 422 – 457 million years ago during the Silurian period, appearing as simple wingless creatures (Grimaldi, 2010). The evolution of bees would come some 300 million years later, diverging from a lineage of hunting wasps that provisioned their developing offspring with paralyzed insects (Michener, 2000). The novelty of bee biology is

seen in their departure from insect provisions as a food source for the development of their young to provisions of pollen (Michener, 2000).

The evolution of the angiosperm group of plants occurred concurrently with the emergence of the bee lineage (Cardinal and Danforth, 2013). Angiosperms were increasing in diversity and abundance during the mid to late cretaceous period (Cardinal and Danforth, 2013). Flowers, and the floral resources they offer such as pollen, would have become increasingly more common during the early evolution and diversification of the bees. It was previously believed that the adaptation of a pollen diet was the salient factor driving bee diversification (Murray et al., 2018); however, an alternative hypothesis elevates the adoption of broader diet breadth and the rise of polylectic foraging strategies as the major driver contributing to bee diversification during this period (Cardinal and Danforth, 2013).

### 1.2.2 Diversity

Bees are a highly diverse taxa of insects belonging to the order Hymenoptera. Hymenoptera is a massively diverse group containing more than 150,000 species, encompassing the entirety of the ants, wasps, sawflies, and bees (Aguiar et al., 2013). Although bees fall within the order Hymenoptera, the biology of bees is unique compared to that of the ancestral apoid wasps from which they evolved. This is due to a novel adaptation in which bees developed a dependance on pollen to complete their life cycle rather than using insect prey like most wasps. This pollen dependence is the result of a 130-million-year-old mutualistic relationship formed between bees and angiosperms (Cardinal and Danforth, 2013).

The energy bees require for their foraging flights, as well as the food provisions used to rear their offspring, come almost exclusively from the floral resources afforded by the flowers of angiosperms in the form of pollen and nectar (Michener, 2000). Flowering plants benefit from

this need for pollen as bees transport pollen between flowers as they forage, facilitating the pollination of visited species. This mutualism places bees in a uniquely pivotal position in the ecology of life on earth, possessing the potential to directly affect the composition of flowering plant species located within their foraging ranges (Su et al., 2022), and indirectly affect organisms that utilize these flowering species as hosts.

The relationship between bees and angiosperms contributed to the diversification of the bee lineage (Cappellari et al., 2013), lending to the diversity we observe today in the more than 20,000 species of bees that have been documented worldwide (Michener, 2000). Six of the seven families of bees are represented by the native bee fauna found in North America (Michener, 2000). They include the families Andrenidae, Apidae, , Colletidae, Halictidae,  Megachilidae and Melittidae.A seventh family – the Stentoidae  is absent from our region and are endemic to the Australian continent (Michener, 2000). It is estimated that nearly 4,000 species constitute the native bee fauna of North America (Ascher and Pickering, 2011). The hymenopteran fauna across the state of Alabama was surveyed by Jones and Jones in the 1980's; they recorded a total of 149 species, with 91 species accounting for new state records (Jones and Jones, 1980). Additional surveys since have been limited (Ray, 2023). Therefore information regarding species occurrences is lacking since it is estimated that as many as 500 species may occur in Alabama based on supplementary data regarding species distributions and checklists made in adjacent states (Ascher and Pickering, 2011).

### 1.2.3 Life Cycle

Bee development adheres to the basic holometabolous stages in which an egg progress to a larva, that later undergoes metamorphosis while encased in a pupa before giving rise to a fully formed, sexually reproductive adult (Michener, 2000). The lifespan of most bees is short; Straka

et al. (2014) investigated adult lifespans and factors that influence the length of life in two

species of bees: *Andrena vaga* Panzer, 1799, and *Anthophora plumipes* (Pallas, 1772). The

lifespan of *Andrena vaga* ranged from 9 – 29 days on average, and the life span of *A. plumipes*

ranged from 8 – 30 days (Straka et al., 2014). The queens of social species like the honeybee

*Apis mellifera* Linnaeus, 1758, typically live longer than non-reproductive workers, on average

between 1-2 years for the queen compared to 15-38 days in the summer for the workers

(Remolina and Hughes, 2008). Most species of bees are solitary (Michener, 2000). Upon

emergence a lone female will disperse, found a nest, and then spend considerable energy

foraging for pollen to rear brood for the season (Michener, 2000).

The number of generations per year varies across taxa. Bees belonging to the genus

*Osmia* Panzer 1806 are typically either univoltine – producing one generation per year – or

semivolitine – taking more than a single year to complete their life cycle (Bosch et al., 2010).

The life cycles of bees displaying varying degrees of sociality is less straightforward than that

described for solitary species. Variations in the number of generations of brood per season, the

addition of multiple reproductive females, and differences in the behaviors of these reproductive

females complicate the topic (Schwarz et al., 2007). This is especially true for instances in which

some species of social bees have been observed practicing multiple strategies (Schwarz et al.,

2007). At times, these species will produce one generation of brood per year, while in other

instances the same species may produce two distinct generations of brood per year, which can

range in size from a few individuals to dozens of female workers. Another variation involves the

addition of sexually reproductive females from the first or second generation of brood in addition

to the founding female. Differences in the behavior of these additional reproductive females adds

another level of complexity due to the fact that they have been observed remaining within the

originally founded and also contributing to the production of brood, or dispersing from the

original nest to found their own (Schwarz et al., 2007).

### 1.2.4 Nesting

The nesting biology of bees is akin to methods practiced by their wasp ancestors; this

includes the construction of belowground nests dug into the soil, and cavity nesting within trees

or the hollowed out stems of pithy plants (Michener, 2000). Ground nesting is practiced by a

substantial majority of wild bees, ranging from 62% -84% of all species (Cane and Neff, 2011;

Harmon-Threatt, 2020). The remaining bee species engage in varieties of cavity nesting

(Michener, 2000). For example bees in the genus *Augochlora* Say, 1837 have been documented

constructing nests in downed trees (Dalmazzo and Alsina, 2012) and members of the family

Megachilidae are frequently found constructing nests within abandoned wood boring beetle

cavities found in the trunks of trees (Michener, 2000; Cane et al., 2007). A smaller subset exhibit

additional nesting strategies, such as bees belonging to the genera *Osmia* and *Hylaeus*, who

construct their nests with the use of snail shells (Hopfenmüller et al., 2020; Graham et al., 2021).

The architecture of belowground nests is variable between genera and species (Clement,

1973; Eickwort and Sakagami, 1979; Packer and Knerer, 1986; Espinoza et al., 2023); however,

the basic elements that constitute a below ground nest consistently includes a main vertical

tunnel dug into the soil, and brood cells that branch off of the main tunnel at varying depths. The

brood cells accommodate provisioned pollen and nectar mass, along with the deposited bee egg;

this provides a safe location for consumption of their food and development (Michener, 2000).

Nest depth varies across bee taxa, Cane (1991) analyzed nest parameters of 36 bee species,

constituting 22 genera across 6 families, and found that nest depth ranged from 2 cm – 180 cm.

The number of brood cells, their depth, and the spatial arrangement of the cells around the main

tunnel differs among and between species. Additional modifications of the basic nest layout includes branching of the main vertical tunnel to accommodate additional secondary tunnels (Potts and Willmer, 1997). Tunnels that completely or incompletely loop around individual brood cells have been hypothesized to aide in regulating soil moisture around developing brood, or they may function to alert nesting females to the presence of brood parasites as they dig their way to brood cells (Packer and Knerer, 1986).

The environmental factors which may be affecting the preferred nest site conditions among different species of ground nesting bees remains elusive. Several key environmental variables have been identified and investigated for their importance in bee nesting including soil composition, soil compaction, and the amount of available bare ground (Cane, 1991). The proportion of sand in soils has been shown to be positively correlated with bee nesting (Cane, 1991); however, too much sand could be detrimental for some species. Very sandy soils may prevent social species of bees from establishing large aggregations as the lack of stability afforded by the sand leads to adjacent nests collapsing into one another (Potts and Willmer, 1997). Additional variables that have been considered in bee nest site preference include soil moisture, soil temperature, slope, aspect, solar insolation, as well as several others (Cane, 1991; Potts and Willmer, 1997; Antoine and Forrest, 2021). Ground slope for example, has the ability to affect the amount of solar insulation and therefore heat within the nest that bees use to warm up their flight muscles at the start of the day and may confer fitness advantages for developing larvae located in brood cells (Antoine and Forrest, 2021). Tolerances to these environmental factors likely differs among bee taxa, with some species having evolved the ability to withstand conditions that other species might not be capable of exploiting. This is especially true for species that possess adaptations that act to stabilize nest site conditions. Many ground nesting

bee species such as those in the family Colletetidae are capable of stabilizing the environments

of their belowground nest through the use of water-resistant secretions produced by an organ

referred to as the Dufors gland (Albans et al., 1980). These 'Cellophane' bees, as they are

commonly referred, rely on these secretions to line the walls of their nest, which aides in

protecting the internal nesting environment (Cane, 1981). The specific nest architecture used by

some species may have very real consequences for the distribution of the species. For example, it

is hypothesized that the range of *Lasioglossum rohweri* (Ellis, 1915) is limited to the eastern U.S.

because their shallowly dug nests do not favor well against the dry soils found in the plains

westward (Breed, 1975).

### *1.2.5 Pollination*

The pollination of angiosperms takes place through interactions with a wide variety of

animal taxa seeking resources from their flowers. As many as 87.5% of flowering plants rely on

aide from animals for pollination; representing a critically important relationship shared between

ecosystems across the globe (Ollerton et al., 2011). The coevolution of flowering plants with

animals over time has led to differences in flower traits among pant taxa. The relationships

between flowers and pollinators can be inferred by differences in flower attractiveness to specific

pollinating groups. To differentiate these interactions, scientists created pollinator syndromes to

describe the pollinating animal that is likely being attracted by specific flower traits.

Ornithophily is reserved for flowers that are large and typically colored red or orange and are

attractive to birds (Cronk and Ojeda, 2008; Faegri and Pijl, 2013). For pollination performed by

insects, a number of more specific terms have been coined to designate the specific insect taxa

that are attracted. Cantharophily and myophily apply to flowers colored white and often

associated with pungent odors thought to be attractive to beetles and flies respectively;

melittophily is reserved for the pollination services rendered by bees, with the flowers often

being yellow to blue (Faegri and Pijl, 2013). Within the United States, pollination by native bees

has been valued to be worth over $3 billion annually (Losey and Vaughan, 2006).

The coevolution and resulting mutualism between bees and angiosperms has led bees to

depend on resources afforded by flowers, and angiosperms to rely on the vectoring of pollen by

bees (Michener, 2000). Even when plants are not dependent on these services, higher fruit set,

quality, and seed set have been observed as a result of successful bee pollination (Walters, 2005;

Roldán Serrano and Guerra-Sanz, 2006; Mallinger and Gratton, 2015). Pollinator network

diagrams allow the visualization of these connections as well as the magnitudes of visitations

between bees and the plant species within a community. Interspecific differences in the diet

breadth of bees has resulted in a spectrum of foraging strategies observed among bees. Generally,

bees can be considered generalist if they forage from a wide diversity of flowering plant species,

and specialist as the variety of species they will forage upon is reduced to varying degrees

(Robertson, 1925; Michener, 2000). Specialist bees, including those that practice either

oligolectic or monolectic foraging species are reliant on the pollen from a limited subset of plant

genera or species (Robertson, 1925). Examples of pollen specialization includes oligolectic bee

species such as is practiced by squash' bees in the genus *Xenoglossa* Smith, 1854- that specialize

on Cucurbita species in North America (Dorchin et al., 2018), as well as species displaying

monolectic foraging strategies such as the coastal bee species *Hesperapis oraria Snelling and*

*Stage, 1997* which forages solely on *the aster Balduina angustifolia* (Cane et al., 1996)

However, the majority of bee species are however polylectic, foraging for pollen across a variety

of flowering plants (Robertson, 1925; Michener, 2000). It is currently believed that higher

diversity of species constituting a pollinator community will provide a level of redundancy in the

plant-insect interactions within an ecosystem (Kopec and Burd, 2017). The overlap in diets breadths among bee species creates redundancy in the pollinator network, increasing the likelihood of continued pollination services (Winfree et al., 2007).

The importance of floral resources to bees, especially pollen, is seen in the array of morphological adaptations that facilitate its collection and storage among different bee taxa. Most bees are relatively hairy insects compared to a typical wasp. These hairs facilitate the collection of pollen, and further modifications of them, which are lacking in wasps, include branched hairs that more effectively ensnare pollen grains (Michener, 2000). More conspicuous examples of structures devoted to the collection of pollen include the corbicula possessed by bumblebees in the genus *Bombus*. This modification of the tibia in which its outer surface is smoothened, slightly concave and bordered by a perimeter of curled hairs essentially allows it to function as a pollen basket (Michener, 2000). When packed with ample amounts of pollen bumblebees can sometimes appear to have bright orange saddle bags on their hind legs. Cavity nesting bees in the genus *Megachile* Latreille, 1802 lack corbicula and abundant scopal hairs on their hind legs. Instead, they harbor dense combs of scopal hairs on the sternites of their abdomen that function to store pollen (Michener, 2000). Other bee taxa lack specialized pollen collecting adaptations altogether and rely on unique methods for transporting pollen such as those seen in bees belonging to the genus *Hylaeus* Fabricius, 1793, who actually store pollen internally within their crop for retrieval at a later time (Müller, 2023). In addition to the morphological adaptations bees possess, they have also evolved behaviors that improve their ability to collect pollen from a diverse assortment of flower morphologies. Pollination by sonification, often referred to as 'buzz' pollination, is a unique method of pollination practiced by several groups of bees such as bumblebees in the genus *Bombus*. Buzz pollination is an

effective adaptation allowing bees who practice it to gather pollen from flowers possessing poricidal anthers, which act to regulate the dispersal of pollen (De Luca and Vallejo-Marín, 2013). The pollen residing on anthers of this type is not easily accessible, therefore bees practicing sonification grab ahold of the flower and rapidly move their flight muscles, vibrating the flower and dislodging the pollen from the anthers (De Luca and Vallejo-Marín, 2013). Pollen and nectar are both essential resources required by bees (Westerkamp, 1996; Michener, 2000). The energy required for foraging flights of adults are fueled by the nectar, providing sugar and water (Westerkamp, 1996; Nicolson, 2011). Pollen is essential for the development of larvae, and provides important nutrients such as protein, lipids, vitamins, and minerals (Nicolson, 2011).

Differences in foraging behaviors across bee taxa has been observed to lead to differences in their pollination efficiency, ultimately leading tangible outcomes such as differences in fruit set and quality (Bosch and Kemp, 2001). Upon visitation to a flower, a bee has the opportunity to collect pollen, nectar, or both. Bee species display differences in the proportion of foraging trips in which both pollen and nectar are collected simultaneously, while others specifically target nectar which does not ensure pollination of the flower, thus reducing its effectiveness as a pollinator (Bosch and Kemp, 2001). Additionally, not all bees respond to inclement weather the same way, and varying bee foraging responses to weather conditions affect the efficiency of species as pollinators. For example, honey bees reduce their foraging efforts during periods of cooler temperatures, while other species such as bumblebees continue to forage as they are affected to a much lesser degree (Tuell and Isaacs, 2010). The accumulation of these differences among bee taxa can greatly affect the overall efficiency of pollination services provided within a system. For example, in apple orchards it has been observed that 250 individuals belonging to

the native bee species *Osmia lignaria* Say, 1837 were capable of providing an equivalent amount of pollination as 15,000-20,000 honey bees (Bosch and Kemp, 2001).

### 1.2.6 Agroecosystems

Agricultural activity has been shown to negatively affect insect populations, and has been implicated as a major driver of ongoing declines in insect abundance and diversity (Sánchez-Bayo and Wyckhuys, 2019). Declines have been reported for populations of native bees (Steffan-Dewenter et al., 2002; Kremen et al., 2004; Kopec and Burd, 2017). The replacement of native plant communities with monocultures of commodity crops reduces the diversity of plants in the landscape. This simplification of the plant community could significantly affect its utility as habitat for bees. This is especially likely when the monoculture is of a wind-pollinating species such as corn, wheat, oat, or barley, which rely on the wind and chance rather than bees for their reproductive success. Unfortunately, there is a lack of robust literature describing pollinator networks and individual relationships between native bee species and commonly planted crop varieties, which limits our current understanding of their value to native bees. Additionally, limited research has been conducted to elucidate the ways in which common management practices used in agricultural production- such as soil tillage or cover crops affect native bee communities existing within the confines of agroecosystems.

### 1.3 Soil Tillage

The intended goal of tillage aims to improve soil conditions so that they are favorable for crop cultivation (Busari et al., 2015). This process entails the physical manipulation of the soil at varying depths, and intensities, which is dependent upon its implementation. Today, soil tillage practices can be described as belonging to either a conventional or conservation tillage system. Differences between these two management practices include the intensity of soil disturbance, as

well as conditions at the soil surface. For example, soil disturbance is typically more intense in conventional than in conservation tillage systems. In conservation tillage, management actions that aid in the accumulation of crop residues on the soil surface are encouraged. Adherence to a conservation tillage system requires that at least 30% of ground cover is composed of crop residues (Claassen et al., 2018). In contrast, the surface crop residues in a conventional tillage system are homogenized and worked into the soil, leaving the surface bare, or nearly so.

Physical modifications of the soil have been made by humans cultivating land throughout history, and were initially accomplished with the use of primitive tools such as branches and sticks referred to as 'digging sticks' to aide in scratching and opening up the soil (Nilles, 1942). In the 17th century, rudimentary ploughs entered into early development, and they saw limited use. However, improvements to British plough shape and design near the end of the 18th century increased the adoption of plowing as an effective, widely adopted tool for the management of weeds (Derpsch, 1998). Conventional tillage practices rely on various implements to physically modify the soil at different depths and intensities. Inversion of the soil accomplished the task of suppressing weeds well, but exposure of the topsoil to erosional forces was an overlooked consideration. The topic was forced due to a severe soil conservation crisis that emerged in the U.S. during the 1930's, which led to questions surrounding the legitimacy of long term continuous plowing as a viable method of crop cultivation (Derpsch, 1998). This paradigm shift away from intensive tillage was strengthened by investigations in the use of reduced tillage practices, and leaving crop residues to conserve both soil and water (Duley and Russel, 1939). These findings represent the beginnings of modern conservation tillage principles and support the intentional buildup of crop residues on the soil surface. This was followed up by the development, and newly discovered utility, of non-selective herbicides for use in weed

suppression (Blevins and Frye, 1993). An increase in the production of herbicides following WWII led to decreasing prices and barriers for their use, which elevated conservation tillage as a viable alternative to conventional tillage systems (Blevins and Frye, 1993). Conventional tillage describes management practices in which primary tillage is performed with the use of a plough implement and then typically followed by secondary tillage operations such as disking, cultivating, and harrowing; this acts to further homogenize and mix the soil. Land use statistics show that conventional tillage methods were used on roughly 32 million hectares of U.S. farmland (2017 Census of Agriculture, 2019). This total represents a 24% decrease in the use of intensive tillage methods in farmland area compared to census data reported in 2012 (2017 Census of Agriculture, 2019). The conclusion that conventional tillage methods were beneficial for the cultivation of crops is rooted in the 1700s when agronomists of the time believed that the finer one could till the soil, the better plants would be able to absorb the fine particles they required for growth (Tull, 1751). This belief and its implementation by farmers of the time would later lead to severe losses of topsoil on farms across the great plains of the United States in the 1930's, thus spurring the development conservation tillage schemes (Blevins and Frye, 1993).

Well-founded benefits attributed to the use of conventional tillage methods are primarily a result of effects caused by soil inversion. Inversion aids in the suppression of weed species when seedings are buried, or when damage is caused to belowground structures that have been exposed to desiccating forces at the soil surface (Subbulakshmi et al., 2009). The magnitude of soil mixing resulting from conventional tillage methods has been shown to increase nutrient availability of elements such as N and K at greater depths in fields under conventional tillage than in no-till systems (Blevins and Frye, 1993). The benefits afforded by conventional tillage systems come at a cost, and have been implicated for causing detrimental effects such as reduced

soil structure, water infiltration, soil moisture, and increased soil erosion (Subbulakshmi et al., 2009).

The magnitude of soil disturbance caused by conventional tillage practices should be of particular concern for scientists studying bee communities in agroecosystems. Considering the prevalence of ground nesting behaviors observed among bee species, it is surprising that literature on interactions between bees and tillage is limited. Review of the work that has been conducted within agroecosystems presents some interesting findings regarding the effects of tillage on bees. The bee species *Eucera Pruinosa* Say, 1837 was subject to field experiments in which mated pairs were confined to mesh cages until nest founding was observed. Following brood development, the cages were removed, and tillage was randomly applied to the ground for a portion of cages which represented the tilled treatment. The mesh cages were reestablished following tillage and the emerging offspring were collected upon emergence, revealing that bee emergence was roughly halved in nests that were subject to soil tillage (Ullmann et al., 2016). Current literature suggests that ground nesting bees prefer to reside in areas of exposed bare ground (Antoine and Forrest, 2021). This is of concern because it is possible that ground nesting species could be attracted to the highly disturbed soils found in conventional tillage systems. Therefore, conventional tillage systems could be acting as a sink.

The development and adoption of early conservation tillage methods were largely founded upon a desire to reduce the negative effects observed as a result of conventional tillage practices. Land use statistics report that a record 81 million hectares of U.S. cropped land fell under the classification of conservation tillage (2017 Census of Agriculture, 2019). The sum of these areas represent a 28% increase in the amount of overall U.S. farmland devoted to conservation tillage since 2012, and amounts to over two times as many hectares than were

farmed using conventional tillage practices in 2017 (2017 Census of Agriculture, 2019). It is likely that producers will continue to adopt conservation tillage practices over conventional tillage into the future because of the advantages it offers in regard to promoting soil health, conserving water, and minimizing the loss of soil to erosional forces (Ogieriakhi and Woodward, 2022). It has been shown that crop residues on the surface in amounts as low as 10% of ground cover are capable of reducing soil erosion by as much as 30% (Sarrantonio and Gallandt, 2003). Another advantage of conservation tillage systems lies is its ability to conserve water by increasing water infiltration; this is caused when surface residues absorb the impact of raindrops and act to slow the overall movement of water across the soil surface (Duley and Russel, 1939; Busari et al., 2015). The soil conditions established as a result of reduced tillage intensities associated with conservation tillage have been shown to increase abundance of earthworms, as well as the preservation of the subterranean tunnels they create, which act to further facilitate water infiltration (Kemper et al., 1987). It is possible that conditions resulting from conservation tillage practices may be beneficial, neutral, or deleterious to bee nest site preference. Conservation tillage may benefit ground nesting bees species because of the lower intensities of soil disturbance associated with these practices; however, it is of interest how crop residues might affect bee nest site preference. It is known that the intentional buildup of crop residues on the soil affects soil characteristics such as soil temperature and moisture (Teasdale and Mohler, 1993), but how these conditions affect the nest site preference or development of ground nesting bee species is largely a mystery. It would not be surprising if crop residues prove to be negatively associated with ground nesting bee activity as many species have been observed preferentially constructing their nests in areas of exposed bare ground (Antoine and Forrest, 2021; Gardein et

al., 2022). It is quite possible that the two are at odds with one another, but a lack of information on the topic currently limits our understanding.

**1.4 Conclusion**

The success of the clade Anthophlia is evidenced by the 20,000 species of bees documented worldwide. The co-evolution of bees with the flowering plants has resulted in varying degrees of dependency on bee mediated pollination for successful reproduction. Thus, bees are a crucial piece of the ecological jigsaw wherever flowering plants exist. Concerns over the decline in bee abundance and diversity need to be addressed in order to buffer against the loss of pollination services provided to flowering plants cultivated in production agriculture as well as those existing in the natural landscape. Agricultural activity, such as expanding cropland and intensification are factors implicated in driving insect decline. Much work is needed to address the mechanisms by which agricultural activity affects beneficial groups of insects – such as ground nesting bees. In the work that follows, I set out to quantify how different tillage regimes affect native ground nesting bees. Due to the intimate relationship that ground dwelling bees have with the soil I believe this research to be a jumping-off point for future work to build upon our understanding of bee ecology in the context of agricultural landscapes.

## 1.5 References

*2017 Census of Agriculture* (Geographic Area Series). (2019). United States department of
Agriculture. https://www.nrcs.usda.gov/sites/default/files/2022-
10/2017NRISummary_Final.pdf

Aguiar, A. P., Deans, A. R., Engel, M. S., Forshage, M., Huber, J. T., Jennings, J. T., Johnson, N.
F., Lelej, A. S., Longino, J. T., Lohrmann, V., Mikó, I., Ohl, M., Rasmussen, C., Taeger, A.,
& Yu, D. S. K. (2013). Order Hymenoptera. *Zootaxa*, *3703*(1), 51-62-51–62.
https://doi.org/10.11646/ZOOTAXA.3703.1.12

Albans, K. R., Aplin, R. T., Brehcist, J., Moore, J. F., & O'toole, C. (1980). Dufour's gland and
its role in secretion of nest cell lining in bees of the genus *Colletes* (Hymenoptera:
Colletidae). *Journal of Chemical Ecology*, *6*(3), 549–564.
https://doi.org/10.1007/BF00987667

Antoine, C. M., & Forrest, J. R. K. (2021). Nesting habitat of ground-nesting bees: A review.
*Ecological Entomology*, *46*(2), 143–159. https://doi.org/10.1111/een.12986

Ascher, J. S., & Pickering, J. (2011). *Bee Species Guide (Hymenoptera: Apoidea: Anthophila)*.
Discover Life. Http://Www. Discoverlife. Org/Mp/20q.

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T.,
Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., & Kunin, W. E.
(2006). Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the
Netherlands. *Science*, *313*(5785), 351–354. https://doi.org/10.1126/science.1127863

Bigelow, D. P., & Borchers, A. (2017). *Major Uses of Land in the United States, 2012* (178; Economic Information Bulletin). United States Department of Agriculture.

Blevins, R. L., & Frye, W. W. (1993). Conservation tillage: an ecological approach to soil management. *Advances in Agronomy*, *51*(C), 33–78. https://doi.org/10.1016/S0065-2113(08)60590-8

Bogusch, P., Bláhová, E., & Horák, J. (2020). Pollen specialists are more endangered than non-specialised bees even though they collect pollen on flowers of non-endangered plants. *Arthropod-Plant Interactions*, *14*, 759–769. https://doi.org/10.1007/s11829-020-09789-y

Bosch, J., & Kemp, W. P. (2001). *How to manage the blue orchard bee: As an orchard pollinator*. Sustainable Agriculture Network.

Bosch, J., Sgolastra, F., & Kemp, W. P. (2010). Timing of eclosion affects diapause development, fat body consumption and longevity in *Osmia lignaria*, a univoltine, adult-wintering solitary bee. *Journal of Insect Physiology*, *56*(12), 1949–1957. https://doi.org/10.1016/j.jinsphys.2010.08.017

Breed, M. D. (1975). Life cycle and behavior of a primitively social bee, *Lasioglossum rohweri* (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society*, *48*(1), 64–80.

Brock, R. E., Cini, A., & Sumner, S. (2021). Ecosystem services provided by aculeate wasps. *Biological Reviews*, *96*(4), 1645–1675. https://doi.org/10.1111/brv.12719

Busari, M. A., Kukal, S. S., Kaur, A., Bhatt, R., & Dulazi, A. A. (2015). Conservation tillage

impacts on soil, crop and the environment. *International Soil and Water Conservation*

*Research*, *3*(2), 119–129. https://doi.org/10.1016/j.iswcr.2015.05.002

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T.

L. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of*

*the National Academy of Sciences of the United States of America*, *108*(2), 662–667.

https://doi.org/10.1073/PNAS.1014743108

Campbell, A. J., Wilby, A., Sutton, P., & Wäckers, F. L. (2017). Do sown flower strips boost wild

pollinator abundance and pollination services in a spring-flowering crop? A case study

from UK cider apple orchards. *Agriculture, Ecosystems & Environment*, *239*, 20–29.

https://doi.org/10.1016/J.AGEE.2017.01.005

Cane, J. H. (1981). Dufour's gland secretion in the cell linings of bees (Hymenoptera: Apoidea).

*Journal of Chemical Ecology*, *7*(2), 403–410. https://doi.org/10.1007/BF00995762

Cane, J. H. (1991). Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell

depth and climate. *Journal of the Kansas Entomological Society*, *64*(4), 406–413.

Cane, J. H., Griswold, T., & Parker, F. D. (2007). Substrates and materials used for nesting by

orth American Osmia bees (Hymenoptera: Apiformes: Megachilidae). *Annals of the*

*Entomological Society of America*, *100*(3), 350–358. https://doi.org/10.1603/0013-

8746(2007)100[350:SAMUFN]2.0.CO;2

Cane, J. H., & Neff, J. L. (2011). Predicted fates of ground-nesting bees in soil heated by

    wildfire: Thermal tolerances of life stages and a survey of nesting depths. *Biological*

    *Conservation*, *144*(11), 2631–2636. https://doi.org/10.1016/j.biocon.2011.07.019

Cane, J. H., Snelling, R. R., & Kervin, L. J. (1996). A new monolectic coastal bee, *Hesperapis*

    *oraria* Snelling and Stage (Hymenoptera: Melittidae), with a review of desert and

    neotropical disjunctives in the Southeastern U.S. *Journal of the Kansas Entomological*

    *Society*, *69*(4), 238–247.

Cappellari, S. C., Schaefer, H., & Davis, C. C. (2013). Evolution: pollen or pollinators — which

    came first? *Current Biology*, *23*(8), R316–R318. https://doi.org/10.1016/j.cub.2013.02.049

Cardinal, S., & Danforth, B. N. (2013). Bees diversified in the age of eudicots. *Proceedings of*

    *the Royal Society B: Biological Sciences*, *280*(1755), 20122686.

    https://doi.org/10.1098/rspb.2012.2686

Claassen, R., Bowman, Maria, McFadden,Jonathan, Smith,David, & Wallander,Steven. (2018).

    *Tillage Intensity and Conservation Cropping in the United States* (197; Economic

    Information Bulletin). United States Department of Agriculture.

    https://www.ers.usda.gov/webdocs/publications/90201/eib-197.pdf

Clement, S. L. (1973). The nesting biology of *Melissodes* (*Eumelissodes*) *rustica* (Say), with a

    description of the larva (Hymenoptera: Anthophoridae). *Journal of the Kansas*

    *Entomological Society*, *46*(4), 516–525.

Cronk, Q., & Ojeda, I. (2008). Bird-pollinated flowers in an evolutionary and molecular context.

    *Journal of Experimental Botany*, *59*(4), 715–727. https://doi.org/10.1093/jxb/ern009

Dalmazzo, M., & Alsina, A. R. (2012). Nest structure and notes on the social behavior of

    *Augochlora amphitrite* (Schrottky) (Hymenoptera, Halictidae). *Journal of Hymenoptera*

    *Research*, *26*, 17–29. https://doi.org/10.3897/jhr.26.2440

De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., Berg,

    M. P., Cipriotti, P., Feld, C. K., Hering, D., Martins Da Silva, P., Potts, S. G., Sandin, L.,

    Sousa, J. P., Storkey, J., Wardle, D. A., & Harrison, P. A. (2010). Towards an assessment of

    multiple ecosystem processes and services via functional traits. *Biodiversity and*

    *Conservation*, *19*(10), 2873–2893. https://doi.org/10.1007/s10531-010-9850-9

De Luca, P. A., & Vallejo-Marín, M. (2013). What's the 'buzz' about? The ecology and

    evolutionary significance of buzz-pollination. *Current Opinion in Plant Biology*, *16*(4),

    429–435. https://doi.org/10.1016/j.pbi.2013.05.002

Derpsch, R. (1998). Historical review of no-tillage cultivation of crops. *Proc. 1st JIRCAS*

    *Seminar on Soybean Research. No-Tillage Cultivation and Future Research Needs*, 1–18.

Dorchin, A., López-Uribe, M. M., Praz, C. J., Griswold, T., & Danforth, B. N. (2018).

    Phylogeny, new generic-level classification, and historical biogeography of the *Eucera*

    complex (Hymenoptera: Apidae). *Molecular Phylogenetics and Evolution*, *119*, 81–92.

    https://doi.org/10.1016/j.ympev.2017.10.007

Duley, F. L., & Russel, J. C. (1939). The use of crop residues for soil and moisture conservation.

    *Agronomy Journal*, *31*(8), 703–709.

    https://doi.org/10.2134/agronj1939.00021962003100080007x

Eickwort, G. C., & Sakagami, S. F. (1979). A classification of nest architecture of bees in the

    tribe augochlorini (Hymenoptera: Halictidae; Halictinae), with description of a Brazilian

    nest of Rhinocorynura inflaticeps. *Biotropica*, *11*(1), 28–37.

    https://doi.org/10.2307/2388168

Espinoza, A. C., Urban-Mead, K. R., Buckner, M. A., Flórez-Gómez, N., Kueneman, J. G., &

    Danforth, B. N. (2023). Biology of *Andrena* (*Callandrena* Sensu Lato) *Asteris* Robertson

    (Hymenoptera: Andrenidae), an eastern aster specialist that makes a very deep nest.

    *Northeastern Naturalist*, *29*(4), 474–491. https://doi.org/10.1656/045.029.0406

Faegri, K., & Pijl, L. V. D. (2013). *Principles of Pollination Ecology*. Elsevier.

Gardein, H., Fabian, Y., Westphal, C., Tscharntke, T., & Hass, A. (2022). Ground-nesting bees

    prefer bare ground areas on calcareous grasslands. *Global Ecology and Conservation*, *39*,

    e02289–e02289. https://doi.org/10.1016/J.GECCO.2022.E02289

Garibaldi, L. A., Gomez Carella, D. S., Nabaes Jodar, D. N., Smith, M. R., Timberlake, T. P., &

    Myers, S. S. (2022). Exploring connections between pollinator health and human health.

    *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1853),

    20210158. https://doi.org/10.1098/rstb.2021.0158

Graham, J. R., Campbell, J. W., Plentovich, S., & King, C. B. A. (2021). Nest architecture of an

    endangered Hawaiian yellow-faced bee, *Hylaeus* anthracinus (Hymenoptera: Colletidae)

    and potential nest-site competition from three introduced solitary bees. *Pacific Science*,

    *75*(3), 361–370. https://doi.org/10.2984/75.3.5

Grimaldi, D. A. (2010). 400 million years on six legs: On the origin and early evolution of

    Hexapoda. *Arthropod Structure & Development*, *39*(2), 191–203.

    https://doi.org/10.1016/j.asd.2009.10.008

Harmon-Threatt, A. (2020). Influence of nesting characteristics on health of wild bee

    communities. *Annual Review of Entomology*, *65*(1), 39–56.

    https://doi.org/10.1146/annurev-ento-011019-024955

Hopfenmüller, S., Holzschuh, A., & Steffan-Dewenter, I. (2020). Effects of grazing intensity,

    habitat area and connectivity on snail-shell nesting bees. *Biological Conservation*, *242*,

    108406. https://doi.org/10.1016/j.biocon.2020.108406

Jones, D., & Jones, G. (1980). Records of bees hymenoptera apoidea from alabama usa. *Journal*

    *of the Georgia Entomological Society*, *15*(1), 56–65.

Kemper, W. D., Trout, T. J., Segeren, A., & Bullock, M. (1987). Worms and water. *Journal of*

    *Soil and Water Conservation*, *42*(6), 401–404.

Klatt, B. K., Nilsson, L., & Smith, H. G. (2020). Annual flowers strips benefit bumble bee

    colony growth and reproduction. *Biological Conservation*, *252*, 108814–108814.

    https://doi.org/10.1016/J.BIOCON.2020.108814

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C.,

    & Tscharntke, T. (2006). Importance of pollinators in changing landscapes for world crops.

    *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 303–313.

    https://doi.org/10.1098/RSPB.2006.3721

Kopec, K., & Burd, L. (2017). Pollinators in Peril: A Systematic Status Review of North American and Hawaiian Native Bees. *Center for Biological Diversity*.

Kremen, C., Williams, N. M., Bugg, R. L., Fay, J. P., & Thorp, R. W. (2004). The area requirements of an ecosystem service: Crop pollination by native bee communities in California. *Ecology Letters*, *7*(11), 1109–1119. https://doi.org/10.1111/j.1461-0248.2004.00662.x

Lark, T. J., Spawn, S. A., Bougie, M., & Gibbs, H. K. (2020). Cropland expansion in the United States produces marginal yields at high costs to wildlife. *Nature Communications*, *11*(1), 4295. https://doi.org/10.1038/s41467-020-18045-z

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, *56*(4), 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

Mallinger, R. E., & Gratton, C. (2015). Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *Journal of Applied Ecology*, *52*(2), 323–330. https://doi.org/10.1111/1365-2664.12377

Michener, C. D. (2000). *The Bees of the World*. JHU Press.

Müller, A. (2023). The hidden diet – examination of crop content reveals distinct patterns of pollen host use by Central European bees of the genus *Hylaeus* (Hymenoptera, Colletidae). *Alpine Entomology*, *7*, 21–35. https://doi.org/10.3897/alpento.7.102639

Murray, E. A., Bossert, S., & Danforth, B. N. (2018). Pollinivory and the diversification

    dynamics of bees. *Biology Letters*, *14*(11), 20180530.

    https://doi.org/10.1098/rsbl.2018.0530

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., & Favila, M. E. (2008).

    Ecological functions and ecosystem services provided by Scarabaeinae dung beetles.

    *Biological Conservation*, *141*(6), 1461–1474.

    https://doi.org/10.1016/J.BIOCON.2008.04.011

Nicolson, S. W. (2011). Bee food: The chemistry and nutritional value of nectar, pollen and

    mixtures of the two. *African Zoology*, *46*(2), 197–204.

    https://doi.org/10.1080/15627020.2011.11407495

Nilles, J. (1942). Digging-sticks, spades, hoes, axes, and adzes of the Kuman people in the

    Bismarck mountains of East-Central New Guinea. *Anthropos*, *37/40*(1/3), 205–212.

Ogieriakhi, M. O., & Woodward, R. T. (2022). Understanding why farmers adopt soil

    conservation tillage: A systematic review. *Soil Security*, *9*, 100077–100077.

    https://doi.org/10.1016/J.SOISEC.2022.100077

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by

    animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Packer, L., & Knerer, G. (1986). An analysis of variation in the nest architecture of *Halictus*

    *ligatus* in Ontario. *Insectes Sociaux*, *33*(2), 190–205. https://doi.org/10.1007/BF02224597

Porto, R. G., de Almeida, R. F., Cruz-Neto, O., Tabarelli, M., Viana, B. F., Peres, C. A., & Lopes,

    A. V. (2020). Pollination ecosystem services: A comprehensive review of economic values,

    research funding and policy actions. *Food Security*, *12*(6), 1425–1442.

    https://doi.org/10.1007/S12571-020-01043-W

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010).

    Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*,

    *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S., & Willmer, P. (1997). Abiotic and biotic factors influencing nest-site selection by

    *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology*, *22*(3), 319–

    328. https://doi.org/10.1046/j.1365-2311.1997.00071.x

Ray, C. (2023). First Survey of the Megachilidae (Hymenoptera: Apoidea) of Alabama.

    *Transactions of the American Entomological Society*, *149*(2), 235–246.

    https://doi.org/10.3157/061.149.0206

Remolina, S. C., & Hughes, K. A. (2008). Evolution and mechanisms of long life and high

    fertility in queen honey bees. *Age*, *30*(2–3), 177–185. https://doi.org/10.1007/s11357-008-

    9061-4

Robertson, C. (1925). Heterotropic Bees. *Ecology*, *6*(4), 412–436.

    https://doi.org/10.2307/1929107

Roldán Serrano, A., & Guerra-Sanz, J. M. (2006). Quality fruit improvement in sweet pepper

    culture by bumblebee pollination. *Scientia Horticulturae*, *110*(2), 160–166.

    https://doi.org/10.1016/j.scienta.2006.06.024

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, *232*, 8–27. https://doi.org/10.1016/J.BIOCON.2019.01.020

Sarrantonio, M., & Gallandt, E. (2003). The role of cover crops in North American cropping systems. *Journal of Crop Production*, *8*(1–2), 53–74. https://doi.org/10.1300/J144v08n01_04

Schwarz, M. P., Richards, M. H., & Danforth, B. N. (2007). Changing Paradigms in Insect Social Evolution: Insights from Halictine and Allodapine Bees. *Annual Review of Entomology*, *52*(1), 127–150. https://doi.org/10.1146/annurev.ento.51.110104.150950

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, *83*(5), 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Straka, J., Černá, K., Macháčková, L., Zemenová, M., & Keil, P. (2014). Life span in the wild: The role of activity and climate in natural populations of bees. *Functional Ecology*, *28*(5), 1235–1244. https://doi.org/10.1111/1365-2435.12261

Su, R., Dai, W., Yang, Y., Wang, X., Gao, R., He, M., Zhao, C., & Mu, J. (2022). Introduced honey bees increase host plant abundance but decrease native bumble bee species richness and abundance. *Ecosphere*, *13*(6), e4085. https://doi.org/10.1002/ecs2.4085

Subbulakshmi, S., Harisudan, C., Saravanan, N., & Subbian, P. (2009). Conservation tillage – an eco friendly management practices for agriculture. *Research Journal of Agriculture and Biological Sciences*, *5*(6), 1098–1103.

Teasdale, J. R., & Mohler, C. L. (1993). Light transmittance, soil temperature, and soil moisture

    under residue of hairy vetch and rye. *Agronomy Journal*, *85*(3), 673–680.

    https://doi.org/10.2134/agronj1993.00021962008500030029x

Tuell, J. K., & Isaacs, R. (2010). Weather during bloom affects pollination and yield of highbush

    blueberry. *Apiculture and Social Insects*, *103*(3), 557–562.

    https://doi.org/10.1603/EC09387

Tull, J. (1751). *Horse-hoeing Husbandry: Or, An Essay on the Principles of Vegetation and*

    *Tillage. Designed to Introduce a New Method of Culture; Whereby the Produce of Land*

    *Will be Increased, and the Usual Expence Lessened. Together with Accurate Descriptions*

    *and Cuts of the Instruments Employed in it*. A. Millar.

Ullmann, K. S., Meisner, M. H., & Williams, N. M. (2016). Impact of tillage on the crop

    pollinating, ground-nesting bee, *Peponapis pruinosa* in California. *Agriculture, Ecosystems*

    *& Environment*, *232*, 240–246. https://doi.org/10.1016/j.agee.2016.08.002

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect

    decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National*

    *Academy of Sciences*, *118*(2). https://doi.org/10.1073/pnas.2023989118

Walters, S. A. (2005). Honey bee pollination requirements for triploid watermelon. *HortScience*,

    *40*(5), 1268–1270. https://doi.org/10.21273/HORTSCI.40.5.1268

Westerkamp, Ch. (1996). Pollen in bee-flower relations some considerations on melittophily.

    *Botanica Acta*, *109*(4), 325–332. https://doi.org/10.1111/j.1438-8677.1996.tb00580.x

Winfree, R., Williams, N. M., Dushoff, J., & Kremen, C. (2007). Native bees provide insurance

against ongoing honey bee losses. *Ecology Letters*, *10*(11), 1105–1113.

https://doi.org/10.1111/j.1461-0248.2007.01110.x

**Chapter 2**

**Effect of tillage type on ground nesting bees in the Southeastern United States**

**2.1 Introduction**

Globally, pollinating insects influence the production of up to two-thirds of agricultural crops, including almonds, blueberries, apples, cucumbers, and melons (Calderone, 2012), and further facilitate the pollination of 87% of all flowering plants (Ollerton et al., 2011). Wild bees (Hymenoptera: Anthophila) are an economically and ecologically important insect taxa because of their role as pollinators of the flowering plants (Porto et al., 2020; Jordan et al., 2021). Due to their importance, recent declines in the abundance and diversity of wild bee communities is concerning. According to a 2017 review of the status of the North American bee fauna, as many as 52% of the 1,437 species included in the study were found to be in decline (Kopec and Burd, 2017). There is a growing consensus that multiple, concurrent factors are likely responsible, including insecticide exposure, introduced parasites, environmental contamination, and habitat loss (Biesmeijer et al., 2006; Potts et al., 2010; Cameron et al., 2011; Willis Chan and Raine, 2021). A significant factor implicated in the degradation of wild bee communities includes land use changes driven by agricultural production and urbanization, both of which leads to the loss of suitable habitat (Biesmeijer et al., 2006; Potts et al., 2010; Abbate et al., 2019; Willis Chan and Raine, 2021).

The magnitude of land used for agricultural activity in the U.S. culminated into 160 million hectares being utilized for crop production in 2017 (2017 Census of Agriculture, 2019). Although the monocultures that are common to agroecosystems are not ideal for supporting a high diversity of bee species, several species have been observed visiting the flowers of common

commodity crops, and nesting within and along the edges of crop fields (Shuler et al., 2005; Cunningham-Minnick et al., 2019). Through experimental manipulation, the abundance of *Lasioglossum callidum* (Sandhouse, 1924), *Lasioglossum hitchensi* Gibbs 2012, and *Agapostemon virescens* (Fabricius, 1775) increased in soybean fields when vegetation was removed from a 1m x 30m area of ground, potentially indicating the ability of these bee species to nest within crop fields when the conditions are suitable (Cunningham-Minnick et al., 2019).

It is estimated that between 64 - 83% of bee species nest below ground (Cane and Neff, 2011; Harmon-Threatt, 2020). The nest structure of ground dwelling bees typically consists of vertical shaft connected to a few brood cells, to more elaborate configurations made up of multiple branching tunnels (Eickwort and Sakagami, 1979; Packer and Knerer, 1986; Dalmazzo and Alsina, 2012). Nest cell depths have been recorded to range from 2 - 180 cm (Cane, 1991). Reproductive females, referred to as 'gynes', provision brood cells with a ball of nectar, pollen, and bee gland secretions that the developing larvae consume (Potts et al., 2010 Michener, 2007). The intimate relationship that most wild bee species have with the soil, and their high sensitivity to disturbances has prompted a call for their representation as part of soil biodiversity conservation efforts (Christmann, 2022). Therefore, wild bees should be considered when deciding on agricultural management practices that disturb the soil, such as pesticide application, irrigation, and tillage.

Tillage is defined as the physical manipulation of the soil in preparation for cultivation. It is implemented utilizing a variety of methods; however, the most commonly practiced tillage methods broadly fall into two main categories, adhering to either Conservation or Conventional tillage regimes. Conservation tillage is a term used to describe tillage practice that reduce soil erosion and minimize water loss; it usually employs the intentional buildup of crop residues on

the soil surface and lower levels of soil disturbance made in conscious effort to minimize disturbance of the reside cover (Claassen et al., 2018). Conservation tillage systems can be further subset into those that practice no till, and others that perform deep tillage but minimize soil disturbance at the surface. This is achieved by subsoiling, which does not disturb surface residues as the subsoiler cuts deep into the soil with a shape similar to a chisel plow. This action loosens and mixes the soil below the surface. Benefits derived from subsoiling have been reported in research conducted in the Tennessee River Valley where no-tillage practices are common. Subsoiling increased cotton yields and lowered levels of soil compaction compared to either the no-tillage or the conventional tillage treatments (Schwab et al., 2002). As a tool, subsoiling offers producers the ability to improve soil conditions for crop cultivation without sacrificing surface residues. This is an important aspect of conservation tillage systems because of the benefits that surface resides provide, such as reduced top soil erosion, water runoff, and increased water infiltration (Brown, 1984; Blevins and Frye, 1993; Ogieriakhi and Woodward, 2022).

Alternatively, in conventional tillage systems there is no goal of generating surface residues (Claassen et al., 2018). As a result, levels of soil disturbance are of higher intensity in conventional tillage, including common use of deep plowing and disking to completely invert the soil, as well as deep tillage by subsoiling. Knowledge of the impact that soil management practices impart on ground-nesting bees is limited. Bees have been observed nesting in soils of varying compositions (Cane, 1991); however, several previous studies have documented bee nesting in soils classified as clay-loams to sandy-loams, but no bees were found nesting in clay soils (Cane, 1991; Potts and Willmer, 1997). In addition to soil texture, soil moisture and availability of bare ground were positively corelated to increased bee nesting (Antoine and

Forrest, 2021; Tsiolis et al., 2022).Agroecosystems often harbor vast areas of exposed soil for much of the year. Even in a conservation tillage regime that values residue cover, the 30% cover goal equates to 70% of the soil surface consisting of exposed bare ground which may be particularly attractive to nesting females. However, these soils are frequently disturbed by tillage practices, and the outcome of bees nesting within their confines are unknown (Shuler et al., 2005; Cunningham-Minnick et al., 2019).

Relevant research regarding tillage bee interactions have involved only a small subset of species and inconsistent results. For example, within squash *Cucurbita* (Curcubitaceae) plantings, the effect of soil tillage delayed and reduced the number of emerging offspring of the squash bee species *Eucera pruinosa* in California (Ullmann et al., 2016); the specific mechanisms responsible were unclear. In contrast, the implementation of soil tillage had no effect on the abundance of *E. pruinosa* or *Bombus impatiens* Cresson 1863 surveyed on pumpkin farms in the mid-Atlantic (Julier and Roulston, 2009). Skidmore et al. (2019) reported higher nesting densities of *E. pruinosa* in strip tilled plots than in no till plots (Skidmore et al., 2019). While additional research suggests that tillage type is not important compared to distance from the field edge (Tschanz et al., 2023). It has been postulated that bee mortality caused by conventional tillage is the result of mechanical act of tillage when implements physically destroy brood, or when the soil surrounding the nest is disturbed, making it difficult for bees to emerge (Shuler et al., 2005; Ullmann et al., 2016; Tsiolis et al., 2022). Furthermore, intentionally generated surface residues fostered under conservation tillage practices may act to limit bee nesting activity, but the effects of these agricultural practices on bee communities is not well understood.

In this work, I investigated how conservation and conventional soil management practices influence the abundance and diversity of bees nesting in agroecosystems by intensively sampling assemblages of ground nesting bees among experimental treatments that are representative of practices used in the Southeastern United States.. The objective of this work was primarily focused on quantifying differences in bee nesting incidence, abundance of bees, and bee species diversity among tillage regimes. I predicted that bee incidence, abundance and diversity would be negatively correlated with increasing disturbance enacted on the soil by tillage operations.

## 2.2 Methods

### 2.2.1 Site Selection and Experimental Design

The study site was located at the E.V. Smith Research Center in Shorter in Alabama (32°25'45.86"N, 85°53'6.69"W), at an experimental agricultural plot used to study conservation tillage for past 35 years (Balkcom et al., 2010). The field was managed according to a two-year crop rotation altering between soybean and cotton, typical of irrigated row crop production in the southeastern United States. The field consisted of 96 experimental plots arranged in a 24 x 4 grid pattern (Figure 1 and 2). Each experimental plot measured 7.3 meters wide x 21.3 meters long and was separated by a minimum of 0.9 meters from surrounding experimental plots on all sides. Twenty-four experimental plots were allocated to one of three infield treatment groups according to historic management: (1) Conventional tillage managed with no winter cover crop, hereinafter referred to as Conventional tillage; (2) Conservation noninversion tillage managed with a winter rye cover crop, hereinafter referred to as Conservation tillage; (3) a non-inversion tillage without a cover crop, hereinafter referred to as Reduced tillage.

Soil tillage was implemented in the spring of each year, occurring on 21 April 2021, and again on 13 May 2022.. The Conventional tillage treatment included disking at a depth of 15.24 cm for 3 passes, followed by leveling the surface with a cultipacker, then subsoiling 35.56 cm deep with rods spaced 91.44 cm apart. Conservation Tillage included planting of Wrens Abruzzi rye at 40.8 kgs/ha using the Great Plains 1206 drill. In the following spring the rye was terminated using an application of glyphosate herbicide at a rate of 2 L/ha, followed by rolling the rye grass flat against the soil surface will a steel roller. This was followed up by subsoiling 35.56 cm deep with rods spaced 91.44 cm apart. The Reduced tillage treatment was historically managed the same way as the Conventional treatment until 2018; however, for the past five years it was maintained in sub-plots that experienced subsoiling 35.56 cm deep with rods spaced 91.44 cm apart and cultivation practices using a no-till drill. In sum, the Conservation, Conventional, and Reduced tillage treatments collectively make up the tilled 'infield' treatment groups and were represented by 24 experimental plots each. In 2021, cotton was planted into each of the 96 experimental plots; soybean followed in 2022. Management of the cash crop followed standard practices used by producers in the area. This included the use of herbicides and pre and post emergence pesticides, as well as fertilizer inputs (Supplementary table 1. Additionally, a fourth treatment was established as a strip measuring 1.8 meters wide x 192 meters long along both the east and western field boundaries, referred to hereinafter as Edge. The Edge treatment received periodic herbicide (Glyphosate) at a rate of 2 L/ha from an ATV mounted sprayer to limit the encroachment of the vegetation adjacent to the field.

**Figure 1:** Satellite image of experimental tillage plot located at the E.V. Smith Research Center in Shorter, Alabama.
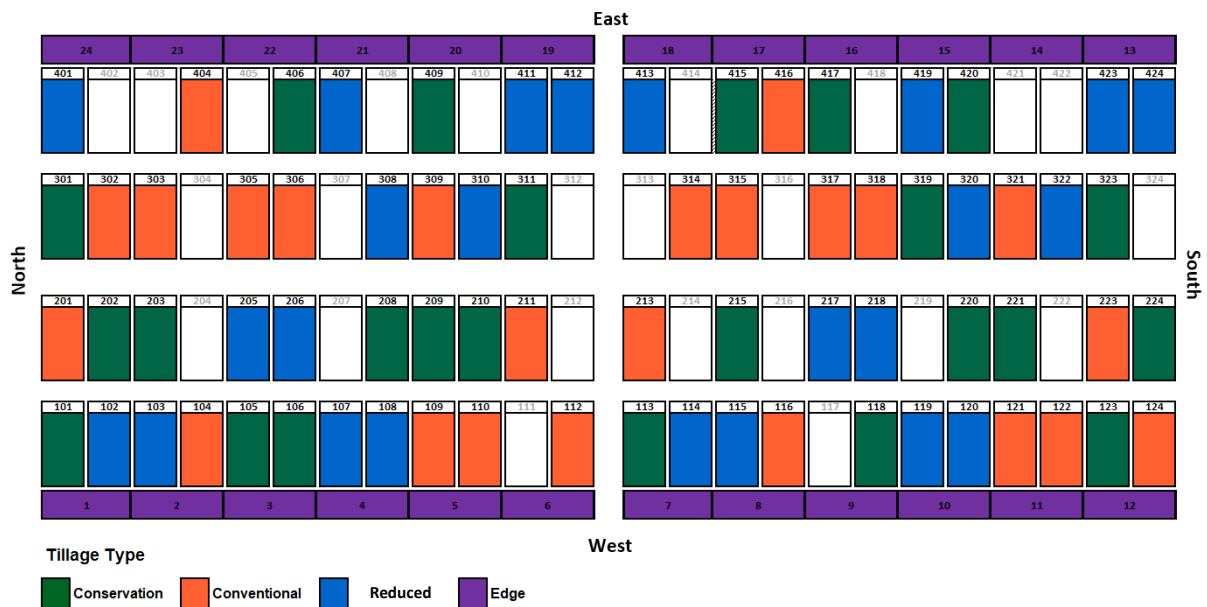


**Figure 2:** Example of experimental plot layout within the tillage filed at E.V. Smith Research Center. Each of the 4 treatment groups: Conservation tillage (Green), Conventional tillage (Orange), Reduced tillage (Blue), Edge (Purple) are represented by 24 experimental plots. Plots represented by the color white were unused in 2021 and 2022.

