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INTRODUCING MANAGED HONEY BEE HIVES INTO NATURAL FYNBOS OF SOUTH AFRICA: EFFECTS ON POLLINATORS AND THEIR DEPENDANT PLANTS

by

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Declaration

I, Robyn Morton, declare that the contents of this dissertation/thesis represent my own unaided work, and that the dissertation/thesis has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

14/04/23

Signed **Date**

Abstract

Honey bees (*Apis mellifera*) are economically important managed pollinators for the agricultural industry. Their use is widespread across the world, however, they are only native to Africa and parts of Europe and Asia. In the Cape Floristic Region (CFR) of South Africa, an indigenous honey bee subspecies, *Apis mellifera capensis* (Cape honey bee) is used for agricultural pollination services. Agricultural crops are used as forage for bees in spring, eucalyptus trees in summer, and natural vegetation is required throughout the winter months. However, honey bees' presence in natural areas in high densities could lead to negative impacts on unmanaged pollinators and their dependent plants, but scientific evidence in support of these actions is largely lacking in the South African context. My objectives in this thesis were to determine the effect of introducing managed honey bee hives (MHBH) on pollination networks, flower visitation rates, community composition of pollinators, insect diversity and abundance, and plant reproduction. To examine these effects, two different study sites were sampled under different conditions. Chapter two investigates these effects with the controlled introduction of 10 MHBH during winter while in chapter three these effects are investigated through the uncontrolled dumping of up to 400 MHBH during summer. There were no other known MHBH within a 3 km radius of the MHBH introduced in this study. For both chapters, data were collected through pollinator flower visit observations and pan traps from four plots within 1 km of MHBH. For chapter two, data was collected for 10 days with no MHBH present (*before hives*) and then for 10 days after MHBH were introduced (*during hives*). In both chapters, increased honey bee hive density increased honey bees flower visitation rate while density of dipteran species decreased, pollination networks were dominated by honey bees and community composition became significantly more homogenous. Abundance of Hymenoptera and flower visitation rates did not decrease due to MHBH introductions. Coleoptera abundance increased significantly in plots where honey bees did not increase significantly. Floral composition and distribution in the landscape affected how honey bees were distributed, with bees showing a preference for generalist Asteraceae flowers. Seed set of *Cullumia reticulata* (Asteraceae) was not affected by the introduction of MHBH. In both instances of the study, where in one case the MHBH introductions were controlled and the other not controlled, some insect groups were affected more than others. Hymenoptera were seemingly unaffected, Diptera was affected and Coleoptera showed some avoidance of areas of high honey bee abundance. Ultimately, the availability of floral resource (type and abundance) will affect how honey bees congregate in the landscape. Even though these findings do have some limitations,

they will contribute towards conservation and management plans for protected areas, where such data is currently lacking, to guide the decision-making process.

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Glossary

Acronyms/Abbreviations

CFR	Cape Floristic Region
MHBH	Managed honey bee hives
Emmeans	Estimated marginal means
GLM	Generalized linear model
ha	Hectare
km	Kilometre
m	Metre
m^2	Square metre
^{o}C	Degrees Celsius

Chapter 1: General introduction

Honey bees (*Apis mellifera*) are generalist pollinators and are the most popular managed pollinators used for pollination services in agriculture (Klein *et al*. 2007). To ensure that honey bee colonies provide effective pollination services, the landscapes that the colonies are placed in need to have adequate forage quantity and diversity to maintain the health and vitality of the honey bees (Alaux *et al*. 2010; Dolezal *et al*. 2019). However, the honey bee is not solely responsible for all pollination services (Rader *et al*. 2016), as different unmanaged pollinators also contribute to pollination in agriculture (Carvalheiro *et al*. 2010; Garibaldi *et al*. 2013). These unmanaged pollinators include beetles, flies, butterflies, moths, and bees other than *Apis mellifera* (Kendall and Solomon 1973; Klein *et al*. 2007). However, the demand for managed honey bee hives (MHBH) in agriculture is increasing, while unmanaged pollinators are declining (Steffan-Dewenter *et al*. 2005; Ellis *et al*. 2020; Osterman *et al*. 2021). Having a diversity of unmanaged pollinators can greatly increase pollination of crops, however, the decline of unmanaged pollinators can also be linked to agricultural practices, namely monocultures, pesticide use and habitat destruction (Steffan-Dewenter *et al*. 2005; Eeraerts *et al*. 2019; Ellis *et al*. 2020). In landscape matrixes where the majority of the land is used for agriculture, and with little natural vegetation, there is a lower abundance and diversity of unmanaged pollinators (Ricketts *et al*. 2008; Newbold *et al*. 2015; Orford *et al*. 2016). In these landscapes, crops are largely dependent on MHBH brought in by beekeepers for pollination (Morse and Calderone 2000).

Honey bees occur naturally in the continent of Africa and parts of Europe and Asia. In other parts of the world, they are considered non-native. Some countries are experiencing a decline in the number of MHBH (Potts *et al*. 2010; VanEngelsdorp *et al*. 2010) even though the number of MHBH is increasing globally (Aizen and Harder 2009). At the same time, the number of crops that rely on animal pollination is increasing five times faster than the growth in the number of MHBH (Aizen and Harder 2009; Aizen *et al*. 2019). As such, the pollination shortfall for pollinator dependent crops is on the increase. In fact, 75% of agricultural crops benefit from pollination by animals, of which the majority is provided by honey bees (Klein *et al*. 2007). The impacts on agricultural production from pollination shortfalls are still limited but are increasing (Aizen *et al*. 2008).

Insect pollinator species are declining worldwide, mainly due to human mediated activities (Potts *et al*. 2010). This may adversely affect plant biodiversity through a loss of pollinator species abundance and richness (Burkle *et al*. 2013). Factors contributing towards the decline of pollinators include habitat loss, habitat fragmentation (Haddad *et al*. 2015), invasive alien species, pesticides, pollution, disease, lack of nutrition and climate change (Vanbergen 2013; Goulson *et al*. 2015). These factors may also have a synergistic effect e.g., pesticides can make pollinators more susceptible to disease, while climate change can exacerbate disease frequency (Goulson *et al*. 2015). These factors could lead to changes in pollinator assemblages. However, there are other factors that can cause changes in pollinator assemblages, which may result in changes among interacting species in pollination networks (Fontaine *et al*. 2005). One of the important factors that could affect species assemblages and co-occurrence of interacting species is the intentional or incidental introductions of alien/non-native pollinator species into the pollination network particularly when these are highly abundant.

The introduction of managed honey bees into areas in which they do not naturally occur can have a negative effect on native pollinators through various forms of competition (Paini *et al*. 2005; Badano and Vergara 2011; Hung *et al*. 2019; Angelella *et al*. 2021). One type of competition is interference competition, which constitutes physical aggressive behaviours (Wojcik *et al*. 2018). Introduced managed honey bees can have aggressive interactions with native insect pollinators, which results in lower flower visitation rates for native bees (Dunpont *et al*. 2004; Pinkus-Rendon *et al*. 2005; Iwasaki and Hogendoorn 2022). The most common form of competition is exploitative competition, where there is competition through resource use (Wojcik *et al*. 2018). This occurs when honey bees reduce floral resources such as nectar and pollen (Mallick and Driessen 2009), as they are known for collecting a large portion of the available pollen and nectar from flowers (Dupont *et al*. 2004). Honey bees are often the dominant pollinator species in a landscape where they are introduced. The dominance of honey bees can force other pollinators to change their behaviour, possibly changing the species on which they forage and the time at which they do so (Magrach *et al*. 2017). This competition becomes more prevalent when resources are limited, for example, in winter when there are fewer plant species flowering (Paini 2004). Negative effects of this competition on native pollinators could include higher energy expenditure on foraging (time and distance to find resources not depleted by honey bees), which may result in unmanaged pollinator having a loss of fitness, reduced body sizes, and lower reproductive successes (Zurbuchen *et al*. 2010).

Introducing non-native managed honey bees could transform the pollinator community and in turn plant species composition (Kenis *et al*. 2009) since honey bees could outcompete native pollinators while not being effective pollinators of native plants thereby reducing native plants seed set. This may then either positively or negatively impact native pollinators. A positive change could entail increasing the abundance of plant species preferred by native pollinators (Wojcik *et al*. 2018). In addition, honey bees are generalist pollinators (Klein *et al*. 2007) and they can sometimes effectively replace pollinators in regions where a native pollinator has gone extinct (Aslan *et al*. 2016). A negative effect could entail honey bees preferring alien invasive plants, thus increasing the abundance of such plants and causing local extinctions of native plants. This may still have further negative consequences in the form of a loss of native pollinators once their dependent plants have disappeared (Abe *et al*. 2011). In this instance, specialist plants could be more at risk of extinction than generalist plant species (Schweiger *et al*. 2010). Generalist plants have floral traits that are aimed at attracting a wide variety of pollinators, while specialists have traits that only attract one, or a small number of pollinator species (Johnson and Steiner 2000). Specialists are more sensitive to environmental changes that can cause population declines and extinctions (Biesmeijer *et al*. 2006; Sekercioglu 2011).

In South Africa where honey bees are native, the introduction of MHBH to new areas is facilitated by beekeepers moving hives to different areas at a certain time of the year to access forage (Masehela 2017). However, beekeepers in the Western Cape Province are prohibited from transporting their Cape honey bee colonies across the Capensis line, which is a line across the southern region of South Africa that indicates the natural range of the Cape honey bee. This is to prevent the Cape honey bee, (*Apis mellifera capensis*) – which is endemic to the Cape floristic region (CFR) – from parasitizing hives of the African honey bee (*Apis melifera scutellate*) which is present in the rest of South Africa and the African continent (Neumann and Hepburn 2002). Cape honey bee workers are able to invade hives of African honey bees, where the Cape worker bee is able to reproduce, which can then cause the colony of African honey bees to collapse (Dietemann *et al*. 2006).

The Western Cape agricultural industry has a high demand for pollination services and there are concerns over sufficient access to forage for MHBH (Masehela 2017). Beekeepers in the Western Cape will periodically move their hives to different sites to follow the seasonal fluctuations of flowering times (Melin *et al*. 2014). These movements are still confined to the "capensis line/border", while beekeepers in other provinces do not face similar restrictions

(Hepburn *et al*.1998; Dietemann *et al*. 2007). Therefore, this already restricts movement, and the type of forage beekeepers can access and utilise within the Western Cape province. Beekeepers forage options are further restricted from being excluded from national parks and nature reserves (collectively recognised as protected areas) as a precautionary measure (SANparks 2022). Beekeepers generally use crops as forage in spring, eucalyptus trees during summer, and fynbos all year round to varying degrees, but fynbos forage is most important during winter (Naug, 2009; Melin *et al*. 2018). In the absence of access to natural vegetation, forage alternatives for MHBH are limited and may compromise the nutritional requirements (and persistence) of the hives during winter (Scofield and Mattila 2015). MHBH that come out of the winter months in poor condition, due to a lack of good nutrition, are not ideal for pollination services. As a result, this escalates the pollination deficit in the agricultural sector. Consequently, this may increase pressure to allow MHBH into protected areas for access to natural vegetation.

Managed honey bees are essential pollinators for the Western Cape agricultural industry (Allsopp and Cherry 2004; Melin *et al.* 2014). The pollination services rendered by bee pollination in the Western Cape is estimated to be valued at R 1 295.7 million for the fruit industry (Turpie *et al*. 2003). Furthermore, the fruit industry has an annual turnover of more than R13 billion and creates over 180 000 job opportunities (Hortgro 2016). The beekeeping industry in the Western Cape consists of 114 512 registered MHBH managed by 1 699 registered beekeepers (DALRRD 2023). Records from two decades ago (2004) show that the industry generated approximately R24 million per annum from honey production and pollination services (Allsopp and Cherry 2004). The availability of fynbos as forage for honey bees directly contributes to honey production, but more importantly a healthy, diverse functioning fynbos ecosystem is indirectly beneficial to the agricultural industry through supporting MHBH used for pollination services (Veldtman 2018).

Publications from outside the African continent suggest that MHBH be excluded from nature reserves where they are alien, to protect other insect pollinators and rare plants (Shavit *et al.* 2009; Valido *et al*. 2019). This is because of the negative impacts that introduced hives of alien honey bees have on native pollinators (Pinkus-Rendon *et al.* 2005; Badano and Vergara 2011; Angelella *et al.* 2021). However, negative impacts have also been recorded in areas in which honey bees are native, but where the numbers are artificially inflated through beekeeping (Hudewenz and Klein 2013; Elbgami *et al*. 2014; Lindström *et al*. 2016; Ropars *et al*. 2022).

From a South African perspective, where honey bees are native, there is almost no research on the16etworts that MHBH have on other pollinators in natural vegetation (but see Brand, 2009; Geerts and Pauw 2011). Although MHBH have been excluded from protected areas (CapeNature2016; SANPparks 2022), MHBH are often placed on reserve boundaries by beekeepers, and the bees fly across the fence boundary to access the protected area (Masehela 2019).

Honey bees in hives are considered by some to be domesticated insects, adding little value to biodiversity within protected areas, and that they may pose several threats to the non-managed pollinators. The common perceived threats include floral resource depletion, resource competition (Mallick and Driessen 2009), rewiring pollination networks (Magrach *et al*. 2017) spreading diseases to other pollinators (Manley *et al*. 2015), reduced pollination success of flowering plant species (Valido *et al*. 2019), reducing the flower visitation rates of other pollinators (Hudewenz and Klein 2013) and reducing the abundance of other pollinators (Ropars *et al*. 2020). This is despite the fact that in South Africa, honey bees may move between being managed (the hive) and wild nesting populations due to trapping by beekeepers to either replenish their lost stocks or when they abscond from managed hives to nest in the surrounding habitat/landscape (Mouton 2011; Masehela 2017). In essence, a swarm of honey bees may be managed today (in the hive) and be back in the wild population the next day – vice versa, and this has been an open system within the South African context when it comes to both indigenous honey bee subspecies and their interaction within the environment.

It is therefore important to investigate the potential impacts that MHBH have on other pollinators in their native range so that there is scientific information available to guide conservation and management decisions.

1.1. Statement of research problem

Managed Cape honey bee hives have been excluded from national parks and nature reserves in the Western Cape province as a precautionary measure to prevent negative impacts on other pollinators. Even so, there are limited scientific data, findings and information documenting and illustrating any of the perceived negative effects that managed Cape honey bee hives have on unmanaged pollinators or on the fruit and seed set of pollinator dependent native plant species. At the same time, there is a continuous increase in demand for honey bee forage. The availability of natural forage is reducing due to habitat destruction for urban and agricultural expansion, this leaves the majority of the forage is within protected areas. It is therefore crucial to determine the impacts of managed Cape honey bee hives on pollinator communities to better support decision making in addressing the protection of biodiversity.

1.2. Aim

In this thesis I aim to quantify the effect of introduced managed Cape honey bee hives – native managed honey bees – on insect pollinators in natural areas. For this, I consider their effects on other pollinators (chapter 2) as well as effects on the reproduction of their dependent plants (chapter 2). I also consider how the ‘dumping’ of hundreds of beehives for short periods into fynbos vegetation influences pollinators (chapter 3).

1.3. Thesis outline

This thesis consists of four chapters, of which two are data chapters. The thesis outline is presented as follows:

- **Chapter 1**: The introduction, provides general background information regarding the research topic, including the aims and research problem.
- **Chapter 2**: Explores the effects that the introduction of 10 managed Cape honey bee hives has on unmanaged pollinators and their dependent plants in natural vegetation. The chapter takes an experimental approach on interactions before MHBH are introduced, and during the MHBH introduction.
- **Chapter 3**: This chapter is a case study assessing how short-term, high-density MHBH dumping in natural vegetation affects unmanaged pollinators. This was an uncontrolled observation where a beekeeper was introducing/removing his beehives to the study area in waves after pollination services were provided.
- **Chapter 4**: Key findings of this study are discussed, along with the study limitations, areas where further research could be pursued and recommendations.

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Chapter 2: To bee chased away: mixed effects of managed native honey bees on pollinator communities in indigenous vegetation of the Cape Floristic Region.

Abstract

Apis mellifera is the most important pollinator in agriculture but has negative impacts on native pollinators in the alien range. High *Apis mellifera* numbers, through beekeeping, can potentially impact on pollinators in its native range, such as South Africa. Surprisingly, this has received very little attention, despite most agricultural crops requiring honey bee pollination. Here I explored the effect of introducing indigenous managed honey bee hives (MHBH) on floral visitation, pollination networks, community composition of floral visitors, and the insect diversity and abundance in close proximity to MHBH in natural areas in the Cape Floristic Region of South Africa. Baseline pollinator data was collected prior to bee hive introduction, thus enabling a rigorous *before hive-during hive* experimental design. Pollinator observations (n = 528 10-minute sampling periods) were conducted in 100 m^2 treatment plots at 20 m, 70 m, 450 m and 960 m away from introduced MHBH. Pan traps were used to evaluate the effects on pollinating and non-pollinating insects. Honey bee numbers increased significantly, and their flower visitation rate increased for the *during hives* treatment. Flower visits for Coleoptera, Hymenoptera and Thysanoptera also increased for the *during hives* treatment, likely due to the onset of spring. Diptera's flower visits decreased by 45%. There was a significant increase for Coleoptera abundance *during hives* in the furthest plots from MHBH. Pollinator networks were significantly more modular *before hives*. Community composition for pollinators and other insects were both significantly more homogenous in the *during hives* treatment. Honey bees dominated the system once introduced; this increase in abundance did have an impact on some pollinator groups. Affected pollinators could have been displaced due to increased competition, whilst pollinators that were not displaced may be unable to do so or there is no niche overlap with honey bees. However, whether the introduction of MHBH affects the long-term health and survival of pollinators and the health and functioning of plant communities remains to be tested.

2.1. Introduction

Pollinators are under pressure from invasive alien species, pesticides, pollution, disease, lack of nutrition, climate change, habitat fragmentation and habitat destruction (Steffan-Dewenter *et al*. 2005; Geerts 2011; Goulson *et al*. 2015; Geerts 2016; Harvey *et al*. 2020; Adedoja *et al*. 2021; Mnisi *et al*. 2021; Duffy *et al*. 2022). In recent years, uncontrolled and too frequent fires in most parts of the world have also added to diminishing floral resources and desired habitats, as natural areas continue to decline and be fragmented (Tulloch *et al*. 2016; Hauber *et al.* 2022). These factors contribute to the global decline of insect pollinator populations (Potts *et al*. 2010). Even in protected areas, insect pollinators have experienced declines, with studies in Denmark and Germany finding an 80% reduction in insect abundance over just a 20-year period (Hallmann *et al*. 2017, Møller 2019). Pesticide use and other intensive agricultural practices are believed to be the main drivers of these declines in agricultural dominated landscapes (Benton *et al*. 2002). Exposure to pesticides has been shown to alter the foraging ability of insects, making them less efficient (Gill and Raine 2014: Stanley and Raine 2016). Additionally, pesticide exposure can alter floral preferences, which in turn, can impair immune system function, leading to increased susceptibility to diseases (Sánchez-Bayo *et al*. 2016). These factors will not only affect the pollinators, but also their dependent plants.

There are pollinators from a variety of classes however insect pollinators are the most prominent. Insect pollinators are essential for yield and quality of crops, with 75% of crops globally reliant on pollinators to some extent (Klein, *et al.* 2007). Pollinators are not only responsible for food quantity but are also linked to human health and wellness since many crops that rely on pollinators are sources of essential vitamins and micronutrients (Ellis *et al*. 2015). Much of the world’s population depend on plant-based medicines to contribute to their healthcare (Bodeker *et al*. 2005), and most of these plants benefit from pollination. Pollinators also contribute towards healthy and functional ecosystems (Fisher and Turner 2008), which in turn provide essential ecosystem services such as carbon sequestering (Kumar *et al.* 2006), contributing to the water cycle (Schlesinger and Jasechko 2014) and air purification (Janhäll 2015).

Honey bees are globally the most widely used managed pollinator for agricultural crop pollination services (Aizen and Harder 2009; IPBES 2016; Osterman *et al.* 2021). The native range of honey bees (*Apis mellifera*) spans across Africa and parts of Europe and Asia, whilst in the rest of the world they are introduced (Requier *et al.* 2019). Honey bees are generalist pollinators and can be managed in large numbers and moved around easily; and are therefore ideal for the provision of pollination services of various crops (Klein *et al*. 2007). Honey bees are the most important managed pollinator, and it is therefore not surprising that the number of MHBH is increasing globally (Aizen *et al*. 2019; Osterman *et al*. 2021). Agricultural land is also increasing, and with almost a third of agricultural land being planted with pollinator dependent crops, the demand for honey bees keeps increasing (Aizen *et al*. 2019; IPBES 2016). Most agricultural land consists of monoculture crops, which makes it less supportive of resident wild pollinators (Aizen *et al*. 2019), but also for managed honey bees (Dolezal *et al*. 2019). With the increasing demand on pollination services provided by MHBH in these intensive agricultural landscapes (Aizen *et al*. 2009), forage from natural vegetation is vital for improving the health and productivity of MHBH before and after providing pollination services (Dolezal *et al*. 2019).

Studies have shown that in parts of the world (Americas, Australasia) in which honey bees are alien, they have a negative impact on native pollinators (Pinkus-Rendon *et al.* 2005; Badano and Vergara 2011; Angelella *et al.* 2021; Pritchard *et al.* 2021). The introduction of MHBH reduces the diversity and abundance of native insect pollinators in these systems (Badano and Vergara 2011). Honey bees do this by displacing native bees from floral resources (Pinkus-Rendon *et al*. 2005) via resource competition or aggressive physical interactions (Gross and Mackay, 1998; Magrach *et al*. 2017). The introduction of MHBH can also lead to a decrease in interactions within pollination networks whereby networks become more homogenous (Valido *et al*. 2019). Proximity and interaction to MHBH can also increase the risk of viruses for closely related pollinators (Pritchard *et al*. 2021).

An influx of honey bees has been shown to have negative impacts on other pollinators, even in parts of the world where honey bees are native (Hudewenz and Klein 2013; Elbgami *et al*. 2014; Henry and Rodet 2018). The introduction of MHBH to natural vegetation is known to increase the abundance of honey bees far beyond natural levels, reducing flower visitation rate of unmanaged bees and reducing wild bee diversity (Hudewenz and Klein 2013; Weekers *et al*. 2021). Introducing MHBH has also been shown to reduce the number of bird pollinators (Geerts and Pauw 2011). Beekeeping inflates honey bee density far above natural levels by providing nest sites in the form of bee boxes, whereas unmanaged honey bee populations have smaller colonies and are more sparsely distributed in natural areas due to limited suitable nesting sites (Melin *et al*. 2018). In contrast, Brand (2009a) found no negative effect on native insects where honey bees are native, aside from honey bee numbers being artificially inflated through beekeeping.

