Spatio-temporal patterns of hover fly (Diptera: Syrphidae) diversity across three habitat types in KwaZulu-Natal, South Africa

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PREFACE

The research contained in this dissertation was completed by the candidate while based in the School of Life Sciences of the College of Agriculture, Engineering and Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa under the supervision of Professor Timotheus van der Niet, Dr John Midgley and Dr Kurt Jordaens from March 2020 to December 2022.

These studies represent original work by the candidate and have not otherwise been submitted in any form for any degree or diploma to another University. Where use has been made of the work of others it is duly acknowledged in the text.

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DECLARATION - PLAGIARISM

I, Luhlumelo Mva, declare that:

1. The research reported in this thesis, except where otherwise indicated or acknowledged, is my original research.

2. This thesis has not been submitted in full or part for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs, or other information unless specifically acknowledged as being sourced from other persons.

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ABSTRACT

Hover flies (Diptera: Syrphidae) are poorly studied in southern Africa and as a result, little is known about their abundance throughout the year. Hover fly abundance is generally expected to vary according to vegetation types, due to differences in the type and diversity of floral resources, but this has not yet been investigated in South Africa. This study aims to investigate temporal and spatial patterns of hover flies across three different, but adjacent habitats (forest, grassland, and plantation) in KwaZulu-Natal (South Africa). This was done in two ways, first, by analysing occurrence data from the Global Biodiversity Information Facility's (GBIF) database across months of the year. Second, by quantifying fly presence and abundance using Malaise traps set up in three different habitats and supplemented with hand-netting data. The Malaise traps were set up from October 2020 - September 2021 and were generally serviced weekly. Hover flies were sorted and identified using available keys at the KwaZulu-Natal Museum. The KZN GBIF database contained 11 tribes that represented three distinct phenological patterns. The Karkloof GBIF dataset contained seven tribes that represented two distinct phenological patterns. The field collection dataset contained eight tribes that represented two distinct monthly patterns, although these slightly differed from the patterns found in the GBIF data. Most records were from January, September and December whereas few records were from May, June and July. Minimum-minimum, average-minimum, average maximum and average temperature showed a positive correlation with hover fly abundance. In terms of spatial patterns, grassland had the highest number of adult hover fly individuals (154), followed by forest (106) and plantation (20). There was an overall effect of habitat type on both the mean number of species and the number of individuals per trap per week. In addition, Shannon's diversity showed variation among the three habitat types whereas Simpsons Evenness index showed no variation. The results show that hover fly populations remain active throughout the year, but with distinct fluctuations in their abundance. They also show that heterogeneous indigenous habitats such as grassland and forest represent high abundance, diversity, evenness and richness of hover flies and this may be due to the diversity in available microhabitats, compared to the plantation, which is a modified habitat that lacks microhabitat diversity. Nonetheless, further studies should be undertaken in different regions of South Africa to better understand the monthly patterns as well as the effect of habitat type on hover fly diversity.

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Chapter One: General Introduction

Although the exact number of species of insects is unknown, as more insect species are continually being discovered worldwide (Stork, 2018), they are the most species-rich group, accounting for more than half of all known species globally (Stork, 2009; Zhang, 2011). They exhibit diverse life history strategies, modes of movement, seasonality, size, trophic levels, and requirements for habitats (Nazir *et al*., 2014). Insects are divided into approximately 30 orders. Of these, the four most speciose are Coleoptera, Lepidoptera, Diptera, and Hymenoptera (Adler & Foottit, 2009; Stork, 2009).

Because of this diversity, insects occupy many niches and are involved in many ecological processes (McGeoch, 1998; Zhang *et al*., 2007). These include pollination, predation/parasitism, nutrient cycling, and decomposition (Pywell *et al*., 2015). Insect presence can also be used as powerful monitoring tool in environmental management as they are sensitive to short-term and long-term impacts of land management and restoration efforts (Underwood & Fisher, 2006). Finally, insects are also commonly used as measures of biodiversity (Purvis & Hector, 2000; Taylor & Doran, 2001).