### 2.2.2 Environmental Factors

**Ground Cover.** I estimated the ground cover composition in 48 of 96 total plots three times in 2021 (April, June, and August), and monthly in 2022 (March – October). Vegetation surveys were conducted in twelve randomly selected plots per experimental treatment; they consisted of randomly placing 3 1-meter squared quadrats within the selected plot and then visually estimating the percent cover of living vegetation, crop residue, and bare ground at the soil surface.

**Soil Texture and Organic Matter.** To quantify differences in soil properties between tillage treatments, I randomly selected six experimental plots from each of 4 treatment groups, then I collected three soil cores at a depth of 30.4 cm from each of the selected plots. The three soil cores collected from each plot were pooled and then submitted to the Soil, Forage and Water Testing Lab at Auburn University for soil texture and organic carbon analysis. Soil particle size analysis was conducted using the hydrometer method (Ashworth et al., 2001). While the amount of organic carbon was determined by loss of ignition analysis (Davies, 1974).

**Soil Strength.** A tractor-mounted with a multiple probe soil cone penetrometer (MPSCP) was used to quantify differences in soil compaction among experimental treatments (R. L. Raper et al., 1999). On 12 April 2021, and 6 June 2022, soil strength was measured three times in six randomly selected plots belonging to each experimental treatment with a 5 probe (MPSCP). Measurements were taken by each probe in 5 cm intervals, up to a maximum depth of 50 cm. In addition, two soil cores were collected at a depth of 30 cm in tandem from each corresponding plot to quantify soil moisture at the time of measurement. Soil from each of the cores was separated into two groups – the first ranging from 0-15 cm and the second from 15-30 cm.

### 2.2.3 Bee Sampling

**Emergence Trap Collections.** Ground nesting bees were assessed at the study site using emergence traps, which were each composed of an enclosed four-sided mesh square pyramid structure measuring 60 by 60 cm that contained a collection jar at its apex (Figure 3). As insects emerged from their nests, they were directed upward towards the top of the trap, where they were collected and temporarily preserved in a jar containing 50% solution of propylene glycol and water (Super Tech RV & Marine Antifreeze, Walmart.Inc, Bentonville, US) (Ulyshen et al., 2021). Each of 24 sub-plots per treatment received one trap held flush to the soil surface using 15 cm long metal ground staples. An additional 12 traps were placed along each of the eastern and western field boundary strips for a total of 24 emergence traps used to assess the Edge treatment. Each of the 72 infield plots consisted of 8 crop rows planted 0.91 meters apart, as well as 7 inter-rows. Initial placement of emergence traps was determined by creating a set of coordinates based on randomly selecting 1 of the 7 plot inter-rows, and also randomly generating a number of steps to take along the interrow before placing the trap. Emergence traps were kept roughly one trap width distance from the edges of experimental plots in attempt to minimize edge effects. Prior studies utilizing soil emergence traps found that periodically moving traps increased the number of bees captured compared to leaving traps stationary all season (Sardiñas and Kremen, 2014; Ulyshen et al., 2021). Emergence traps were deployed continuously for seven days, ±1-2 days due to inclement weather or because of field wide management actions needing to be carried out, such as application of pesticides Upon collection of the samples, the traps were moved a randomly generated distance in steps either east or west within the interrow, moving to the adjacent interrow when reaching the edge of the plot to ensure appropriate sampling of each sub-plot. In 2021, emergence trap sampling occurred between March - September, for a total of 20 collection events. In 2022, soil emergence trap sampling was extended into the first week of

November due to an observed increase in *Lasioglossum* bees captured in the fall of 2021. This resulted in 28 collection events taking place in 2022. For the combined years of 2021 and 2022, I sampled for 48 weeks, amounting to a total of 1,152-week long emergence trap sampling events per experimental treatment, or a grand total of 4,608-week long emergence trap deployments over the course of the study.



**Figure 3:** Example of soil emergence trap used in the study, manufacturer: Bugdorm.com, Taichung, Taiwan

*2.2.4 Statistical Analysis*

**Environmental Factors.**

*Ground Cover.* Initial exploration of the ground cover data revealed differences in variance around both the mean and the median among treatments (Package car, Function leveneTest, center = mean, median). An indication that the data were not normally distributed. Therefore, I conducted Kruskal Wallis H tests (package ggbetweenstats, function ggbetweenstats, type = "nonparametric") for percentages of Residue, Bare Ground, and Living Vegetation in order to quantify differences in ground cover among experimental treatments (Moreno-de las Heras et al., 2009). Following the Kruskal Wallis tests, pairwise comparisons were made by post hoc Dunns tests (package ggbetweenstats, function ggbetweenstats, , p.adjust.method = "holm").

*Soil Texture and Organic matter.* For percentages of sand, silt, clay, and organic matter, I used linear regression to investigate differences in soil composition across experimental treatments (Package Stats, Function lm). Model building was done via a stepwise approach, and selection of the best fitting model included testing for correct distribution, dispersion and outliers as well as visual inspection of model residuals plotted against predicted values (DHARMa package, function simulateResiduals). For each soil constituent the best fitting model included the constituent of interest as the response variable, and Treatment as the dependent variable. Linear regression was followed by post hoc Tukey tests (emmeans package, function emmeans, adjust="Tukey").

*Soil Strength.* I evaluated soil compaction among experimental treatments following the methods outlined by (Balkcom et al., 2016), in which cone index values were averaged for each soil probe and then the area under the curve was calculated using a formula derived from the trapezoid formula (Pruessner et al., 2003). The first step in calculating the area under the curve

for cone index values ($AUC_{C.I.}$) required calculating a single mean cone index value for each of five probe positions across all soil depth classes from the three penetrometer measurements taken per plot. This was followed by calculation of plot level $AUC_{C.I.}$ values based on the mean cone index value for each probe position (Package DescTools, Method=Trapezoid). The resulting plot level $AUC_{C.I.}$ values were fitted to a linear model to analyze differences in soil compaction among treatments (Package Stats, Function lm). The final model included $AUC_{C.I.}$ as the response variable, and Treatment as a fixed effect. Model selection was carried out by testing for correct distribution, dispersion and outliers, as well as visual inspection of model residuals plotted against predicted values (DHARMa package, function simulateResiduals). The linear model was followed by post hoc Tukey tests (package emmeans, function emmeans, adjust="Tukey"). Ground cover and soil analyses were conducted in R v.4.3.1 (2023).

**Bee Sampling.** I analyzed the incidence, abundance, and diversity of bees collected in soil emergence traps located in each experimental treatment. Due to the low rate of capture associated with soil emergence traps in previous studies (Ulyshen et al., 2021), I pooled emergence trap collections from all 24 plots for each sampling round (n=24 emergence traps) and used these data to analyze bee incidence and abundance among treatments.

*Bee Incidence*. Logistic analysis of bee incidence across treatments required that I denote bee presence in each treatment per sampling round with either a '0' for bee absence or a '1' for bee presence. The incidence of bee capture among treatments was analyzed using a generalized linear mixed effect model (Package glmmTMB, Function glmmTMB) with a binomial distribution to account for the binary response. Model building followed a stepwise approach, and fit was assessed by testing for correct distribution, dispersion, and outliers, as well as visual inspection of model residuals plotted against predicted values (DHARMa package, function

simulateResiduals). The final model included bee presence as the response variable with treatment as a fixed effect, and sampling round as a random effect to account for differences in the flight periods of bee species across sampling rounds. The generalized linear model was followed by post hoc Tukey tests (emmeans package, function emmeans, adjust="Tukey").

*Bee Abundance*. I analyzed bee abundance in each treatment per sampling round with a generalized linear mixed model (Package glmmTMB, Function glmmTMB). Model building followed a stepwise approach and fit was assessed by testing for correct distribution, dispersion and outliers, as well as visual inspection of model residuals plotted against predicted values (DHARMa package, function simulateResiduals). The final fitted model included a negative binomial distribution to accommodate overdispersion in the dataset, and bee abundance was used as the response variable with treatment as a fixed effect. Sampling round was included as a random effect due to differences in the flight periods of bee species across sampling rounds. Significant results from the generalized linear model were followed by post hoc Tukey tests (emmeans package, function emmeans, adjust="Tukey").

*Bee Diversity.* I investigated bee diversity among treatment groups by analyzing the bee assemblages collected by emergence traps deployed in each treatment during the 2021 and 2022 field seasons (n=1,152 traps/treatment). I identified bees to species with the use of a stereomicroscope (Leica S9 D) and relevant taxonomic literature (Ascher and Pickering, 2011; Gibbs, 2011; Gibbs et al., 2013). I then used Hill Shannon and Hill Simpson diversity metrics based on hill numbers which are a more robust way of investigating the diversity of different assemblages than traditional metrics because hill numbers possess the replication principle and allows comparisons among traditional Shannon and Simpson diversity metrics possible (Jost, 2018; Roswell et al., 2021). I calculated the effective number of species (ENS) for Shannon

diversity (Hill number q =1), and ENS for Simpson diversity (Hill number q = 2) at the sample

coverage level equal to that of the treatment with the lowest maximum coverage (Chao and Jost,

2012; Roswell et al., 2021) (Package iNEXT, Function estimateD, datatype = "abundance",

base="coverage", conf = 0.95, level=0.89). I plotted the effective number of species for Shannon

and Simpson diversities at the rarified coverage and visually examined the overlap of 95%

confidence intervals among treatments. All bee analyses were conducted in R v.4.3.1 (2023).

## 2.3 Results

### 2.3.1 Environmental Factors

**Ground Cover**. Residue cover was observed to have the highest percentages in the

Conservation tillage treatment (Supplementary Table 2). Residue cover differed significantly

among treatment groups (Kruskal-Wallis rank test, $\chi2 = 852.06$, DF = 3, $p < 0.0001$)

(Supplementary Figure 1). Pairwise comparisons among experimental treatments revealed that

residue cover was significantly higher in the Conservation tillage treatment than the Edge

treatment ($p < 0.0001$), Reduced tillage treatment ($p < 0.0001$), and the Conventional tillage

treatment ($p < 0.0001$) (Dunn's Test of Multiple Comparisons) (Supplementary Table 3).

Additionally, residue cover was significantly higher in the Edge treatment than in the Reduced

tillage treatment ($p < 0.0001$) and the Conventional tillage treatment ($p < 0.0001$) (Dunn's Test

of Multiple Comparisons). The Reduced tillage treatment had significantly higher amounts of

residue cover than the Conventional tillage treatment ($p < 0.0001$) (Dunn's Test of Multiple

Comparisons).

I found significant difference in the amount of bare ground among treatments (Kruskal-

Wallis rank test, $\chi2 = 852.06$, DF = 3, $p < 0.0001$)(Supplementary Figure 2). The Conventional

tillage treatment had significantly higher amounts of bare ground than the Reduced (p = 0.0002), Edge (p < 0.0001) and Conservation tillage (p < 0.0001) treatments (Dunn's Test of Multiple Comparisons)(Supplementary Table 3). The Reduced tillage treatment had significantly more bare ground than the Edge (p < 0.0001) and Conservation tillage (p < 0.0001) treatments (Dunn's Test of Multiple Comparisons), and the Edge treatment possessed significantly higher amounts of bare ground than the Conservation tillage treatment (p = 0.0138) (Dunn's Test of Multiple Comparisons).

The percent of living vegetation cover differed significantly among treatment groups (Kruskal-Wallis rank test, $\chi^2$ = 852.06, DF = 3, p < 0.0001)(Supplementary Figure 3). The amount of vegetation cover was significantly higher in the Edge treatment than the Reduced ( p < 0.0001), Conservation tillage (p < 0.0001), and Conventional tillage (p < 0.0001) treatment groups (Dunn's Test of Multiple Comparisons), whereas the Reduced tillage treatment had significantly higher amounts of living vegetation cover than the Conventional tillage treatment (p = 0.009) (Dunn's Test of Multiple Comparisons)(Supplementary Table 3). The amount of living vegetation cover was not statistically different between the Reduced and Conservation treatments, or between the Conventional and Conservation treatments (p > 0.05) (Dunn's Test of Multiple Comparisons)

**Soil Texture and Organic Matter.** Overall, average percentages of sand, silt, clay and organic matter were similar among the infield tilled treatment groups, with larger differences observed between the Edge and the infield tilled treatments (Supplementary Table 5). The fitted linear regression model for percent sand indicated significant differences among treatments ($R^2$ = 0.483, F = 6.237, p = 0.0036)(Supplementary Figure 5, Supplementary Table 8). I found that the Edge treatment possessed significantly lower percentages of sand than all other treatments (p <

0.05) (Post hoc Tukey tests) (Figure 5A, Supplementary Table 9). The percentage of sand was found to be 4.05% (95% CI [2.51, 5.59], p = 0.0047) lower in the Edge treatment than in the Conventional tillage treatment (Figure 5A). As well as being 3.63% (95% CI [2.09, 5.17], p = 0.0115), and 3.11% (95% CI [1.57, 4.65], p = 0.0335) lower than the Reduced tillage and Conservation tillage treatments. I found no significant differences for the percentage of silt found in soils among all experimental treatments ($R^2$ = 0.0467, F = 0.326, p = 0.806)(Figure 5B, Supplementary Figure 7, Supplementary Table 12); however, the fitted linear regression modeling percent clay revealed significant differences among treatments ($R^2$ = 0.748, F = 19.86, p < 0.0001) (Figure 5C, Supplementary Figure 6, Supplementary Table 10). Soil in the Edge treatment possessed a significantly higher percentage of clay than all of the tilled infield treatments (p < 0.05)(Supplementary Table 11). The percentage of clay was 2.95% (95% CI [2.30, 3.59], p = 0.0001) higher in the Edge than the Conventional tillage treatment, 2.83% (95% CI [2.18, 3.47], p < 0.0001) higher compared to the Reduced tillage treatment, and 2.40% (95% CI [1.75, 3.04], p < 0.0001) higher than in the Conservation tillage treatment. The amount of organic matter differed significantly between treatments ($R^2$ = 0.518, F = 7.178, p = 0.0018) (Figure 4D, Supplementary Figure 4, Supplementary Table 6). The Edge treatment possessed significantly higher percentages of organic matter than both the Reduced tillage and Conventional tillage treatments (p < 0.05) (Post hoc Tukey tests) (Figure 5D, Supplementary Table 7) but was not significantly different than the Conservation tillage treatment. The percentage of organic matter was 0.467% (95% CI [0.15, 0.78], p = 0.0026) higher in the Edge than the Conventional tillage treatment, and 0.367% (95% CI [0.05, 0.68], p = 0.019) higher compared to the Reduced tillage treatment. Additionally, organic matter in the soil of the Conservation tillage treatment was 0.333% (95% CI [0.02, 0.65], p = 0.0357) higher than in the

Conventional tillage treatment.
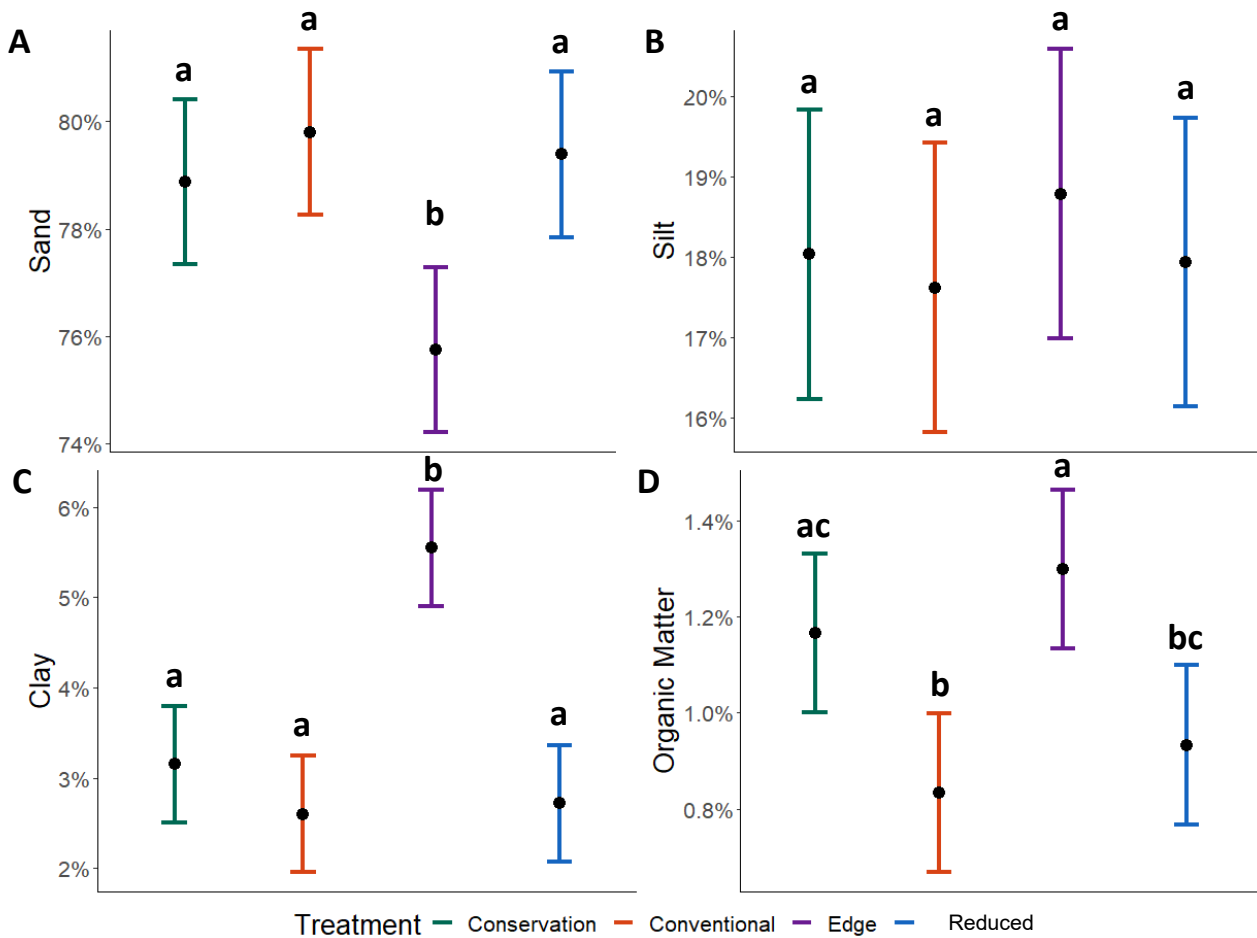


**Figure 4:** Point estimates of means and 95 % C.I.s from fitted linear models (Package Emmeans, Function emmeans) for percentages of A) Sand, B) Silt, C) Clay, and D) Organic Matter found in 3 pooled soil cores collected from each of 6 randomly selected experimental plots per treatment group in 2021. Significant differences between groups denoted by the letter above.

**Soil Strength.** For both penetrometer survey dates I found significant differences in soil compaction among treatments (2021: $R^2 = 0.909$, F = 66.63, p < 0.0001; 2022: $R^2 = 0.801$, F = 26.7, p < 0.0001)(Supplementary Tables 14 & 16, Supplementary Figures 8 & 9). Soil compaction in the Edge treatment was found to be significantly higher than all other treatment groups for both surveys (p < 0.0001) (Post hoc Tukey tests)(Supplementary Table 15 & 17).

Results from the survey conducted on 12 April 2021 indicate that soil strength in the Edge was 230.31 (95% CI [175.03, 285.59], p = 0.0001) MPa-cm higher than the Conventional tillage treatment, 229.92 (95% CI [174.64, 285.20], p = 0.0001) MPa-cm higher compared to the Conservation tillage treatment, and 223.64 (95% CI [168.38, 278.9], p = 0.0001) MPa-cm more than was found in the Reduced tillage treatment (Post hoc Tukey tests) (Figure 6A, Supplementary Table 15). A second penetrometer survey performed on 27 June 2022 found that soil compaction in the Edge treatment was 192.57 (95% CI [123.24, 261.90], p = 0.0001) MPa-cm higher than in the Conventional tillage treatment, 191.8 (95% CI [122.40, 261.20], p = 0.0001) MPa-cm higher than the Conservation tillage treatment, and 159.78 (95% CI [90.46, 229.10], p = 0.0001) MPa- cm higher compared to the Reduced tillage treatment (Figure 6B, Supplementary Table 17).
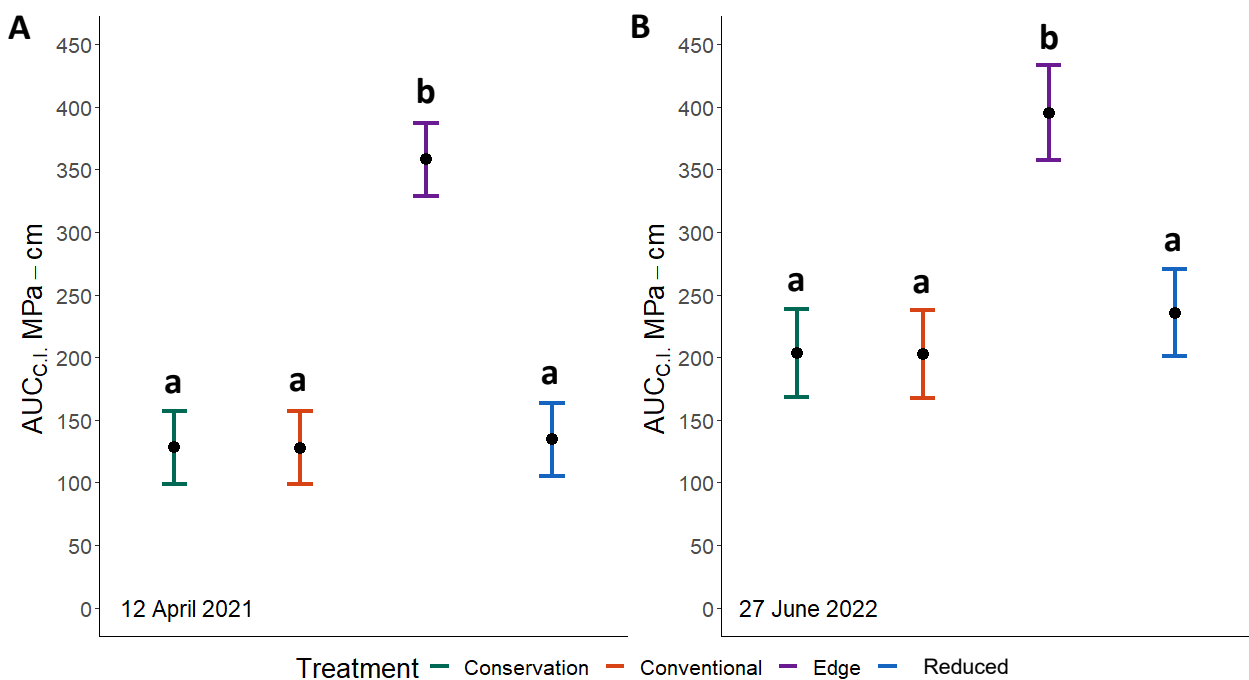


**Figure 5 :** Mean area under the curve for cone index ($AUC_{C.I.}$) values and 95% Confidence intervals (Package Emmeans, Function emmeans) resulting from fitted linear models (Package Stats, Function lm, n = 18) for soil penetrometer surveys conducted on A) 12 April 2021, and B)

27 June 2022. Significant differences between groups denoted by the letter above each treatment group.

### 2.3.2 Bee Sampling

**Bee Incidence**. I investigated the incidence of bee presence and absence among tillage treatments and found significant differences in the odds of collecting bees in soil emergence traps among experimental treatments (Supplementary Table 18). The odds of collecting a bee were significantly higher in the Edge treatment than all other treatment groups (all p-values < 0.005) (Figure 7, Supplementary Table 19). The odds of collecting a bee in the Edge were 12.46 (95% CL [2.561, 60.63 ], p = 0.0003) times as likely compared to emergence trap collections made in the Reduced tillage, 11.29 (95% CL [2.340, 54.51], p = 0.0005) times as likely than collections made in the Conventional tillage treatment, and 7.6 (95% CL [1.611, 35.86], p = 0.0047) times as likely compared to collections made in the Conservation tillage treatment (Post hoc Tukey tests). For full statistical output see Supplementary Tables 18 and 19, and Supplementary Figure 12.
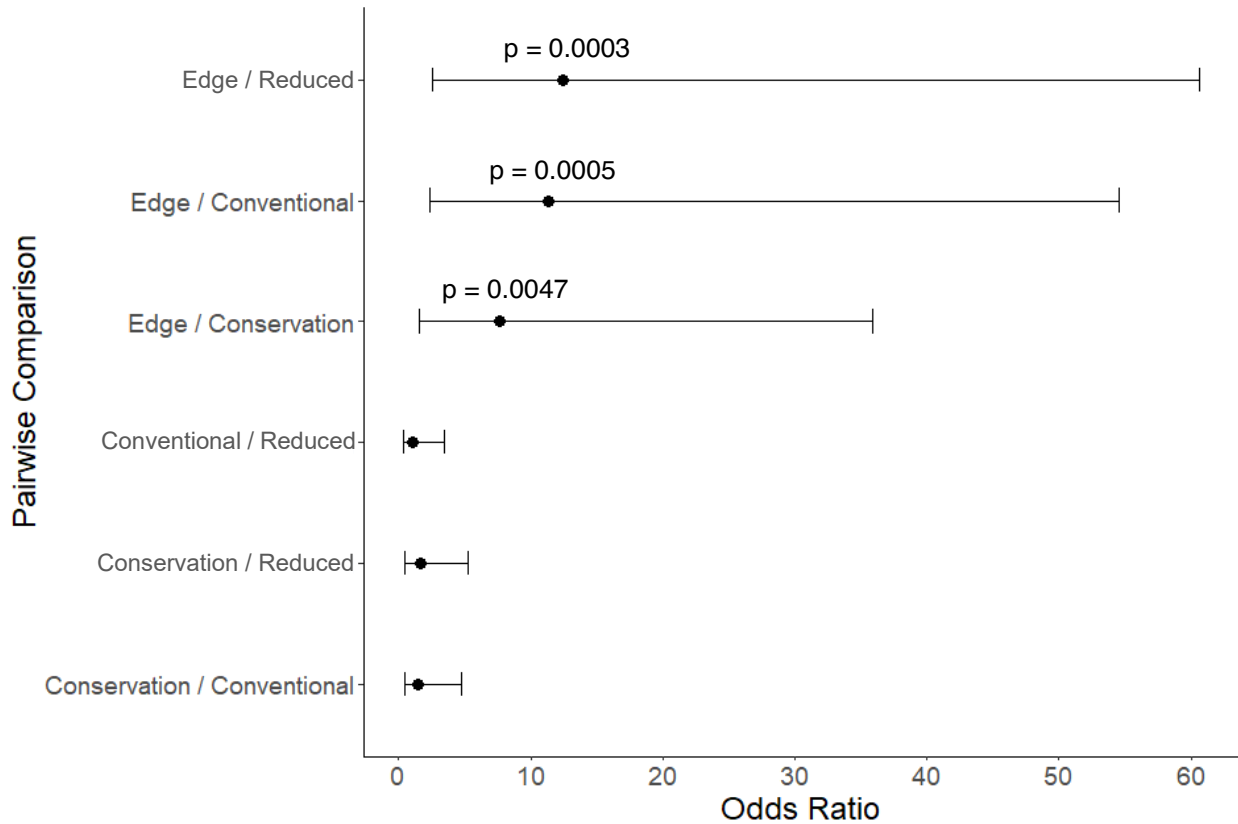
**Figure 6:** Results of pairwise post hoc Tukey tests comparing differences in bee incidence from emergence trap collections made in 2021 and 2022 (n = 48 sampling rounds) between treatment groups (Package Emmeans, Function emmeans, adjust="tukey"). Estimates are back transformed from the log scale as odds ratios that represent the differences in likelihood of collecting a bee between treatment groups as "times as likely".