There are several impacts associated with the influx of MHBH in the surrounding natural landscape. Potential impacts can extend far from a hive, since honey bees can travel up to 10 km in search of forage (Levin *et al*. 1960) but if there are abundant floral resources surrounding the hives, they will largely forage within 1 km of their hive (Hagler *et al*. 2011). Seasonality, the complexity of the landscape and the genetics of the colony can also influence forage distance (Steffan-Dewenter and Kuhn 2003). However, honey bees' ability to scout for suitable forage and then communicate through dance back to the colony (Von Frisch 1967), gives them a competitive edge over most other pollinators that are solitary. This enables honey bees to exploit the most abundant floral resources efficiently (Hung *et al*. 2019). When floral abundance increases, honey bee abundance at these resources will therefore increase faster than other pollinator groups (Hung *et al*. 2019).

Honey bees are generalist pollinators and will therefore have many links in a pollination network (Giannini *et al*. 2015). Honey bees visit the most abundant and rewarding floral resource causing wild pollinators to shift their diets to other flowers, thus changing the structure and properties of pollination networks (Magrach *et al*. 2017). Honey bees can reduce the diversity of wild pollinators, through dominating pollination networks and outcompeting other pollinators for floral resources (Lindström *et al*. 2016; Magrach *et al*. 2017; Ropars *et al*. 2019). Since the make-up of pollinator assemblages can influence plant communities (Fontaine *et al*. 2006), changes to this make up can lead to lower reproductive success in plants (Potts *et al*. 2010). Pollinators vary in how effective they are at pollination (Wilcock and Neiland 2002) replacement of an effective pollinator by an ineffective generalist could have negative consequences on plant reproduction. Honey bees are generalist and have a high flower visitation rate, however, this does not necessarily equate to an effective pollination event (Rader *et al*. 2016). Various factors influence pollinator effectiveness when visiting flowers (e.g., body size, pollen load capacity and flight time). When honey bees are ineffective at pollinating, but still obtain resources from the flower, they reduce the floral resources, making flowers less attractive to other more effective pollinators, thereby reducing the reproductive success of the plant (Padyšáková *et al*. 2013).

Having an overabundance of honey bees in their alien range has raised concerns about impacts on native pollinators since they have not evolved with honey bees (Mallinger *et al*. 2017). However, the effects of high-density beekeeping in the native range is less well understood (Goulson and Sparrow 2009; Hudewenz and Klein 2013; Elbgami *et al*. 2014; Henry and Rodet 2018). The fynbos biome at the Cape of South Africa, is home to the indigenous Cape honey bee (*Apis mellifera capensis*), which is also very important agriculturally (Turpie *et al*. 2003). Fynbos is rich in plant species (Myers *et al*. 2000) which is linked to richness in insects (Kemp and Ellis 2017). In spring, the agricultural industry relies on pollination services of managed indigenous Cape honey bees (Masehela 2017) which overwinter in fynbos sites (Melin *et al*. 2014) when little other food sources are available (Melin *et al*. 2018). Whilst in summer, alien eucalyptus trees are an essential source of forage for managed honey bees (Allsopp and Cherry 2004; Hirsch *et al*. 2020). The overabundance of honey bees in fynbos could have a positive or negative effect on pollination rates (Geerts and Pauw 2011). It might be positive in small fynbos patches – in which some pollinators might have been lost – by providing additional pollination services to plants that have become pollen limited (Garibaldi *et al*. 2013). Alternatively, it could negatively impact other pollinator species by outcompeting and depleting their food resources (Geldmann and González-Varo 2018). However, increased honey bee numbers in fynbos vegetation, beyond what occurs naturally, may reduce floral resources such as nectar and pollen resulting in interference competition with other pollinator species (Mallick and Driessen 2009).

Currently, MHBH are not permitted in protected areas in the fynbos biome as a precautionary measure (Brand 2009b; CapeNature 2016; Sanparks 2022). However, beekeepers in the fynbos biome are increasing their usage of natural vegetation forage (Hutton-Squire 2014). The impacts of artificially inflated honey bee numbers on other pollinators in their native range in South Africa has largely been ignored (but see Geerts and Pauw 2011). Therefore, here I explore whether the addition of managed Cape honey bee hives to natural areas 1) increases the number of honey bees on native flowers; 2) change the pollination networks; 3) change the composition of the pollinator communities; 4) affects the abundance and richness of insects; and 5) reduces plant reproduction. Also, I test whether the distance from MHBH has an influence on pollinator communities.

2.2. Methods

2.2.1. Study site and experimental design

The study was conducted in the Cape floristic region (CFR) of South Africa. The CFR is a biodiversity hotspot with a high level of plant endemism (Myers *et al*. 2000). The study site was located on Lourensford Wine Estate, which covers 4000 hectares, most of which is farmland. However, the estate has 1200 hectares dedicated to being a biodiversity area, adjacent and linked to the Hottentots Holland and Helderberg nature reserves, which together protect over 70 000 hectares of natural fynbos, a fire driven, evergreen shrubland (Rebelo *et al*. 2006). Vegetation types in the area include endangered Cape Winelands Shale Fynbos, Boland Granite Fynbos and the critically endangered Lourensford Alluvium Fynbos with small pockets of Afromontane Forest (Rebelo *et al*. 2006; Lourensford 2022). The area has a Mediterranean climate with cold wet winters and hot dry summers with a mean annual precipitation of 470–980 mm and average temperature ranges from a high of 26°C in summer to a low of 7°C in winter (Rebelo *et al*. 2006).

Pollinator observations were carried out at Lourensford Wine Estate (Figure 2.1). The study site was placed in natural fynbos vegetation away from human activity and more than 3 km away from the nearest agricultural fields, which were not in bloom during the study period. There were 2 phases to this study, 1) data was collected without any MHBH present (*before hives* treatment); and 2) data was collected after MHBH were introduced to the study site (*during hives* treatment). There were 4 observation plots of 10x10 m placed along a transect of 1000 m. This distance was selected since competition between honey bees and other pollinators is highest within a 1 km radius of the MHBH (Henry and Rodet 2020), especially with abundant floral resources available (Hagler *et al*. 2011). The plots were placed at a 20 m, 70 m, 450 m and 960 m interval from the MHBH. These distances were chosen due to the topography of the region such as streams (and thus riparian vegetation) and rocky outcrops (no or very little vegetation) that prevented plots at 100, 500 and a 1000 m since plots were selected to be representative of the vegetation. There were no known MHBH within 3 km of the study site. But it is very likely that there were wild colonies in the area.

The introduced *Apis mellifera capensis* hives came from a fynbos patch on a farm about 10 km away from the study site. Hives were inspected before use to ensure the honey bee colonies were in good health based on the Western Cape Bee Industry Association pollination standards (WCBA 2022). Ten hives were introduced on 18/8/20 and placed at -34.017340, 18.951380 in the study area (Figure 2.1). All 10 hives were placed (clustered) within one spot (in yellow, Figure 2.1) using wooden pallets, and not spread out across the study area.

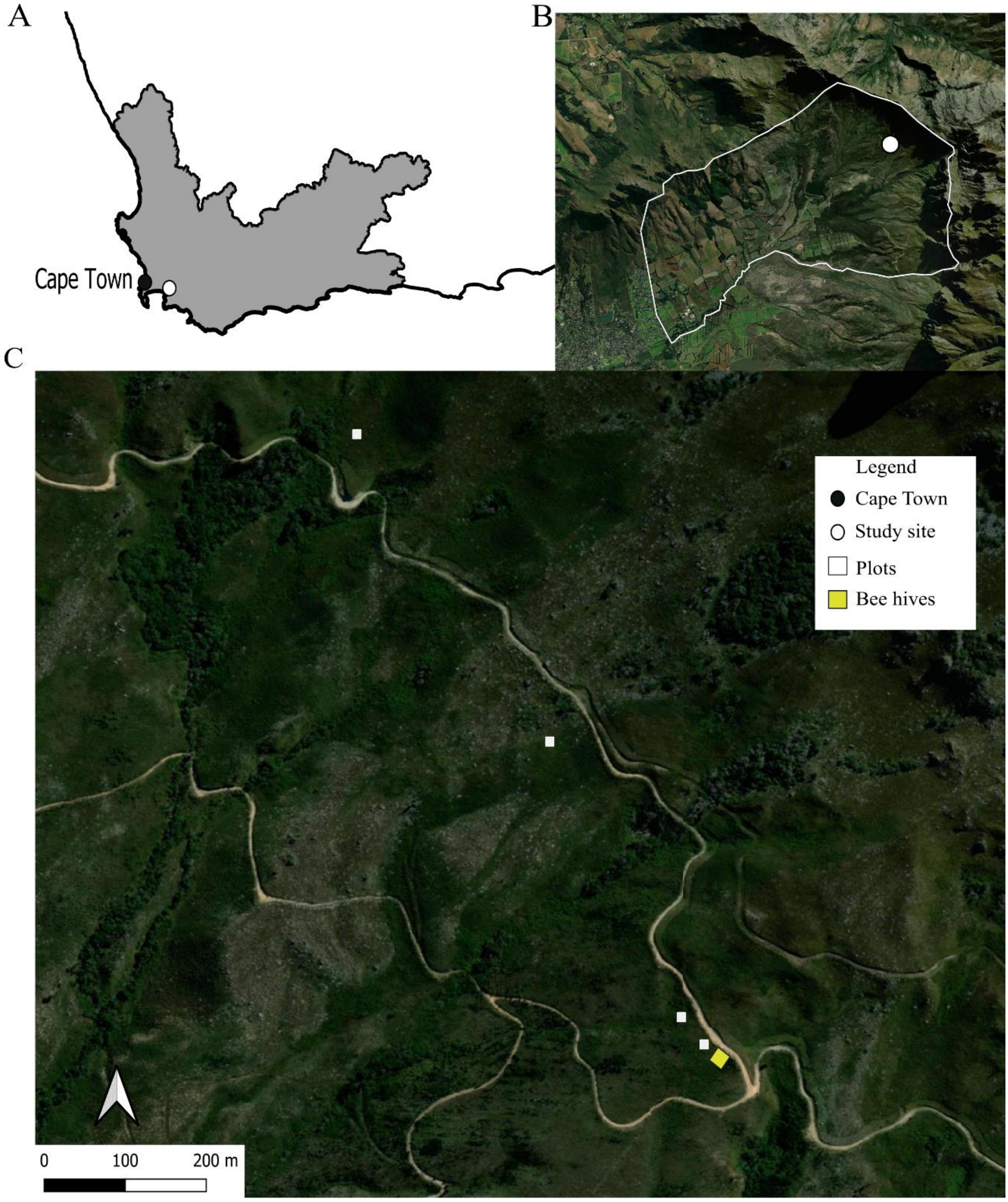


Figure 2.1: Map of study site located on Lourensford Wine estate. Location of study site within the Western Cape (A). Location of study site (white dot) showing Lourensford Wines Estate (white line represents the boundary of the farm) and surrounding landscape (B). Location of the study plots and location of the managed honey bee hives (C).

2.2.2. Honey bees' effect on pollinators

Observations of pollinator visits to flowers took place in each plot for a period of 10 minutes per flowering plant (Shavit *et al*. 2009). All pollinator visits to flowers and the number of flowers they visited were recorded. Only legitimate visits to flowers were scored; the pollinator had to make contact with the reproductive parts of the flower. Pollinators were identified to morphospecies in the field, where possible. Insect pollinators were captured and placed in vials with ethanol for further identification. All observations were done between 10:00 and 16:00, when the temperature was above 16°C and on days with no inclement weather. Observation periods were rotated in a structured way, ensuring that each plot was observed in the morning and afternoon. Data collection took place mainly during winter and into early spring for 20 days between late July and early September, when weather allowed, observations were done on consecutive days, or every other day. This is also the period when beekeepers rely most on natural vegetation as forage for their bees (Melin *et al*. 2014). The first 10 days of data collection was done without any MHBH present (*before hives*), then 10 days after MHBH were introduced (*during hives*). The MHBH were allowed to settle for 3 days before data collection started for the *during hives* treatment. There was a total of 528 observation periods which equates to 88 hours of observation time.

2.2.3. Honey bees' effect on insect community

Pan traps were set up adjacent (within 5 m) to the observational plots to determine impacts on the broader insect community. There were 3 different coloured (white, yellow, and purple) pan traps per plot to attract a diversity of insects. Each pan trap contained water and a drop of dishwashing liquid (Wilson *et al*. 2016). Pan traps were set for an average of 36 hours. The pan traps were collected 10 times for the '*before hive*' and the '*during hive*' treatments. Insects were collected from pan traps and placed in vials with 70% ethanol whereafter they were identified. The orders that were abundant enough for data analysis were Diptera, Coleoptera, Hymenoptera, and Thysanoptera. The Hymenoptera species in refences here excludes honey bees. Only a few spiders and moths were captured, and these were therefore excluded from all analyses, as well as 12 species that could not be identified to a taxonomic level.

2.2.4. Honey bees' effect on plant reproduction

Cullumia reticulata (Asteraceae) was chosen as the focal plant species, since it has a generalist inflorescence, it was widespread across the study area and present in all the plots. Since *Cullumia reticulata* is a generalist, this ensured that honey bees would visit the inflorescence and the competition between the honey bees and other pollinators could be observed. If honey bees outcompete other floral visitors and are less effective pollinators then will seed set decline, or honey bees don’t outcompete and seed set remains the same/increases, or honey bees are effective pollinators and seed set remains the same/increases. At least 19 or more individual inflorescences were chosen for each treatment. Inflorescences were subjected to either one of the following treatments: bagged as buds to determine percentage of autonomous self-pollination, marked and left open (natural pollination) before MHBH were introduced (*before* inflorescences), marked and left open after the MHBH have been introduced (*during* inflorescences). The *during* inflorescences were marked as buds when the MHBH were introduced, they were only open for the *during hives* treatment and not for the *before hives* treatment. Whilst the *before hives* inflorescences were finished flowering when hives were introduced. After flowering finished, the mature fruits were collected, and the seeds counted.

2.3. Statistical analysis

Pollinator visits were converted to visits per flower per hour to obtain flower visitation rates for each pollinator taxon. Data from all the plots was used to construct two general plant-pollinator interaction networks for each treatment. Plant-pollinator interaction networks for each treatment were constructed using the R package *bipartite* (Dormann *et al*. 2009). Network metrices were computed for each treatment and a paired t-test was conducted for each of the metrics to compare *during hives* and *before hive*. Network metrics were computed for the individual plots for before hive and during hive treatments. The t-test was conducted to test the difference in network metrics across all plots before hive vs during hive treatments. Bonferroni was used to correct for false discovery rates.

To examine how bee hive treatment affected community composition of pollinator species and the insect community (pan traps) across study plots, I estimated the Bray-Curtis dissimilarity index using insect abundance data, and I ran a PERMANOVA with bee hive treatment as fixed effect. PERMANOVA as a multivariate approach was used to analyse the difference in the composition of species between hive treatment and among plots. A significant PERMANOVA (p<0.05) indicated that species composition of pollinators was different across plot or between treatments. PERMANOVA showcases the similarity of the data points for each treatment based on the spread of the data. A non-metric multidimensional scaling (NMDS) plot was used to visualise the difference in community composition between treatments for both the observation and pan trap datasets. NMDS was done to visualize the data points to simply interpret the spread of data points into patterns. This method allows for visualizing the level of similarity of data points and is displayed in a distance matrix. Interpreting the spread of the datapoint helps to understand the disimilarity/similarity in species assemblages in the community. Analyses were conducted using the *vegan* package in R (Oksanen *et al*. 2013).

The pan trap data was used to examine the effect of the MHBH treatments on the abundance and species richness of different insect groups. Shapiro Wilk's test was used to test normality of response variables and a general linear model (GLM) was fitted with negative binomial error using the *MASS* package in R (Venables and Ripley 2002). Statistical significance for fixed effects were determined using the Type II sum of squared ANOVA. I used the *emmeans* package (Lenth *et al*. 2021) to evaluate the pairwise differences in abundance and species richness among different plots and between beehive treatments.

To test for differences in seed production from all the selected inflorescences of *Cullumia reticulata* between treatments (autonomous, *before hives* and *during hive*), a GLM with poisson error was used, and we tested for model overdispersion using the R package *AER*. All statistical analyses were performed in R version 3.5.3 (R Development Core Team 2020).

2.4. Results

2.4.1. Honey bees' effect on pollinators

Honey bee numbers could artificially be manipulated and honey bee visits per flower per hour increased from 0.8 in *before hives* to 1.2 for *during hives* (Table 2.1). Total flower visits by honey bees increased from 95 in the *before hives* to 652 flower visits for the *during hives* treatment. Honey bee abundance increased significantly in the *during hives* treatment, mostly closer to the MHBH (Figure 2.2; Appendix 2.1). For the *before hives* treatment, honey bee abundance was low at all distances and not significantly different between plots (Figure 2.2).

A total of 1941 plant-pollinator interactions were recorded, 557 flower visits for *before hives* and 1395 visits for *during hives* (Table 2.1). There were 16 pollinator species recorded for the *before hives* treatment (which included 7 Coleoptera, 3 Hymenoptera, 4 Diptera, and 2 Passeriformes) and 38 species recorded for the *during hives* treatment (which included 22 Coleoptera, 5 Hymenoptera, 10 Diptera, and 1 Passeriformes) (Appendix 2.2). The visits per flower per hour for *before hives,* compared to *during hives,* was higher for Diptera and Passeriformes, but lower for Coleoptera, Thysanoptera and Hymenoptera (Table 2.1). There was no significant difference in network nestedness (t = 0.067, *P* = 0.95), whilst modularity was significantly higher in *before hives* (Figure 2.3A and 2.4A) than for *during hives* (t = 2.57, *P* = 0.053; Figure 2.3B and 2.4B) and this difference is strongest closer to MHBH (Appendix 2.3).

For *before hives* treatment, there were 11 plant species in flower and for *during hives* treatment there were10 (Figure 2.3). Honey bees increased and so did the number of plant species they visited, from visiting 6 plant species in the *before hives* treatment to visiting 9 plant species in the *during hives* treatment (Figure 2.4). The number of plant species Diptera visited decreased from 10 plant species *before hives* to 5 plant species for the *during hives* treatment. Thysanoptera and Hymenoptera increased the number of plant species they visited slightly between the treatments. Coleoptera visited 11 plant species *before hive*s but visited 9 plant species *during hives* (Figure 2.4).

2.4.2. Honey bees' effect on insect abundance and richness

The pan traps collected 150 different species. For the *before hives* treatment there were 83 different species (of which 26 Coleoptera, 9 Hymenoptera and 48 Diptera) and the *during hives* treatment there were 94 (of which 34 Coleoptera, 11 Hymenoptera and 48 Diptera) (Appendix 2.2). The abundance for *before hives* was 999 (168 Coleoptera, 13 Hymenoptera, 415 Diptera and 403 Thysanoptera) which increased for *during hives* to 1150 (460 Coleoptera, 47 Hymenoptera, 393 Diptera and 250 Thysanoptera). The number of honey bees captured for *before hives* was 3 and for *during hives* this increased to 19.

The distance from introduced MHBH had varied effects on the abundance and richness of the different insect taxa collected from pan traps (Table 2.2; Figure 2.5; Appendix 2.4). The pairwise comparison for Diptera showed no significant difference in abundance and species richness between the treatments for each distance (Figure 2.5A and B). Hymenoptera had no significant difference in abundance and species richness between the treatments at each distance from the MHBH (Figure 2.5C and D). Coleoptera had no significant difference in abundance and species richness between the treatments at each distance from the MHBH (Figure 2.5E and F), except for plot 450 m where the abundance significantly increased for *during hives,* which is the plot where the honey bees were the least abundant. MHBH introductions had no significant effects on Thysanoptera abundance and richness (Figure 2.5G).

2.4.3. Honey bees' effect on the pollinator and insect community composition

To determine whether the introduction of MHBH affected the composition of the insect and pollinator communities, NMDS graphs were created for both the pollinator observation and pan trap data sets (Figure 2.6A and B). Observations had 9 unique species and pan traps had 11 unique species sharing 32 common species. There was a clear distinction between the treatments, once the MHBH were introduced the community composition of insects became more homogenous compared to the *before hives* treatment (Figure 2.6A and B). There was a significant difference in species composition between treatments and plots for both data sets, but not for the interaction between plot and treatment for the pan trap data (Table 2.3).

2.4.4. Honey bees' effect on plant reproduction

To determine whether the introduction of MHBH and the distance from MHBH influenced plant reproduction, fruit set of *Cullumia reticulata* was tested. There was no significant difference in fruit set between the *before hives* and *during hives* at each distance from MHBH (Figure 2.7; 20 m P = 1.0, plot 70 m P = 0.94, plot 450 m P =1.000 and plot 960 m P =1.000). There was always one seed per fruit, and the number of fruits per inflorescence ranged from 1 to 4. *Cullumia reticulata* is unable of autonomous selfing since the inflorescences in the pollinator excluded treatment produced no fruit or seeds.

2.5. Figures and tables

Table 2.1: Flower visitation rate (visits/flower/hour) of the different pollinator taxa for all plots combined. Flower visits is the total number of flowers visited by each pollinator taxa from all the plots per treatment. Flower visits percentage is the percentage of flower visits performed by each pollinator group.

	Apis mellifera capensis	Diptera	Coleoptera	Hymenoptera	Passeriformes
Flower visitation rate					
Before hive	0.8	0.5	0.2	0.1	1.8
During hive	1.2	0.3	0.4	0.9	1.5
Flower visits					
Before hive	95	283	116	30	28
During hive	652	152	343	223	10
Flower visits percentage					
Before hive	17	50,8	20,8	5,4	5
During hive	47,7	10,8	24,6	15,9	0,7

Table 2.2: The effect of managed honey bee hives treatments and sampling distance on the abundance and species richness of insects collected in pan traps (honey bees are not included in Hymenoptera). The columns represent the statically differences for the plots, treatments and then the interaction of plots and treatments had on insect abundance and richness. * Indicates the significant *P* values.

Pan traps	Plot		Treatment		Plot + Treatment	
Abundance	χ^2	*P*	χ^2	*P*	χ^2	*P*
Diptera	13.43	0.004*	0.04	0.833	7.39	0.061
Hymenoptera	13.72	0.003*	4.26	0.039*	2.02	0.569
Coleoptera	5.29	0.152	15.61	<0.0001*	9.56	0.023*
Thysanoptera	26.46	<0.0001*	0.29	0.588	4.56	0.207
Richness						
Diptera	0.65	0.885	0.0002	0.9874	4.64	0.200
Hymenoptera	5.49	0.139	0.77	0.3800	3.79	0.285
Coleoptera	2.38	0.497	11.22	0.0008*	5.44	0.142

Table 2.3: The differences in treatment, distance from managed honey bee hives and the interaction between these for community composition of observation and pan trap data sets. All pollinator groups were included for these analyses.