Regardless of the positive impact insects have on the general functioning of ecosystems, some species also have a negative impact on crops, livestock, and humans. Insects pose an important constraint to socio-economic development due to the huge losses they cause in the agricultural sector because insects and insect-borne diseases affect the worldwide crop and livestock industry at various scales (Harris, 2017; Villet, 2017; Garros *et al*., 2018). Some insect species are pests or potential pests that may affect the health and vigor of the animal (Jankielsohn, 2018). Insects can cause a reduction in weight gain, cause abortion of embryos, and reduction of meat, wool, and milk production and, in extreme cases, they may be responsible for animal deaths (Eldridge & Folman, 2012). Additionally, *ca* 10,000 insect pests destroy up to 40% of the world's food crops annually (Dhaliwal *et al*., 2007). The damage usually results from direct feeding by larvae of phytophagous insect species on harvested products or by causing plant damage by leaf-mining, stem-boring, root-feeding, or gall-forming (Harris, 2017).

Despite their diversity, abundance and the various roles insects play, they are rarely included in biodiversity studies. If insects are included, the focus is usually only on a few specific insect groups (Clark & May, 2002; Hawksworth, 2011). This is likely due to the limited resources invested in the study of this highly diverse group of invertebrates. Their small body size and variability in physical features also makes insect identification and diversity studies more challenging than studies of other animal and plant groups (Yi *et al.*, 2011). Nonetheless, it is important to have a solid understanding of how insects respond to human activities and climate change, as this necessarily informs conservation management decisions and assessments of the anthropogenic and climate change effects on the ecosystem (Nicholsa *et al.*, 2007).

Hover flies

Diptera, or true flies, are an order of ubiquitous insects that occur in almost all ecosystems worldwide, including urban areas (Alder & Foottit, 2009; Courtney *et al.*, 2009). Furthermore, they are important for delivering ecosystem services including pollination, but they are also among the worst pests for humans and livestock (Pywell *et al.*, 2015). One of the most important fly groups from an ecological point of view comprises hover flies (also known as flower flies, or syrphids). The systematic study of hover flies (Diptera: Syrphidae) has gradually progressed since the 17th century, and approximately 6200 species in 210 genera are currently recognized worldwide (Thompson & Rotheray, 1998). About 610 hover fly species in 60 genera are known from the Afrotropical Region, but the highest species diversity (*ca* 1800 species) is found in the Neotropical Region (Thompson, 1999; Ssymank *et al.*, 2021). The Afrotropical Region has species from three out of the four hover fly subfamilies: Eristalinae, Microdontinae, and Syrphinae (Thompson & Rotheray, 1998; Whittington, 2003; Jordaens *et al.*, 2015), while the subfamily Pipizinae, has the greatest diversity in the Palaearctic and Nearctic Regions, it is absent from the Afrotropical Region (Mengual *et al.*, 2015).

Adult hover flies are small- to large-bodied flies (4–25 mm), with a petiolate to wide and robust abdomen (Thompson & Rotheray, 1998; Ssymank *et al.*, 2021). Adult hover flies vary in colouration, usually among, rather than within genera. They are usually black or brown with yellow or orange abdominal bands, though some are entirely black or metallic green to blue (Thompson & Rotheray, 1998; Figure 1.1). Many hover fly species mimic wasps or bees, as the banded yellow and black colouration is thought to protect them from predators as it likely deceives these into thinking they are venomous (or otherwise harmful) insects (Edmunds, 2000; Penney *et al.*, 2014). Hover flies have large basal wing cells *br*, *bm,* and *cua,* a closed cell *dm*, the branches of vein M_1 are turned up to run parallel to the wing margin joining an unbranched vein R_{4+5}, thereby forming a closed cell r_{4+5}, and, with a few exceptions, a so-called spurious vein located in cell *br* and r_{4+5} which distinguishes them from all other flies (Ssymank *et al.*, 2021).