**Bee Abundance.** I found significant differences in bee abundance across experimental treatments (Supplementary Table 19). The Edge harbored the highest number of bees per sampling round compared to all other treatments ($p < 0.0001$) (Post hoc Tukey tests) (Figure 7, Supplementary Table 21). There were 5.71 (95% CL [2.718, 11.98 ], $p < 0.0001$) times as many bees collected in the Edge treatment than in the Conventional tillage treatment, 3.99 (95% CL [1.937, 8.24], $p < 0.0001$) times as many bees than the Reduced tillage treatment, and 3.65 (95% CL [1.774, 7.50], $p < 0.0001$) times as many bees compared to the Conservation tillage treatment

(Post hoc Tukey tests). For full statistical output see supplementary Tables 20, 21 and

Supplementary Figure 13.
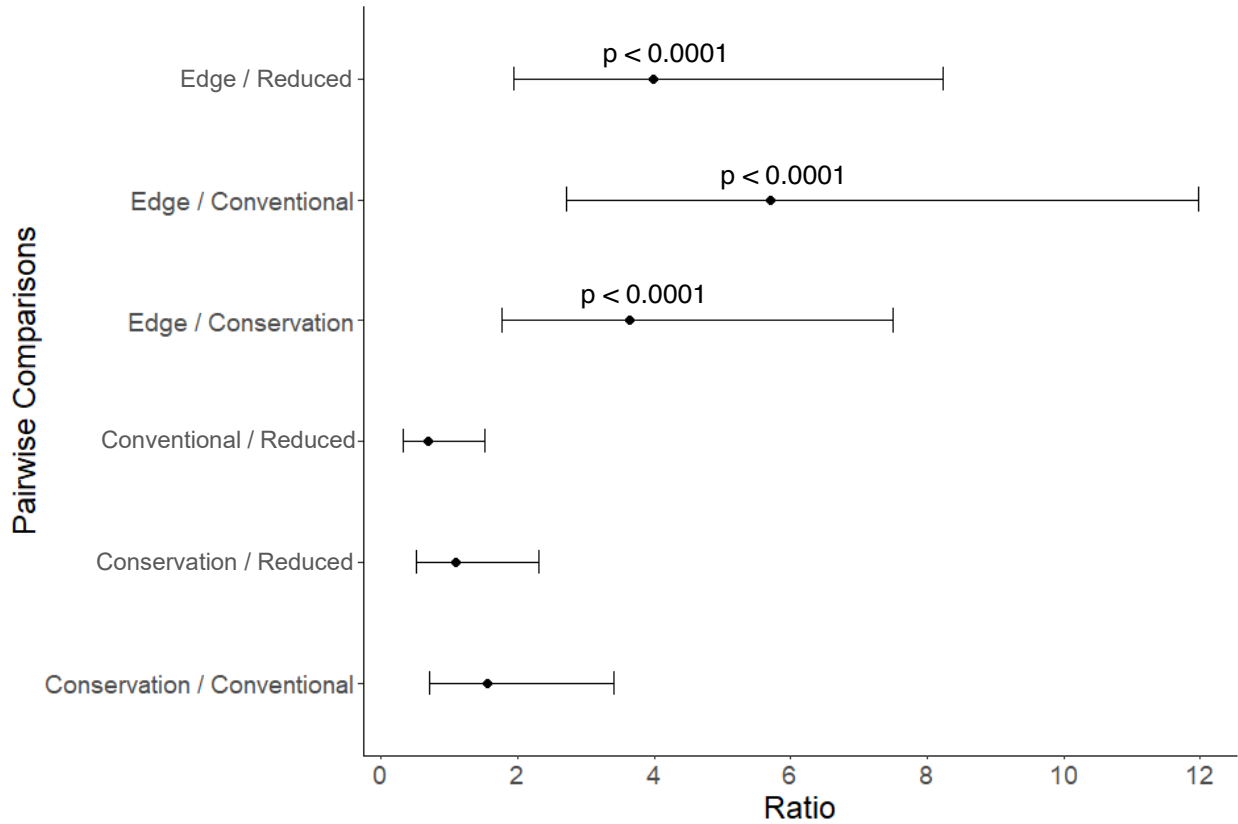


**Figure 7:** Results of pairwise post hoc Tukey tests comparing differences in bee abundance from emergence trap collections made in 2021 and 2022 (n = 48 sampling rounds) between treatment groups (Package Emmeans, Function emmeans, adjust="tukey"). Estimates are back transformed from the log scale as rate ratios that represent the differences in bee abundance between treatment groups as "times as many bees".

**Bee Diversity.** Sampling completeness of bee assemblages was found to be sufficient among treatments, with the Reduced tillage treatment possessing the lowest sampling coverage at a level equal to 0.89, and the Edge with the highest coverage equal to 0.97 (Package iNEXT, Function $DataInfo)(Supplementary Figure 14). This indicates that a relatively low number of unobserved species were missing from collections made among treatments. In total, 529

individuals belonging to 33 species of ground nesting bees were collected from emergence traps deployed for the duration of the study (Supplementary Table 22). Bees in the genus *Lasioglossum* made up 81.5% of all bees collected from emergence traps. Furthermore, 18 species of *Lasioglossum* were detected by emergence traps in both years of the study, but only 4 species were represented by 10 or more individuals (Supplementary Table 22; bees belonging to what is referred to in this work as the *Lasioglossum tegulare/puteulanum* species constituted 31% of all bees collected.

Analysis of bee diversities across orders of q revealed significant differences in bee diversity among treatment groups. No significant differences were observed in species richness (q=0) among treatment groups (Figure 8A). The Shannon diversity of bee assemblages (q=1) found in the Edge treatment harbored a higher number of bee species (6.01 species, 95% CI [5.25, 6.77]) compared to both the Conservation tillage (1.93 species, 95% CI [1.17, 2.69]) and Conventional tillage (2.97 species, 95% CI [1.56, 4.38]) treatments (non-overlapping 95% CI's) (Figure 8B, Supplementary Table 23 & 24); however, the diversity of common bee species in the Reduced tillage treatment (4.61 species, 95% CI [2.17, 6.78]) did not differ significantly from that of the Edge. When providing more leverage to species at higher relative abundances for the effective number of species at Simpson diversity (q = 2), I found that the Edge (4.5 species, 95% CI [3.84, 5.16]) contained a higher effective number of abundant bee species than the Conservation tillage (1.55 species, 95% CI [1.28, 1.82]), Conventional tillage (1.99 species, 95% CI [1.45, 2.53]), and the Reduced (2.57 species, 95% CI [1.79, 3.35]) (non-overlapping 95% CI's) treatments (Figure 8C). Detailed diversity statistics can be found in supplementary tables 23 and 24, as well as supplementary figures 15 and 16.
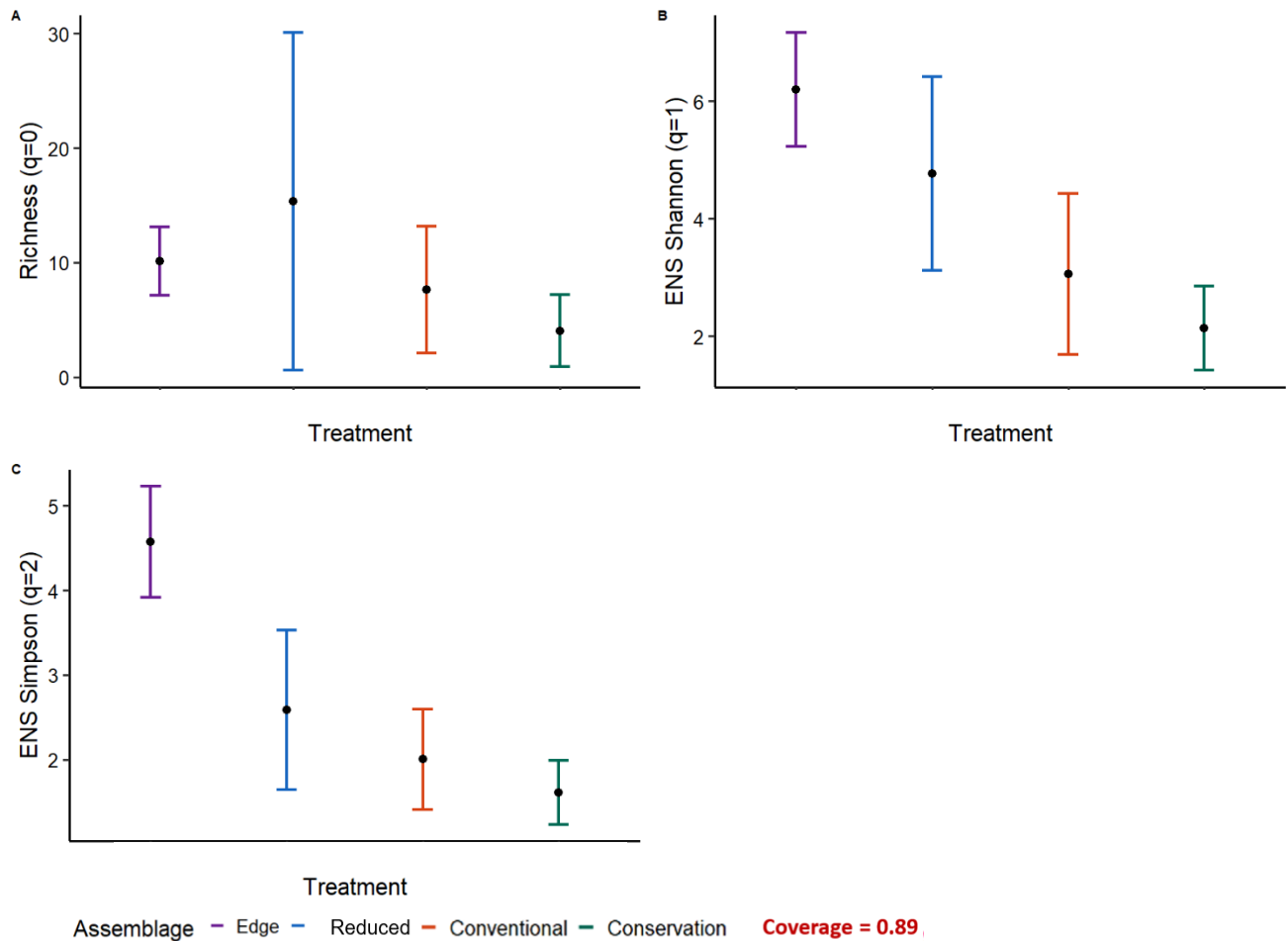
**Figure 8**: Estimated number of effective species and 95% confidence intervals for **A)** Species Richness (hill number q = 0), **B)** Shannon diversity (Hill number q = 1), and **C)** Simpson diversity (Hill number q=2) at sampling coverage equal to 0.89 (Package iNEXT, Function estimateD, q = 0,1,2, level = 0.89) among tillage treatments. Significant differences are denoted by the letter above each treatment group.

## 2.4 Discussion

Increasing our knowledge of how soil management practices used in agricultural production affect native bee communities is a necessary step forward in efforts aimed at their conservation, as well as increasing their utility to producers as pollinators. Altogether I found strong evidence that bee incidence, abundance, and diversity were depreciated in cultivated

fields, regardless of the tillage regime implemented when compared to the field edge. Findings from this study reinforce the importance of uncultivated areas to native ground-nesting bee communities persisting within agricultural landscapes and highlight what could be seen as an incompatibility between agricultural practices and ground nesting bee ecology.

Numerous studies have documented depauperate bee communities occupying agricultural landscapes (Winfree and Kremen, 2009; Potts et al., 2010). There is strong evidence that lower bee diversity is correlated with increasing distance from natural areas and an overall simplification of the landscape (Kim et al., 2006; Schubert et al., 2022). As well as evidence that routine practices such as irrigation and fertilizer applications negatively affect bee abundance (Steinhübel et al., 2022). In this study, significantly less abundant and diverse assemblages of bees were found nesting among all of the tilled infield treatments compared to the edge treatment located just outside of the cultivated plots.

Bees belonging to the genus *Lasioglossum* constituted 81.5% of all bees collected in emergence traps for the combined 2021 and 2022 field seasons. The use of emergence traps in previous studies produced similar proportions of *Lasioglossum* bees as was found in this study (Sardiñas and Kremen, 2014; Pane and Harmon-Threatt, 2017; Ulyshen et al., 2021). Both the bee species *Lasioglossum imitatum* (Smith,1853) and *Lasioglossum illinoiense* (Robertson, 1892) were commonly collected in this study and may represent very common species to the southeast as they were also readily collected in emergence trap collections made in forests of the Southeastern United States (Ulyshen et al., 2021), suggesting that these species are common in both agricultural and natural systems. As floral generalists, bees in the genus *Lasioglossum* readily visit a wide range of flowering plants and can be effective pollinators when foraging in high numbers (Garantonakis et al., 2016; Elliott et al., 2021). The contributions toward

pollination services that *Lasioglossum* bees afford has been overlooked in the past (Nelson et al., 2023), as multiple studies have observed *Lasioglossum* bees to be the dominant crop flower visitor (Batra and Batra, 1997; Garantonakis et al., 2016; O'Brien and Arathi, 2018). Therefore, the inclusion and fostering of *Lasioglossum* in the agricultural landscape would result in an increase to pollination services rendered to producers.

However, management practices such as the intentional build-up of crop residues on the soil surface, as is found in conservation tillage practices, may be at odds with the preferable nesting site conditions of ground nesting bees. The composition of ground cover may be an explanatory variable that has been of interest among researchers studying ground nesting bee site selection (Antoine and Forrest, 2021; Orr et al., 2022), with particular attention on the availability of bare ground because it has been correlated with higher bee abundances. However, management practices such as the intentional build-up of crop residues on the soil surface, as is found in conservation tillage practices, may be at odds with the preferable nesting site conditions of ground nesting bees. The composition of ground cover may be an explanatory variable that has been of interest among researchers studying ground nesting bee site selection (Antoine and Forrest, 2021; Orr et al., 2022), with particular attention on the availability of bare ground because it has been correlated with higher bee abundances (Gardein et al., 2022). However, I observed that bee abundances were not statistically higher in either the conventional or Reduced tillage treatments whose ground cover was primarily composed of bare ground. In fact, bee abundance and incidence were non significantly different among all infield treatment groups even though the conservation treatment possessed significantly lower percentages of bare ground due to the high percentage of residue cover on the soil surface. This may be an indication that the total amount of available bare ground was not a limiting factor affecting bee nesting in this

instance, as I observed the highest incidences, abundances, and diversities of bees in the edge treatment where percentages of bare ground cover were the most variable, but second lowest among treatments.

The effective number of species for both Shannon and Simpson diversities were the lowest in the conservation treatment compared to all other treatment groups, suggesting that the disturbance caused from subsoiling paired with the thick reside layer on the soil surface may be limiting the diversity of bee species able or willing to nest in these areas. Ground cover in the conservation treatment was dominated by high percentages of residue cover which could be influencing bee nesting by altering soil conditions such as soil temperature and moisture (Johnson and Lowery, 1985; Blevins and Frye, 1993). Increased soil temperature was shown to decrease the nesting cycle of the sweat bee *Lasioglossum malachurum* (Kirby,1802). While additional studies conducted with emergence traps have reported increased bee capture rates corelated with lower soil moisture, providing evidence of bees responding to changes in abiotic conditions (Weissel et al., 2006; Pane and Harmon-Threatt, 2017). The high percentages of residue cover found on the soil surface in the conservation tillage treatment may increase soil moisture content in the soil and in turn result in lower bee nesting activity. Overall, I observed significantly lower Shannon and Simpson diversities of bee species in the conservation tillage treatment compared to the edge treatment, and although the diversity of bee assemblages were not significantly different among any of the tilled experimental treatments, the conservation tillage treatment possessed the least diverse assemblages of bee species, which is of concern because of the increasing adoption of conservation tillage practices across the United States (Claassen et al., 2018). If crop residues left on the soil surface are acting to limit the subset of

bee species occupying agricultural landscapes, then the role that field edges play becomes increasingly more important for supporting native ground nesting bees.

Canopy cover from the cultivated crop may be a factor confounding inferences on the effect of ground cover. In this study cotton and soybean were not planted until late April/May, resulting in experimental plots being nearly void of living vegetation between crop harvest the previous year, up until crop emergence and development the following year - except for the conservation treatment due to the use of a winter planted rye grass used as a cover crop. Near the middle of each summer, the planted crop increased in size and its branches eventually covered large portions of the inner rows that were surveyed. Cover from cotton or soy was not included in the 'living vegetation' class during the ground cover surveys because the focus was placed on differences that existed at the soil surface, and because it was observed to affect the infield treatment groups equally. Cover from the planted crop likely has an unknown effect in this study and its absence on the edge may be a factor related to the increase in bee nesting activity. It is possible that the increase in solar insolation as a result of not being shaded by the cash crop could make the Edge a more favorable nesting location.

Previous investigations into which specific soil characteristics are correlated with belowground bee nesting activity include soil texture-specifically the ratio of sand, silt, and clay (Cane 1991). In this study, the soil among all experimental treatments was classified as a loamy sand. I found that the edge had significantly less sand and more clay than all other treatment groups. Much is unknown in regard to how soil physical properties affect different bee species ability to construct their belowground nest. Potts and Willmer, 1997 proposed an interesting idea that the percentage of sand, specifically at high levels, could be limiting, especially for species that are known to nest in aggregations because these excessively sandy soils cause the nests to

collapse into one another (Potts and Willmer 1997). The percentages of sand among treatment groups varied by a small amount compared to the ranges of sand content found in soils where bees have been documented nesting (Cane, 1991). Therefore, additional soil properties such as soil aggregate stability and soil structure  may further explain bees ability to construct their belowground nests.

The percentage of clay found in soils of experimental treatments for instance may be an important explanatory variable. Overall, clay contents of soils among all treatments were very low; however, the edge treatment possessed significantly more clay than the infield treatments, at less than 6% on average. The very low amount of clay may be limiting bee nesting, as Cane (1991) documented only 6 out of 36 bee species nesting in soils with less than 6% clay content and Tsiolis (2022) reported clay percentages where bees were nesting to be between 12.8% - 23.6%, with an optimum at around 17.4% (Tsiolis et al., 2022). This may be an indication that clay content in the Edge treatment was located near a lower bound that is conductive to bee nesting compared to levels of clay found in the infield treatments. Overall, the difference in percentages of clay among treatments was small in magnitude and unlikely to be driving differences in bee nesting activity. Additional soil physical properties such as levels of soil compaction differed among treatments in the study, with the edge treatment having the most compacted soils as well as the highest levels of bee nesting (Supplementary Figures 10 & 11, Supplementary Table 21). This aligns with previous work that included the relationship of soil compaction with bee nesting density and found that maximum nesting density was higher at sites with harder substrates (Potts and Willmer, 1997); however further research is needed to better understand the effect of soil strength on the ability of different bee species ability to construct their belowground nests.

In addition to the environmental factors that differed due to tillage practice, the intensity of soil disturbance differed among treatments due to the inclusion of different tractor pulled implements commonly employed in tillage operations. The edge treatment received no soil disturbance other than wheel traffic (occasional tractor traffic during field wide management) while in-row subsoiling at a depth of 24" was conducted in the conservation, conventional, and Reduced tillage treatment groups. Additional tillage was applied in the Conventional tillage treatment by disking of the entire plot at a depth of 6" for multiple passes. Overall, the conventional treatment harbored the lowest abundance of bees among all treatments and also experienced the most intensive form of tillage among treatment groups. The actual implementation of tillage in the conventional and Reduced tillage treatment groups differed only by the removal of disking. Therefore the difference between these two treatment groups essentially represents the effect of disking, or reduced tillage intensity on ground nesting bees. I observed no biologically meaningful difference in bee abundance or incidence when the act of disking was removed from tillage operations. This implies that some shared variable among the infield treatment groups could be acting to limit bee nesting. It is possible that the act of subsoiling could be a confounding factor among treatments since none of the 'in-field' treatments showed significant differences in abundances, and they all received subsoiling as part of their tillage implementation. The soil disturbance enacted by subsoiling could decrease bee incidence and abundance in the tilled in-field treatments if it is the cause of nest destruction or bee mortality. As far back as 1922, Frison (1922) noted the discovery of unearthed pupae belonging to the Eucerine bee *Melissoides bimaculatus* (Lepeletier,1825) that had become exposed to the soil surface after plowing. Despite this, only a few studies have attempted to quantify the effect of tillage operations on ground nesting bees in past century.

## 2.5 Conclusion

The loss of suitable habitat is a major driver associated with global insect decline (Potts et al., 2010; Cameron et al., 2011). Nearly 160 million hectares of land in the United States has been converted for use in agricultural production (2017 Census of Agriculture, 2019), affecting aspects of native bee biology and ecology in ways yet to be explored. The work in this study provides strong evidence that bee nesting incidence, abundance and diversity were significantly lower among all of the infield tillage treatments. This demonstrated the elevated role that field edges play in supporting ground nesting bee abundance and diversity in agroecosystems. Evidence that bee nesting was significantly lower in tilled fields could manifest as a decrease in pollination services provided by native ground nesting bees in cultivated fields. If the majority of ground nesting bee activity occurs on the perimeter of crop fields, it would likely have the effect of concentrating pollination services around the field exterior because bees are central place foragers, with limited flight ranges (Greenleaf et al., 2007; Grüter and Hayes, 2022). The implications of which support the addition of areas with undisturbed soils into agricultural fields to increase native ground nesting bee abundances.

Overall, it remains unclear if the lower levels of bee nesting observed in all of the tilled infield treatments is the result of bee nest site selection, mortality caused by soil tillage, or driven by a combination of the two, in addition to other factors such as the availability of floral resources. Future work should look to isolate and quantify bee mortality caused by tillage practices that employee the use of different farm implements, like plows, subsoilers, and discs. Understanding whether tilled fields are simply unattractive to ground nesting bees, or acting as ecological sinks will greatly benefit efforts to conserve the biodiversity of native bee species.

**2.6 References**

*2017 Census of Agriculture* (Geographic Area Series). (2019). United States department of

   Agriculture. https://www.nrcs.usda.gov/sites/default/files/2022-

   10/2017NRISummary_Final.pdf

Abbate, A., Campbell, J. W., Kimmel, C. B., & Kern, W. H. (2019). Urban development

   decreases bee abundance and diversity within coastal dune systems. *Global Ecology and

   Conservation*, *20*, e00711. https://doi.org/10.1016/j.gecco.2019.e00711

Antoine, C. M., & Forrest, J. R. K. (2021). Nesting habitat of ground-nesting bees: A review.

   *Ecological Entomology*, *46*(2), 143–159. https://doi.org/10.1111/een.12986

Ascher, J. S., & Pickering, J. (2011). *Bee Species Guide (Hymenoptera: Apoidea: Anthophila)*.

   Discover Life. Http://Www. Discoverlife. Org/Mp/20q.

Ashworth, J., Keyes, D., Kirk, R., & Lessard, R. (2001). Standard procedure in the hydrometer

   method for particle size analysis. *Communications in Soil Science and Plant Analysis*,

   *32*(5–6), 633–642. https://doi.org/10.1081/CSS-100103897

Balkcom, K. S., Duzy, L. M., Mitchell, C. C., & Delaney, D. P. (2016). A simple approach to

   enhance multiprobe soil cone penetrometer analyses. *Soil Science Society of America

   Journal*, *80*(6), 1619–1628. https://doi.org/10.2136/sssaj2016.05.0157

Balkcom, K. S., Price, A. J., Van Santen, E., Delaney, D. P., Boykin, D. L., Arriaga, F. J.,

   Bergtold, J. S., Kornecki, T. S., & Raper, R. L. (2010). Row spacing, tillage system, and

   herbicide technology affects cotton plant growth and yield. *Field Crops Research*, *117*(2–

   3), 219–225. https://doi.org/10.1016/j.fcr.2010.03.003

Batra, S. W. T., & Batra, S. W. T. (1997). Bionomics of *Lasioglossum (Evylaeus) matianense* (Blüthgen) (Hymenoptera: Halictidae), the predominant pollinating bee in orchards at high altitude in the great Himalaya of Garhwal, U.P., India. *Proceedings of the Entomological Society of Washington*, *99*, 162--170.

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., & Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, *313*(5785), 351–354. https://doi.org/10.1126/science.1127863

Blevins, R. L., & Frye, W. W. (1993). Conservation tillage: an ecological approach to soil management. *Advances in Agronomy*, *51*(C), 33–78. https://doi.org/10.1016/S0065-2113(08)60590-8

Brown, L. R. (1984). The global loss of topsoil. *Journal of Soil and Water Conservation*, *39*(3), 162–165.

Calderone, N. W. (2012). Insect pollinated crops, insect pollinators and US Agriculture: trend analysis of aggregate data for the period 1992–2009. *PLoS ONE*, *7*(5), e37235. https://doi.org/10.1371/journal.pone.0037235

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(2), 662–667. https://doi.org/10.1073/PNAS.1014743108

Cane, J. H. (1991). Soils of ground-besting bees (Hymenoptera: Apoidea): texture, moisture, cell

    depth and climate. *Journal of the Kansas Entomological Society*, *64*(4), 406–413.

Cane, J. H., & Neff, J. L. (2011). Predicted fates of ground-nesting bees in soil heated by

    wildfire: Thermal tolerances of life stages and a survey of nesting depths. *Biological*

    *Conservation*, *144*(11), 2631–2636. https://doi.org/10.1016/j.biocon.2011.07.019

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing

    samples by completeness rather than size. *Ecology*, *93*(12), 2533–2547.

    https://doi.org/10.1890/11-1952.1

Christmann, S. (2022). Regard and protect ground-nesting pollinators as part of soil biodiversity.

    *Ecological Applications*, *32*(3). https://doi.org/10.1002/EAP.2564

Claassen, R., Bowman, Maria, McFadden,Jonathan, Smith,David, & Wallander,Steven. (2018).