	Observation		Pan traps	
	P	PsedoF	*P*	PsedoF
Treatment	0.001	5.1038	0.001	4.7276
Plot	0.009	1.8417	0.001	2.7845
Treatment + Plot	0.589	0.9229	0.015	1.5149

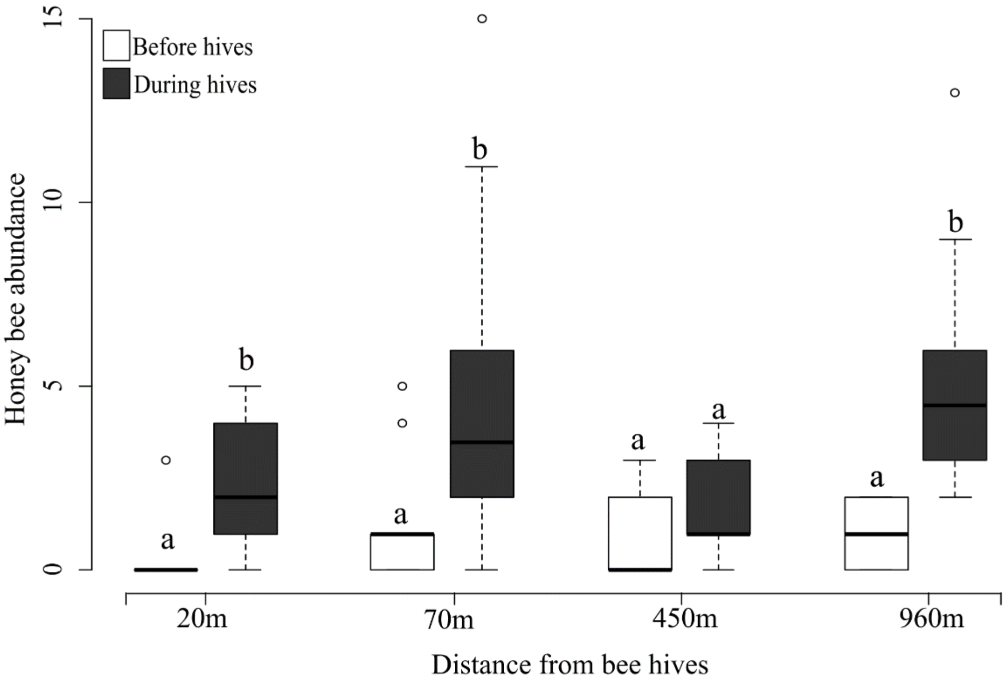


Figure 2.2: The effect of introducing managed honey bee hives on the abundance of honey bees in natural fynbos with increasing distance from the hives. Different letters show the significant difference in honey bee abundance between treatments with distance from the managed honey bee hives.

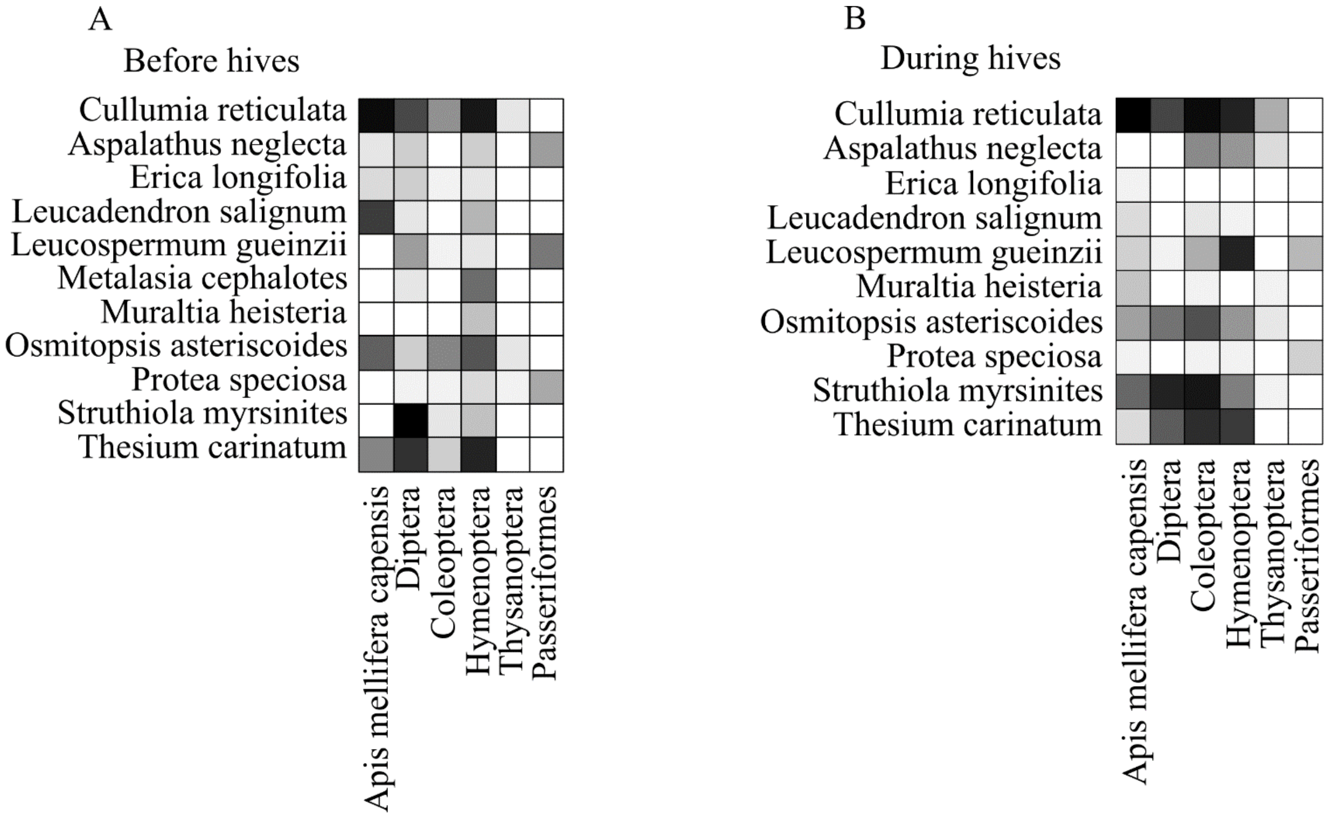
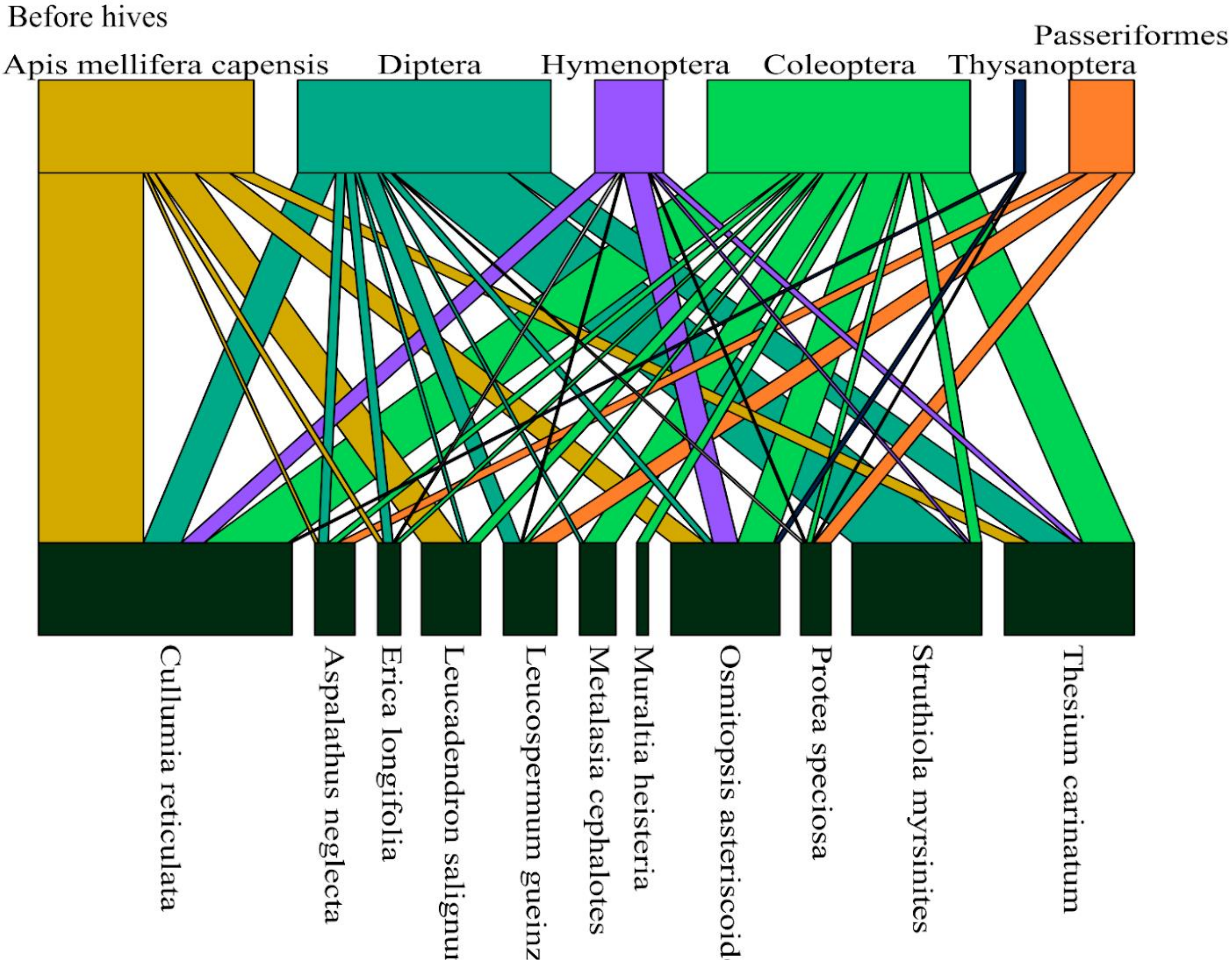


Figure 2.3: The interaction frequency at which pollinator groups visited different plant species calculated for each treatment individually *before hives* (A) and *during hives* (B). All flowering plants from each plot and every observation of a pollinator visiting a flower was included. With the darkest shades of grey being the most visited and the lightest grey being the least visited and white indicates no visits. The plant species are ordered from top to bottom by most visited to least visited. The pollinator groups are ordered from left to right by most frequent to least frequent.

A
Before hives



B
During hives

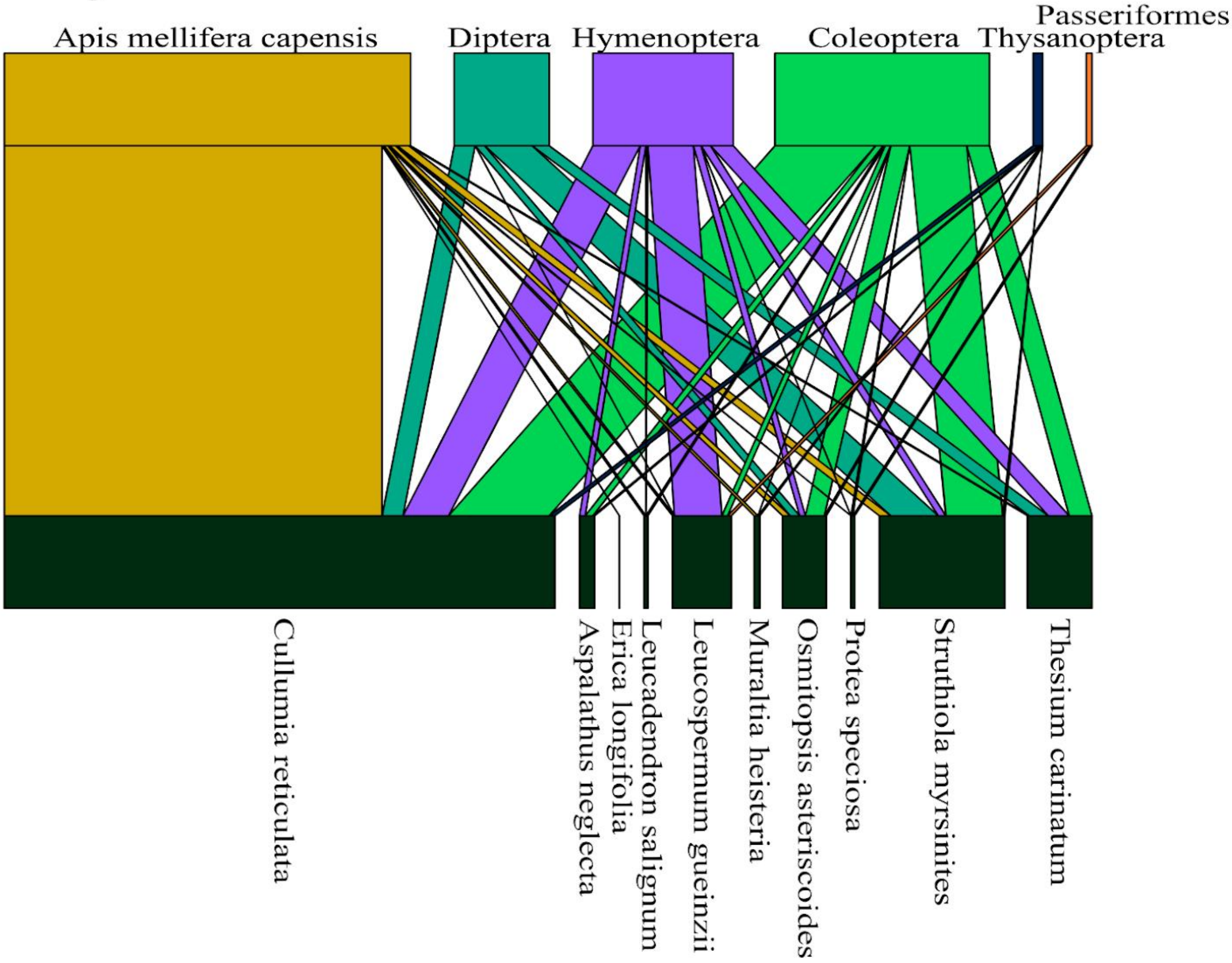


Figure 2.4: Pollinator network representing the flower visits of different pollination taxa for *before hives* (A) and *during hives* (B). Pollinator groups are represented by the coloured bar on the top of the network while the plant species are represented by the dark green bars on the bottom. The lines connecting the pollinators and plants represent flower visitation, with the thickness of the line indicating visitation frequency.

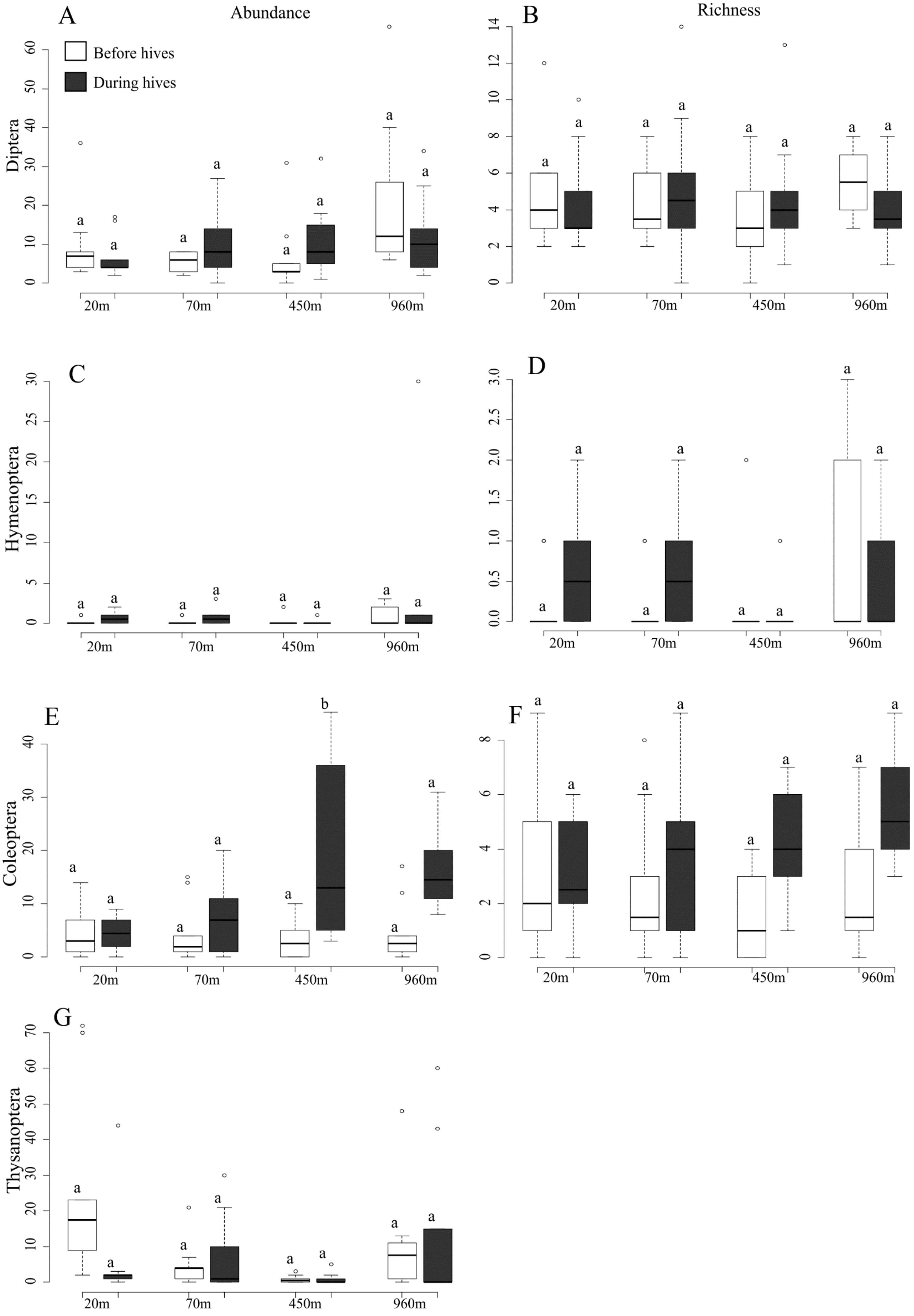

A
Abundance
B
Richness
Before hives
During hives
Diptera
Hymenoptera
Coleoptera
Thysanoptera
C
D
E
F
G
20m
70m
450m
960m
a
b

Figure 2.5: The effect of bee hive treatment on Diptera abundance (A), Diptera species richness (B), Hymenoptera abundance (C), Hymenoptera species richness (D), Coleoptera abundance I, Coleoptera species richness (F), and Thysanoptera abundance (G) collected in pan traps across sampling distance from the managed honey bee hives. For Thysanoptera only the abundance was recorded, and I did not differentiate between the different species to record species richness. The box represents the interquartile range, the thick black line in the boxes represents the median, and the lines extending from the boxes represent the minimum and maximum values. Bars with the same letters are not significantly different at alpha = 0.05. The x-axis represents the distance from managed honey bee hives.

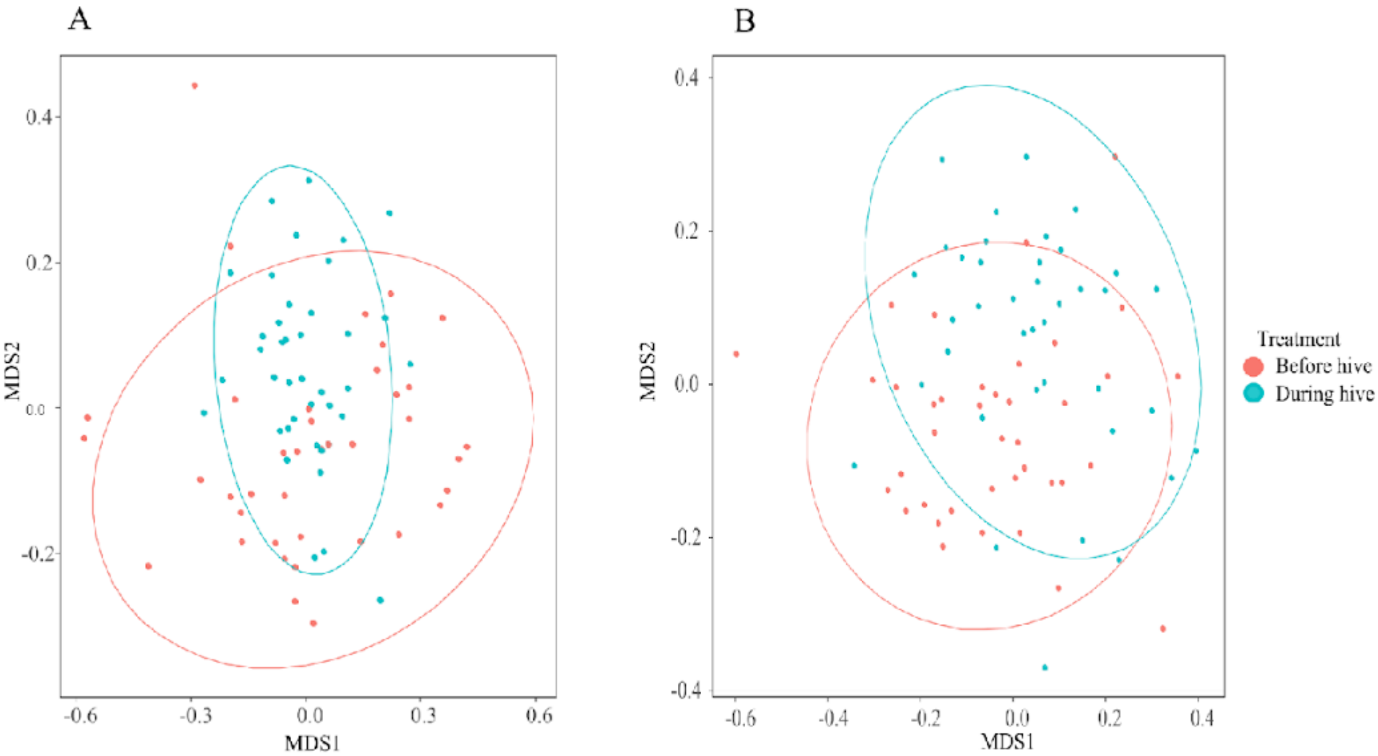


Figure 2.6: Non-metric multidimensional scaling displaying the differences in species composition of the insect communities through observations (A) and pan trap (B). Data *before hives* is in red and *during hives* in blue. The ovals represent the standard deviation around the centroids of the groups. The *before hives* points are more dispersed, indicating these communities are more dissimilar than those from the *during hives* treatment.