Feeding behaviour of adult hover flies and larvae

Adult hover flies have a feeding preference for floral resources, specifically pollen and nectar (Branquart & Hemptinne, 2000; Rotheray & Gilbert, 2011). Females consume pollen for nutrients (proteins, lipids, and vitamins) that are critical for egg production and nectar is consumed by both males and females to provide energy for flight (Haslett, 1989; Sajjad *et al.*, 2010; Woodcock *et al.*, 2014; Moquet *et al.*, 2018). Hover fly flower preference varies, depending on the availability of local plant species, and since flowering is often highly seasonal, preference may vary over time (Cowgill *et al.*, 1993; Colley & Luna, 2000). Hover flies exhibit innate colour preferences, with some species preferring yellow flowers (Sutherland *et al.*, 1999; Doyle *et al.*, 2020) and others preferring blue flowers (Lunau, 2014; Doyle *et al.*, 2020). In general, hover flies prefer visiting plants with open flowers in which nectar and pollen are readily accessible for the majority of species with short proboscises, but hover fly species with longer proboscises, particularly in the genera *Asarkina* and *Rhingia*, exploit flowers with relatively long nectar tubes (Gilbert, 1981; Vlaśánková *et al.*, 2017).

Hover fly larvae exhibit a variety of feeding modes that vary for each subfamily (Larde, 1989; Thompson & Rotheray, 1998). The larvae of the subfamily Microdontinae are predatory inquilines in ant nests, where they feed on the early stages of their ant host (Rotheray & Gilbert, 2011). The larvae of the subfamily Syrphinae are zoophagous in nature and most feed on soft-bodied, colonial insects, such as aphids, scale insects, and whiteflies, yet some feed on other insect larvae or are pollinivorous (Rotheray & Gilbert, 2011; Ssymank *et al.*, 2021). The larvae of the subfamily Eristalinae comprise a range of phytophagous, saproxylic, and saprophagous forms. Those that are saprophagous feed on the decaying organic material of plants as well as animals (Rotheray & Gilbert, 2011; Ricarte *et al.*, 2008). The larvae of phytophagous species feed on live plants as borers, on either or both the underground and aerial parts (Thompson & Rotheray, 1998; Ricarte *et al.*, 2008). Eristalinae also includes occasional zoophages, where third-instars are facultative predators of dead or dying bees and wasps (Rupp, 1989; Ssymank *et al.*, 2021).

Ecosystem services of hover flies

Adult hover flies are thought to be the second most important group of pollinating insects in certain parts of the world (Petanidou *et al.*, 2011; De Groot & Bevk, 2012) and can be among the most abundant groups of flower-visiting insects (Inouye *et al*., 2015). They are considered an essential group of insects in agriculture as they play a crucial role in the pollination of different agricultural and horticultural crops, vegetables, and wildflowers (Lapchin *et al*., 1987). Some of the crop species for which hover flies contribute to pollination include apple (Solomon & Kendall, 1970), strawberry (Kendall *et al*., 1971), pepper (Jarlan *et al*., 1997), oilseed rape (Stanley *et al*., 2013) and avocado (Dymond *et al*., 2021). When compared to honeybees, hover flies seem more effective pollinators across various crop systems (Garibaldi *et al*., 2013). Finally, adult hover flies are highly mobile and may facilitate gene flow among plant populations through long-distance pollen transport (Doyle *et al*., 2020).

Hover fly larvae perform various key roles in ecosystems (Larde, 1989; Thompson & Rotheray, 1998). Saprophagous hover fly larvae play a crucial role in the recycling and decomposition of organic matter as they feed on decaying plant or animal matter (Rotheray & Gilbert, 2011; Djellab *et al*., 2019). Zoophagous hover fly larvae provide biocontrol of agricultural crops as they feed on other insect species (e.g. aphids, thrips, ants, etc) (Stubbs & Falk, 2002; Moquet *et al*., 2018). Some hover fly species have been proposed as biological indicators to assess the conservation state of a specific ecosystem (Speight *et al*., 2000). This is due to the specialized larval diet that restricts hover flies to a specific microhabitat during larval development (Sommaggio, 1999; Burgio & Sommaggio, 2007).