    *Tillage Intensity and Conservation Cropping in the United States* (197; Economic

    Information Bulletin). United States Department of Agriculture.

    https://www.ers.usda.gov/webdocs/publications/90201/eib-197.pdf

Cunningham-Minnick, M. J., Peters, V. E., & Crist, T. O. (2019). Nesting habitat enhancement

    for wild bees within soybean fields increases crop production. *Apidologie*, *50*, 833–844.

    https://doi.org/10.1007/s13592-019-00691-y

Dalmazzo, M., & Alsina, A. R. (2012). Nest structure and notes on the social behavior of

    *Augochlora amphitrite* (Schrottky) (Hymenoptera, Halictidae). *Journal of Hymenoptera*

    *Research*, *26*, 17–29. https://doi.org/10.3897/jhr.26.2440

Davies, B. E. (1974). Loss-on-ignition as an estimate of soil organic matter. *Soil Science Society of America Journal*, *38*(1), 150–151. https://doi.org/10.2136/sssaj1974.03615995003800010046x

Eickwort, G. C., & Sakagami, S. F. (1979). A classification of nest architecture of bees in the tribe Augochlorini (Hymenoptera: Halictidae; Halictinae), with description of a Brazilian nest of *Rhinocorynura inflaticeps*. *Biotropica*, *11*(1), 28–37. https://doi.org/10.2307/2388168

Elliott, B., Wilson, R., Shapcott, A., Keller, A., Newis, R., Cannizzaro, C., Burwell, C., Smith, T., Leonhardt, S. D., Kämper, W., & Wallace, H. M. (2021). Pollen diets and niche overlap of honey bees and native bees in protected areas. *Basic and Applied Ecology*, *50*, 169–180. https://doi.org/10.1016/j.baae.2020.12.002

Garantonakis, N., Varikou, K., Birouraki, A., Edwards, M., Kalliakaki, V., & Andrinopoulos, F. (2016). Comparing the pollination services of honey bees and wild bees in a watermelon field. *Scientia Horticulturae*, *204*, 138–144. https://doi.org/10.1016/j.scienta.2016.04.006

Gardein, H., Fabian, Y., Westphal, C., Tscharntke, T., & Hass, A. (2022). Ground-nesting bees prefer bare ground areas on calcareous grasslands. *Global Ecology and Conservation*, *39*, e02289–e02289. https://doi.org/10.1016/J.GECCO.2022.E02289

Gibbs, J. (2011). Revision of the metallic *Lasioglossum* (*Dialictus*) of eastern North America (Hymenoptera: Halictidae: Halictini). *Zootaxa*, *3073*(1), 1. https://doi.org/10.11646/zootaxa.3073.1.1

Gibbs, J., Packer, L., Dumesh, S., & Danforth, B. N. (2013). Revision and reclassification of *Lasioglossum* (*Evylaeus*), *L.* (*Hemihalictus*) and *L.* (*Sphecodogastra*) in eastern North America (Hymenoptera: Apoidea: Halictidae). *Zootaxa*, *3672*(1), 1. https://doi.org/10.11646/zootaxa.3672.1.1

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589–596. https://doi.org/10.1007/s00442-007-0752-9

Grüter, C., & Hayes, L. (2022). Sociality is a key driver of foraging ranges in bees. *Current Biology*, *32*(24), 5390-5397.e3. https://doi.org/10.1016/j.cub.2022.10.064

Harmon-Threatt, A. (2020). Influence of Nesting Characteristics on Health of Wild Bee Communities. *Annual Review of Entomology*, *65*(1), 39–56. https://doi.org/10.1146/annurev-ento-011019-024955

Johnson, M. D., & Lowery, B. (1985). Effect of three conservation tillage practices on soil temperature and thermal properties. *Soil Science Society of America Journal*, *49*(6), 1547–1552. https://doi.org/10.2136/sssaj1985.03615995004900060043x

Jordan, A., Patch, H. M., Grozinger, C. M., & Khanna, V. (2021). Economic dependence and vulnerability of United States agricultural sector on insect-mediated pollination service. *Environmental Science & Technology*, *55*(4), 2243–2253. https://doi.org/10.1021/acs.est.0c04786

Jost, L. (2018). What do we mean by diversity? The path towards quantification. *Mètode Revista de Difusió de La Investigació*, *9*. https://doi.org/10.7203/metode.9.11472

Julier, H. E., & Roulston, T. H. (2009). Wild bee abundance and pollination service in cultivated

    pumpkins: Farm management, nesting behavior and landscape effects. *Journal of Economic*

    *Entomology*, *102*(2), 563–573. https://doi.org/10.1603/029.102.0214

Kim, J., Williams, N., & Kremen, C. (2006). Effects of cultivation and proximity to natural

    habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas*

    *Entomological Society*, *79*(4), 309–320. https://doi.org/10.2317/0507.11.1

Kopec, K., & Burd, L. (2017). Pollinators in peril: A systematic status review of North American

    and Hawaiian native bees. *Center for Biological Diversity*.

Moreno-de las Heras, M., Merino-Martín, L., & Nicolau, J. M. (2009). Effect of vegetation cover

    on the hydrology of reclaimed mining soils under Mediterranean-Continental climate.

    *CATENA*, *77*(1), 39–47. https://doi.org/10.1016/j.catena.2008.12.005

Nelson, W., Evans, L., Donovan, B., & Howlett, B. (2023). *Lasioglossum* bees – the forgotten

    pollinators. *Journal of Apicultural Research*, *62*(1), 39–46.

    https://doi.org/10.1080/00218839.2022.2028966

O'Brien, C., & Arathi, H. S. (2018). Bee genera, diversity and abundance in genetically modified

    canola fields. *GM Crops & Food*, *9*(1), 31–38.

    https://doi.org/10.1080/21645698.2018.1445470

Ogieriakhi, M. O., & Woodward, R. T. (2022). Understanding why farmers adopt soil

    conservation tillage: A systematic review. *Soil Security*, *9*, 100077–100077.

    https://doi.org/10.1016/J.SOISEC.2022.100077

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Orr, M. C., Jakob, M., Harmon-Threatt, A., & Mupepele, A.-C. (2022). A review of global trends in the study types used to investigate bee nesting biology. *Basic and Applied Ecology*. https://doi.org/10.1016/j.baae.2022.03.012

Packer, L., & Knerer, G. (1986). An analysis of variation in the nest architecture *of Halictus ligatus* in Ontario. *Insectes Sociaux*, *33*(2), 190–205. https://doi.org/10.1007/BF02224597

Pane, A. M., & Harmon-Threatt, A. N. (2017). An assessment of the efficacy and peak catch rates of emergence tents for measuring bee nesting. *Applications in Plant Sciences*, *5*(6), 1700007. https://doi.org/10.3732/apps.1700007

Porto, R. G., de Almeida, R. F., Cruz-Neto, O., Tabarelli, M., Viana, B. F., Peres, C. A., & Lopes, A. V. (2020). Pollination ecosystem services: A comprehensive review of economic values, research funding and policy actions. *Food Security*, *12*(6), 1425–1442. https://doi.org/10.1007/S12571-020-01043-W

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S., & Willmer, P. (1997). Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology*, *22*(3), 319–328. https://doi.org/10.1046/j.1365-2311.1997.00071.x

Pruessner, J. C., Kirschbaum, C., Meinlschmid, G., & Hellhammer, D. H. (2003). Two formulas for computation of the area under the curve represent measures of total hormone concentration versus time-dependent change. *Psychoneuroendocrinology*, *28*(7), 916–931. https://doi.org/10.1016/S0306-4530(02)00108-7

R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

R. L. Raper, B. H. Washington, & J. D. Jarrell. (1999). Technical notes: a tractor-mounted multiple-prob soil cone penetrometer. *Applied Engineering in Agriculture*, *15*(4), 287–290. https://doi.org/10.13031/2013.5779

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*(3), 321–338. https://doi.org/10.1111/oik.07202

Sardiñas, H. S., & Kremen, C. (2014). Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic and Applied Ecology*, *15*(2), 161–168. https://doi.org/10.1016/j.baae.2014.02.004

Schubert, L. F., Hellwig, N., Kirmer, A., Schmid-Egger, C., Schmidt, A., Dieker, P., & Tischew, S. (2022). Habitat quality and surrounding landscape structures influence wild bee occurrence in perennial wildflower strips. *Basic and Applied Ecology*, *60*, 76–86. https://doi.org/10.1016/j.baae.2021.12.007

Schwab, E. B., Reeves, D. W., Burmester, C. H., & Raper, R. L. (2002). Conservation Tillage

    Systems for Cotton in the Tennessee Valley. *Soil Science Society of America Journal*, *66*(2),

    569–577. https://doi.org/10.2136/sssaj2002.5690

Shuler, R. E., Roulston, T. H., & Farris, G. E. (2005). Farming Practices Influence Wild

    Pollinator Populations on Squash and Pumpkin. *Journal of Economic Entomology*, *98*(3),

    790–795. https://doi.org/10.1603/0022-0493-98.3.790

Skidmore, A. R., Short, C. A., Dills, C., Goodell, K., & Bessin, R. T. (2019). Preference of

    *Peponapis pruinosa* (Hymenoptera: Apoidea) for Tilled Soils Regardless of Soil

    Management System. *Environmental Entomology*, *48*(4), 961–967.

    https://doi.org/10.1093/ee/nvz052

Steinhübel, L., Wenzel, A., Hulamani, P., von Cramon-Taubadel, S., & Mason, N. M. (2022).

    Effects of local farm management on wild bees through temporal and spatial spillovers:

    Evidence from Southern India. *Landscape Ecology*, *37*(10), 2635–2649.

    https://doi.org/10.1007/s10980-022-01507-8

Tschanz, P., Vogel, S., Walter, A., Keller, T., & Albrecht, M. (2023). Nesting of ground-nesting

    bees in arable fields is not associated with tillage system per se, but with distance to field

    edge, crop cover, soil and landscape context. *Journal of Applied Ecology*, *60*(1), 158–169.

    https://doi.org/10.1111/1365-2664.14317

Tsiolis, K., Potts, S., Garratt, M., Tilston, E., Burman, J., Rintoul-Hynes, N., & Fountain, M. (2022). The importance of soil and vegetation characteristics for establishing ground-nesting bee aggregations. *Journal of Pollination Ecology*, *32*, 186–200. https://doi.org/10.26786/1920-7603(2022)682

Ullmann, K. S., Meisner, M. H., & Williams, N. M. (2016). Impact of tillage on the crop pollinating, ground-nesting bee, *Peponapis pruinosa* in California. *Agriculture, Ecosystems & Environment*, *232*, 240–246. https://doi.org/10.1016/j.agee.2016.08.002

Ulyshen, M. D., Wilson, A. C., Ohlson, G. C., Pokswinksi, S. M., & Hiers, J. K. (2021). Frequent prescribed fires favor ground-nesting bees in southeastern U.S. forests. *Insect Conservation and Diversity*, *14*(4), 527–534. https://doi.org/10.1111/icad.12484

Weissel, N., Mitesser, O., Liebig, J., Poethke, H.-J., & Strohm, E. (2006). The influence of soil temperature on the nesting cycle of the halictid bee *Lasioglossum malachurum*. *Insectes Sociaux*, *53*(4), 390–398. https://doi.org/10.1007/s00040-005-0884-7

Willis Chan, D. S., & Raine, N. E. (2021). Population decline in a ground-nesting solitary squash bee (*Eucera pruinosa*) following exposure to a neonicotinoid insecticide treated crop (*Cucurbita pepo*). *Scientific Reports*, *11*(1), Article 1. https://doi.org/10.1038/s41598-021-83341-7

Winfree, R., & Kremen, C. (2009). Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1655), 229–237. https://doi.org/10.1098/rspb.2008.0709

**Appendix 1 – Supplementary material for chapter 2**

Environmental Factors

*Ground Cover*

**Supplementary Table 1:** Management records for pesticides and herbicides applied in 2021 at the experimental field site located at the E.V. Smith Research center in Shorter, AL. Columns from left to right indicate: Application date, product name, target crop or pest, application rate in Liters per Hectare, and identity of applicator.

| Application Date | Product Name | Crop/Target Pest | Rate (L/ha) | Applicator |
|---|---|---|---|---|
| 4/20/2021 | Roundup | burndown rolled | 2 | Mote |
| 4/20/2021 | Liberty | rye/clover cover | 2 | Mote |
| 4/23/2021 | Valor | Pre-Plant | 0.07 | Scott |
| 4/23/2021 | surfactant | | 0.58 | Scott |
| 5/14/2021 | Direx | Pre emerge with | 1.5 | Scott |
| 5/14/2021 | Reflex | more burndown | 0.87 | Scott |
| 5/14/2021 | Roundup | | 1.75 | Scott |
| 5/14/2021 | Liberty | | 2.1 | Scott |
| 6/29/2021 | Roundup | post emerge | 2.1 | Mote |
| 6/29/2021 | Liberty | post emerge | 2.1 | Mote |
| 6/29/2021 | Dual Magnum | | 1 | Mote |
| 10/11/2021 | Boll Buster | Defoliant | 1.75 | Ruff |
| 10/11/2021 | Takedown | Defoliant | 0.44 | Ruff |
| 10/11/2021 | DFT 6 | Defoliant | 2.1 | Ruff |
| 10/11/2021 | Aim | weeds | 0.1 | Ruff |

**Supplementary Table 2:** Summary statistics for ground cover classes: Bare, Residue, and Vegetation among treatment groups

| Cover Class | Treatment | n | min | max | median | iqr | mean | sd | se | ci |
|---|---|---|---|---|---|---|---|---|---|---|
| Bare | Conservation | 324 | 0 | 94 | 10 | 12.2 | 13.5 | 11.8 | 0.653 | 1.28 |
| | Conventional | 323 | 10 | 100 | 95 | 16 | 86.9 | 18.4 | 1.02 | 2.02 |
| | Edge | 315 | 0 | 94 | 15 | 35 | 26.5 | 27.2 | 1.53 | 3.01 |
| | Reduced | 324 | 3 | 100 | 89 | 23.5 | 79.7 | 21.1 | 1.17 | 2.31 |
| Residue | Conservation | 324 | 3 | 98 | 85 | 30.5 | 70.778 | 31.225 | 1.735 | 3.413 |
| | Conventional | 324 | 0 | 80 | 3 | 10 | 8.185 | 13.269 | 0.737 | 1.45 |
| | Edge | 315 | 0 | 97 | 15 | 40 | 28.086 | 28.543 | 1.608 | 3.164 |
| | Reduced | 324 | 0 | 97 | 6 | 11.25 | 11.799 | 15.231 | 0.846 | 1.665 |
| Vegetation | Conservation | 324 | 0 | 94 | 1 | 10 | 15.682 | 26.618 | 1.479 | 2.909 |
| | Conventional | 324 | 0 | 88 | 1.5 | 5 | 4.944 | 8.747 | 0.486 | 0.956 |
| | Edge | 315 | 0 | 98 | 45 | 60 | 45.422 | 31.93 | 1.799 | 3.54 |
| | Reduced | 324 | 0 | 85 | 3 | 12 | 8.522 | 12.943 | 0.719 | 1.415 |

**Supplementary Table 3:** Results of Dunns Tests of pairwise comparisons among treatment groups for Bare Ground, Residue, and Vegetation cover.

| Cover Class | group1 | group2 | n1 | n2 | statistic | p | p.adj | p.adj.signif |
|---|---|---|---|---|---|---|---|---|
| Bare | Conservation | Conventional | 324 | 323 | 23.94 | 1.22E-126 | 7.34E-126 | **** |
| | Conservation | Edge | 324 | 315 | 3.05 | 2.29E-03 | 1.38E-02 | * |
| | Conservation | Reduced | 324 | 324 | 19.89 | 5.40E-88 | 3.24E-87 | **** |
| | Conventional | Edge | 323 | 315 | -20.72 | 2.18E-95 | 1.31E-94 | **** |
| | Conventional | Reduced | 323 | 324 | -4.07 | 4.74E-05 | 2.85E-04 | *** |
| | Edge | Reduced | 315 | 324 | 16.70 | 1.40E-62 | 8.42E-62 | **** |
| Residue | Conservation | Conventional | 324 | 324 | -23.25 | 1.46E-119 | 8.77E-119 | **** |
| | Conservation | Edge | 324 | 315 | -12.29 | 1.05E-34 | 6.32E-34 | **** |
| | Conservation | Reduced | 324 | 324 | -18.40 | 1.24E-75 | 7.45E-75 | **** |
| | Conventional | Edge | 324 | 315 | 10.80 | 3.57E-27 | 2.14E-26 | **** |
| | Conventional | Reduced | 324 | 324 | 4.85 | 1.26E-06 | 7.57E-06 | **** |
| | Edge | Reduced | 315 | 324 | -5.99 | 2.16E-09 | 1.30E-08 | **** |
| Vegetation | Conservation | Conventional | 324 | 324 | -1.64 | 1.02E-01 | 6.10E-01 | ns |
| | Conservation | Edge | 324 | 315 | 15.66 | 2.83E-55 | 1.70E-54 | **** |
| | Conservation | Reduced | 324 | 324 | 1.52 | 1.28E-01 | 7.66E-01 | ns |
| | Conventional | Edge | 324 | 315 | 17.29 | 6.06E-67 | 3.63E-66 | **** |
| | Conventional | Reduced | 324 | 324 | 3.16 | 1.58E-03 | 9.46E-03 | ** |
| | Edge | Reduced | 315 | 324 | -14.15 | 1.93E-45 | 1.16E-44 | **** |

$\chi^2_{\text{Kruskal-Wallis}}(3) = 605.12, p = 7.83e\text{-}131, \hat{\varepsilon}^2_{\text{ordinal}} = 0.47, \text{CI}_{95\%} [0.44, 1.00], n_{\text{obs}} = 1{,}287$
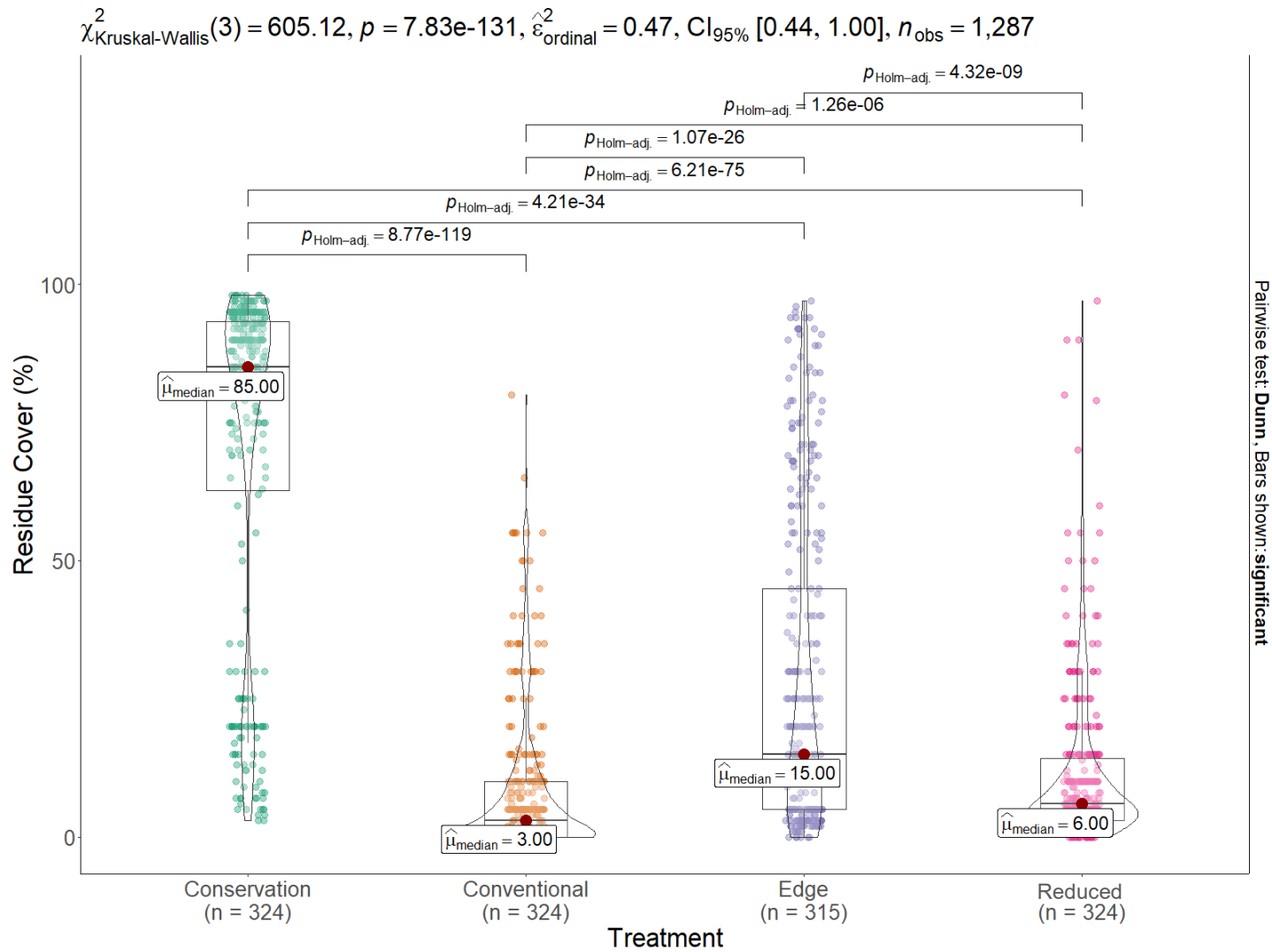
**Supplementary Figure 1:** Box and Violin plot produced with R package ggbetweenstats of Kruskal Wallis analysis of percent residue cover among experimental treatments. Percent reside cover was visually estimated following random placement of 3 - 1m$^2$ quadrats in 12 randomly selected experimental plots of each treatment group in 2021 and 2022.

$\chi^2_{\text{Kruskal-Wallis}}(3) = 852.06, p = 2.22\text{e-}184, \hat{\epsilon}^2_{\text{ordinal}} = 0.66, \text{CI}_{95\%} [0.64, 1.00], n_{\text{obs}} = 1,286$
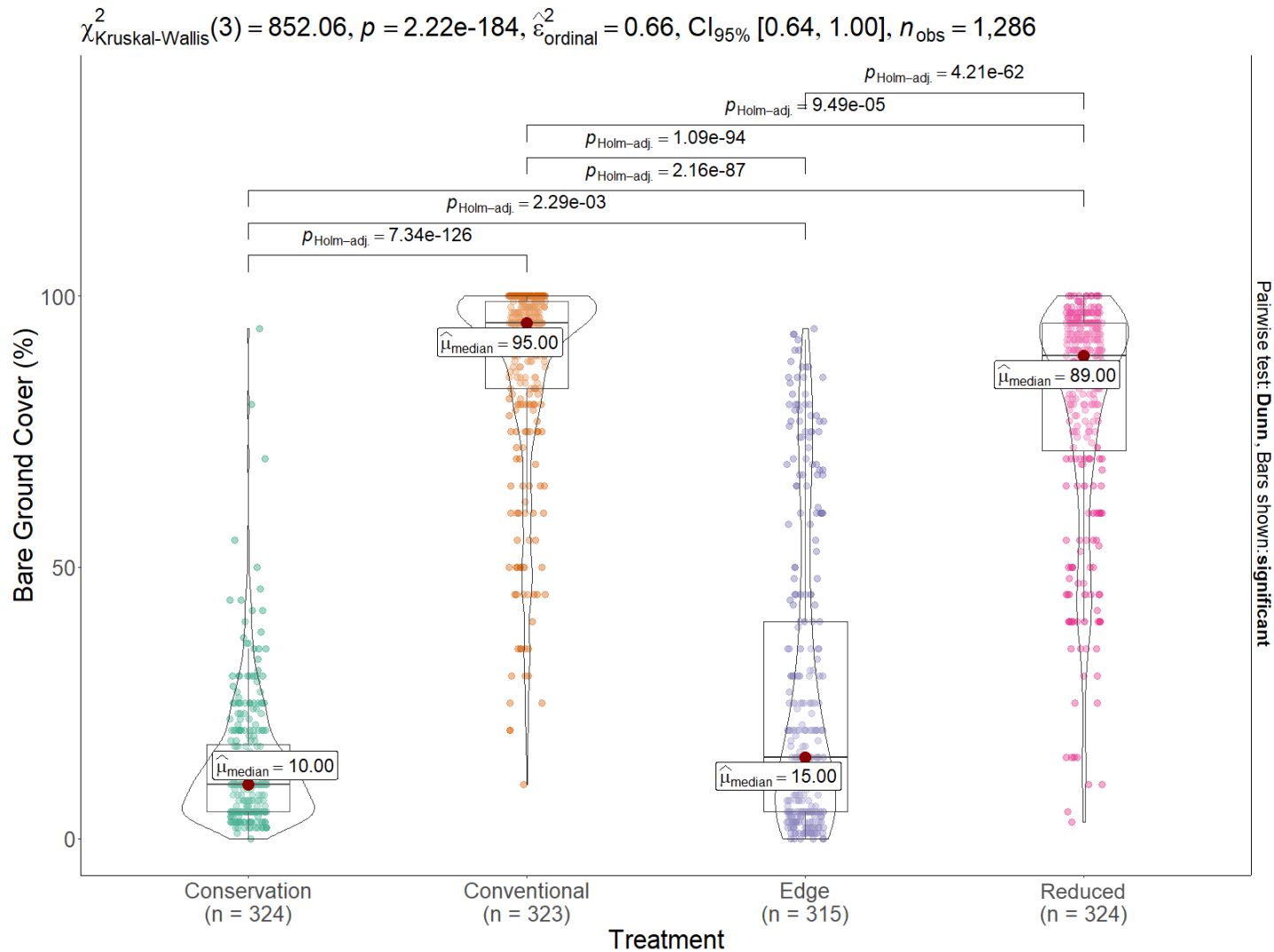
**Supplementary Figure 2:** Box and Violin plot produced with R package ggbetweenstats of Kruskal Wallis analysis of percent bare ground cover among experimental treatments. Percent bare ground cover was visually estimated following random placement of 3 - 1m$^2$ quadrats in 12 randomly selected experimental plots of each treatment group in 2021 and 2022.

$\chi^2_{\text{Kruskal-Wallis}}(3) = 377.03, p = 2.09e{-}81, \hat{\varepsilon}^2_{\text{ordinal}} = 0.29, CI_{95\%} [0.26, 1.00], n_{\text{obs}} = 1{,}287$
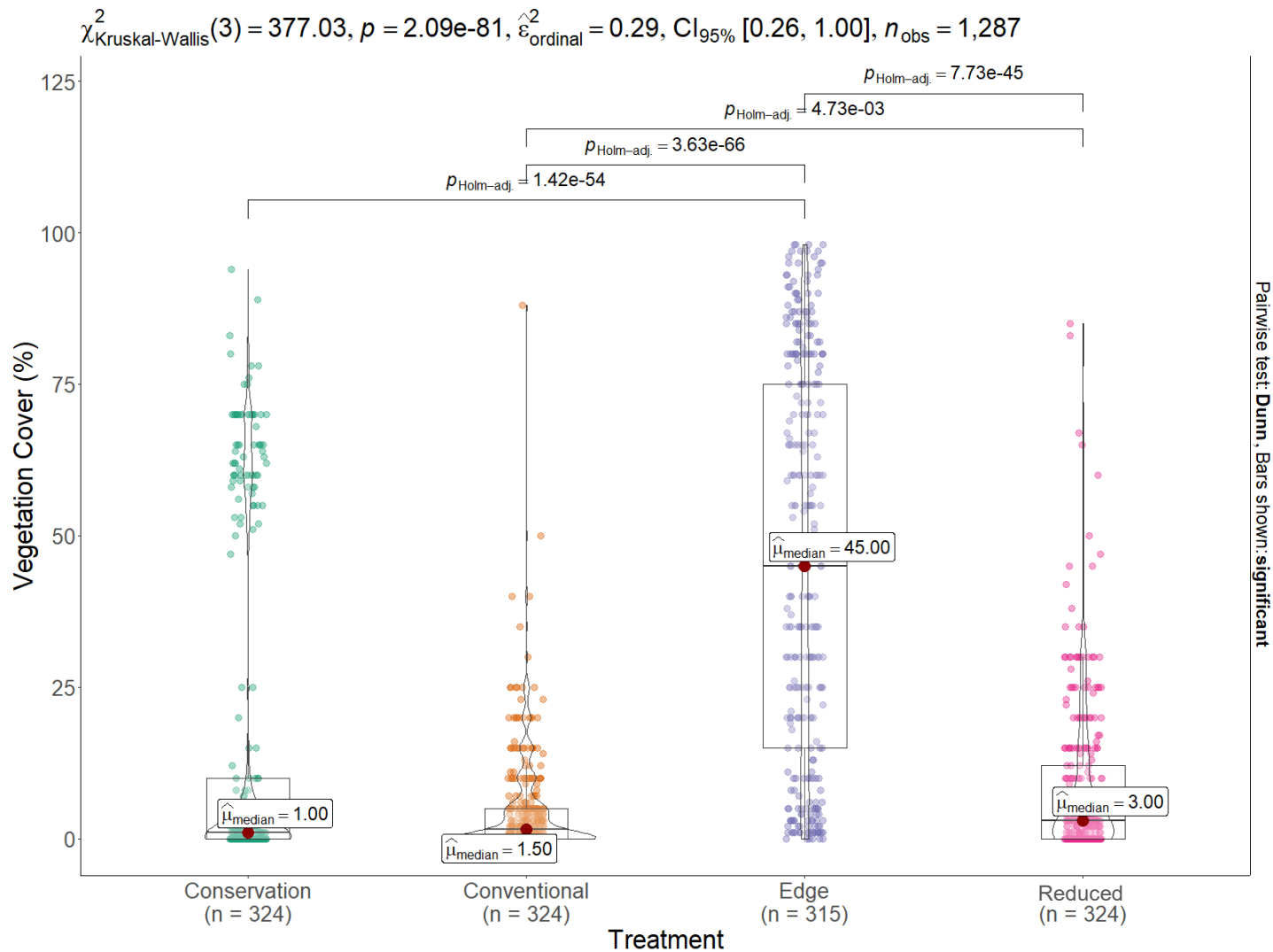
**Supplementary Figure 3:** Box and Violin plot produced with R package ggbetweenstats of Kruskal Wallis analysis of percent vegetation cover among experimental treatments. Percent vegetation cover was visually estimated following random placement of 3 - 1m² quadrats in 12 randomly selected experimental plots of each treatment group in 2021 and 2022.