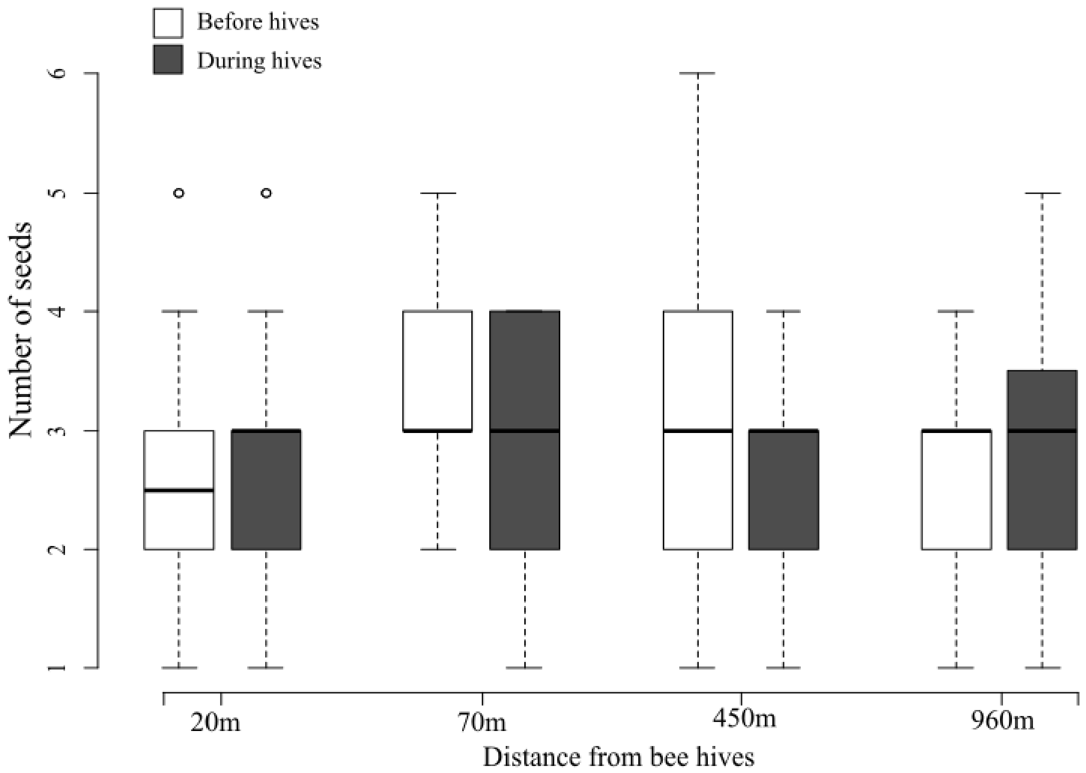


Figure 2.7: Seed set for the *before hives* inflorescence and *during hives* inflorescence with distance from managed honey bee hives. There were no significant differences between the treatments. The box represents the interquartile range, the thick black line in the boxes represents the median, and the lines extending from the boxes represent the minimum and maximum values, while the dots are the outliers. Autonomous seed production was zero, therefore it was not included in the figure.

2.6. Discussion

2.6.1. Honey bee abundance and its effect on community composition

The introduction of MHBH led to a significant increase in honey bee numbers across the study area. This is consistent with previous studies that reported significant increase in honey bee abundance after honey bee hive introductions, dominating floral resources and becoming the predominant floral visitor (Hudewenz and Klein 2013; Magrach *et al*. 2017; Hung *et al*. 2019; Valido *et al*. 2019). In my findings, the increase in honey bee abundance did not follow expectations of having the biggest increase closer to the MHBH and then decreasing as distance increased. The biggest increases were recorded in plots close to hives or in plots with the highest abundance of the plant, *Cullumia reticulata. Cullumia reticulata* was the most common plant species across the plots and honey bees visited these flowers frequently. This observation is in agreement with other studies that showed honey bees to monopolise areas with the best floral resources (Magrach *et al*. 2017; Hung *et al*. 2019; Elliott *et al.* 2021). The body size of pollinators could also have an influence on whether honey bees have an impact on pollinators. Ropars *et al*. (2019) found Hymenoptera with larger bodies were more impacted by honey bee presence than smaller bodied Hymenoptera. Shared traits between other pollinators and honey bees increase the likelihood of negative effects from honey bees, these shared traits include having similar proboscis length and foraging behaviour to honey bees (Cappellari *et al*. 2022). These shared traits probably cause foraging niche overlap with honey bees and wild pollinators. Though these honey bees are native, their unnaturally high abundance from introduced MHBH could trigger the same type of competition and negative effects from niche overlap that comes from an introduced alien species (Goulson *et al*. 2002; Inoue *et al*. 2008; Córdova-Tapia *et al*. 2015). The introduction of MHBH did affect community composition of the pollinators and insects with the composition being significantly different between treatments, becoming more homogenous for the *during hives* treatment. However, the different pollinator taxa were affected differently.

2.6.2. The effect of honey bees on Hymenoptera

The dominance of honey bees did not have a negative effect on Hymenoptera. Hymenoptera flower visitation rate increased after the MHBH were introduced, which contrasts with other studies where Hymenoptera flower visits decrease with an increase in honey bees (Shavit *et al*. 2009; Lindström *et al*. 2016; Magrach *et al*. 2017; Ropars *et al*. 2019; Valido *et al*. 2019; Lázaro *et al*. 2021). However, Lázaro *et al*. (2021) found that honey bees did not affect all species of Hymenoptera negatively, as bees from the Apidae family were more tolerant to an increase in honey bee abundance. At the same time, Ropars *et al* (2020) showed that the richness of larger bodied bees decreased in response to honey bees while smaller bodied bees were not affected. Furthermore, there are a few studies that also found increasing honey bee abundance had no negative affect on Hymenoptera abundance and richness (Steffan-Dewenter and Tscharntke 2000; Russo *et al*. 2015). The onset of spring could have influenced the increase in Hymenoptera flower visitation rate (Lowman 1982; Gilbert and Raworth 1996). However, despite Hymenoptera not negatively impacted by honey bees, they may be central place foragers whereby they bring floral resources back to the nest, and this would limit their forage range and prevent the escape from honey bee competition. Therefore, they could be negatively impacted in the long-term through limited access to floral resources, but this remains to be tested.

Throughout my observations, almost no aggressive behaviour from honey bees were noted, which has been found in other studies (Gross and Mackay 1998; Pinkus-Rendon *et al*. 2005). However, the three instances of aggressive resource guarding behaviour from a solitary bee species all happened in the *during hives* treatment, which could indicate that the increase of honey bee abundance leads to increased competition of forage for this solitary bee species. There is evidence that other bee species can exhibit aggressive behaviour towards honey bees (Roubik and Villanueva-Gutiérrez 2017), and especially when resources become scarce these aggressive bees can increase the frequency of attacks (Roubik 1981).

2.6.3. Honey bees' effect on Coleoptera

The introduction of MHBH had no significant negative impact on Coleoptera. Coleoptera abundance only significantly increased at a distance of 450 m (Figure 2.5 E and F) for the *during hives* treatment, but this plot also had the least amount of honey bees present (Figure 2.2). Flower visits and flower visitation rate increased, though the number of plant species visited decreased. Comparably, Ropars *et al* (2019) found Coleoptera flower visits decreased with increasing honey bee abundance in areas where honey bees are native. In contrast, Worthy (2021) found that there was a positive relationship between honey bee abundance and Coleoptera diversity where honey bees were not native to the study area. In contrast. In my findings, Coleoptera abundance decreased in the closest plot to the MHBH but increased in all other plots. This general increase in abundance could be attributed to the start of spring. Generally, warmer temperatures correspond to increased insect abundance as it signals the abundance in availability of flowering plants – thus foraging resources (Birch 1948; Lowman 1982; Gilbert and Raworth 1996; Logan *et al*. 2003), suggesting that the increase in abundance was not related to honey bees. However, the only plot where Coleoptera increased significantly was in the one plot where honey bees did not increase significantly (Figure 2.2 and 2.5E). This could be an indication that Coleoptera prefer areas with lower honey bee abundance and that it is an avoidance mechanism to escape high competition. Coleoptera were thus not completely displaced from the study area but seemingly altered their foraging patterns at a local scale to reduce competition with honey bees.

2.6.4. Honey bees' effect on Diptera

There was no significant effect of introduced MHBH on the abundance and richness of Diptera. Interestingly, the abundance and richness of Diptera observed was similar for both treatments but the number of flowers visited by Diptera declined by 45% after hives were introduced and the number of plant species visited decreased from ten to five. Despite the importance of Dipterans as pollinators (Raguso 2020), studies investigating the effect of honey bees on Diptera are scarce, as the focus tends to be on Hymenoptera. The few studies that have evaluated the effects of honey bees on Diptera have mixed results. For example, Ropars *et al* (2019) and Worthy (2021) found no negative effect on Diptera abundance or diversity where honey bees are introduced. In contrast, Lindström *et al* (2016) found honey bee presence reduced the densities of Diptera significantly. Where honey bees have no negative impact on Diptera, this could be a result of having a limited forage niche overlap with honey bees. However, where Diptera are affected, they may have been displaced due to high forage niche overlap with honey bees (Goulson *et al*. 2002; Inoue *et al*. 2008). Diptera fulfils a crucial pollination niche in the CFR (de Jager and Ellis 2017; Theron *et al*. 2023), and honey bees reducing the flower vitiation rate of Diptera could negatively affect reproduction in Diptera dependent plants.

2.6.5. Honey bees' effect on Passeriformes

Passeriformes flower visitation rate decreased and visited one less flowering plant species *during hives*. There were two species of nectar feeding birds (Passeriformes) observed, the Cape Sugar Bird (*Promerops cafer)* and the Orange Breasted Sunbird (*Anthobaphes violacea*), which utilised two Proteaceae species, which were not often visited by honey bees. However, other Hymenoptera species did increase their visits to Proteaceae species *during hives*, which could indicate that honey bees did not directly compete with Passeriformes but could increase the competition between Passeriformes and other Hymenoptera species. Geerts and Pauw (2011) found that increased honey bee abundance through MHBH reduced Sugarbird numbers while not reducing floral resource availability, suggesting that interference competition rather than resource competition is at play.

2.6.6. Honey bees' effect on plant reproduction

Honey bee abundance and proximity to MHBH did not influence fruit set for *Cullumia reticulata*, even though it was the most frequently visited plant species by honey bees. These results are robust since *C. reticulata* is not capable of autonomous seed production. These results do contrast with other studies where increased honey bee abundance led to decreased seed set (Magrach *et al*. 2017; Valido *et al*. 2019). Valido *et al* (2019) found that for certain plant species, the seed set was lower with increasing proximity of the plants to MHBH, however this effect was not found for all plant species studied. Honey bees' effectiveness at pollination has been found to vary depending on the plant species, however, as generalists they can be effective pollinators for most plant species even where they are not native (Goulson *et al*. 2003). Here I found that the increase in honey bee visits did not lead to a decline in seed production. Illustrating that even though honey bees may compete for floral resources, as expected, they are able to successfully pollinate *C. reticulata*. However, other pollinators still visited *C. reticulata* and could have contributed to the majority of pollination. Even if honey bees were less effective pollinators of *C. reticulata* they may make up for that with their high visitation rate. Some pollinator guilds may be more sensitive to the increased presence of honey bees. This might be different in more specialised flowers in which honey bees might be ineffective pollinators or rob nectar and pollen, and in doing so reduce visitation by the appropriate pollinators, which could lead to a decline in reproduction (Irwin and Brody 1998; Dedej and Delaplane 2004; Burkle *et al*. 2007; Magrach *et al*. 2017; Valido *et al*. 2019). Though honey bees may not frequently visit specialist flowers since honey bees are generalist themselves. This is a key area for future studies.

2.6.7. Limitations

This study provides valuable insight into the impacts MHBH can have on local pollinators. However, it is important to acknowledge a potential limitation inherent in the study design, some variables change over time within the study site that could affect insect abundance and richness such factors include climate, weather, and flower abundance. The results from the study offer insight into the impact of MHBH for a specific time frame, they may not fully account for the nuanced variations caused by environmental changes. To overcome these limitation controls and replicates could be implemented, unfortunately the topography of the study area limited the amount of study plots that could have been set up. However, studies have shown impacts from MHBH introductions therefore it is not unlikely that impacts found in this study can be attributed to the introduction of MHBH. Though future studies should incorporate controls and replicates for more robust results. By recognizing these limitations allows for a more informed interpretation of the results.

2.7. Conclusion

There is mounting evidence that increase in honey bee abundance can have a negative effect on other pollinators, pollination networks and seed set, regardless of whether honey bees are native or introduced. There are however studies that show that increased honey bee numbers have no negative effect on the aforementioned factors (Steffan-Dewenter and Tscharntke 2000; Giannini *et al*. 2015). But I found that despite introducing a modest number of MHBH, honey bees dominated the study area once introduced, and this increase in abundance of honey bees did have an impact on some pollinator groups, reducing the flowers visits of Diptera. The pollinator community composition of the study area became significantly more homogenous once the MHBH were introduced. Increasing honey bees' numbers therefore does have the potential to have a negative effect on some parts of the pollinator community. Although natural systems are dynamic, and many variables can contribute to whether honey bees will have a negative effect, my findings here do indicate that there are impacts, even with a low number of MHBH. These negative impacts could be exacerbated by introducing MHBH at a higher density, which can be a common occurrence from beekeepers with a large amount of MHBH. Though environmental factors can affect how severe these impacts may be. Floral abundance and richness can influence the impact honey bees might have on local pollinators, and with high floral abundances in spring, impacts might be largely absent, but this need to be tested (Lázaro and Totland 2010; Magrach *et al*. 2017; Hung *et al.* 2019).

Having a diversity of pollinators is beneficial for both natural ecosystems and agricultural systems (Richards 2001; Klein *et al*. 2007; Garibaldi *et al*. 2011). However, pollinators are under threat and on the decline due to various anthropogenic factors (Steffan-Dewenter *et al*. 2005; Geerts 2011; Goulson *et al*. 2015). Increased pressure from high density MHBH could exasperate these declines. It is therefore crucial to find a balance between beekeeping practices and safeguarding wild pollinators; especially since I found some negative effects from the introduction of only 10 MHBH, which is a relatively small number. Effects were studied for a short period, and studies over longer time frames and multiple years are urgently needed given the contested nature of this topic/subject area. Although it could be argued that it ultimately the responsibility of growers and/or beekeeper to provide forage for the managed bees, Conservation organisations will unfortunately need a more scientifically robust approach and evidence to support their decisions to not allow MHBH into or around protected areas. It is therefore important that they consider a more robust research approach since pressure for forage is ever increasing. In future, the large number of MHBH on or close to conservation area fence lines will increase to more than what is currently being observed. At the same time, my findings are presented with caution as the study area has had low density MHBH at some stage in the past and long-term legacy effects might have persisted, masking impacts. Also, beekeepers own hundreds to thousands of MHBH that need natural vegetation to forage on simultaneously. This applies in particular after pollination services were rendered and hundreds of hives are put into natural vegetation during summer when fewer species are flowering than during late winter/early spring when this study was conducted. The massive increase in honey bee numbers, gradually or rapidly, could lead to increased competition for resources and ultimately the displacement of pollinators that cannot coexist with these extremely high honey bee numbers. However, with potentially fewer pollinator species and fewer plant species in flower, impacts might be limited. This question will be addressed in chapter 3 of this thesis.

2.8. References

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2.9. Appendix A

Appendix 2.1: The pairwise comparison of honey bee abundance. Comparison of honey abundance between treatments for each plot expressed in *P* values and standard error (SE).

Observations abundance

Plots	20 m		70 m		450 m		960 m	
	P	SE	*P*	SE	*P*	SE	*P*	SE
Apis mellifera capensis	0.042*	0.652	0.011*	0.380	0.657	0.496	0.001*	0.407

Appendix 2.2: Total abundance and species richness of all taxa captured in the pan traps (A) and observed pollinators (B).

A. Pan traps	Abundance		Richness	
	Before	During	Before	During
Diptera				
Asilidae	5	4	4	4
Empididae	16	25	4	5
Mycetophilidae	5	1	2	1
Mydidae	1	1	1	1
Platystomatidae	1	2	1	1
Sciaridae	47	27	8	7
Simuliidae	11	11	4	4
Stratiomyiidae	3	1	2	1
Syrphidae	0	6	0	2
Tabanidae	23	48	1	2
Tipulidae	111	82	12	9
Species unknown	192	185	9	11
Coleoptera				
Cerambycidae	1	2	1	1
Curculionidae	5	2	2	2
Meloidae	0	1	0	1
Scarabaeidae	4	63	2	5
Species unknown	158	392	20	25
Hymenoptera				
Colletidae	2	0	1	0
Sphecidae	3	1	2	1
Species unknown	8	46	6	10
Thysanoptera	403	250	1	1

B. Observations

	Abundance		Richness	
	Before	During	Before	During
Diptera				
Empididae	1	8	1	2
Tabanidae	46	25	3	3
Syrphidae	0	1	0	1
Species unknown	1	8	1	4
Coleoptera				
chrysomelidae	3	14	1	1
Coccinellidae	3	5	2	2
Curculionidae	1	5	1	3
Pentatomidae	11	9	3	4
meloidae	2	1	1	1
Scarabaeidae	4	56	2	2
Species unknown	59	214	4	9
Hymenoptera				
Colletidea	13	21	1	1
Xylocopa	1	4	1	1
Species unknown	3	6	1	3
Passeriformes				
Promerops cafer	5	4	1	1
Anthobaphes violacea	8	0	1	0

Appendix 2.3: Network metrices (in rows) for each plot (in columns) showing the difference between before hives and during hives using paired t-test for each of the metrics.

	20 m		70 m		450 m		960 m			
Network metrics	Before hives	During hives	Before hives	During hives	Before hives	During hives	Before hives	During hives	t-value	p-value
Number of pollinators species	5	4	6	6	5	6	6	6		
Number of plants species	6	5	7	6	7	8	5	6		
Network size	30	20	42	36	35	48	30	36	−0.117	0.911
Connectance	0.60	0.65	0.41	0.47	0.54	0.5	0.47	0.44	−0.160	0.878
Link per species	1.64	1.44	1.31	1.42	1.58	1.71	1.27	1.33	−0.201	0.847
Nestedness	20.32	18.22	36.95	29.47	27.03	24.16	5.15	19.53	−0.068	0.948
Weighted nestedness	0.36	0.50	0.26	0.22	0.23	0.28	0.55	0.47	−0.175	0.867
NODF	68.00	81.25	43.29	50.00	64.52	62.40	81.67	64.17	−0.008	0.994
Weighted NODF	39.27	52.08	28.01	28.33	29.03	29.03	34.66	51.94	−1.051	0.333
H2	0.46	0.15	0.47	0.52	0.46	0.35	0.54	0.53	1.039	0.339
Network diversity	1.57	2.31	2.26	1.37	2.63	2.58	2.14	1.67	0.471	0.654
Modularity	0.32	0.17	0.34	0.18	0.41	0.31	0.33	0.30	2.569	0.042
Interaction eveness	0.46	0.76	0.60	0.38	0.74	0.66	0.63	0.47	0.384	0.714
Linkage density	1.99	2.99	2.50	1.87	3.06	3.17	2.53	2.03	0.013	0.990
Vulnerability	1.82	3.35	2.41	2.18	2.53	2.58	2.94	2.37	−0.564	0.593
Generality	2.18	2.64	2.59	1.56	3.59	3.75	2.11	1.69	−0.339	0.746

Appendix 2.4: The pairwise comparison between the treatments for the abundance and richness of taxa from pollinator pan traps for each plot represented in *P* values and standard error (SE).

Pan traps

Abundance	20 m		70 m		450 m		960 m	
	P	SE	*P*	SE	*P*	SE	*P*	SE
Diptera	0.977	0.360	0.779	0.364	0.857	0.358	0.828	0.342
Coleoptera	1.000	0.450	0.917	0.444	0.002*	0.442	0.060	0.434
Hymenoptera	0.972	1.080	0.939	1.069	0.999	1.414	0.557	0.820
Thysanoptera^	0.356	0.676	0.999	0.687	1.000	0.819	1.000	0.674
Richness								
Diptera	0.999	0.246	0.981	0.244	0.952	0.256	0.824	0.246
Coleoptera	1.000	0.332	0.931	0.337	0.093	0.366	0.165	0.322
Hymenoptera	0.895	0.837	0.895	0.837	0.999	1.239	0.999	0.614

Chapter 3: High-density beekeeping of native honey bees homogenises fynbos pollinator communities.

Abstract

Managed honey bees require a constant supply of good quality forage to maintain colony health and productivity. Wildflowers constitute quality forage resources for managed honey bees, providing adequate nutrition before, during and after rendering pollination services to revitalise the colony. However, introducing managed honey bee hives (MHBH) to areas of natural vegetation can have negative impacts on wild pollinators. I explored the impact of high-density MHBH introductions in natural vegetation on flower visitors, pollination networks, insect abundance and diversity, and community composition of insects and pollinators at a study site in the Cape Floristic Region, South Africa. I observed plant-pollinator interactions in a study site where 66, 400 and 200 MHBH were introduced. The MHBH introductions was uncontrolled and happened in waves, creating a "*bee hive*" dumping effect. Pollinator observations were conducted in 100 m^2 plots at 30 m, 150 m, 500 m and 850 m away from the placed MHBH. Pan traps were used to estimate insect abundance and diversity. As expected, honey bee visitation rates were highest during the 400 hives treatment while Diptera and Coleoptera visitation rates decreased, but Hymenoptera visitation rate increased. Insect community composition for the 400 hives treatment was significantly more homogenous. Honey bees were dominant in the pollination network for the 66 and 400 hives treatments. Honey bees were not as abundant in the observation plots as expected for such a high density of MHBH, possibly due to the uneven distribution of attractive floral resources. MHBH treatments did affect the overall foraging activities of pollinators. Some pollinators had reduced flower visits in response to MHBH treatments, suggesting that increased competition from honey bees could have displaced these pollinators. Therefore, to safeguard the most sensitive wild pollinators, high-density MHBH introductions are not recommended especially when there is a low abundance of floral resources.

3.1. Introduction

Intensive agriculture and the lack of diversity in crops does not promote wild pollinator abundance and diversity (Eeraerts *et al*. 2017), yet the agricultural crop industry continues to rely on animal mediated pollination services. Without effective pollination service, yield and quality for pollinator dependent crops can suffer (Bartomeus *et al.* 2014; Khalifa *et al.* 2021).

Wild pollinators can be very beneficial for pollination services in agriculture, though natural vegetation in and around the farm lands is required to facilitate these pollination services (Eeraerts *et al*. 2017; Garibaldi *et al*. 2013). At the same time, intensive agriculture drives wild pollinator decline primarily through loss of suitable habitat and forage resources in agricultural landscapes (Steffan-Dewenter and Westphal 2008). As a result of declining wild pollinator diversity, many farmers rely on managed honey bees, which are highly effective pollinators of many agricultural crops (Thapa 2006) and are easily managed and transported. The demand for managed honey bee hives (MHBH) is growing (Aizen *et al*. 2019).