Seasonal variation of hover fly abundance

Like most insects, seasonal variation in the abundance of hover flies is affected by abiotic and biotic environmental factors. These environmental factors play a role in determining hover fly survival and affect their population dynamics, distribution, abundance and feeding behaviour (Palumbo, 2011). Hover flies have evolved in response to these factors by showing a wide range of adaptations in *e.g.*, body size and colour (Aguirre-Gutiérrez *et al*., 2016; Badejo *et al*., 2020).

Hover flies thrive in hot and sunny weather conditions and are then mostly observed hovering near flowers and/or feeding on pollen and nectar (Thompson & Rotheray, 1998; Ansari & Memon, 2017). Adult hover flies also often bask in sunlight to increase their body temperature (Thompson & Rotheray, 1998). However, in extremely hot weather they are less active due to the associated risk of dehydration and heat stress (Terry & Nelson, 2018). In cold weather, hover flies are less active and they can often be found sitting motionless in thick vegetation or other protected sites (Hondelmann & Poehling, 2007).

Given the need for various and specific resources (food, temperature, sunlight, larval habitat requirements) that are critical for the life cycle of hover flies, it is expected that their abundance varies in time and space, depending on the presence of the required resources. Seasonal patterns of hover fly presence and abundance have been studied in different parts of the world. General seasonal pattern suggests that they occur in low abundance in cold months and high abundance in hot months, as a result they are characteristic elements of spring and summer (Souva-Silva *et al.*, 2001; Sajjad *et al.*, 2010; Ansari & Memon, 2017; Terry & Nelson, 2018; Djellab *et al.*, 2019). Nonetheless, hover flies are found to be active all year round in some areas, albeit with temporal fluctuations in abundance. For instance, Ansari & Memon (2017) investigated the seasonal variation of hover fly abundance in various habitat types in central Sindh, Pakistan. They found that hover fly abundance indeed varied seasonally with the highest abundance being recorded in spring and the lowest in autumn. They explained that this variation was due to the abundance of flowering plant species and that most of the plants were flowering during spring. Their study also showed that environmental factors such as rainfall, cloudiness, relative humidity and temperature played a role in determining the seasonal patterns. Yet, among these factors only temperature showed a significant correlation with hover fly abundance.

Diversity of hover flies in different habitat types

Hover flies have a nearly worldwide distribution, and are only absent from the Antarctic and some remote oceanic islands (Thompson & Rotheray, 1998). They occur in a variety of habitats including both open and those with closed canopies but do not occur in deserts (Stubbs & Falk, 2002). The distribution of adult hover flies across different habitats is often determined by the niche of the larvae as the larvae are more specialised than adults in their feeding preference (Dziock, 2006; D'Amen *et al.*, 2013). For instance, hover flies with aphidophagous larvae species require a habitat with sufficient aphid colonies before they could lay eggs. The microhabitat must also supply adult hover flies with resources such as food and shelter (Földesi & Kovács-Hostyánszki, 2014; Naderloo & Rad, 2014; Ansari & Memon, 2017; Gaytán *et al.*, 2020).

An example of how hover flies are distributed across habitats, and how degradation of pristine habitats may affect hover fly abundance is provided by Naderloo & Rad (2014). They studied the diversity of hover fly communities in four different habitats (riverside, woodland, fruit garden, and rice field) in Zanjan, Iran. Their results showed that hover fly composition differed among the four habitats. They also found similar hover fly composition between a fruit garden and woodland habitats, and between a fruit garden and riverside, whereas rice fields had a different composition than all other habitats. They suggested that the riverside was very diverse and rich in vegetation, shrubs, mud, and water that attracted hover flies, while the rice field was homogeneous as it had a simple vegetation which consisted mostly of rice bunches.