*Soil Texture and Organic Matter*

**Supplementary Table 4:** Results of soil analysis report for percentages of: Organic Matter, Sand, Silt, and Clay

| Lab ID | Sample Name | % Organic Matter | % Sand | % Silt | % Clay | Soil Textural Class |
|---|---|---|---|---|---|---|
| 23.S0590 | 421E | 1.2 | 76.9 | 16.3 | 6.9 | loamy sand |
| 23.S0591 | 404E | 0.9 | 77.5 | 16.3 | 6.3 | loamy sand |
| 23.S0592 | 408E | 1.1 | 76.9 | 16.9 | 6.3 | loamy sand |
| 23.S0593 | 110W | 1.4 | 76.3 | 19.4 | 4.4 | loamy sand |
| 23.S0594 | 104W | 1.6 | 72.5 | 21.9 | 5.6 | sandy loam |
| 23.S0595 | 114W | 1.6 | 74.4 | 21.9 | 3.8 | loamy sand |
| 23.S0596 | 117S | 1.4 | 76.9 | 19.4 | 3.8 | loamy sand |
| 23.S0597 | 418S | 1.3 | 80.6 | 15.6 | 3.8 | loamy sand |
| 23.S0598 | 319S | 1.2 | 81.9 | 14.4 | 3.8 | loamy sand |
| 23.S0599 | 304N | 1 | 78.1 | 19.4 | 2.5 | loamy sand |
| 23.S0600 | 301N | 0.9 | 76.3 | 21.3 | 2.5 | loamy sand |
| 23.S0601 | 405N | 1.2 | 79.4 | 18.1 | 2.5 | loamy sand |
| 23.S0602 | 122S | 0.7 | 80.6 | 16.9 | 2.5 | loamy sand |
| 23.S0603 | 315S | 0.7 | 81.9 | 15.6 | 2.5 | loamy sand |
| 23.S0604 | 121S | 0.9 | 79.4 | 18.1 | 2.5 | loamy sand |
| 23.S0605 | 104N | 0.9 | 78.8 | 18.8 | 2.5 | loamy sand |
| 23.S0606 | 109N | 0.7 | 80.6 | 16.9 | 2.5 | loamy sand |
| 23.S0607 | 404N | 1.1 | 77.5 | 19.4 | 3.1 | loamy sand |
| 23.S0608 | 423S | 1.1 | 80 | 17.5 | 2.5 | loamy sand |
| 23.S0609 | 320S | 0.9 | 80.6 | 16.9 | 2.5 | loamy sand |
| 23.S0610 | 322S | 0.9 | 81.3 | 16.3 | 2.5 | loamy sand |
| 23.S0611 | 103N | 0.9 | 77.5 | 20 | 2.5 | loamy sand |
| 23.S0612 | 108N | 0.8 | 78.1 | 19.4 | 2.5 | loamy sand |
| 23.S0613 | 407N | 1 | 78.8 | 17.5 | 3.8 | loamy sand |

**Supplementary Table 5:** Summary descriptive statistics for percentages of organic matter, sand, silt, and clay

| | Treatment | n | min | max | median | iqr | mean | sd | se | ci |
|---|---|---|---|---|---|---|---|---|---|---|
| **Organic Matter** | Conservation | 6.00 | 0.90 | 1.40 | 1.20 | 0.23 | 1.17 | 0.19 | 0.08 | 0.20 |
| | Conventional | 6.00 | 0.70 | 1.10 | 0.80 | 0.20 | 0.83 | 0.16 | 0.07 | 0.17 |
| | Edge | 6.00 | 0.90 | 1.60 | 1.30 | 0.43 | 1.30 | 0.28 | 0.12 | 0.30 |
| | Reduced | 6.00 | 0.80 | 1.10 | 0.90 | 0.08 | 0.93 | 0.10 | 0.04 | 0.11 |
| **Sand** | Conservation | 6.00 | 76.30 | 81.90 | 78.75 | 3.10 | 78.87 | 2.17 | 0.89 | 2.28 |
| | Conventional | 6.00 | 77.50 | 81.90 | 80.00 | 1.65 | 79.80 | 1.56 | 0.64 | 1.64 |
| | Edge | 6.00 | 72.50 | 77.50 | 76.60 | 2.03 | 75.75 | 1.92 | 0.78 | 2.01 |
| | Reduced | 6.00 | 77.50 | 81.30 | 79.40 | 2.18 | 79.38 | 1.49 | 0.61 | 1.56 |
| **Silt** | Conservation | 6.00 | 14.40 | 21.30 | 18.75 | 3.18 | 18.03 | 2.59 | 1.06 | 2.72 |
| | Conventional | 6.00 | 15.60 | 19.40 | 17.50 | 1.73 | 17.62 | 1.41 | 0.58 | 1.48 |
| | Edge | 6.00 | 16.30 | 21.90 | 18.15 | 4.83 | 18.78 | 2.67 | 1.09 | 2.80 |
| | Reduced | 6.00 | 16.30 | 20.00 | 17.50 | 1.88 | 17.93 | 1.45 | 0.59 | 1.52 |
| **Clay** | Conservation | 6.00 | 2.50 | 3.80 | 3.15 | 1.30 | 3.15 | 0.71 | 0.29 | 0.75 |
| | Conventional | 6.00 | 2.50 | 3.10 | 2.50 | 0.00 | 2.60 | 0.25 | 0.10 | 0.26 |
| | Edge | 6.00 | 3.80 | 6.90 | 5.95 | 1.60 | 5.55 | 1.21 | 0.49 | 1.27 |
| | Reduced | 6.00 | 2.50 | 3.80 | 2.50 | 0.00 | 2.72 | 0.53 | 0.22 | 0.56 |

**Supplementary Table 6** Linear regression summary for percentage organic matter among treatment groups

| Treatment | Organic Matter | | Std.Error | t-value | p-value |
|---|---|---|---|---|---|
| | *Dependent variable:* | | | | |
| (Intercept) | 1.167 | *** | 0.080 | 14.660 | 3.67E-12 |
| Conventional | -0.333 | *** | 0.113 | -2.962 | 0.008 |
| Edge | 0.133 | | 0.113 | 1.185 | 0.250 |
| Reduced | -0.233 | * | 0.113 | -2.073 | 0.051 |
| | | | | | |
| **Observations** | 24 | | **F Statistic** | | 7.178*** (df = 3; 20) |
| **$R^2$** | 0.519 | | **Residual Std. Error** | | 0.1949 (df = 20) |
| **Adjusted $R^2$** | 0.446 | | **p-value** | | 0.002 |

*Note: Conservation treatment as reference category; ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

**Supplementary Table 7:** Summary of post hoc Tukey tests conducted using R package Emmeans (function emmeans, adjust = "tukey") for percentage of organic matter among treatments

| Contrast | Estimate | Std.Error | df | lower.CL | upper.CL | t.ratio | p.value | |
|---|---|---|---|---|---|---|---|---|
| Conservation - Conventional | 0.333 | 0.113 | 20 | 0.018 | 0.648 | 2.962 | 0.036 | ** |
| Conservation – Edge | -0.133 | 0.113 | 20 | -0.448 | 0.182 | -1.185 | 0.643 | |
| Conservation – Reduced | 0.233 | 0.113 | 20 | -0.082 | 0.548 | 2.073 | 0.196 | |
| Conventional – Edge | -0.467 | 0.113 | 20 | -0.782 | -0.152 | -4.146 | 0.003 | *** |
| Conventional – Reduced | -0.100 | 0.113 | 20 | -0.415 | 0.215 | -0.889 | 0.811 | |
| Edge – Reduced | 0.367 | 0.113 | 20 | 0.052 | 0.682 | 3.258 | 0.019 | ** |

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01
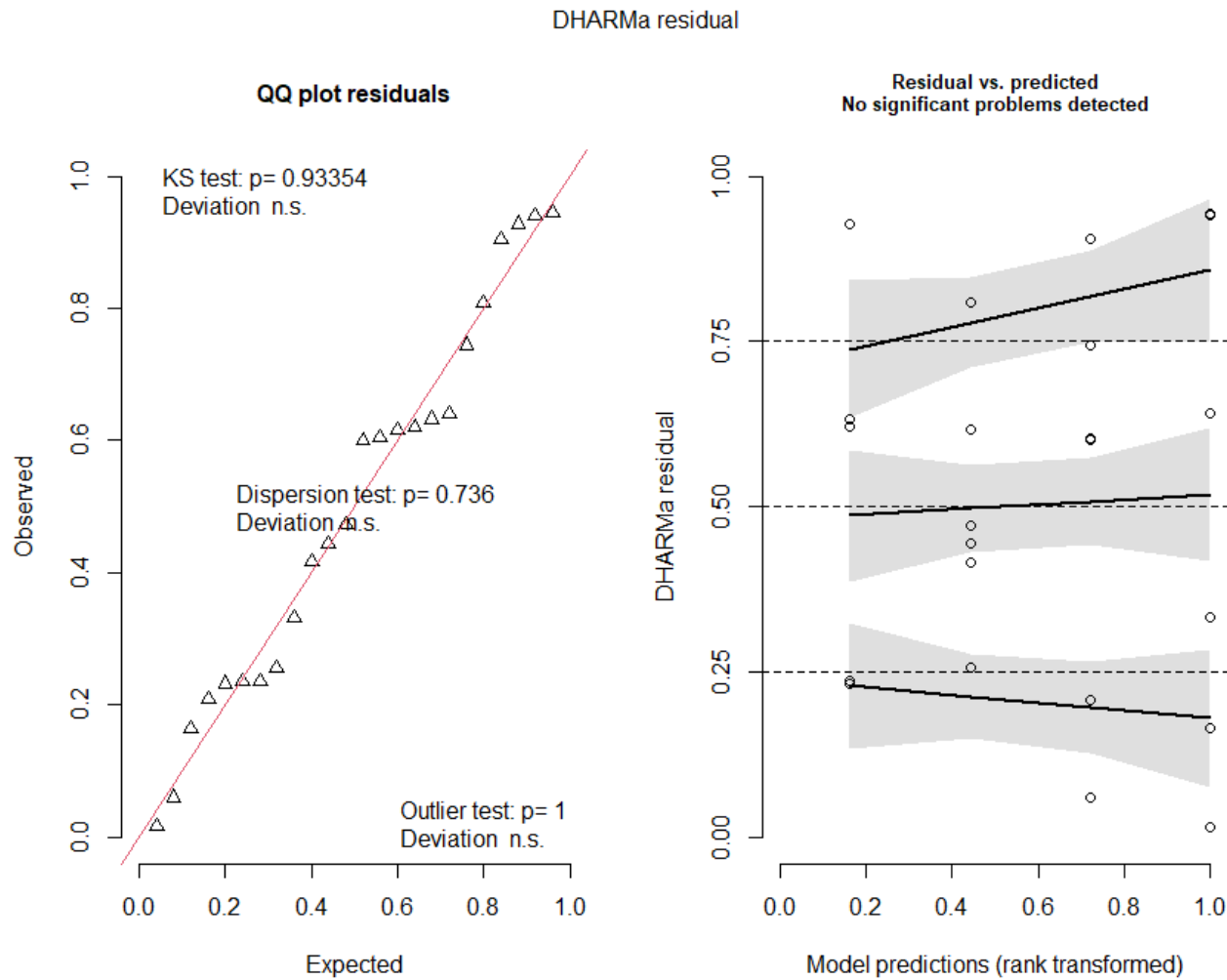
**Supplementary Figure 4:** QQ plot and Residual vs. predicted output from R package dHARMA, (function simulateResiduals) for linear model of percent organic matter among treatment groups

**Supplementary Table 8:** Linear regression summary for percentage sand among treatment groups

| Treatment | Dependent variable: Sand | | Std.Error | t-value | p-value |
|---|---|---|---|---|---|
| (Intercept) | 78.867 | *** | 0.737 | 107.046 | 4.55E-29 |
| Conventional | 0.933 | | 1.042 | 0.896 | 0.381 |
| Edge | -3.117 | *** | 1.042 | -2.991 | 0.007 |
| Reduced | 0.517 | | 1.042 | 0.496 | 0.625 |
| | | | | | |
| **Observations** | 24 | | **F Statistic** | | 6.237*** (df = 3; 20) |
| **R²** | 0.483 | | **Residual Std. Error** | | 1.805 (df = 20) |
| **Adjusted R²** | 0.406 | | **p-value** | | 0.003 |

*Note: Conservation treatment as reference category; *p<0.1; **p<0.05; ***p<0.01

**Supplementary Table 9:** Summary of post hoc Tukey tests conducted using R package Emmeans (function emmeans, adjust = "tukey") for percentage of sand among treatments

| Contrast | Estimate | Std.Error | df | lower.CL | upper.CL | t.ratio | p.value | |
|---|---|---|---|---|---|---|---|---|
| Conservation - Conventional | -0.933 | 1.042 | 20 | -3.850 | 1.983 | -0.896 | 0.807 | |
| Conservation - Edge | 3.117 | 1.042 | 20 | 0.200 | 6.033 | 2.991 | 0.034 | ** |
| Conservation - Reduced | -0.517 | 1.042 | 20 | -3.433 | 2.400 | -0.496 | 0.959 | |
| Conventional - Edge | 4.050 | 1.042 | 20 | 1.134 | 6.966 | 3.887 | 0.005 | *** |
| Conventional - Reduced | 0.417 | 1.042 | 20 | -2.500 | 3.333 | 0.400 | 0.978 | |
| Edge - Reduced | -3.633 | 1.042 | 20 | -6.550 | -0.717 | -3.487 | 0.011 | ** |

Note: *p<0.1; **p<0.05; ***p<0.01

DHARMa residual

**QQ plot residuals**

KS test: p= 0.78449
Deviation n.s.

Dispersion test: p= 0.736
Deviation n.s.

Outlier test: p= 1
Deviation n.s.

Observed

Expected

**Residual vs. predicted**
**No significant problems detected**

DHARMa residual

Model predictions (rank transformed)

**Supplementary Figure 5:** QQ plot and Residual vs. predicted output from R package dHARMA, (function simulateResiduals) for linear model of percent sand among treatment groups

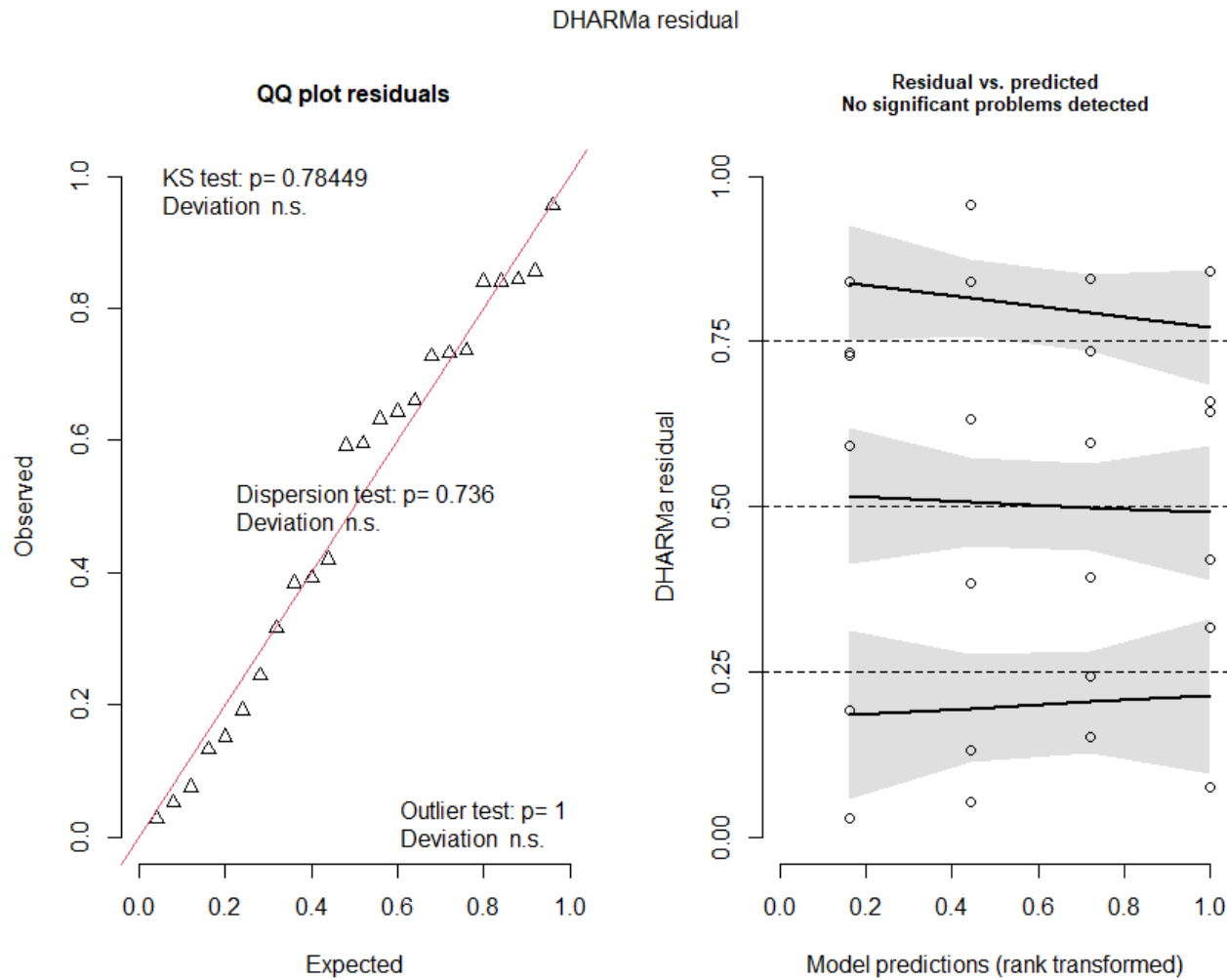**Supplementary Table 10:** Linear regression summary for percentage of clay among treatment groups

| Treatment | Clay | | std.error | t-value | p-value |
|---|---|---|---|---|---|
| | *Dependent variable:* | | | | |
| (Intercept) | 3.150 | *** | 0.311 | 10.141 | 2.50E-09 |
| Conventional | -0.550 | | 0.439 | -1.252 | 2.25E-01 |
| Edge | 2.400 | *** | 0.439 | 5.463 | 2.39E-05 |
| Reduced | -0.433 | | 0.439 | -0.986 | 3.36E-01 |
| | | | | | |
| **Observations** | 24 | | **F Statistic** | | 19.860*** (df = 3; 20) |
| **R²** | 0.749 | | **Residual Std. Error** | | 0.761 (df = 20) |
| **Adjusted R²** | 0.711 | | **p-value** | | |

*Note: Conservation treatment as reference category; *p<0.1; **p<0.05; ***p<0.01

**Supplementary Table 11:** Summary of post hoc Tukey tests conducted using R package Emmeans (function emmeans, adjust = "tukey") for percentage of clay among treatments

| Contrast | Estimate | Std.Error | df | lower.CL | upper.CL | t.ratio | p.value | |
|---|---|---|---|---|---|---|---|---|
| Conservation - Conventional | 0.550 | 0.439 | 20 | -0.680 | 1.780 | 1.252 | 0.602 | |
| Conservation - Edge | -2.400 | 0.439 | 20 | -3.630 | -1.170 | -5.463 | 1.31E-04 | *** |
| Conservation - Reduced | 0.433 | 0.439 | 20 | -0.796 | 1.663 | 0.986 | 0.759 | |
| Conventional - Edge | -2.950 | 0.439 | 20 | -4.180 | -1.720 | -6.715 | 8.71E-06 | *** |
| Conventional - Reduced | -0.117 | 0.439 | 20 | -1.346 | 1.113 | -0.266 | 0.993 | |
| Edge - Reduced | 2.833 | 0.439 | 20 | 1.604 | 4.063 | 6.450 | 1.52E-05 | *** |

Note: *p<0.1; **p<0.05; ***p<0.01
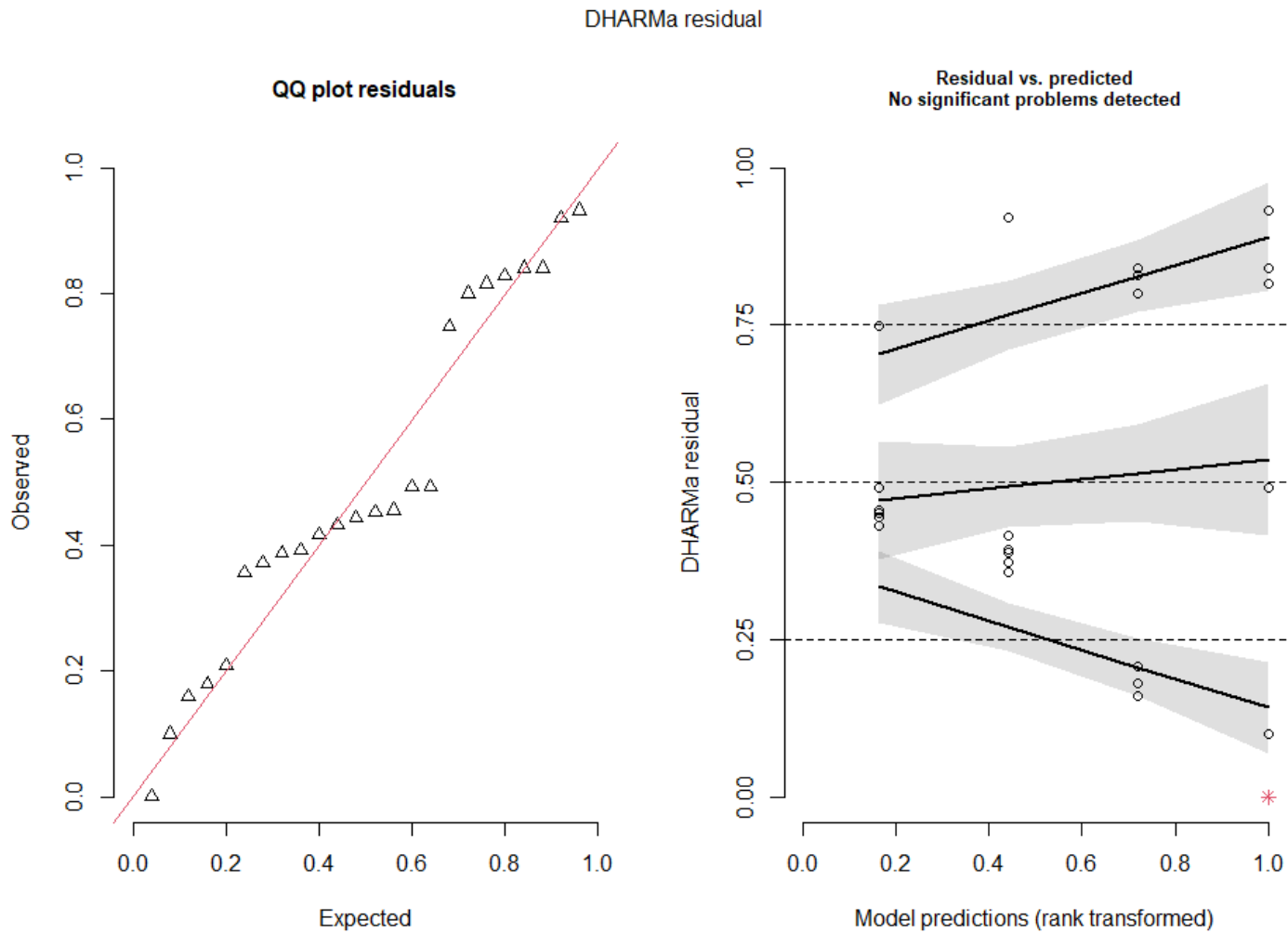
**Supplementary Figure 6:** QQ plot and Residual vs. predicted output from R package dHARMA, (function simulateResiduals) for linear model of percent clay among treatment groups

**Supplementary Table 12:** Linear regression summary for percentage of silt among treatment groups

| Treatment | Clay | | std.error | t-value | p-value |
|---|---|---|---|---|---|
| *Dependent variable:* | | | | | |
| (Intercept) | 18.033 | *** | 0.864 | 20.862 | 4.82E-15 |
| Conventional | -0.417 | | 1.222 | -0.341 | 0.737 |
| Edge | 0.750 | | 1.222 | 0.614 | 0.546 |
| Reduced | -0.100 | | 1.222 | -0.082 | 0.936 |
| | | | | | |
| **Observations** | 24 | | **F Statistic** | | 0.326 (df = 3; 20) |
| **R²** | 0.046 | | **Residual Std. Error** | | 2.117 (df = 20) |
| **Adjusted R²** | -0.096 | | **p-value** | | 0.806 |

*Note: Conservation treatment as reference category; ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

**Supplementary Table 13:** Summary of post hoc Tukey tests conducted using R package Emmeans (function emmeans, adjust = "tu*key")* for percentage of silt among treatments

| Contrast | Estimate | Std.Error | df | lower.CL | upper.CL | t.ratio | p.value |
|---|---|---|---|---|---|---|---|
| Conservation - Conventional | 0.417 | 1.222 | 20 | -3.005 | 3.838 | 0.341 | 0.986 |
| Conservation - Edge | -0.750 | 1.222 | 20 | -4.172 | 2.672 | -0.614 | 0.927 |
| Conservation - Reduced | 0.100 | 1.222 | 20 | -3.322 | 3.522 | 0.082 | 1.000 |
| Conventional - Edge | -1.167 | 1.222 | 20 | -4.588 | 2.255 | -0.954 | 0.776 |
| Conventional - Reduced | -0.317 | 1.222 | 20 | -3.738 | 3.105 | -0.259 | 0.994 |
| Edge - Reduced | 0.850 | 1.222 | 20 | -2.572 | 4.272 | 0.695 | 0.898 |