Honey bee health and the strength of the colony are dependent on diverse forage providing good quality nutrition (Alaux *et al*. 2010; Hutton-Squire 2014). Good quality forage (pollen and nectar sources) is used to strengthen honey bee colonies before being rendered out for pollination services (Mouton 2011; Hutton-Squire 2014; Masehela 2017). This is known as colony build-up, ensuring a honey bee colony is strong and able to effectively provide pollination service (Dolezal *et al*. 2016; Dolezal *et al*. 2019; Durant 2019). Honey bee health depends largely on the dietary value of floral resources, especially pollen, which contains good quality and essential proteins (Di Pasquale *et al.* 2016). Honey bees with limited access to quality pollen, can become malnourished (Brodschneider and Crailsheim 2010) this can lead to weak honey bee workers and poor foragers with shorter life span compared to honey bees with access to adequate pollen (Scofield and Mattila 2015). A diversity of forage sources is needed otherwise an inadequate diet compromises the immune system of honey bees (Alaux *et al*. 2010; DeGrandi-Hoffman *et al*. 2010) and a colony with a weak immune system will be more susceptible to the negative effects from environmental stressors such as the exposure to pesticides (Tosi *et al*. 2017). Pesticides cause honey bees to be more susceptible to diseases by weakening of their immune system (Sánchez-Bayo *et al*. 2016), this can change foraging behaviour (Gill and Raine 2014: Stanley and Raine 2016) impair motor function (Tosi and Nieh 2017), cause navigational impairments, and shorten life spans of honey bees (Henry *et al.* 2012). The synergistic effects of poor diet and pesticide can be detrimental to colony strength, and both can cause the shortening of honey bees life spans (Tosi *et al*. 2017). Premature ageing and early deaths of adult honey bees leaves the colony without enough workers to attend the brood, a poorly attended brood leads to a weakened colony or the complete collapse of the colony (Oldroyd 2007; Stindl and Stindl 2010; Nearman and vanEngelsdorp 2022).

Since crops do not always offer the ideal floral resource for colony health, beekeepers often need to relocate (migrate) their MHBH to sites with good forage to revitalize their colonies at the end of the pollination season. However, their options for good forage sites can be limited due to safety concerns, especially theft and vandalism (Masehela 2017). In addition, beekeepers move MHBH over long distances across forage locations to the farms where honey bee pollinator services are required. This can also result in additional stress for honey bees. When searching for forage, beekeepers may overstock an area of good forage, which means a large influx of honey bees in these areas (Al-Ghamdi *et al.* 2016; Durant 2019; Newstrom-Lloyd 2016). Another limiting factor to forage is that beekeepers do not own the land required for ideal forage and MHBH are prohibited from nature reserves. However, honey bees have an effective foraging radius of about 5 km (Beekman and Ratnieks 2000) and can forage a maximum distance of 10 km (Levin *et al*. 1960). As a result, forage in nature reserves can be utilised despite the physical exclusion of MHBH. This potentially threatens wild pollinators, since artificially increasing honey bee abundance in natural vegetation could lead to negative impact on wild pollinator abundance and diversity through competition for floral resources (Hudewenz and Klein 2013; Weekers *et al*. 2022; Magrach *et al*. 2017). Honey bees can have strong floral preferences (Aronne *et al*. 2012), which could result in resources competition where honey bees reduce floral resources before other pollinators have a chance to forage (Mallick and Driessen 2009). Even where honey bees are native, high-density beekeeping reduces the flower visitation rate of solitary bee species (Hudewenz and Klein 2013), changes pollination networks (Magrach *et al*. 2017), reduces the densities of other pollinators (Lindström *et al*. 2016) reduces wild bee diversity (Weekers *et al*. 2022) and reduce wild bee abundance (Ropars *et al*. 2020).

There is also the concern that managed honey bee populations can be a vector of pathogens to wild pollinators (Manley *et al*. 2015). Viruses can be transmitted indirectly through shared floral resources (Singh *et al*. 2010). Viruses that emerged in wild pollinator populations have been linked to honey bee presence (Fürst *et al*. 2014; Pritchard *et al*. 2021). Beekeeping could increase the spread of pathogens (Goulson *et al*. 2015; Owen 2017) through high stocking densities, allowing for pathogens to spread via close contact (Singh *et al*. 2010; Manley *et al*. 2015), and through the movement of MHBH creating larger geographic range for pathogens to spread. This is evident in the global spread of the Varroa mite (*Varroa destructor*) due to the transportation and trade of MHBH (Griffiths and Bowman 1981). The Varroa mite infestation facilitates the transmittance of viruses (Traynor *et al*. 2020). In South Africa, wild and managed colonies interchange constantly, but studies on the current status of disease, pest and pathogen spread, or exchange is not fully understood or documented (see Allsopp 2006; Dietemann *et al*. 2009; Human *et al*. 2011; Strauss *et al*. 2013).

*Apis mellifera capensi*s, the Cape honey bee, is indigenous to the Cape Floristic Region (CFR), however it is not naturally found at the high densities resulting from beekeeping practices (Melin *et al*. 2018). Furthermore, studies looking at the effect of beekeeping on other pollinators in the CFR are scarce (see Brand, 2009a; Geerts and Pauw 2011). In this case study, I explore the real-time scenario of the MHBH post pollination "dumping effect", whereby a beekeeper seeks forage for MHBH that have just come out of pollination. I refer to this scenario as the "dumping effect" since the beekeeper "drops off" a high amount of MHBH in one area. The "dumping effect" is dependent on factors such as that MHBH must be removed from orchards after pollination, the need to find suitable and adequate forage for recovery post pollination, travel distance and labour requirements in delivering MHBH and the safety aspect as MHBH need to be protected from theft and vandalism. In some instances, these sites can become semi-permanent sites (apiaries) for MHBH should alternative viable forage be unavailable. This dumping of MHBH could potentially cause negative effects for local pollinators by increasing honey bee abundance beyond that of natural levels (Hudewenz and Klein 2013; Weekers *et al*. 2021). These negative effects are especially prominent within the 1 km forage range from MHBH (Henry and Rodet 2020). Possible negative effects include in changes pollination networks, reducing flower visitation rates and reducing richness and abundance of local pollinators (Hudewenz and Klein 2013; Lindström *et al*. 2016; Magrach *et al*. 2017; Ropars *et al*. 2020; Weekers *et al*. 2022).

In this case study, I specifically explored whether the high-density of MHBH: 1) increases the number of honey bees on native flowers; 2) affect pollination 69etworks and flower visitation rates; 3) impact the composition of the pollinator and insect communities; and 4) affect the abundance and richness of insects. I also evaluate if the distance from MHBH has an influence on the aforementioned factors. Answering these questions will allow me to understand the various dynamics behind the "dumping effect" and how this affects other pollinators.

3.2. Methods

3.2.1. Study site and experimental design

The study was conducted in the Cape Floristic Region (CFR) of South Africa. The study site was located on a Fruitways farm in the Grabouw valley, which is an active fruit farm (Figure 3.1). No crops were in bloom during the study period; therefore, MHBH were to rely on fynbos vegetation in and around the farm. The study was conducted within an area that was mostly natural with 800 ha of natural vegetation, However, the MHBH were placed close together over a 3 ha area on the edge of natural vegetation within disturbed environments. The study plots were within natural vegetation with plots 1 and 2 being within close proximity to the grazing lawn while plots 3 and 4 were surrounded by natural vegetation. The placement of the MHBH within disturbed environments should not affect there foraging, as they will move out of the disturbed environment to find the closest adequate forage. The study area was adjacent to the Hottentots Holland Nature Reserve (70 000 ha). The vegetation type of the study area consists of the critically endangered Elgin Shale Fynbos, characterised by a semi open shrubland with a prevalence of species from the Proteaceae and Asteraceae families (Rebelo *et al*. 2006). The climate is Mediterranean, the wet season is from May to August with mean average rainfall of 830 mm. The average daily temperatures for winter and summer are 6.2 °C and 26.2 °C respectively (Rebelo *et al*. 2006). The majority of this vegetation type has been lost to make way for fruit farms and flooded for the creation of dams (Rebelo *et al.* 2006).

Three different MHBH treatments were established in the study area. A total of 66 MHBH were initially “dumped” at the study site (66 hives) from 26/10/20 – 30/10/20, then the MHBH were increased to 400 MHBH (400 hives) from 31/10/20 – 16/11/20 and then reduced to 200 MHBH (200 hives) from 18/11/20 – 4/12/20. Data collection included pollinator observations and the application of pan traps. Pollinator observations were conducted in four 10 m x 10 m plots situated along a 1000 m transect (Figure 3.1). The plots were placed at 30 m, 150 m, 500 m and 850 m from where MHBH were placed. Plots were selected based on appropriate vegetation cover e.g., avoiding roads, streams, grass patches and rocky outcrops. Plots needed to have plants that were in flower to facilitate flower visitor observations with a preference for high floral diversity and abundance. Data collection took place during summer from the end of October to the beginning of December, over a 5-week period.

Data collection started on 29/10/20 and concluded on the 20/11/20. Two days were given after MHBH introductions to allow honey bees to settle before data collection, but this was not done after the reduction in MHBH. The data collection plots were set up based on the placement of the initial 66 hives. However, when the additional MHBH were added, these were placed at a different location – approximately 1 km away from the initial placement of the 66 hives. The first plot was placed 30 m away from where the MHBH were initially placed at -33.996088, 19.123496. With the placement of additional MHBH, I did not adjust the plot distances as this would have altered the observation distance already made by using the 66-hives. Since this was a MHBH dumping scen–rio, I had no control over MHBH placements and the timing thereof. The MHBH being placed at a different location was not ideal, however this was an opportunistic and real time study. And since the effect of hundreds of additional MHBH will spill over for at least 5 km (Levin *et al*. 1960) and since honeybees will be concentrated on areas with the most resources (chapter 2), i.e., my plots, this change in placement is unlikely to significantly influence results. Even more so since this study was undertaken in summer when floral resources are low, and honey bees will therefore increase their foraging distance (Levin *et al*. 1960), as opposed to having a shorter foraging distance when floral resources are abundant (Hagler *et al*. 2011).

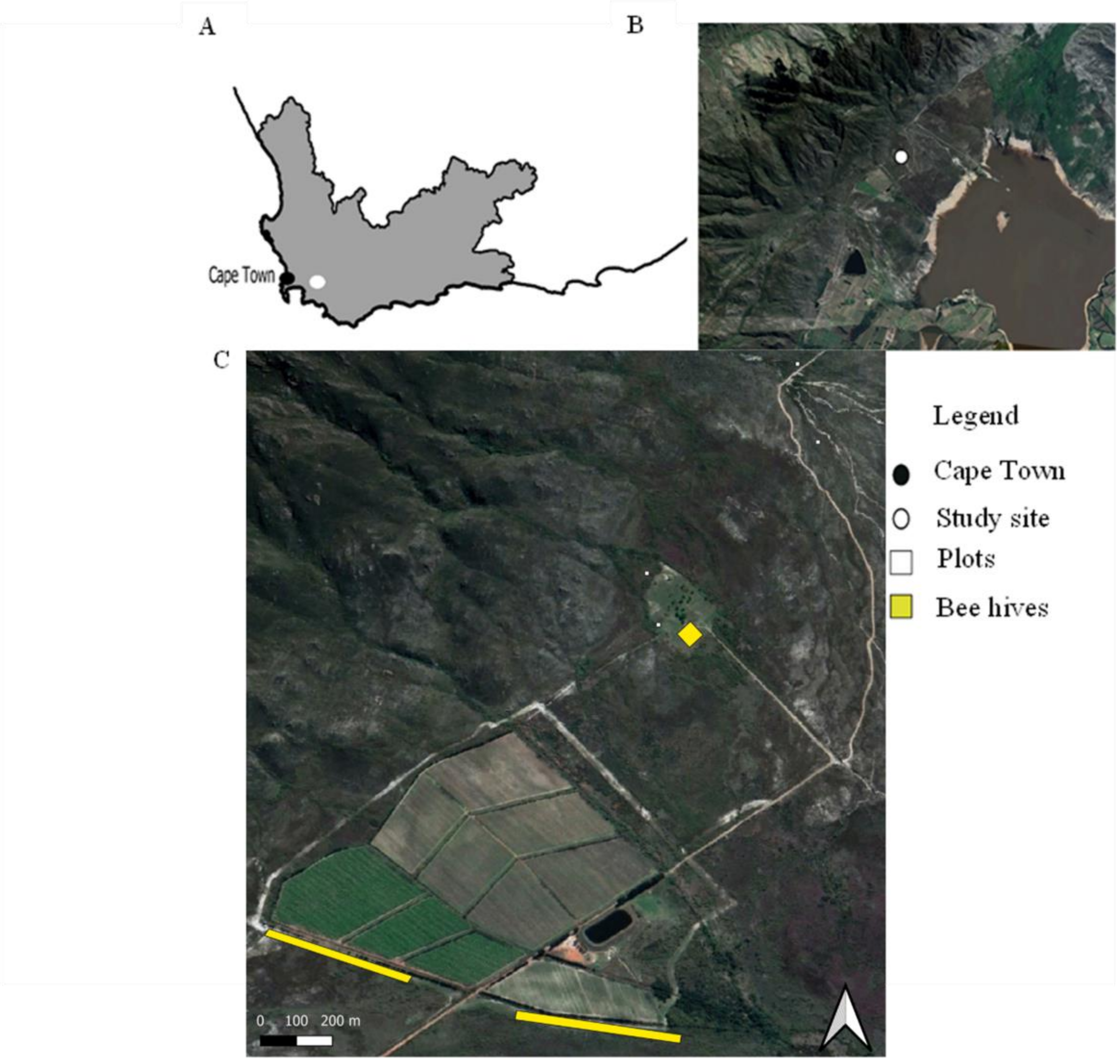


Figure 3.1: Map illustrating the location of study site within the Western Cape (A). The general landscape around where the study site (Fruitways farm) is situated (B). The location of study plots in white and managed honey bee hives are represented by the yellow square (initial managed honey bee hives placement) and yellow rectangles (additional managed honey bee hives placement) (C).

3.2.2. Honey bees' effect on pollinators

Observations of pollinator visits to flowers were conducted in each plot for 10-minute intervals, with a total of 6 intervals per plot equating to an hour of observation time for each plot for every day of observations. Observations were conducted for 3 days during each treatment. There was a total of 216 observation periods which equates to 36 hours of observation time. Flower abundance was visually estimated for each observation period. All floral visitors that made contact with the reproductive parts of the flower were recorded. Observations were conducted between 10:00 and 16:00, with temperatures above 16 ^{o}C and on days with fair weather. An anemometer was used to record the wind speed and temperature to ensure sampling took place on days with low wind speeds. The order in which plots were observed was rotated sequentially to ensure that each plot was observed in both the morning and afternoon. Flower visitors were caught and identified to morphospecies in the field, then placed in vials with ethanol for preservation and further identification.

3.2.3. Honey bees' effect on insect community

Pan traps were set within 5 m of observation plots. Three pan traps were set at each plot, each a different colour (white, yellow, and purple). The different colour pan traps were used to attract a wider variety of flower visitors (Vrdoljak and Samways 2012). Pan traps were half filled with water and a few drops of dishwashing liquid. Pan traps were set for 29 hours on average. Pan traps were collected from each plot on the same day. Insects collected from pan traps were placed in vials with 70% ethanol for preservation until they were sorted and identified. The data collected from the different coloured pan traps were combined for analyses. The orders that were abundant enough for data analysis were Diptera, Coleoptera, Hymenoptera, Lepidoptera and Thysanoptera. The Hymenoptera species in refences here excludes honey bees.

3.3. Statistical analysis

Pollinator visitation rate was quantified as visits per flower per hour. Observation data was used to construct plant-pollinator interaction networks for each treatment using the *bipartite* R package (Dormann *et al*. 2009). Data from all four plots was used to construct two general plant-pollinator interaction networks for each treatment.

Pan trap data was used to assess how insect abundance and species richness vary among MHBH treatments and distances from MHBH. Shapiro Wilk's test was used to ensure normality assumptions of response variables were not violated. A general linear model (GLM) fitted with negative binomial error using the *MASS* package (Ripley *et al*. 2013) was used to determine the effect of MHBH treatments on insect abundance and species richness with MHBH treatment as the predictor, and insect abundance and richness as response variables. The model included Plot+Treatment+Plot*Treatment. Type II sum of squared ANOVA was conducted to determine statistical significance for fixed effect, and pairwise comparison was conducted using the *emmeans* package (Lenth *et al*. 2021) to evaluate the pairwise differences in abundance and species richness among different plots and between beehive treatments. The above methods were also used for honey bee visitation rates.

To examine how high-density MHBH affected pollinator and insect community composition across study plots, datasets from observation and pan traps were analysed separately. I constructed a Bray-Curtis dissimilarity matrix using datasets from observation and pan traps in each plot and conducted a PERMANOVA on the dissimilarity matrix with MHBH treatment as a fixed effect. To visually display the difference in community composition between treatments, the non-Metric Multidimensional Scaling (NMDS) was used. Analyses were conducted using the *vegan* package (Oksanen *et al*. 2013). All statistical analyses were conducted in R version 3.5.3 (R Development Core Team 2020).

3.4. Results

3.4.1. Honey bee abundance and flower visitation rate

Honey bee visitation rate was highest in 400 hives and lowest in the 200 hives treatments (Table 3.1). Honey bee visitation rates increased by 85% in the 400 hives compared to the 66 hives treatment. However, there was a sharp decrease (81%) in the 200 hives treatment. Honey bee abundance was comparable among MHBH treatments at 30 m, 150 m and 850 m from MHBH, but honey bee abundance was significantly higher in the 400 hives treatment compared to 66 and 200 hives treatments at 500 m from MHBH (Figure 3.2; Appendix 3.1). There were 7 flower species in total from the study plots. Honey bees visited 6 flowering species in the 66 hives treatment, 4 during the 400 hives treatment and only 2 species in the 200 hives treatment (Figures 3.3 and 3.4). Honey bees visited *Erica hispidula* the most in the 66 hives treatment. For both the 400 and 200 hives treatments, *Pteronia aspera* was visited most frequently. Also, *Pteronia aspera* was most abundant at the 500 m plot where honey bees were most abundant (Table 3.2).

3.4.2. Honey bees' effect on pollinators

Five pollinator groups (Diptera, Coleoptera, Hymenoptera, Lepidoptera and honey bees) were recorded visiting flowers during observations (Table 3.1). These five groups had a total of 360 flower visits in the 66 hives treatment, 1142 flower visits in the 400 hives treatment and 541 flower visits in the 200 hives treatment. A breakdown for these groups revealed a total of 20 pollinator species records in the 66 hives treatment (11 Coleoptera, 2 Hymenoptera, and 7 Diptera), 21 species in the 400 hives treatment (14 Coleoptera, 8 Hymenoptera, and 9 Diptera), and 40 species in the 200 hives treatment (17 Coleoptera, 10 Hymenoptera, 11 Diptera and 2 Lepidoptera). Diptera visitation rate declined by 63% in the 400 hives compared to the 66 hives treatment (Table 3.1). Coleoptera visitation rate decreased by 18% in the 400-hive compared to 66 hives treatment, and then increased by 134% in the 200 hives treatment. All pollinator taxa except Lepidoptera, visited *Othonna quinquedentate* during the 66 hives treatment, while *Pteronia aspera* and *Cullumia reticulata* were visited by all pollinator taxa except Lepidoptera during the 400 and 200 hives treatments. Diptera visited 5 flowering species in all treatments (Figure 3.4). Hymenoptera visited 2 plant species in the 66 hives treatment, which then increased to 4 species in both the 400 and 200 hives treatments (Figure 3.4). Coleoptera visited 4 plant species in the 66 hives treatment, which increased to 5 species in both the 400 and 200 hives treatments (Figure 3.4). There were no Lepidoptera visits recorded in the 66 and 400 hives treatments, but 2 plant species were visited in the 200 hives treatments (Figure 3.4).

3.4.3. Honey bees' effect on the pollinator and insect community composition

Honey bee abundance had a significant influence on both the pollinator and insect communities (Table 3.3). In both data sets communities were the most homogenous for the 400 hives treatment (Figure 3.5).

3.4.4. Honey bees' effect on the insect community

The pan traps collected 186 different species with a total of 1643 individuals (Appendix 3.2). A total of 77 species with 228 individuals were collected in the 66 hives treatment, 106 species with 728 individuals in the 400 hives treatment and 107 species with 687 individuals in the 200 hives treatment. There was a significant difference in the abundance and species richness of Diptera with distance from MHBH, but not with MHBH treatments (Appendix 3.3). However, there was a significant difference in the abundance of Hymenoptera (excluding honey bees) across plots and treatments, but species richness of Hymenoptera differed significantly across treatment but not plot (Appendix 3.3). Similarly, there was a significant difference in the abundance of Coleoptera for treatments and plots, but species richness of Coleoptera differed significantly among treatments, but not plots (Appendix 3.3). There was no significant difference in the abundance and species richness of Lepidoptera across plots and treatments (Appendix 3.3).

Pairwise comparison was used to determine the significant difference between treatments for each plot to ascertain if the distance from MHBH influenced abundance and richness. Diptera, Hymenoptera and Lepidoptera had no significant differences in abundance and richness among MHBH treatments in all plots (Figure 3.6; Appendix 3.4). Coleoptera abundance increased significantly from the 66 hives treatment to both the 400 and 200 hives treatments except for plot 450m (Figure 3.6 E and F; Appendix 3.4).

3.5. Figures and Tables

Table 3.1: Flower visitation rate (visits/flower/hour) of the different pollinator taxa. Flower visits is the total number of visits to flowers by each pollinator taxa during each treatment. Flower visits percentage is the percentage of flower visits performed by each pollinator group.

	Apis mellifera capensis	Diptera	Coleoptera	Hymenoptera	Lepidoptera
Visitation rates					
66	2.48	0.44	0.32	0.31	0
400	4.60	0.16	0.26	0.46	0
200	0.83	0.12	0.61	0.51	0.64
Flower visits					
66	213	38	82	27	0
400	871	32	151	88	0
200	136	20	301	84	103
Flower visits percentage					
66	60,2	9,3	22,9	7,6	0
400	69,1	3,9	21,2	5,8	0
200	27,9	3,5	41,5	12,2	14,9

Table 3.2: Average flower abundance (open flowers/inflorescences) for each plant species in the different plots over the 3 days of observation during each managed honey bee hives treatment. The numbers 66, 400, 200 refer to the number of managed honey bee hives at the site.