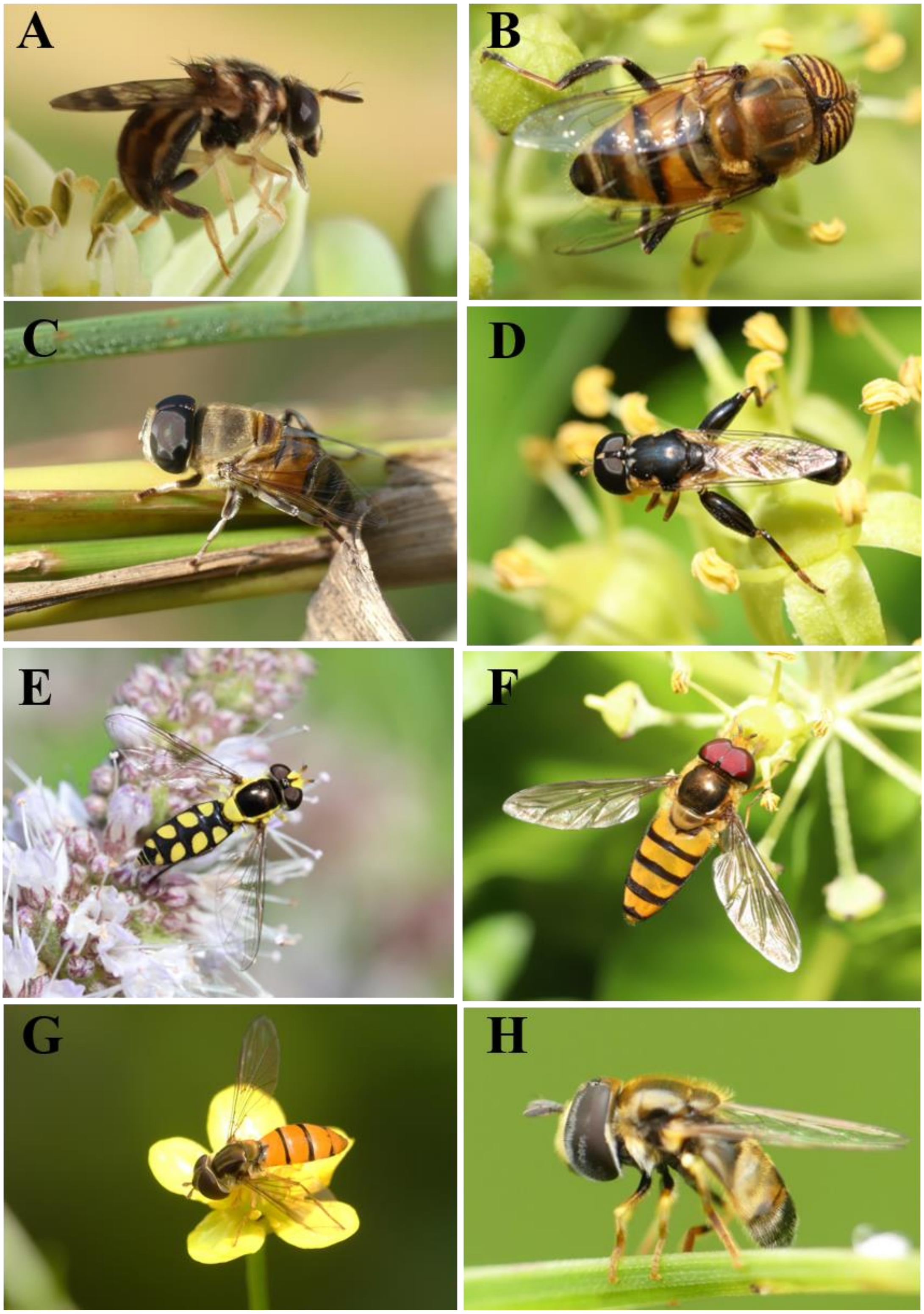

Figure 1.1: Examples of hover fly species: A–D: subfamily Eristalinae; A: *Graptomyza* sp.; B: *Eristalinus taeniops* (Wiedemann, 1818); C: *Phytomia incisa* (Wiedemann, 1830); D: *Syritta* sp. - E–F: subfamily Syrphinae; E: *Allograpta* sp.; F: *Asarkina* sp.; G: *Episyrphus trisectus* (Loew, 1858); H: *Paragus borbonicus* (Macquart, 1842). A, B, D, E, F, Terence Bellingan; C, G and H: Menno Reemer.