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01
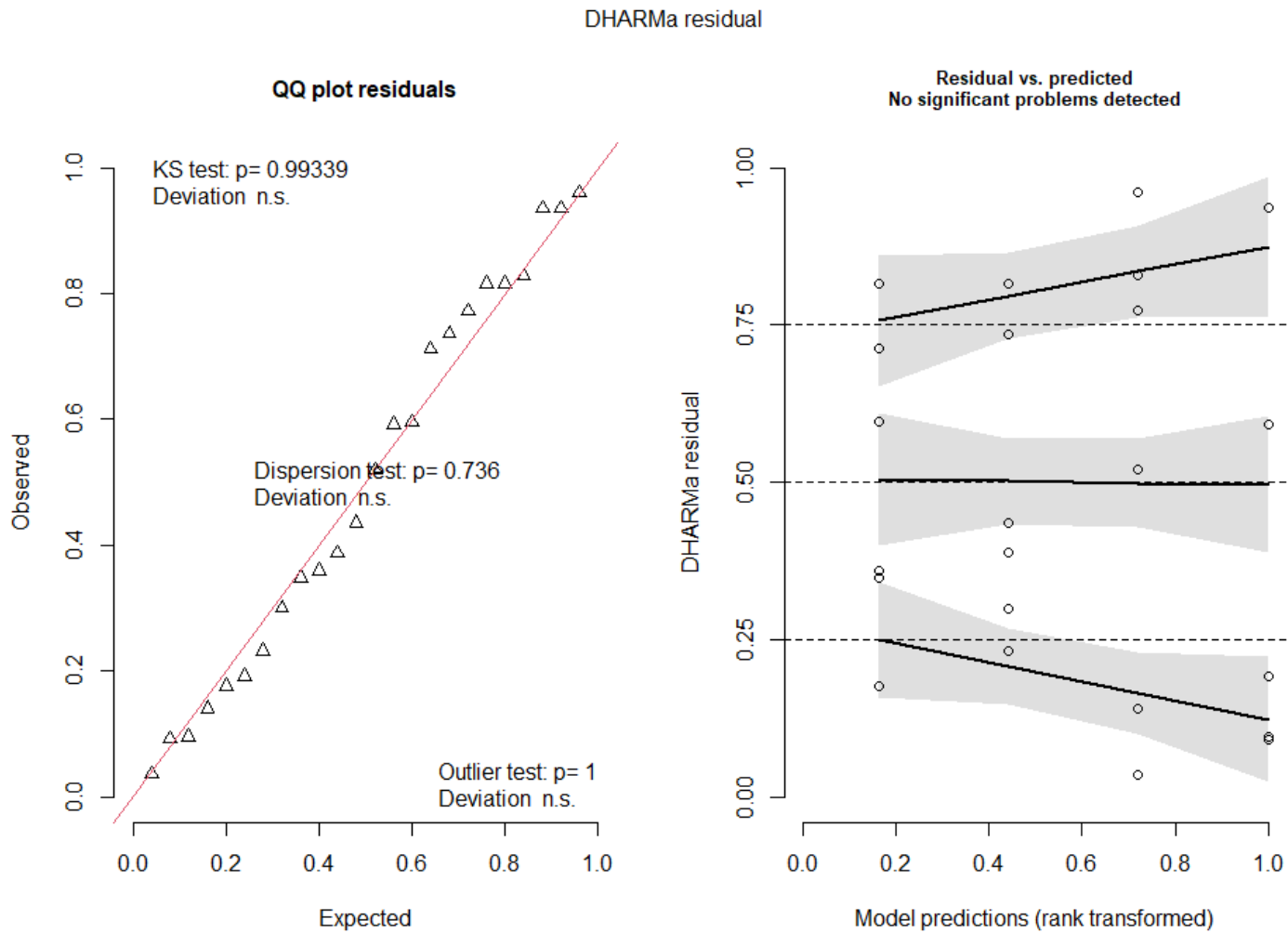
**Supplementary Figure 7:** QQ plot and Residual vs. predicted output from R package dHARMA, (function simulateResiduals) for linear model of percent silt among treatment groups

*Soil Compaction*

**Supplementary Table 14:** Linear regression summary of soil compaction for penetrometer survey conducted on 12 April 2021

| Treatment | *Dependent variable:*<br>AUC | | std.error | t-value | p-value |
|---|---|---|---|---|---|
| (Intercept) | 128.179 | *** | 13.969 | 9.176 | 1.32E-08 |
| Conventional | -0.393 | | 19.754 | -0.020 | 0.984 |
| Edge | 229.919 | *** | 19.754 | 11.639 | 2.33E-10 |
| Reduced | 6.283 | | 19.754 | 0.318 | 0.754 |
| | | | | | |
| **Observations** | 24 | | **F Statistic** | | 66.627*** (df = 3; 20) |
| **$R^2$** | 0.909 | | **Residual Std. Error** | | 34.216 (df = 20) |
| **Adjusted $R^2$** | 0.895 | | **p-value** | | 1.37E-10 |

*Note: Conservation treatment as reference category; $*p<0.1$; $**p<0.05$; $***p<0.01$

**Supplementary Table 15:** Summary of post hoc Tukey tests conducted using R package Emmeans (function emmeans, adjust = "tukey") For soil compaction (AUC) among treatment groups for penetrometer survey conducted on 12 April 2021

| Contrast | Estimate | Std.Error | df | lower.CL | upper.CL | t.ratio | p.value | |
|---|---|---|---|---|---|---|---|---|
| Conservation - Conventional | 0.393 | 19.754 | 20 | -54.898 | 55.685 | 0.020 | 1.00 | |
| Conservation - Edge | -229.919 | 19.754 | 20 | -285.211 | -174.628 | -11.639 | 1.34E-09 | *** |
| Conservation - Reduced | -6.283 | 19.754 | 20 | -61.574 | 49.009 | -0.318 | 0.989 | |
| Conventional - Edge | -230.312 | 19.754 | 20 | -285.604 | -175.021 | -11.659 | 1.30E-09 | *** |
| Conventional - Reduced | -6.676 | 19.754 | 20 | -61.967 | 48.616 | -0.338 | 0.986 | |
| Edge - Reduced | 223.637 | 19.754 | 20 | 168.345 | 278.928 | 11.321 | 2.17E-09 | *** |

Note: $*p<0.1$; $**p<0.05$; $***p<0.01$
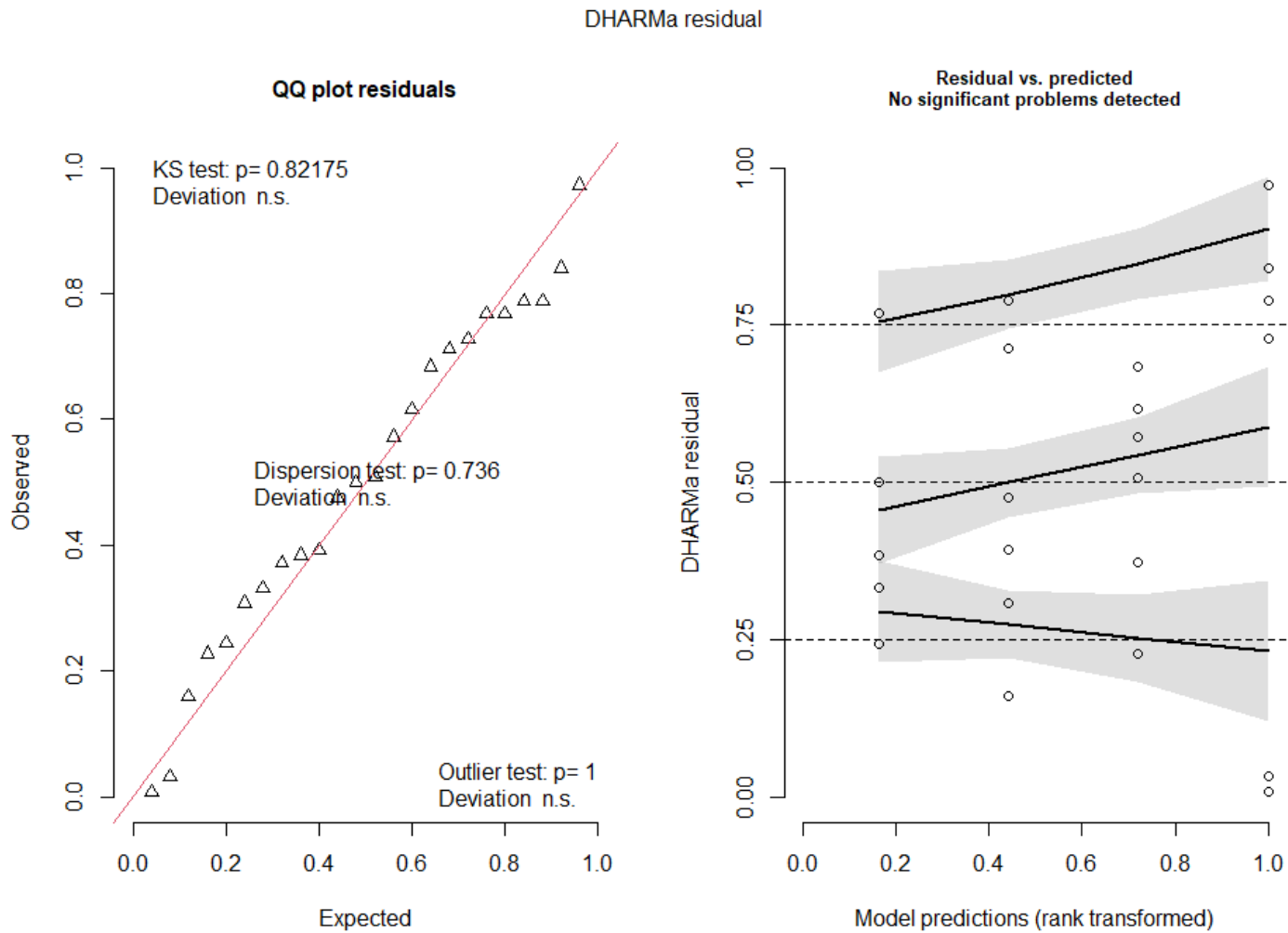
**Supplementary Figure 8:** QQ plot and Residual vs. predicted output from R package dHARMA, (function simulateResiduals) of linear model fitted for penetrometer survey conducted on 12 April 2021

**Supplementary Table 16:** Linear regression summary of soil compaction for penetrometer survey conducted on 6 June 2022

| Treatment | AUC | | std.error | t-value | p-value |
|---|---|---|---|---|---|
| | *Dependent variable:* | | | | |
| (Intercept) | 203.354 | *** | 16.631 | 12.227 | 1.89E-10 |
| Conventional | -0.773 | | 23.520 | -0.033 | 0.974 |
| Edge | 191.800 | *** | 24.668 | 7.775 | 2.55E-07 |
| Reduced | 32.017 | | 23.520 | 1.361 | 0.189 |
| **Observations** | 23 | | **F Statistic** | | 26.702*** (df = 3; 19) |
| **R²** | 0.808 | | **Residual Std. Error** | | 40.738 (df = 19) |
| **Adjusted R²** | 0.778 | | **p-value** | | 5.04E-07 |

*Note: Conservation treatment as reference category; ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

**Supplementary Table 17:** Summary of post hoc Tukey tests conducted using R package Emmeans (function emmeans, adjust = "tukey") of soil compaction (AUC) among treatment groups for penetrometer survey conducted on 6 June 2022

| Contrast | Estimate | Std.Error | df | lower.CL | upper.CL | t.ratio | p.value | |
|---|---|---|---|---|---|---|---|---|
| Conservation - Conventional | 0.773 | 23.520 | 19 | -65.362 | 66.909 | 0.033 | 1.000 | |
| Conservation - Edge | -191.800 | 24.668 | 19 | -261.163 | -122.436 | -7.775 | 1.44E-06 | *** |
| Conservation - Reduced | -32.017 | 23.520 | 19 | -98.152 | 34.119 | -1.361 | 0.537 | |
| Conventional - Edge | -192.573 | 24.668 | 19 | -261.937 | -123.210 | -7.806 | 1.35E-06 | *** |
| Conventional - Reduced | -32.790 | 23.520 | 19 | -98.925 | 33.346 | -1.394 | 0.518 | |
| Edge - Reduced | 159.783 | 24.668 | 19 | 90.420 | 229.147 | 6.477 | 1.83E-05 | *** |

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01
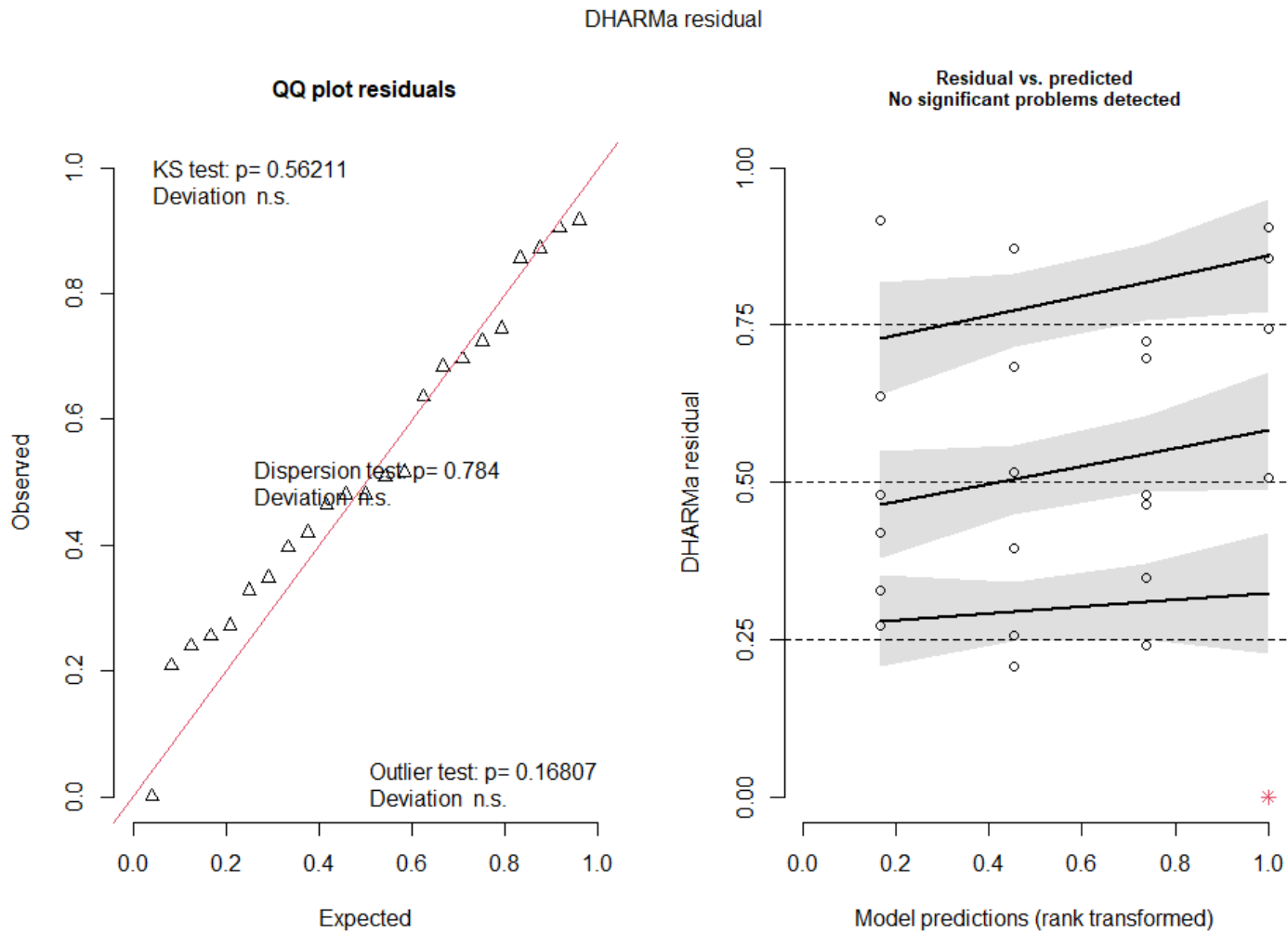
**Supplementary Figure 9:** QQ plot and Residual vs. predicted output from R package dHARMA, (function simulateResiduals) of linear model fitted for penetrometer survey conducted on 6 June 2022
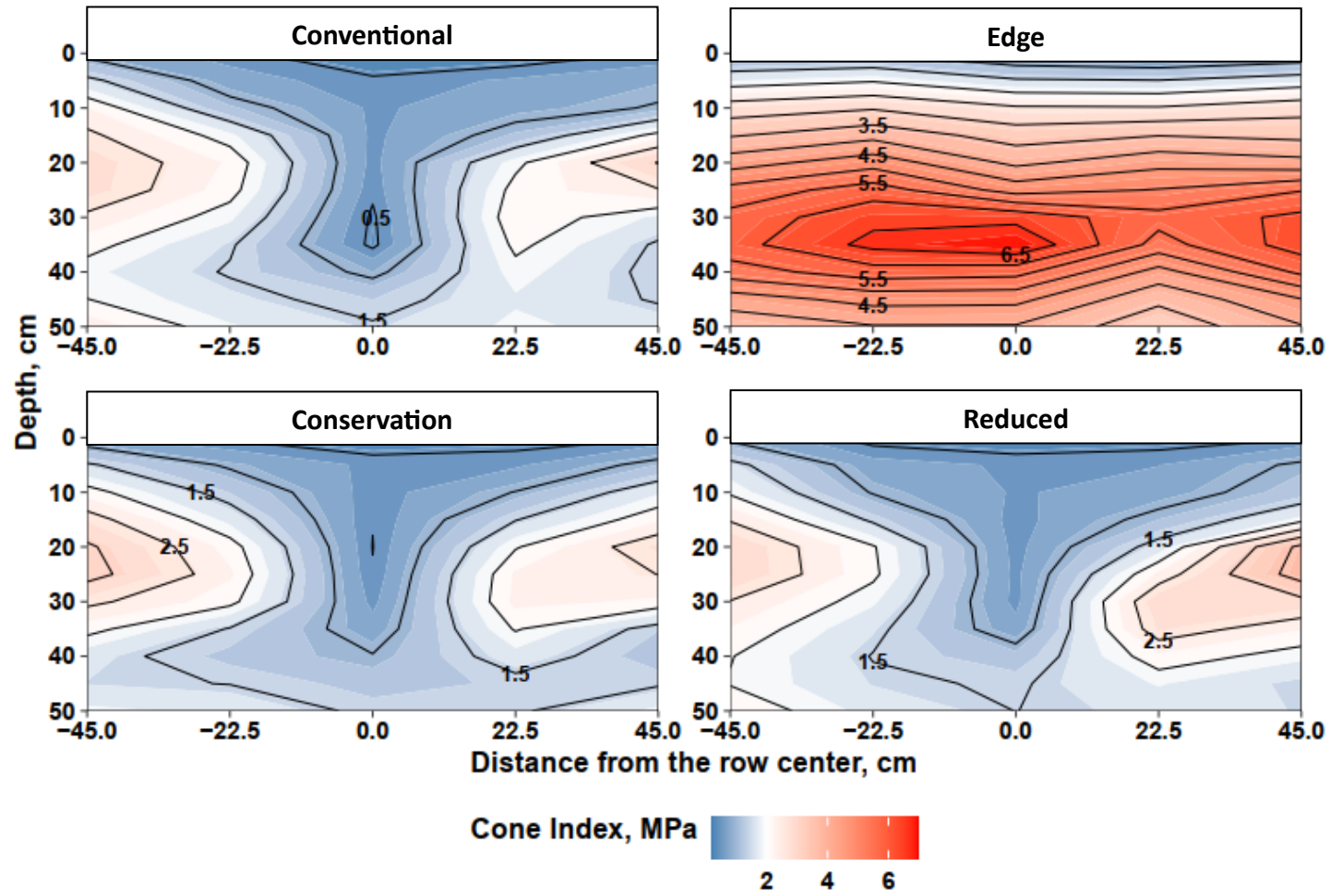
**Supplementary Figure 10:** Contour plot of soil strength among treatment groups for penetrometer survey conducted on 12 April 202. The vertical axis depicts soil probe depth and the horizontal axis corresponds to the 5 probe positions. Soil strength is depicted as a blue to red color gradient with lower levels of soil strength being blue and higher colored red.
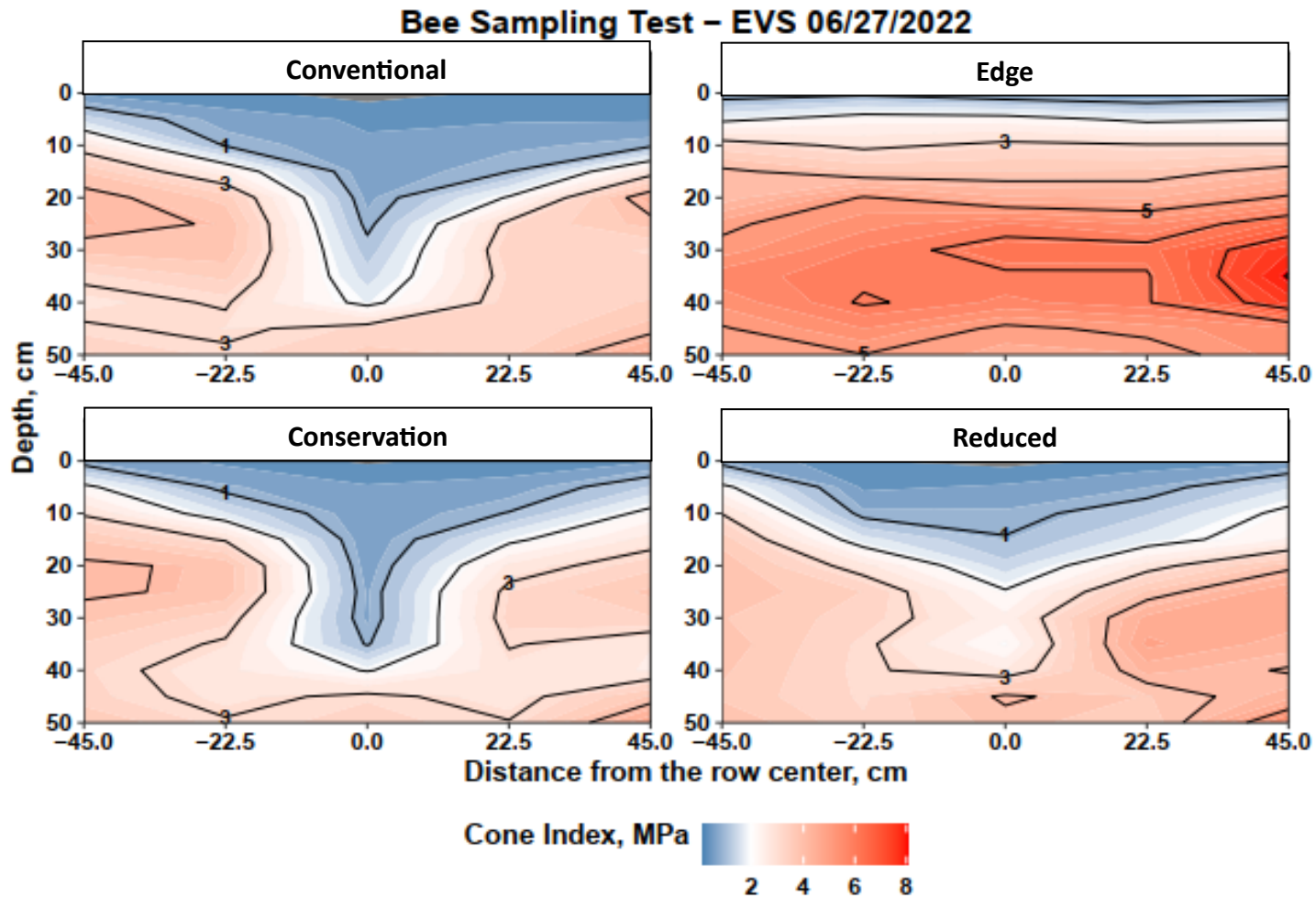
**Supplementary Figure 11:** Contour plot of soil strength among treatment groups for penetrometer survey conducted on 6 June 2022. The vertical axis depicts soil probe depth and the horizontal axis corresponds to the 5 probe positions. Soil strength is depicted as a blue to red color gradient with lower levels of soil strength being blue and higher colored red.