		30 m			**150 m**			**450 m**			**850 m**		
Family	**Species**	66	400	200	66	400	200	66	400	200	66	400	200
Asteraceae	*Corymibum africanum*	16	16	44			13						
Thymelaeaceae	*Struthiola myrsinites*	114	75	31	23	19							
Asteraceae	*Osmitopsis asteriscoides*	15	21	5			2						
Ericaceae	*Erica hispidula*				800	2750	333						
Asteraceae	*Peteronia aspera*							310	909	432	7	23	10
Asteraceae	*Cullumia reticulata*							24	19	9	71	476	130
Iridaceae	*Aristea capitata*										3	4	3

Table 3.3: Community composition was compared between the three treatments of managed honey bee hives for both the observation and pan trap data sets.

Treatments	**Observation**		**Pan traps**	
	P	PseudoF	*P*	PseudoF
66 and 400	0.021*	2.297	0.001*	2.681
66 and 200	0.002*	2.988	0.001*	2.434
400 and 200	0.014*	1.965	0.337	1.066

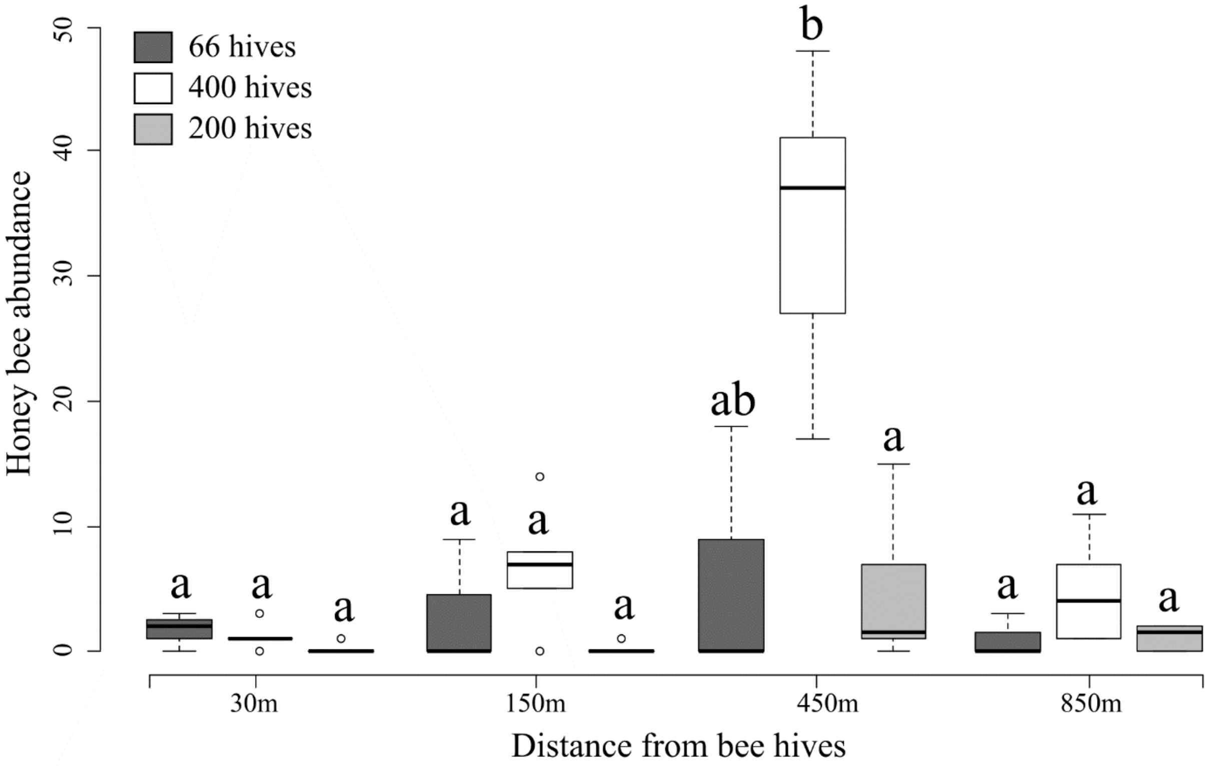


Figure 3.2: The effect of high-density managed honey bee hives treatments on the abundance of honey bees per distance. The box represents the interquartile range, the thick black line in the boxes represents the median, and the lines extending from the boxes represent the minimum and maximum values. Different letters show the significant difference (at alpha = 0.05) in honey bee abundance between the different treatments for each plot.

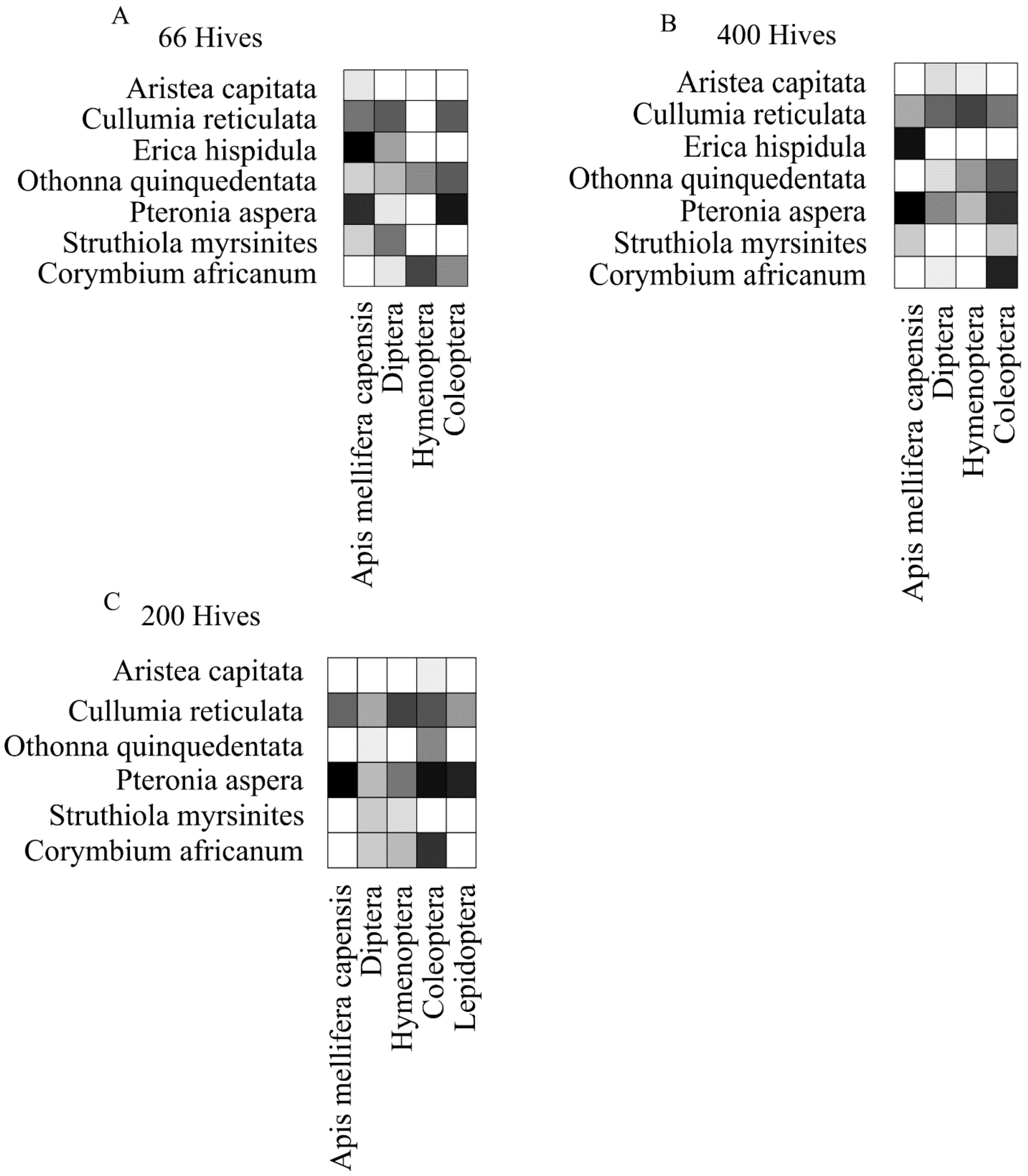
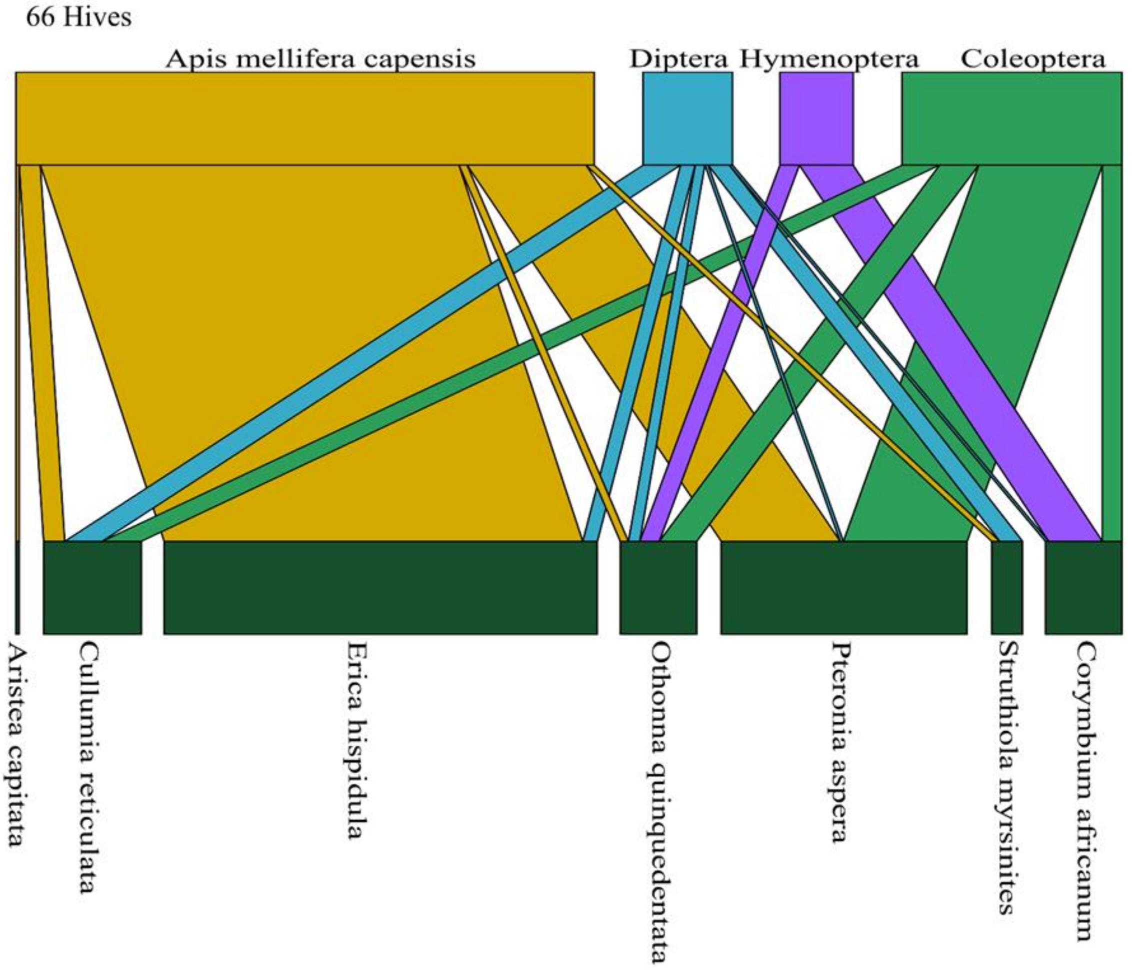
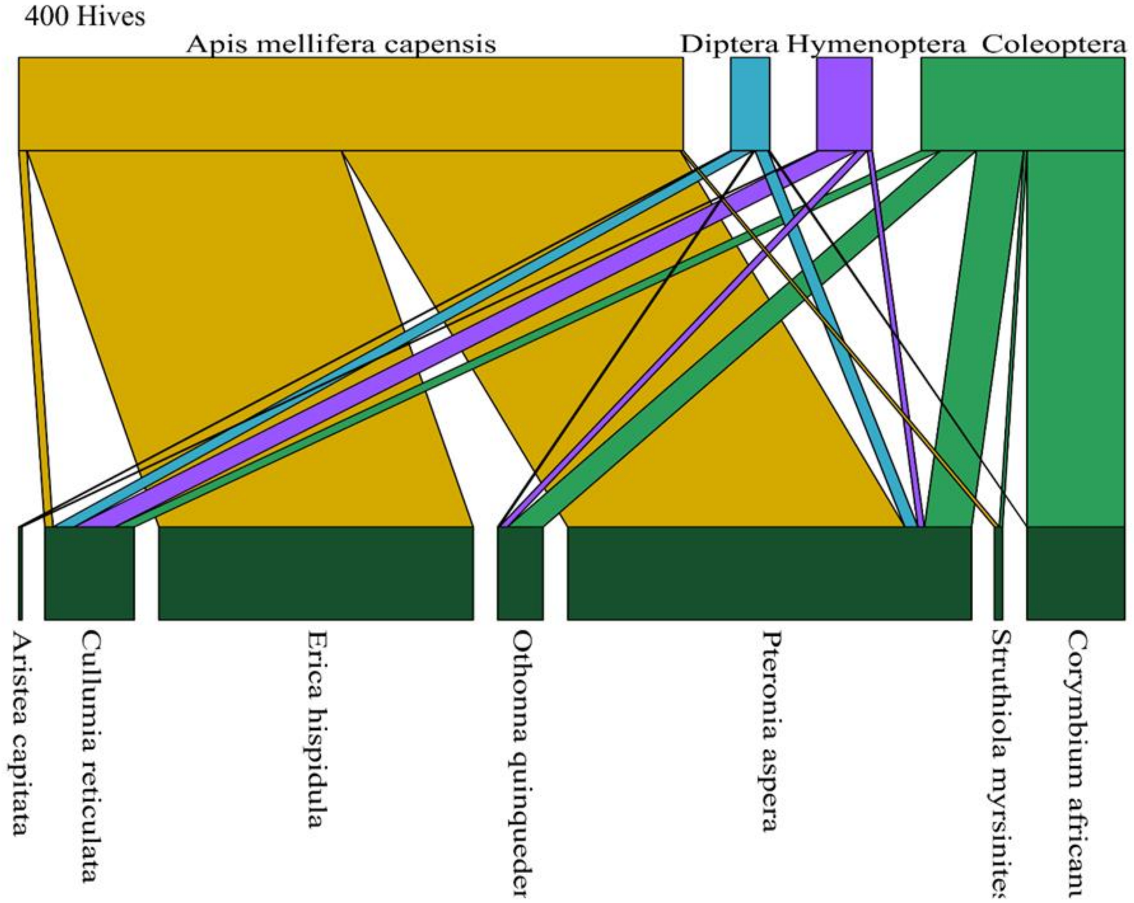


Figure 3.3: The interaction frequency of which pollinator groups visited different species of flowering plants calculated for each of the different managed honey bee hives treatments individually (A, B and C). All flowering plants from each plot and every observation of a pollinator visiting a flower were included in the analysis. The darkest shades of grey represent the most visits and the lightest grey being the least number of visits and white indicates no visits.

A


66 Hives
Apis mellifera capensis
Diptera
Hymenoptera
Coleoptera
Aristea capitata
Cullumia reticulata
Erica hispidula
Othonna quinquedentata
Pteronia aspera
Struthiola myrsinites
Corymbium africanum

B


400 Hives
Apis mellifera capensis
Diptera
Hymenoptera
Coleoptera
Aristea capitata
Cullumia reticulata
Erica hispidula
Othonna quinqueder
Pteronia aspera
Struthiola myrsinite
Corymbium africanu

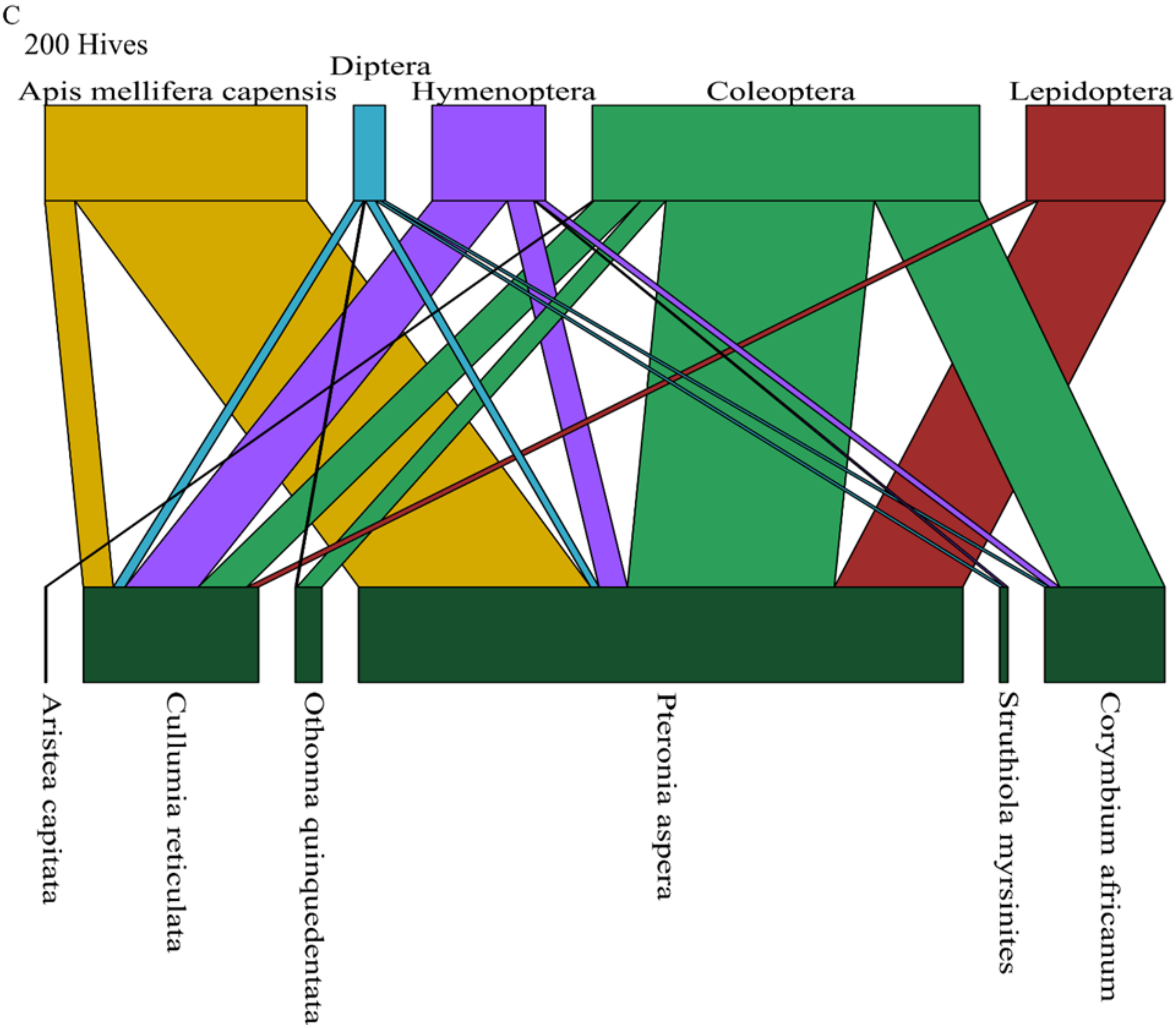


Figure 3.4: Pollination network of the different managed honey bee hives treatments (A, B and C). Pollination groups are represented by the top bar of the network while the plant species are represented by the bars on the bottom. The lines connecting the top bars to the bottom bars represent the flower visitation and the thickness of the line represents the number of visits to flowers, thicker lines indicate more visits.