Problem statement

Ecological research on Syrphidae in the Afrotropical region is still in the discovery phase, with a focus on taxonomic revisions. Recently, taxonomic works have been published on a variety of Eristalinae such as *Mesembrius* (Jordaens *et al*., 2021) and *Meromacroides* (Bellingan *et al*., 2021). Publications on Syrphinae and Microdontinae are rarer, but *Afrosyrphus* (Mengual *et al*., 2020) and *Ischiodon* (Mengual, 2018) have been revised. In regions where the taxonomy is better understood (*e.g.* the Palaearctic, Nearctic and Neotropic Regions), research has been expanded to include hover flies as important components of the ecosystem in terms of pollination, biological control, and decomposers, but these are rare in the Afrotropical Region. Investigating the patterns in hover fly occurrence (both spatial and temporal) will provide a better understanding of the ecology of Afrotropical species and the roles they play in the environment, this will allow us to compare patterns of occurrence of Afrotropical syrphids to syrphids of other, better-studied regions.

Aims and Objectives

This study aims to investigate temporal and spatial patterns of hover fly diversity and abundance across three different habitat types (forest, grassland, and plantation) in KwaZulu-Natal (South Africa).

The objectives were:

1. To analyse occurrence data from the Global Biodiversity Information Facility (GBIF) database across months of the year.
2. To quantify hover fly presence and abundance using Malaise traps and supplemented with data of hover flies collected using hand-nets.

Study sites

This study was conducted in three different but adjacent habitats in the Karkloof region within the uMgungundlovu district in the KwaZulu-Natal province, South Africa (Figure 1.2). The Karkloof region was chosen as it contains a variety of habitats ranging from mist-belt grasslands, wetlands, and huge tracts of indigenous mist-belt forests, farmland, and plantations. Additionally, the Karkloof region is diverse in microhabitats as well as floristic diversity, which offers potential nectar and pollen rewards as a food source to insects (Wirminghaus, 1990; Johnson *et al*., 2009). The three chosen habitats experience the same climatic conditions and rainfall patterns. The first habitat, forest, is an indigenous Southern Mist-belt Forest (FOz3) with large trees and a variety of flowering plants (Mucina *et al*., 2009). The second habitat, grassland, is a rocky Midlands Mist-belt Grassland (Gs9) without trees, but with shrubs and rich in diversity of flowering plants (Mucina *et al*., 2006). The third habitat, plantation, is a modified monoculture with almost no understory and is dominated by equally spaced pine trees. The plantation is also exposed to logging and other management practices.