**Bee Sampling**

*Bee Incidence*

**Supplementary Table 18:** Summary for fitted binomial generalized linear mixed effect model of bee incidence among treatment groups, n = 48 sampling rounds

| | *Dependent variable:* | | | |
|---|---|---|---|---|
| **Treatment** | **Bee Incidence** | **std.error** | **z value** | **p-value** |
| (Intercept) | 0.395 | 0.342 | 1.155 | 0.25 |
| Conventional | -0.396 | 0.448 | -0.885 | 0.376 |
| Edge | 2.028 *** | 0.598 | 3.390 | 7.00E-04 |
| Reduced | -0.494 | 0.449 | -1.101 | 0.271 |
| | | | | |
| **Observations** | 192 | **σ²** | | 3.290 |
| **Marginal R²** | 0.208 | **df.resid** | | 187 |
| **Conditional R²** | 0.351 | | | |

*Note: Conservation treatment as reference category; ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

**Supplementary Table 19:** Summary of post hoc Tukey tests conducted using R package Emmeans (function emmeans, adjust = "tukey") for differences in bee incidence among treatments

| Contrast | Odds Ratio | Std.Error | df | lower.CL | upper.CL | t.ratio | p.value | |
|---|---|---|---|---|---|---|---|---|
| Conservation - Conventional | 1.486 | 0.665 | 187 | 0.466 | 4.739 | 0.885 | 0.813 | |
| Conservation - Edge | 0.132 | 0.079 | 187 | 0.028 | 0.621 | -3.390 | 4.70E-03 | *** |
| Conservation - Reduced | 1.639 | 0.735 | 187 | 0.512 | 5.244 | 1.101 | 0.689 | |
| Conventional - Edge | 0.089 | 0.054 | 187 | 0.018 | 0.427 | -3.992 | 5.41E-04 | *** |
| Conventional - Reduced | 1.103 | 0.489 | 187 | 0.349 | 3.483 | 0.222 | 0.996 | |
| Edge - Reduced | 12.460 | 7.606 | 187 | 2.561 | 60.633 | 4.133 | 3.13E-04 | *** |

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01
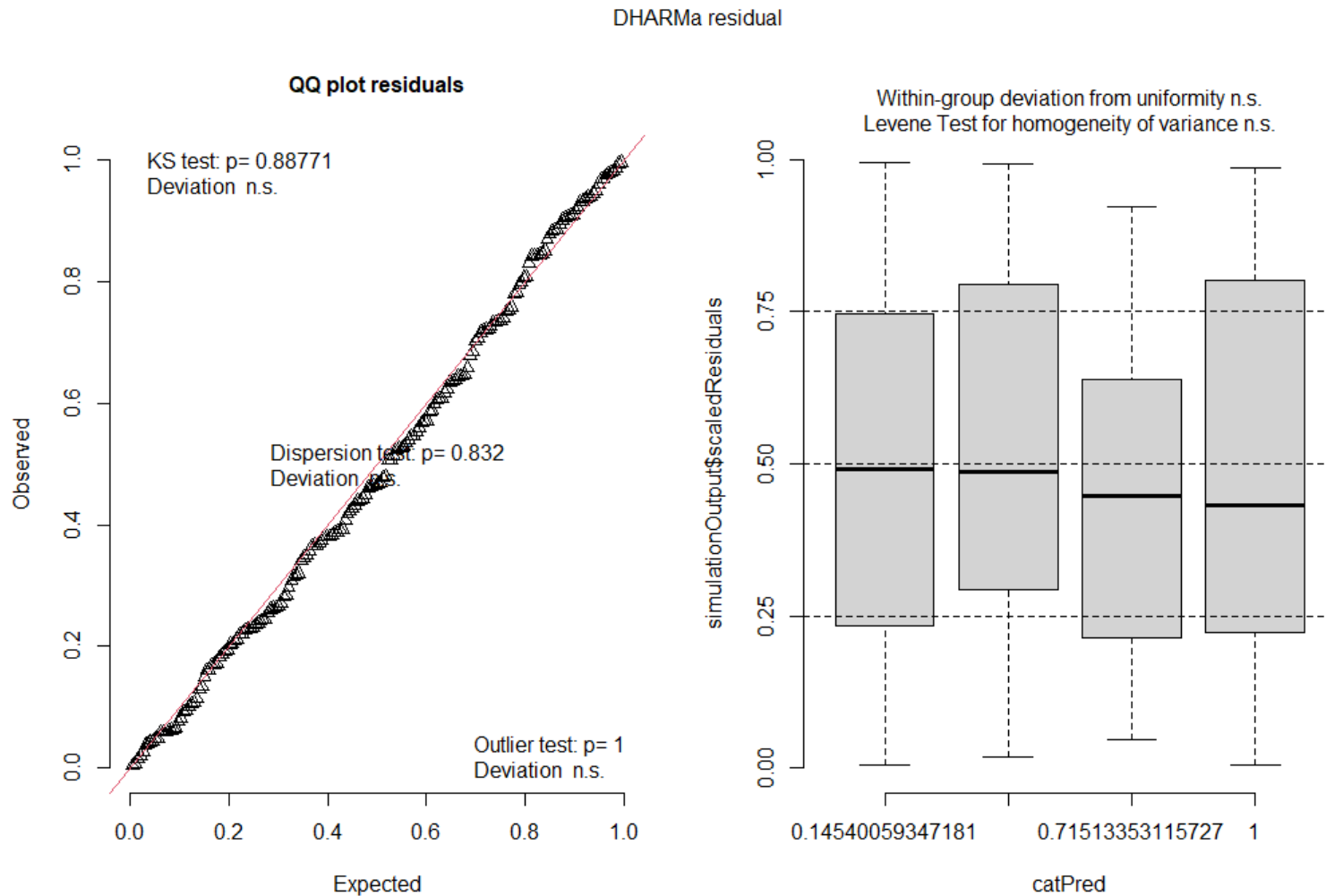
**Supplementary Figure 12:** QQ plot and Residual vs. predicted output from R package dHARMA, (function simulateResiduals) of fitted GLMER for bee incidence. Model formula: Bee Incidence ~ Treatment + (1|Round)

*Bee Abundance*

**Supplementary Table 20:** Summary for fitted negative binomial generalized linear mixed effect model of bee abundances among treatment groups, n = 48 sampling rounds

| Treatment | Bee Abundance | | std.error | z value | p-value |
|---|---|---|---|---|---|
| | *Dependent variable:* | | | | |
| (Intercept) | 0.473 | * | 0.226 | 2.096 | 0.036 |
| Conventional | -0.447 | | 0.301 | -1.490 | 0.136 |
| Edge | 1.294 | *** | 0.278 | 4.653 | 3.26E-06 |
| Reduced | -0.091 | | 0.288 | -0.315 | 0.752 |
| | | | | | |
| **Observations** | 192 | | $\sigma^2$ | | 0.960 |
| **Marginal R$^2$** | 0.267 | | df.resid | | 186 |
| **Conditional R$^2$** | 0.413 | | | | |

*Note: Conservation treatment as reference category; $*p<0.1$; $**p<0.05$; $***p<0.01$

**Supplementary Table 21:** Summary of post hoc Tukey tests conducted using R package Emmeans (function emmeans, adjust = "tukey") for differences in bee abundance among treatments

| Contrast | Ratio | Std.Error | df | lower.CL | upper.CL | t.ratio | p.value | |
|---|---|---|---|---|---|---|---|---|
| Conservation - Conventional | 1.564 | 0.469 | 186 | 0.718 | 3.404 | 1.490 | 0.446 | |
| Conservation - Edge | 0.274 | 0.076 | 186 | 0.133 | 0.564 | -4.653 | 3.65E-05 | *** |
| Conservation - Reduced | 1.095 | 0.315 | 186 | 0.520 | 2.307 | 0.315 | 0.989 | |
| Conventional - Edge | 0.175 | 0.050 | 186 | 0.084 | 0.368 | -6.088 | 3.83E-08 | *** |
| Conventional - Reduced | 0.700 | 0.210 | 186 | 0.321 | 1.526 | -1.186 | 0.636 | |
| Edge - Reduced | 3.995 | 1.115 | 186 | 1.938 | 8.236 | 4.962 | 9.30E-06 | *** |

Note: $*p<0.1$; $**p<0.05$; $***p<0.01$
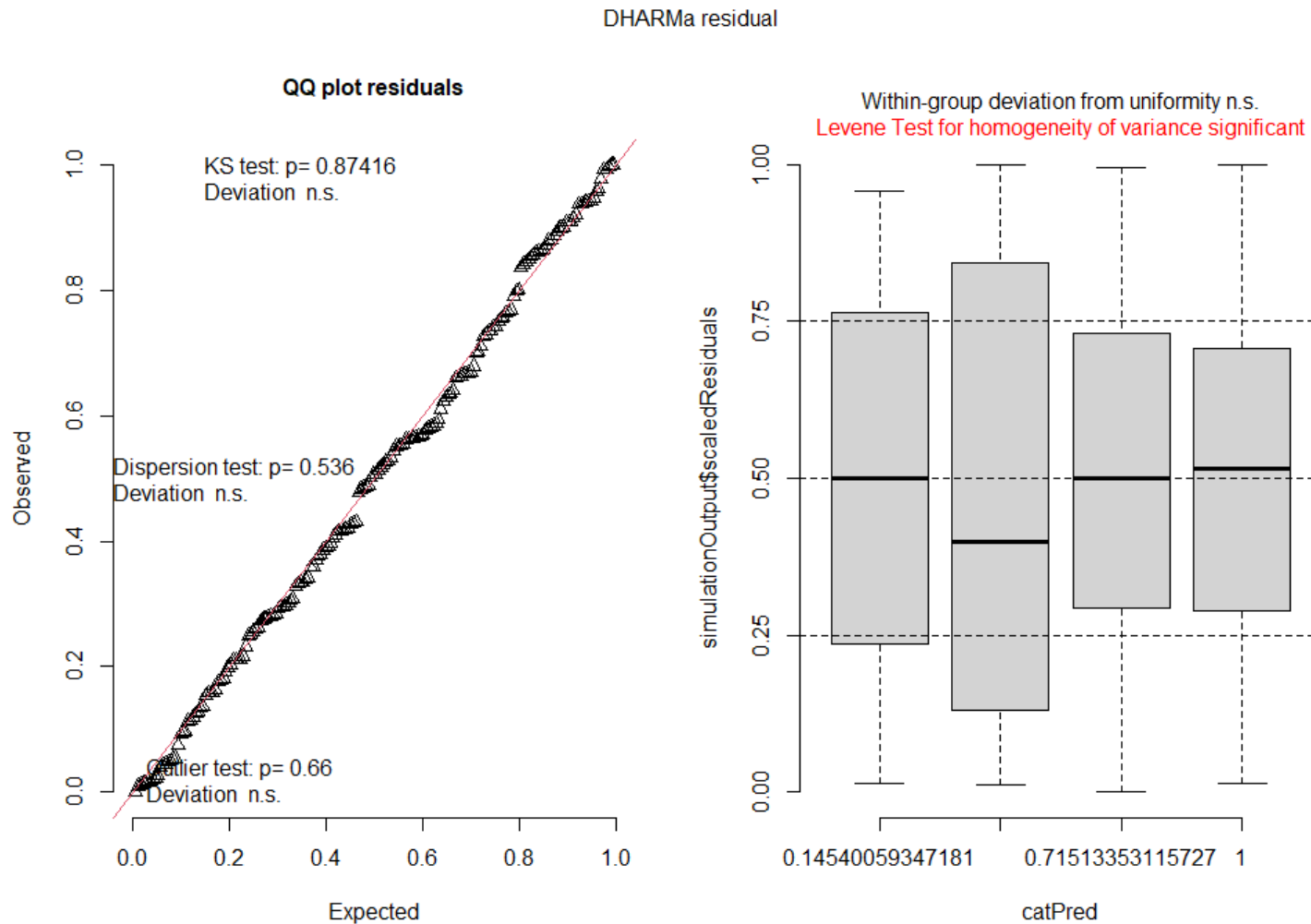
**Supplementary Figure 13**: QQ plot and Residual vs. predicted output from R package dHARMA, (function simulateResiduals) of fitted GLMER for bee abundances. Model formula: Bee Abundance ~ Treatment + (1|Round)

*Bee Diversity*

**Supplementary Table 22:** Bee taxa collected from soil emergence traps (n = 4,608) for the combined years of 2021 and 2022 among treatments

| Family | Subfamily | Tribe | Genus | Species | Edge | Conservation | Conventional | Reduced | Total Species Abundance |
|---|---|---|---|---|---|---|---|---|---|
| Andrenidae | Andreninae | Andrenini | *Andrena* Fabricius, 1775 | *krigiana* Robertson, 1901 | 1 | 0 | 0 | 0 | 1 |
| | | | | *lamelliterga* Ribble, 1968 | 1 | 0 | 0 | 0 | 1 |
| | | | | *miserabilis* Cresson, 1872 | 1 | 0 | 2 | 4 | 7 |
| Apidae | Apinae | Bobbini | *Bombus* Latreille, 1802 | *impatiens* Cresson 1863 | 2 | 0 | 1 | 0 | 3 |
| | | | | *pensylvanicus* (De Geer, 1773) | 0 | 2 | 0 | 0 | 2 |
| Apidae | Apinae | Eucerini | *Melissodes* Latreille, 1829 | *bimaculatus* (Lepeletier, 1825) | 0 | 1 | 0 | 1 | 2 |
| | | | | *communis* Cresson, 1878 | 0 | 1 | 1 | 1 | 3 |
| Apidae | Nomadinae | Nomadini | *Nomada* Scopoli, 1770 | *sp.1* | 0 | 0 | 1 | 0 | 1 |
| | | | | *sp.2* | 1 | 0 | 0 | 0 | 1 |
| Halictidae | Halictinae | Augochlorini | *Augochlora* Smith, 1853 | *pura* (Say, 1837) | 1 | 0 | 0 | 0 | 1 |
| Halictidae | Halictinae | Augochlorini | *Augochlorella* Sandhouse, 1937 | *aurata* (Smith, 1853) | 5 | 0 | 0 | 1 | 6 |
| | | | | *gratiosa* (Smith, 1853) | 1 | 0 | 0 | 0 | 1 |
| Halictidae | Halictinae | Halictini | *Agapostemon* Guerin-Meneville, 1844 | *splendens* (Lepeletier, 1841) | 2 | 1 | 8 | 11 | 22 |
| | | | *Lasioglossum* Curtis, 1833 | *bruneri* (Crawford, 1902) | 2 | 0 | 0 | 0 | 2 |
| | | | | *callidum* (Sandhouse, 1924) | 7 | 0 | 0 | 0 | 7 |
| | | | | *coreopsis* (Robertson, 1902) | 3 | 0 | 0 | 1 | 4 |
| | | | | *creberrimum* (Smith, 1853) | 0 | 0 | 1 | 0 | 1 |
| | | | | *fattigi* (Mitchell, 1960) | 1 | 0 | 0 | 0 | 1 |
| | | | | *floridanum* (Robertson, 1892) | 0 | 0 | 0 | 2 | 2 |
| | | | | *illinoense* (Robertson, 1892) | 41 | 0 | 1 | 1 | 43 |
| | | | | *imitatum* (Smith, 1853) | 65 | 0 | 0 | 1 | 66 |
| | | | | *longifrons* (Baker, 1906) | 1 | 0 | 0 | 2 | 3 |
| | | | | *pectorale* (Smith, 1853) | 1 | 0 | 0 | 0 | 1 |
| | | | | *pilosum* (Smith, 1853) | 2 | 0 | 2 | 1 | 5 |
| | | | | *pruinosum* (Robertson, 1892) | 4 | 2 | 0 | 1 | 7 |
| | | | | *quebecense* (Crawford, 1907) | 0 | 1 | 0 | 0 | 1 |
| | | | | *subviridatum* (Cockerell, 1938) | 7 | 0 | 0 | 0 | 7 |
| | | | | *tamiamense* (Mitchell, 1960) | 0 | 0 | 0 | 1 | 1 |
| | | | | *tegulare/puteulanum* | 108 | 69 | 37 | 48 | 262 |
| | | | | *trigeminum* Gibbs, 2011 | 16 | 0 | 0 | 0 | 16 |
| | | | | *apopkense* (Robertson, 1892) | 3 | 0 | 0 | 0 | 3 |
| | | | Sphecodes Latreille, 1804 | *sp.1* | 30 | 11 | 0 | 4 | 45 |
| Megachilida | Megachilina | Megachilini | Coelioxys Latreille, 1809 | *sayi* Robertson, 1897 | 0 | 1 | 0 | 0 | 1 |
| | | | | **Total bee Abundance** | 306 | 89 | 54 | 80 | 529 |
| | | | | **Species Richness** | 24 | 9 | 9 | 15 | 33 |

**Supplementary Table 23:** Summary of basic diversity statistics among treatments, package iNEXT (function $DataInfo). Displaying sample size of bees collected among treatments (n), as well as observed species richness, sample coverage and the frequencies of the first 10 species.

| Assemblage | n | Observed Species Richness | Sample Coverage | First 10 species frequencies: | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | f1 | f2 | f3 | f4 | f5 | f6 | f7 | f8 | f9 | f10 |
| Edge | 306 | 24 | 0.971 | 9 | 4 | 2 | 1 | 1 | 0 | 2 | 0 | 0 | 0 |
| Conservation | 90 | 9 | 0.934 | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Conventional | 54 | 9 | 0.909 | 5 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Reduced | 80 | 15 | 0.888 | 9 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |

**Supplementary Table 24:** Sample-coverage-based estimates of bee assemblage diversity among treatments for ENS Shannon (q = 1), and ENS Simpson (q = 2) at sample coverage equal to 0.88, package iNEXT (function estimateD). Assemblage indicates treatment group, SC = selected Sample coverage. For Hill Shannon and Hill Simpson the column qD displays the estimated effective number of species, with qd.LCL and qd.UCL indicating the lower and upper 95% confidence limits.

| Assemblage | SC | Richness (q = 0) | | | Hill Shannon (q = 1) | | | Hill Simpson (q = 2) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | qD | qD.LCL | qD.UCL | qD | qD.LCL | qD.UCL | qD | qD.LCL | qD.UCL |
| Edge | 0.88 | 10.082 | 7.849 | 12.315 | 6.013 | 5.250 | 6.776 | 4.501 | 3.837 | 5.164 |
| Conservation | 0.88 | 3.366 | 0.274 | 6.459 | 1.933 | 1.165 | 2.702 | 1.550 | 1.277 | 1.823 |
| Conventional | 0.88 | 7.637 | 0.000 | 16.071 | 2.970 | 1.556 | 4.383 | 1.993 | 1.454 | 2.532 |
| Reduced | 0.88 | 15.334 | 0.000 | 33.367 | 4.619 | 2.176 | 7.063 | 2.577 | 1.795 | 3.359 |
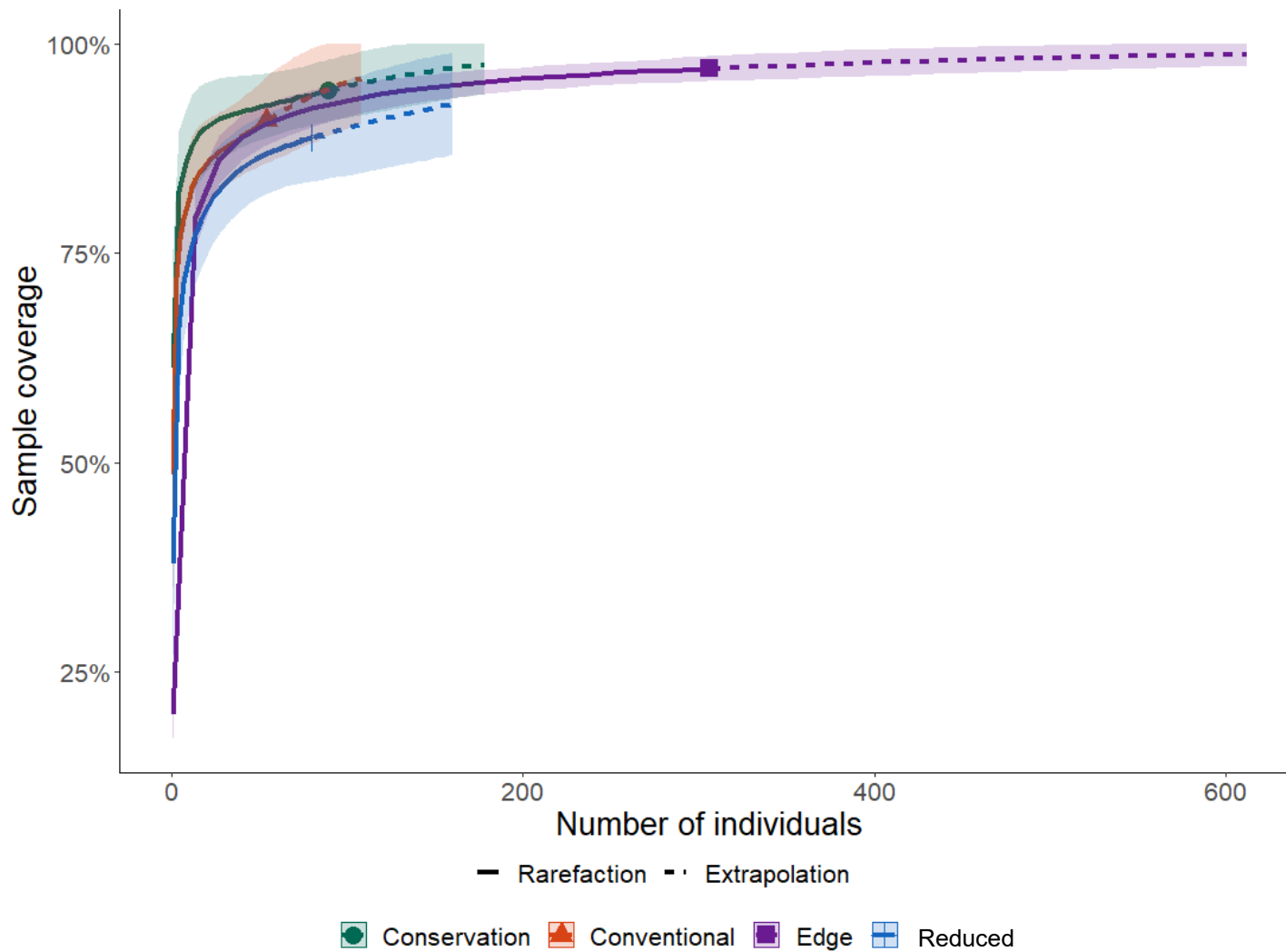
**Supplementary Figure 14:** Sampling completeness curves of bee assemblages among treatments, created in package iNEXT, (function gginext, type = 2).
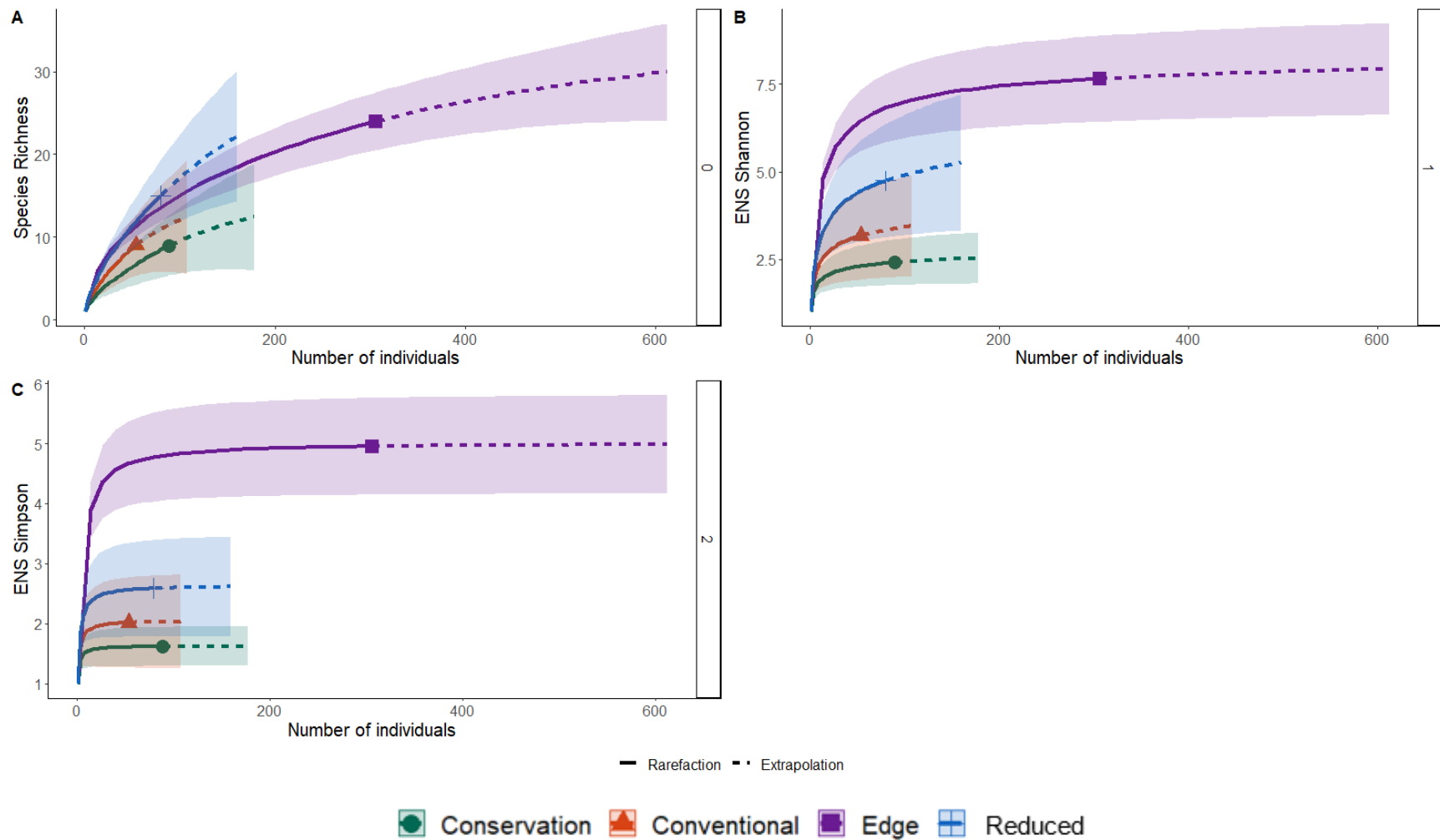
**Supplementary Figure 15:** Sample-size-based rarefaction and extrapolation curves for estimates of bee diversity among treatments along with 95% CI for: **A)** Species richness q = 0, **B)** Hill Shannon q = 1, **C)** Hill Simpson q = 2. Created with package iNEXT, (function ggiNEXT, q = 0, 1, 2, type = 1).
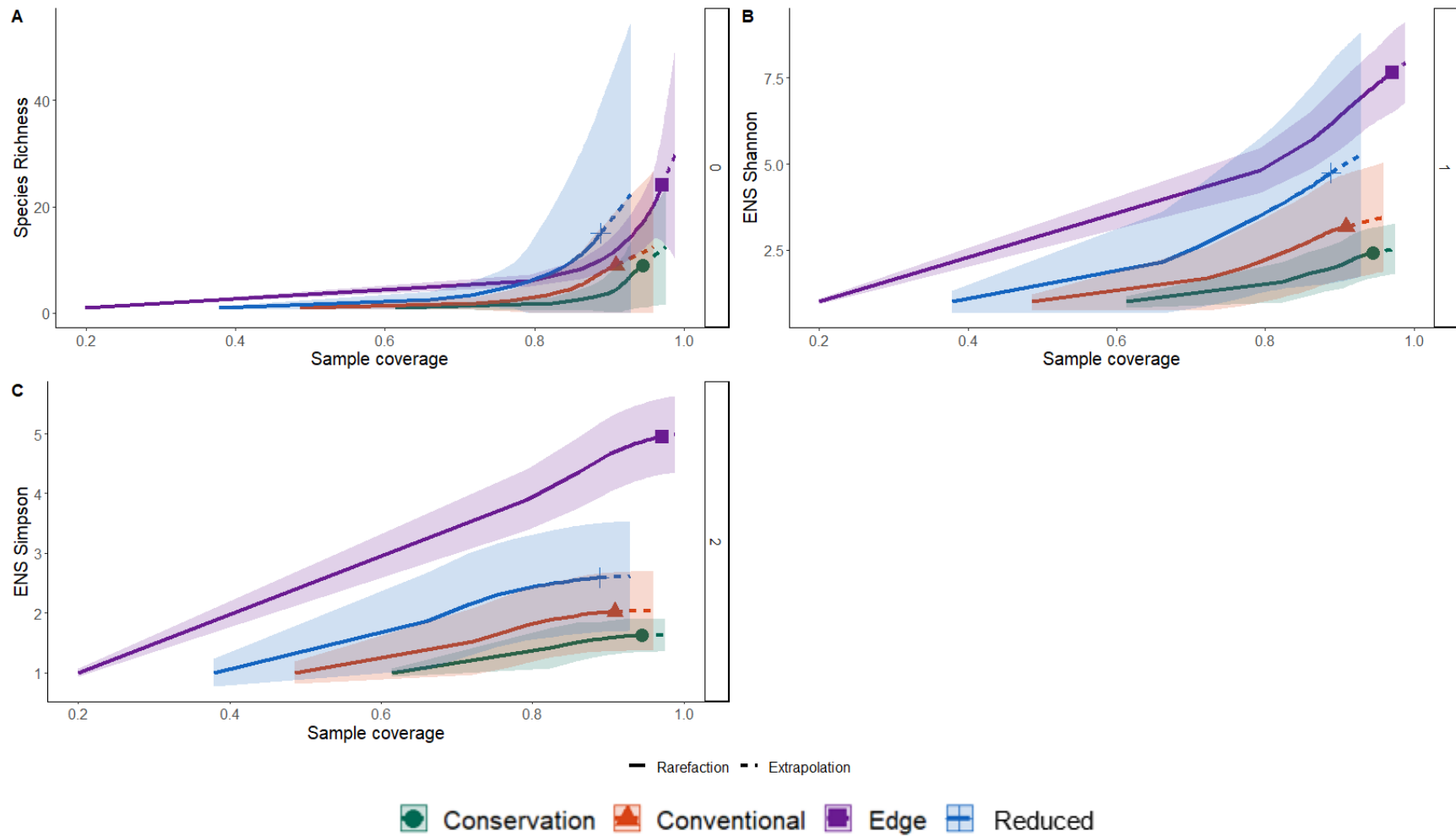
**Supplementary Figure 16:** Sample-coverage -based rarefaction and extrapolation curves for estimates of bee diversity among treatments along with 95% CI for: **A)** Species richness q = 0, **B)** Hill Shannon q = 1, **C)** Hill Simpson q = 2. Created with package iNEXT, (function ggiNEXT, q = 0, 1, 2, type = 3).