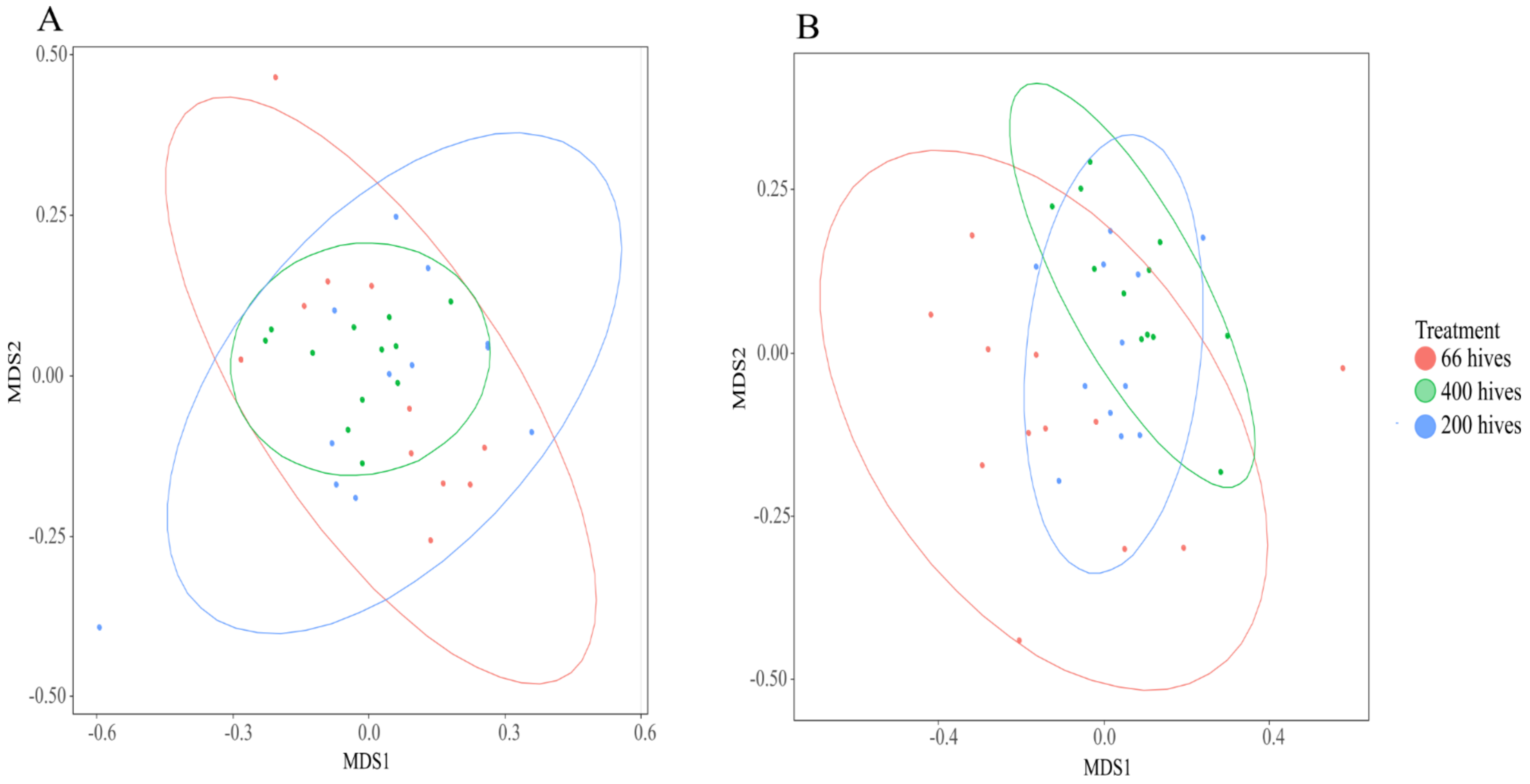
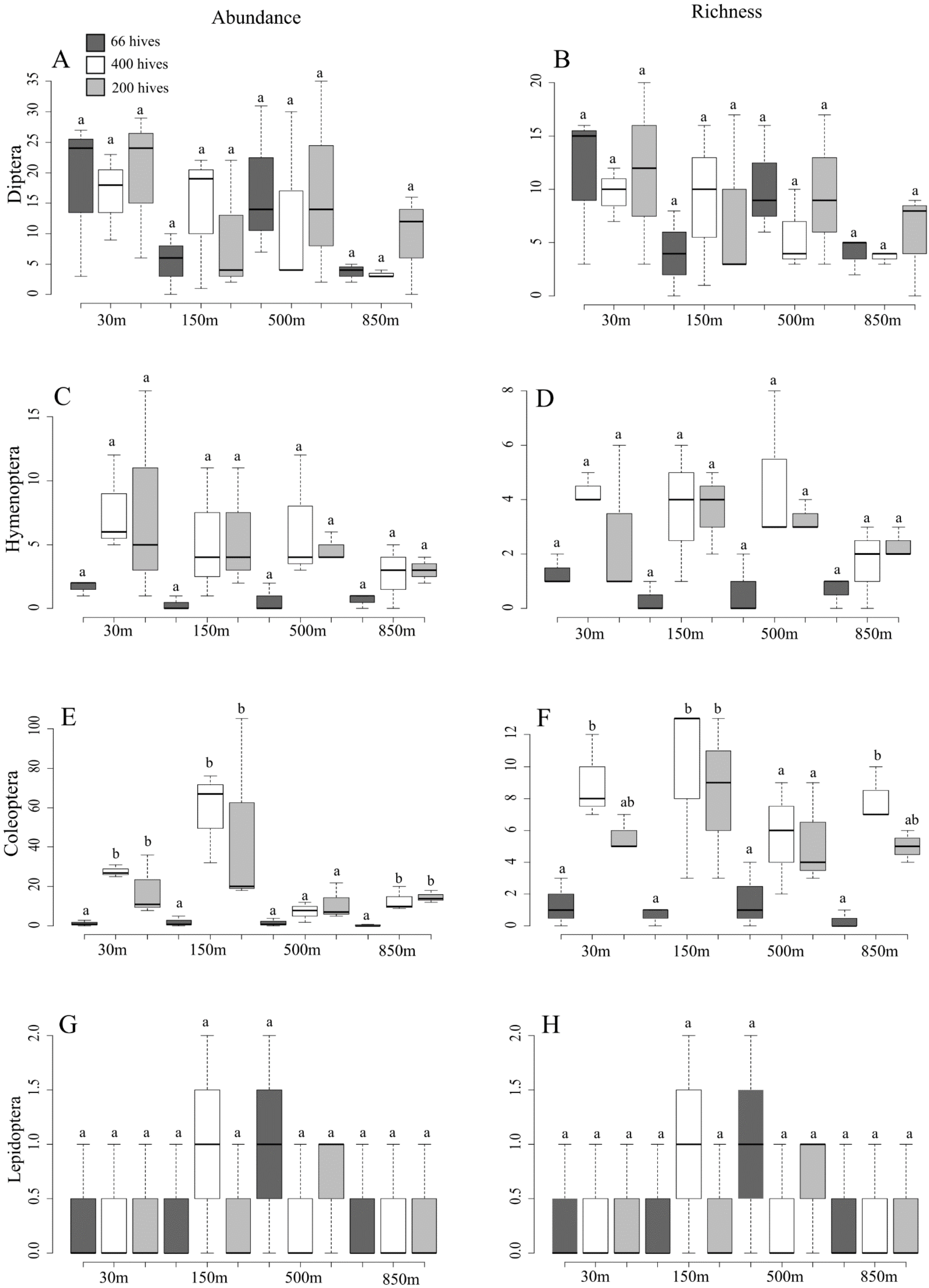


Figure 3.5: Non-metric multidimensional scaling showing differences in species composition of the pollinator and insect communities between the different managed honey bee hives treatments for (A) observations and (B) pan trap data. The 66 hives treatment is in red, 400 hives treatment is in green and 200 hives treatment is in blue. The ovals represent the standard deviation around the centroids of the groups.

Abundance
Richness
66 hives
400 hives
200 hives
A
B
C
D
E
F
G
H
Diptera
Hymenoptera
Coleoptera
Lepidoptera
30m
150m
500m
850m
a
b
ab

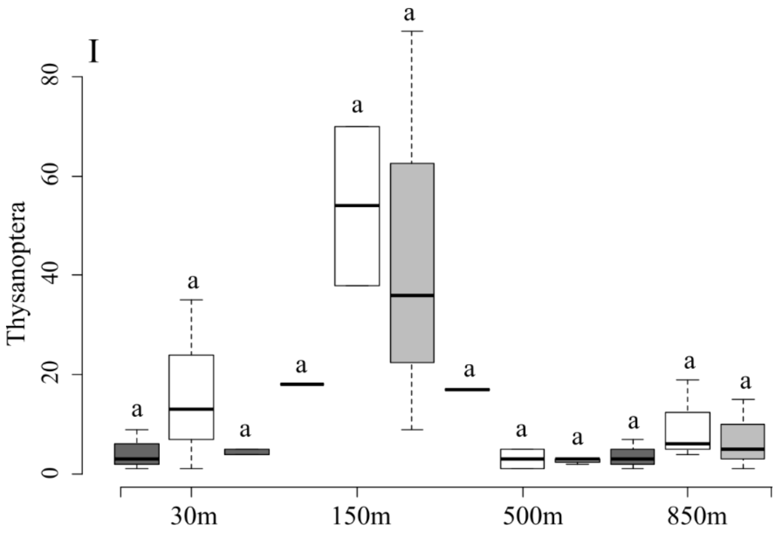


Figure 3.6: The effect managed honey bee hives treatments on Diptera abundance (A), Diptera species richness (B), Hymenoptera abundance (C), Hymenoptera species richness (D). Coleoptera abundance (E), Coleoptera species richness (F), Lepidoptera abundance (G), Lepidoptera species richness (H) and Thysanoptera abundance (I) collected in pan traps across sampling distance from the managed honey bee hives. For Thysanoptera only the abundance was recorded, and I did not differentiate between the different species. The box represents the interquartile range, the thick black line in the boxes represents the median, and the lines extending from the boxes represent the minimum and maximum values. Bars with the same letters are not significantly different at alpha = 0.05. The x-axis represents the distance from managed honey bee hives.

3.6. Discussion

3.6.1. Honey bee abundance

Honey bee abundance did not increase uniformly with distance from the MHBH, even though MHBH were being introduced at a high density. This is most likely due to the uneven spatial abundance of floral resources in the landscape that are attractive to honey bees. Floral traits and abundance can influence honey bee visitation to different flowering plant species (Courcelles *et al*. 2013; Martin 2004; Lázaro and Totland 2010), and this may explain the low honey bee abundance in plots with *Erica hispidula* and *Struthiola myrsinites,* which both have small white flowers that may not be as attractive to honey bees and were most abundant in the two closest plots to the MHBH (Table 3.2). In plots further away from the MHBH, generalist Asteraceae species *Pteronia aspera* and *Cullumia reticulata* dominated and received high floral visitation rates from honey bees, especially during the 400 hives treatments. Honey bees require optimal and abundant floral resources for colony build-up, but even in sites with diverse floral resources, honey bees can have a preferred flowering species on which they mainly forage (Lázaro and Totland 2010). This floral preference during foraging can lead to honey bees ignoring flowers close to the hive, instead, they tend to select for high pollen and nectar volumes (Aronne *et al*. 2012). The floral preferences of honey bees will impact pollinators differentially. Thus, pollinators with a larger floral overlap with honey bees are more likely to be negatively impacted from the high abundance of honey bees and increased competition for floral resources. Especially if honey bees exhaust the floral resources of their preferred flowers and leave little resources for other pollinators. This increased competition with honey bees could lead to other pollinators having to change their diets (Magrach *et al*. 2017) which could be detrimental to their health and long-term survival. This would be detrimental more especially to insects that have a limited flying range and are unable to escape from competition with honey bees.

3.6.2. Honey bees' effect on pollination networks

Honey bees dominated the pollination networks, once large numbers of MHBH were introduced to this site. Honey bees represented 56% of all flower visits throughout the study, their flower visitation rates were highest while MHBH density was highest in the 400 hives treatment, however honey bee visitation rates declined over time, even though MHBH numbers remained high. Magrach *et al*. (2017) found that the increasing honey bee abundance affected pollination networks, as honey bees became dominant and monopolised the most abundant floral resources, which led to other pollinators shifting their diets. Hung *et al*. (2019) also found that honey bees became dominant in pollination networks with a preference for the most abundant resources. Valido *et al*. (2019) recorded that honey bee abundance reduced the diversity of other pollinators in the networks. Having 400 MHBH present in the landscape could have exhausted floral resources, reducing flower visitation rate for the 200 hives treatment. This finding supports that of Dupont *et al*. (2004) who found high honey bee abundance to deplete floral resources. In instances where resident wild pollinators rely on floral resources shared with honey bees, this could mean that they are left with little to no resources which could negatively affect their populations and survival (Biesmeijer *et al*. 2006).

3.6.3. Honey bees' effect on Hymenoptera

Hymenoptera flower visitation rate increased with an increase in MHBH irrespective of distance. Their abundance and richness in the pan traps also increased in all plots with increased MHBH density, though not significantly. This is in line with studies that found no negative effect of increasing honey bee abundance on Hymenoptera abundance and richness (Steffan-Dewenter and Tscharntke 2000; Russo *et al*. 2015). However, other studies have found that increased honey bee abundance does have a negative impact on Hymenoptera (Lázaro *et al*. 2021; Lindström *et al*. 2016; Magrach *et al*. 2017; Shavit *et al*. 2009; Ropars *et al*. 2019; Valido *et al*. 2019). Even where negative effects were found, there were some mitigating factors that made some groups of Hymenoptera not as susceptible to these negative effects. Ropars *et al*. (2020) found that smaller bodied bees were more tolerant to increased honey bees than larger bodied bees. For example, Lázaro *et al*. (2021) found Hymenoptera from the Apidae family were less susceptible to the negative impacts from increased honey bee abundance than other Hymenoptera not as closely related to honey bees. However, Hymenopterans that are not affected by increased MHBH density could be central place foragers and are not able to escape the competitive pressure from increased honey bees, and thus will have limited access to floral resources. Central place foragers such as bumblebees suffered from weight loss and produced smaller workers when their hives were placed near MHBH (Elbgami *et al*. 2014; Goulson and Sparrow 2009). Therefore, for central place foragers whose abundance and richness are not affected by high MBHH density since they cannot move to better locations, could suffer long-term from limited forage access and ultimately nutrition and population viability effects.

3.6.4. Honey bees' effect on Coleoptera

Coleoptera flower visitation rate was the lowest when honey bee visitation was the highest and *vice versa*. Coleoptera abundance from pan traps increased significantly in the 400 and 200 hives treatments, with the only exception being in the plot that had a significant increase in honey bee abundance. This suggests that high abundance of honey bees could be a deterrent for Coleoptera. Ropars *et al*. (2019) also found that increased MHBH density significantly decreased flower visitation by Coleoptera. This indicates that Coleoptera exhibit an avoidance to floral patches where honey bees are most abundant, thus avoiding direct competition with honey bees. Coleoptera can still be abundant in a landscape with high-density MHBH treatment, however, avoiding the areas of highest competition with honey bees they ensure their access to floral resources. Therefore, this could be a co-existence survival strategy for Coleoptera in honey bee dominated areas.

3.6.5. Honey bees' effect on Diptera

Diptera flower visitation rate generally decreased as the number of MHBH increased. However, their abundance and richness in pan traps was not significantly affected. Ropars *et al*. (2019) found no negative effects on the flower visits of Diptera with increased honey bee abundance. In contrast, Lindström *et al* (2016) found depressed densities of Diptera with the addition of MHBH and the effects were stronger in close proximity to MHBH. Diptera may be more mobile and move away from areas of high competition with honey bees. This could increase their likelihood of survival since they avoid the possible long-term negative effects that increased honey bee abundance could have on Diptera's access to good forage resources. Diptera could then fare better compared to central place foragers that will be exposed to the negative consequences of increased competition within their home range (Boyd *et al*. 2014) through having limited access to resources. If Diptera are more mobile and able to move to areas of abundant resources outside the reach of honey bees, this adaptation would then be limited to areas of natural vegetation that are large enough for Diptera to escape the range of honey bees. At the same time, it is also crucial to note that there is currently severe pressure on various landscapes related to different land use practices – and in most instances, these have resulted in habitat loss and landscape destruction (Haddad *et al*. 2015). These activities have also been shown to be some of the leading factors resulting in pollinator declines globally (Steffan-Dewenter and Westphal 2008). Therefore, landscape activities, management and practices should consider these dynamics in areas of high honey bee densities given their potential impacts on Diptera.

3.6.6. Honey bees' effect on community composition

Community composition for pollinator observations and pan traps were more homogenous for the 400 hives treatment. Community composition refers to the makeup of the community, with regards to the identity of species present, their relative abundance and the distribution of individual species. There is mounting evidence that high honey bee abundance affects different facets of the make-up of pollinator and insect communities. Abundance and richness of wild pollinator taxa have been found to declined due to the introduction of MHBH (Vergara 2011; Valido *et al*. 2019; Lázaro *et al*. 2021; Weekers *et al*. 2022). In contrast some studies found some wild pollinator taxa to be unaffected by increased honey bee abundance (Steffan-Dewenter and Tscharntke 2000; Ropars *et al*. 2019). However, changing composition of pollinator communities can in turn affect pollination for various plant species, subsequent seed, and fruit set (Valido *et al*. 2019). My results agree with those studies that found negative impacts on the different facets of wild pollinator community composition. The increased presence of honey bees can affect the community composition of wild pollinators and insect communities.

This opportunist case study was able to provide data on the real-world (and time) scenario of introducing a high density of MHBH into natural vegetation. This MHBH dumping scenario is common practise in summer for the Western Cape Province as MHBH come out of pollination. This may become more common as land with natural vegetation for forage becomes scarcer and the demand for pollination services from managed honey bees increases. Therefore, it is of value to study the impacts thereof, especially since introducing so many MHBH into a protected area is not advised, as the concern for the potential negative impacts would be too great.

3.7. Conclusion

This case study, to the best of my knowledge, was a first of its kind testing the MHBH dumping effect. Therefore, all findings were real time scenarios, laying an important foundation for future studies. My results show that high-density MHBH introductions does increase the number of honey bees on native flowers, affects pollination networks and the flower visitation rates of other pollinators, impact on the composition of pollinator and insect communities; and affects the abundance and richness of some insect groups. Honey bee abundance only had a significant increase in one plot however, honey bee flower visitation rate was highest when MHBH density was at its highest during the 400 hives treatment, and they were responsible for 56% of all flower visits and dominated pollination networks. The floral distribution of the landscape affected how honey bees aggregate in a landscape. Honey bees were more prominent in the 66 hives treatment than in the 200 hives treatment. Possibly due to the abundance of honey bees during the 400 hives treatment reducing the abundance of floral resources, making the study plots less attractive to the honey bees during the 200 hives treatment. My results show that the high-density introduction of MHBH does affect some wild pollinator and insect taxa, in particular flower visitation rates by Coleoptera and Diptera. Coleoptera abundance increased significantly in all plots except for the plot where honey bee abundance significantly increased, suggesting honey bee abundance suppresses Coleoptera abundance. MHBH treatments did not seem to affect the abundance, species richness and visitation rates of Hymenoptera which contrasts with many other studies (Lázaro *et al*. 2021; Lindström *et al*. 2016; Weekers *et al*.

2022). However, they could still be negatively impacted if they are central place foragers and are not able to move to areas of less competition therefore their access to resources is then limited which could reduce their health and ultimately their survival (Elbgami *et al*. 2014; Goulson and Sparrow 2009). In contrast, the taxa whose presence was reduced due to honey bee introduction could be mobile foragers and may be able to escape from the competition that introduced MHBH bring. This study looked at the short-term effects of high-density MHBH introduction, and not the long-term impacts. Further exploration should be done on the long-term impacts that high honey bee abundance has on the health and fecundity of other insect taxa. Future studies should focus of the effects of MHBH at a distance of 1-5 km from MHBH. Since floral abundance, distribution and the makeup of floral communities seems to be a better predictor of how honey bees aggregate in the landscape than distance within 1 km of MHBH. Therefore, these factors should be investigated to determine how they influence the impacts of introducing MHBH. Future studies should also investigate how introducing MHBH affects Diptera as they seem sensitive to increased abundance of honey bees from introducing MHBH.

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3.9. Appendix B

Appendix 3.1: Pairwise comparison showing the *P* values and standard error (SE) from comparing the abundance of honey bees in each plot between each treatment of managed honey bee hives.

Observations abundance	**Treatment**			30m		70m		450m		850m	
				P	SE	*P*	SE	*P*	SE	*P*	SE
Apis mellifera capensis	66	and	400	1.000	0.975	0.998	0.814	0.259	0.754	0.993	0.972
Apis mellifera capensis	66	and	200	0.986	1.304	1.000	3301	0.999	0.828	0.999	1.001
Apis mellifera capensis	400	and	200	0.997	1.323	1.000	3301	0.029*	0.796	1.000	0.883

Appendix 3.2: The abundance and richness of different taxa collected from pan traps.

Treatment					
Abundance	Coleoptera	Hymenoptera	Diptera	Lepidoptera	Thysanoptera
66	19	10	134	6	59
400	322	66	142	6	192
200	277	63	170	5	172
Richness					
66	10	8	53	5	
400	31	26	46	3	
200	22	22	5	5	

Appendix 3.3: The statistical differences for plot, treatment and the interaction of plots and treatment for insect abundance and richness from pan trap data for each pollinator group. * Indicates a significant *P* value.

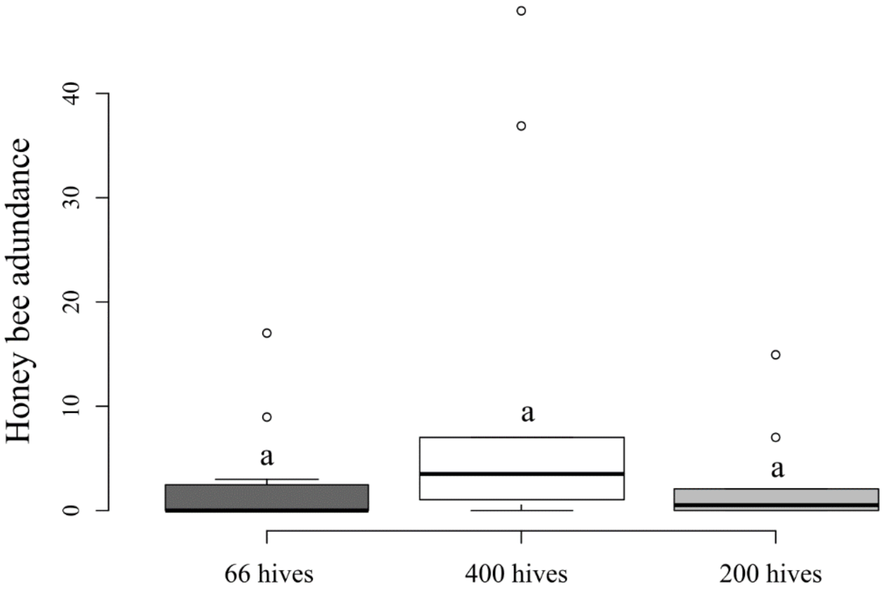
Pan traps	Plot		Treatment		Plot + Treatment	
Abundance	χ^2	*P*	χ^2	*P*	χ^2	*P*
Diptera	12.09	0.007*	1.21	0.55	4.09	0.665
Hymenoptera	7.94	0.047*	33.44	<0.001*	2.04	0.916
Coleoptera	36.05	<0.001*	97.72	<0.001*	6.80	0.339
Lepidoptera	1.58	0.663	0.12	0.942	2.41	0.878
Thysanoptera	42.19	<0.001*	3.98	0.137	13.56	0.035*
Richness						
Diptera	9.09	0.028*	0.83	0.659	3.86	0.696
Hymenoptera	4.47	0.215	26.38	<0.001*	3.89	0.693
Coleoptera	3.85	0.278	73.98	<0.001*	5.79	0.448
Lepidoptera	1.58	0.663	0.12	0.942	2.41	0.878

Appendix 3.4: Pairwise comparison showing the *P* values and standard error (SE) from the abundance and richness for all insect taxa in each plot compared between each treatment.