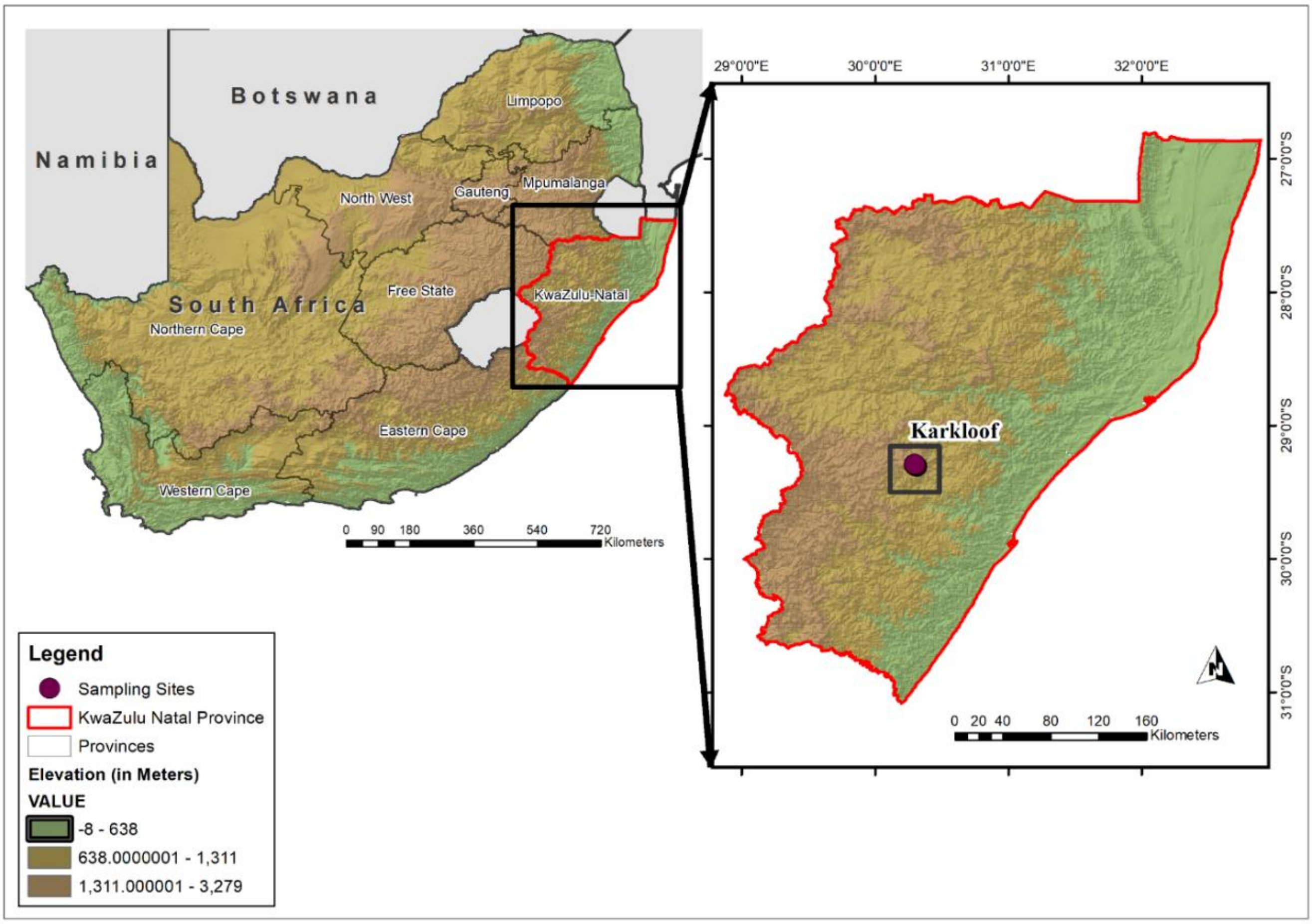

Figure 1.2: Map showing South Africa and the location of the Karkloof within the province of KwaZulu-Natal. (Photo: ArcGIS).

Outline of dissertation structure

This dissertation consists of four chapters: a general introduction, two data chapters and a general discussion. Chapter 1 is the general introduction which provides a literature review of the concepts covered in this study. Chapter 2 investigates temporal patterns of KwaZulu-Natal hover flies at two spatial scales (province wide and focused on the Karkloof region) by analysing existing collection data from the Global Biodiversity Information Facility (GBIF) database across months of the year and by quantifying hover fly abundance using Malaise traps in the Karkloof region and comparing this to the GBIF data. Chapter 3 explores hover fly abundance and diversity in three different, but adjacent, habitats (forest, grassland and plantation) in the Karkloof region, KwaZulu-Natal, South Africa, using Malaise traps and hand-nets. Chapter 4 is a general discussion where I sum up and discuss the important findings of the study and reflect on limitations of the study. Additionally, it provides recommendations for additional studies to further understand temporal and spatial variation in Afrotropical hover fly abundancies.