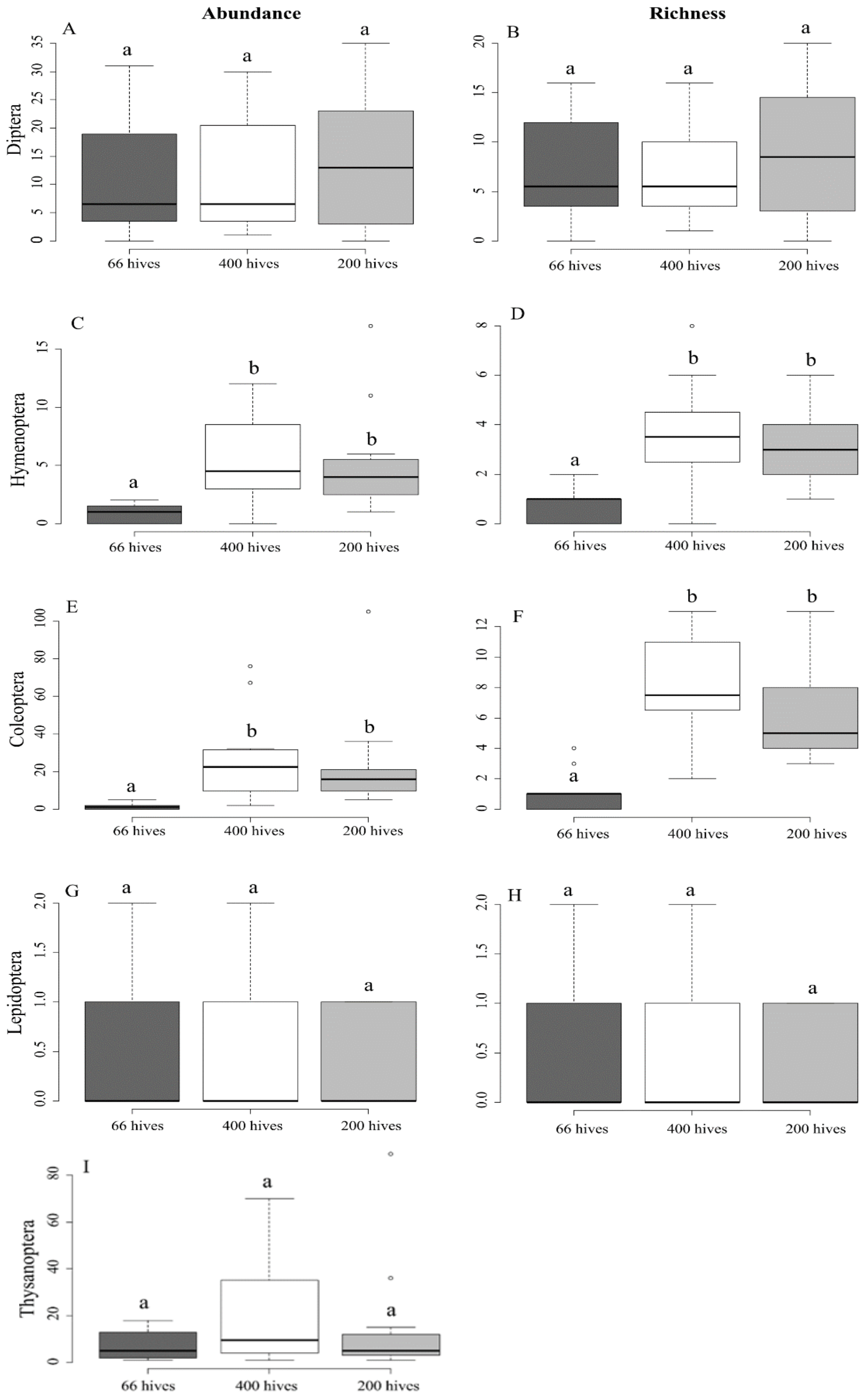
Pan traps

Abundance	**Treatment**	30m		70m		450m		850m	
		P	SE	*P*	SE	*P*	SE	*P*	SE
Diptera	66 and 400	1.000	0.631	0.955	0.668	1.000	0.637	1.000	0.742
Diptera	66 and 200	1.000	0.629	0.999	0.677	1.000	0.632	0.974	0.698
Diptera	400 and 200	1.000	0.630	1.000	0.648	1.000	0.637	0.951	0.704
Coleoptera	66 and 400	0.0002*	0.646	<.0001*	0.572	0.448	0.633	0.036*	1.087
Coleoptera	66 and 200	0.003*	0.651	<.0001*	0.574	0.085	0.620	0.025*	1.085
Coleoptera	400 and 200	0.999	0.431	1.000	0.410	0.999	0.480	1.000	0.451
Hymenoptera	66 and 400	0.363	0.619	0.322	1.097	0.224	0.832	0.915	0.875
Hymenoptera	66 and 200	0.363	0.619	0.288	1.095	0.472	0.844	0.852	0.867
Hymenoptera	400 and 200	1.000	0.477	1.000	0.511	1.000	0.514	1.000	0.613
Lepidoptera	66 and 400	1.000	1.414	0.999	1.155	0.998	1.155	1.000	1.414
Lepidoptera	66 and 200	1.000	1.414	1.000	1.414	1.000	0.913	1.000	1.414
Lepidoptera	400 and 200	1.000	1.414	0.999	1.155	1.000	1.225	1.000	1.414
Thysanoptera	66 and 400	0.524	0.594	0.968	0.799	0.734	0.894	0.919	0.617
Thysanoptera	66 and 200	1.000	0.712	0.989	0.757	0.532	0.833	0.997	0.627
Thysanoptera	400 and 200	0.746	0.671	1.000	0.579	1.000	0.781	1.000	0.581
Richness									
Diptera	66 and 400	1.000	0.495	0.947	0.549	0.992	0.521	1.000	0.596
Diptera	66 and 200	1.000	0.489	0.991	0.555	1.000	0.498	1.000	0.568
Diptera	400 and 200	1.000	0.494	1.000	0.511	0.997	0.524	0.999	0.575
Coleoptera	66 and 400	0.024*	0.546	0.016*	0.739	0.437	0.520	0.083*	1.026
Coleoptera	66 and 200	0.304	0.566	0.033*	0.742	0.533	0.523	0.275	1.038
Coleoptera	400 and 200	0.961	0.327	1.000	0.293	1.000	0.364	0.971	0.346
Hymenoptera	66 and 400	0.651	0.572	0.479	1.044	0.294	0.756	0.995	0.837
Hymenoptera	66 and 200	0.993	0.612	0.479	1.044	0.639	0.775	0.923	0.802
Hymenoptera	400 and 200	0.996	0.449	1.000	0.426	0.999	0.414	1.000	0.586
Lepidoptera	66 and 400	1.000	1.414	0.999	1.155	0.999	1.155	1.000	1.414
Lepidoptera	66 and 200	1.000	1.414	1.000	1.414	1.000	0.913	1.000	1.414
Lepidoptera	400 and 200	1.000	1.414	0.999	1.155	1.000	1.225	1.000	1.414

Appendix 3.5: Honey bee abundance for each managed honey bee hives treatment. The box represents the interquartile range, the thick black line in the boxes represents the median, and the lines extending from the boxes represent the minimum and maximum values. The lower-case letters refer to the statistical difference in abundance between the different managed honey bee hives treatments.



Appendix 3.6: The effect managed honey bee hives treatments on Diptera abundance (A), Diptera species richness (B), Hymenoptera abundance (C), Hymenoptera species richness (D), Coleoptera abundance (E), Coleoptera species richness (F), Lepidoptera abundance (G) Lepidoptera species richness (H) and Thysanoptera abundance (I). The box represents the interquartile range, the thick black line in the boxes represents the median, and the lines extending from the boxes represent the minimum and maximum values. The lower-case letters refer to the statistical difference in abundance and richness in each plot between the managed honey bee hives treatments for the different pollinator groups.



Chapter 4: General discussion

4.1. Managed honey bee in the context of my study

Managed honey bees are important for agricultural crop pollination as they can be easily managed and moved around to the various areas requiring pollination services. To effectively provide these pollination services, colonies of managed honey bees need to be healthy. To maintain the health and strength of these colonies, honey bees need access to diverse, good quality forage. Areas that provide such forage vary across the landscape, for example, agricultural crops and natural areas. In fact, natural areas have been shown to provide a diversity of good quality forage when other sources of forage are unavailable (Hutton-Squire 2014; Masehela 2017). In South Africa, there is an abundance of natural forage available in protected areas, though managed honey bees have been excluded from accessing these areas (CapeNature 2016; SANParks 2022).

Globally, there is mounting evidence that high density bee hive placement can negatively influence local pollinator communities. Where honey bees are introduced, negative impacts on native pollinators have been recorded, native pollinator abundance and richness are reduced, and their foraging patterns are altered (Angelella *et al*. 2021; Badano 2011; Pinkus-Rendon *et al*. 2005). However, negative impacts have also been found where honey bees are native, through the introduction of managed honey bees hives (MHBH) at high densities (Henry *et al*. 2018; Ropars *et al.* 2020). An increase in native honey bees, due to beekeeping, can alter foraging patterns, reduce foraging success, and reduce the abundance and richness of wild pollinators (Lindström *et al*. 2016; Henry *et al*. 2018; Ropars *et al.* 2020; Lázaro *et al.* 2021; Cappellari *et al*. 2022). At the same time, there is some evidence that increased honey bee abundance does not negatively affect other Hymenoptera in areas where honey bees are native (Giannini 2015; Steffan-Dewenter and Tscharntke 2000). Therefore, different groups of wild pollinators are or may be affected differently by increased honey bee abundance as a result of beekeeping practices, through the placement of managed bee hives.

4.2. Exploring effects of managed bee hives of pollinators

There are currently limited and inconclusive studie***s*** exploring MHBH effects/impacts on local pollinator communities in South Africa and this calls for more studies to address the data and knowledge gaps (but see Brand, 2009; Geerts and Pauw 2011). Here, I explored the effect on pollinators by introducing MHBH into natural vegetation. Furthermore, the effects on the reproduction of their dependent plants. It is essential to keep in mind that the honey bee species in reference here, the Cape honey bee (*Apis mellifera capensis*), is native to the study area – the Cape Floristic Region (CFR). In both Chapters two and three, I specifically investigated whether the addition of managed honey bee hives increased the number of honey bees on native flowers, affected pollination networks and pollinators flower visitation rate. I also investigated how the introduction of MHBH influenced the composition of the pollinator and other insect communities, affected the abundance and richness of insects and if distance from MHBH has an influence on the aforementioned factors. In Chapter two, I also investigated whether the addition of honey bee hives affected the seed set of *Cullumia reticulata*.

My findings from chapter two show that the addition of MHBH did increase the number of honey bees on native flowers relative to before MHBH introduction. Also, in chapter three the introduction of MHBH at the highest density (400 hives) did increase the number of honey bees on native flowers from the lowest density (66 hives). For both chapters, pollination networks were dominated by honey bees and their flower visitation rate increased significantly following the introduction of beehives. Similarly for chapter three with the introduction of MHBH at their highest density pollination networks were dominated by honey bees and their flower visitation rate increased significantly. For Chapter two results in particular, the introduction of MHBH did not influence *Cullumia reticulata* seed set, indicating that honey bees may be effective pollinators of this species. This is not surprising as honey bees are well known generalists (Klein *et al*. 2007). Honey bees were most abundant in plots that had plenty of generalist Asteraceae flowers. Honey bees are known to show floral preference and are attracted to high density flower patch irrespective of the distance or where hives are placed (Lázaro and Totland 2010; Hagler *et al*. 2011; Hung *et al*. 2019), although foraging activities of honeybees are also most effective within 5 km radius (Beekman and Ratnieks 2000) and have the biggest impact on wild pollinators within 1 km of MHBH (Henry and Rodet 2020). This study showed that within 1 km of MHBH distance did not affect the variables investigated, plots closest to the MHBH did not have the highest abundance of honey bees or the highest impact on other pollinators. However, floral composition and distribution in the landscape shaped honey bee abundance and visitation rates rather than distance from MHBH within 1 km. This may also vary from season to season, area to area as not all plants flower at the same time and provide similar rewards for honey bees (Allsopp and Cherry 2004; Hutton-Squire 2014; Masehela 2017).

The introduction of MHBH resulted in a mixed effect on the flower visits of different taxa. In essence, the different pollinator groups were affected differently, an indication that there is some level of tolerance and co-existence in resource sharing (foraging) with honey bees, while other groups are displaced and/or chased away. Therefore, my findings support what has been shown in other parts of the world, whether honey bees are native or introduced, that high density bee hive placement impacts wild pollinators differentially (see Angelella *et al*. 2021; Cappellari *et al*. 2022; Lindström *et al*. 2016; Pinkus-Rendon *et al*. 2005). Diptera were the most sensitive group to the MHBH introduction, whereas Coleoptera were avoidant of areas with high honey bee abundance, and Hymenoptera seemed unaffected. The fact that these different groups behaved or responded differently to high honey bee densities, suggest that they have different coping mechanisms, but it is not fully established if these mechanisms are viable for the survival of any of the groups in the long term. Although the full implications of these effects are still poorly understood for South Africa, other studies (Magrach *et al.* 2017; Ropars *et al*. 2019; Ropars *et al.* 2020 Weekers *et al*. 2021) have already indicated that other pollinators are at risk from not being able to co-exist with high honey bee numbers in the same area as they are chased out and outcompeted for resources. These findings further highlight the need to find effective landscape management approaches that seek to address the floral competitive behaviour of high-density MHBH towards other pollinators. However, this can only be done if or when the full scope in terms of interaction and resource requirements for the different groups is well established, therefore, highlighting the need for more research in the South African context. Priority taxa for future research should include Diptera and Coleoptera.

4.3. Cape honey bee co-existence, evolution, and interaction within the CFR

The Cape honey bee is indigenous to the CFR and has evolved alongside the plants and pollinators in the region. Therefore, it could be argued that the potential negative effects on pollinators and plants should not be as prominent as in their alien range. However, in reality, honey bee colonies would usually be at much lower densities under natural conditions. Even though there has been coevolution, the increased densities from MHBH could potentially cause local extinctions of sensitive pollinators, such as Diptera which had declined flower visitation rates. Key pollinator losses can cause reduction in plant reproduction (Anderson *et al*. 2011; Brosi and Briggs 2013). These losses can have negative cascading effects on other species (Aslan *et al*. 2013) and on ecosystem functioning and services (Estes *et al*. 2011). Specialist plants and pollinators are known to be more sensitive to population declines due to environmental changes (Biesmeijer *et al*. 2006; Sekercioglu 2011). The introduction of MHBH at high densities could trigger this sensitivity through increased competition and changing pollination networks which could then lead to population declines and disrupt ecosystem functioning, even though the Cape honey bee is native. Therefore, it would be an area of further research to investigate how the native honey bee could negatively impact specialist pollinators and plants if introduced at high densities. Again here, the investigations must consider the different area and seasonal differences and/or scenarios.

South African conservation authorities have given consideration to the concerns over the possible effect MHBH could have on wild pollinators in their protected areas, and thus exclude MHBH from being placed in protected areas at local provincial and national levels (CapeNature 2016; SANParks 2022). However, MHBH can still be placed on the fence line of protected areas, and this has been a common practice by beekeepers in some parts of the Western Cape Province. SANParks has indicated the desire to institute MHBH free buffer zones around their protected areas, however they did not state how big these buffer zones would be (SANParks 2022). They also indicated that this would be a collaborative effort with landowners around protected areas rather than an enforceable law at this current time. Here I show that distance from MHBH within 1 km is not important for honey bee abundance. Floral resources will have a larger impact on honey bee abundance. Whether an effective buffer zone around protected areas will need to be up to 5 km away from their fence lines (Beekman and Ratnieks 2000) needs to be determined to evaluate whether a buffer zone is feasible.

Over the years, beekeepers have argued that suitable forage habitat continues to be destroyed, removed and transformed leaving MHBH without adequate forage to maintain their health and ability to render pollination services. This has also been captured in several studies conducted in the Western Cape Province (Allsopp and Cherry 2004; Mouton 2011; Melin *et al.* 2018; Hutton-Squire 2014; Masehela 2017). Beekeepers are particularly concerned with the removal of alien eucalyptus trees, which is one of the most important forage sources for honey bees (Allsopp and Cherry 2004). However there has been an initiative to keep some alien eucalyptus trees as it is vital forage to honey bees. The loss of the critical forage for MHBH means that there is more pressure to find alternative forage to keep up with honey production and pollination services for the agricultural industry. Already, the demand for pollination services increases annually for provinces such as the Western Cape, and more hives means more forage required for the managed bee hives. There are currently various initiatives to encourage the planting of more bee forage (The Bee Effect 2021; SANBI 2023). At the same time, beekeepers also need to explore planting their own forage to sustain their hive, although they have long argued that they do not have land nor funds for bee forage planting (Masehela 2019). Beekeepers must also ensure that the there is enough forage available for the density of their MHBH.

Realising the economic importance of MHBH for the agricultural sector, job creation and the economy of the country, the lawmakers might soon have to deal with strong arguments for MHBH to be given access to protected areas. Should this happen, the need for habitat provision and forage protection for wild pollinators' might be drawn into the limelight of arguments, if not politics, with the science having limited merit to address the potential conflict. Therefore, more and longer-term rigorous studies like I present in this thesis are urgently required. To favour MHBH over wild pollinators could be risky to the long-term stability of ecosystems and our agricultural food systems. It is essential to have conservation areas for wild pollinators to have a refuge away from the anthropogenic pressures placed upon them, since ecosystem functioning and agriculture benefit from the diverse pollinator assemblages that come from these protected areas (Richards 2001; Fontaine *et al*. 2005; Garibaldi *et al*. 2014). Relying too heavily on managed honey bees for pollination services at the detriment of wild pollinators, could cause robust populations of diverse wild pollinators to be lost, and leaving managed honey bees as one of the only pollinators available would put ecosystems and food security at risk. Honey bees are vulnerable to population declines due to how they are managed, as was seen with the varroa mite and the spread of disease it facilitated (Schroeder and Martin 2012) and then we would be left without large populations of functional pollinators. Therefore, it remains crucial to champion the conservation of wild pollinator populations. Thus, mindful consideration to the effect that high-density MHBH have on wild pollinators should be applied when placing bee hives in natural areas. Consideration should be given to balancing honey bees' need for forage and maintaining healthy populations of wild pollinators.

4.4. Concluding remarks

My results show that introducing managed honey bee hives into natural vegetation did have some impacts on the local pollinator and insect communities. However, this is based on data collected over a limited time frame and these findings should be viewed and interpreted with caution. However, even though my study was conducted over a short time frame, impacts were still found. More studies over a longer time frame are needed to get a deeper understanding of long-term impacts. Longer term studies will provide more robust results on the impacts of MHBH, because the impacts of short-term studies could be attributed to other uncontrollable factors that can affect the abundance of pollinators such as weather. For short-term studies pollinator abundances changes could be due to pollinators moving away from the area of MHBH introductions while long term studies will be able to observe population declines. The number of MHBH that are introduced could be increased for future studies, as only 10 MHBH were introduced in chapter 2. An increased number of MHBH could reveal stronger impacts and would be in line with the high number of MHBH that beekeepers introduce. Studies should also investigate how floral resource distribution and abundance affects the impacts from MHBH. Having a control study area where no MHBH are introduced can be beneficial to create more robust results by having baseline data to compare to study areas where MHBH are introduced. This will provide insight into whether the effects on pollinators are caused by MHBH or if they are related to natural environmental variability. Having studies in different vegetation types could also be beneficial to ascertain how the impacts of MHBH present themselves within different environments and floral makeups.

As insect populations continue to decline globally, the preservation and protection of insects and other pollinators across the different landscapes, including protected areas, will become increasingly vital for their conservation and management. This includes protecting pollinator habitat, restoring pollinator habitat, and creating corridors between pollinator habitats. At the same time, the agricultural crop pollination demand increases annually, meaning that beekeepers must find additional forage to maintain the colonies to meet these pollination requirements. The escalating pressure is on beekeepers, and they are already seeking to utilize the vegetation in nature reserves and protected areas for forage. Over the years, this issue has become controversial and is already causing tension and conflict between the beekeeping industry and conservation bodies, particularly in the Western Cape Province. For the conservation authorities, protecting the diversity and abundance of wild pollinators, and biodiversity in general, is a priority, especially in all protected areas. In their view, the beekeeping (and agriculture) industry should find ways that ensure suitable forage for managed bees to maintain their health and strength thus enabling honey bees to effectively render their pollination services. They further argue that beekeeping is an agricultural practice, and not conservation. In the below section, I propose a number of recommendations to assist both the beekeeping industry and conservation authorities in working towards finding tangible solutions around this matter.

4.5. Recommendations

4.5.1. For the beekeeping industry:

- **Finding alternative forage sources:** increasing the diversity of flowers in and around agricultural landscapes can be beneficial. The addition of wildflower strips and cover crops to agricultural fields to maintain honey bee health during pollination season could be an appropriate option (Carvalheiro *et al*. 2012). Planting programmes could be initiated where high quality forage plants that are favoured by honey bees are planted. Old farmlands could be rewilded/rehabilitated to create islands of natural forage in agricultural landscapes. Pollinator habitat restoration in agricultural landscapes has been undertaken in other countries, which has increased pollination nutrition, and had secondary benefits such as pest reduction and soil restoration (Wratten *et al*. 2012). Weeds that grow along the edges of agricultural fields are beneficial sources of forage for honey bees. These weeds could be allowed grow instead of being removed or being sprayed with herbicide.
- **Implication of increasing MHBH numbers:** beekeepers need to be aware that they cannot just keep increasing their hives to meet the pollination demand while they have no land or good forage to keep these hives. Beekeepers should then be mindful of the available forage sites they have access to and keep the appropriate numbers of bee hives. Beekeepers should take an active role in planting appropriate forage for their honey bee colonies.
- **Sharing of apiary/forage sites:** beekeepers could look into the options of sharing forage sites. Where access to these sites would be rotated depending on the different crops, they render their services too which will have varying flowering times. This is one practice that can be managed or regulated by provincial beekeeping bodies (associations), or the government since all regulations and beekeeper registrations are already overseen by the National Department of Agriculture, Land Reform and Rural Development (DALRRD).
- **Tax incentives for providing bee forage:** DALRRD and the Department of Forestry, Fisheries and the Environment (DFFE) could consider providing tax incentives for

landowners in the agricultural landscape that maintain honey bee forage on their land or that rehab areas with honey bee forage.

- **Honey bee friendly certification:** Agricultural products that were produced on land that maintains/provide bee forage could get a honey bee friendly certification sticker to indicate that buying these products promotes honey bee health. Similar initiatives have been introduced for commodities such as wine and olives; and have proved to be effective for a number of years.

4.5.2. For conservation authorities:

- **Future studies are needed:** evidence should be gathered from protected areas before MHBH are introduced and then while MHBH are present. My results showed effects from MHBH within 1 km of MHBH, therefore, the maximum distance at which MHBH can still have a measurable negative impact on wild pollinators should be investigated. A study of this nature could help inform the appropriate size of MHBH free buffer zones around protected areas. Multiyear studies should be undertaken to investigate whether there could be long-term impacts from high-density beekeeping on wild pollinator health, fecundity, and survival. The effect of high-density beekeeping on the seed set of specialist plants should be investigated. The effects on wild pollinators should be examined under different densities and stocking rates of MHBH. The impacts on Diptera should be focused on since they were sensitive to MHBH introductions. Hymenoptera should also be investigated even though I found no negative impact on their abundance and richness, they may still suffer from exploitative competition. Megachilid bees could be a taxon for further research since they have proven to be effective pollinators of some crop plants and wildflowers species (Steiner and Whitehead 1991; Johnson and Steiner 1994; Watmough 1999; Wousla *et al*. 2020). They will make their nest in artificial glass tubes to allow for studying (Skaife 1950). This would give insight into their fecundity and the number of resources they gather and how introducing MHBH would affect these factors. Other areas of research could investigate whether the proximity of MHBH increases the rate of disease in wild pollinator populations. Alternative natural forage resources for managed honey bees should be investigated, such as restoration of degraded areas in agricultural landscapes for the purpose of providing forage for managed honey bees. This could be a beneficial collaboration between the two industries.

4.6. References

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