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Chapter 2: Seasonal patterns of hover fly diversity (Diptera: Syrphidae) in KwaZulu-Natal, South Africa.

Abstract

Hover fly (Diptera: Syrphidae) species composition and abundance in time and space are generally expected to be determined by abiotic climatic factors and biotic interactions such as the abundance of flowers on which they rely for nectar and/or pollen. Here I focus on South Africa, which is well-known for its high plant diversity, but for which studies of insect diversity are largely lacking, to investigate temporal patterns of adult hover fly diversity at two spatial scales in the subtropical KwaZulu-Natal province. I first analyse existing collection data from the Global Biodiversity Information Facility (GBIF) database across months of the year and then compare this to quantitative patterns of hover fly abundance derived from Malaise traps set up in the Karkloof region. The province-wide GBIF dataset contained 5617 hover fly records belonging to 11 tribes that represented three distinct phenological patterns. The local GBIF dataset contained 268 records belonging to seven tribes that represented two distinct phenological patterns. The dataset collected in the field contained 280 individuals belonging to eight tribes that represented two distinct phenology patterns, although these differed slightly from the patterns found in the GBIF data. The most common pattern illustrated by most tribes in all three datasets was characterized by taxa that were present from late spring, throughout summer and, sometimes, in late autumn. This pattern was illustrated by hover flies that had larvae that are mostly saprophagous feeders. Correlations with weather variables confirmed the importance of climate for explaining abundance patterns, as minimum-minimum, average minimum, average maximum and average temperature showed a positive correlation. These correlations may perhaps be due to the presence of a diversity of flowering plants during these seasons. The fact that historical data from the Karkloof gave very similar results to field-collected data from a single year suggests that either approach to quantifying variation in temporal diversity may be useful. The findings of this study suggest that although adult hover flies can be found all year round, there is variation in the monthly patterns exhibited by tribes that may belong to the same subfamily. Future work focusing on the monthly patterns of hover flies in other parts of KwaZulu-Natal and the rest of South Africa should be considered as well as investigating the drivers behind the phenological patterns.

Keywords: *GBIF, Karkloof, phenology, occurrence patterns, abundance patterns*

Introduction

Insect diversity is affected by a variety of abiotic (*e.g.*, temperature, rainfall, relative humidity) and biotic (*e.g.*, resource availability, host plant quality) environmental factors (Kevan & Baker, 1983; Ben-Yosef *et al*., 2021). These environmental factors play a role in determining insect survival and affect their population dynamics, distribution, abundance, and feeding behaviour (Palumbo, 2011). Due to variation in these factors, many insect populations fluctuate throughout the year but and show distinct phenological patterns that vary over time (Kevan & Baker, 1983).

Abiotic factors affecting seasonality of insects

Insects are poikilothermic, which means that their body temperature is usually linked to changes in ambient temperature (Nedvěld, 2009). The majority of insect species have an optimal temperature range to complete their life cycle (Block, 1990; Chapman, 1998; Cooper & Cave, 2016). When exposed to temperatures below their optimal range (cold temperature), many insect species will enter a chill coma state (Mellanby, 1939). This is a state where the insect is immobilized by the cold and insect development and reproductive rate are slowed (Dank, 1987). Temperatures exceeding the optimal range may rapidly increase insect death rate due to the risks associated with desiccation (Cooper & Cave, 2016). Some insects can mitigate against temperature stress using behavioural thermoregulation, heating up using sunlight through basking behaviour or by shivering, where they vibrate their wings during warm-up (Heinrich, 2009). High temperatures are avoided by accessing cooler microhabitats (Bodlah *et al*., 2017) or evaporative cooling (Prange, 1996).

While temperature is a highly influential factor affecting insects (Souza-Silva *et al*., 2001; Jaworski & Hilszczański, 2013; Du Plessis *et al*., 2020), other climatic factors may also influence the seasonality of insects, such as relative humidity and wind (Kevan & Baker, 1983). Relative humidity determines the seasonality of insect populations as it affects the insect's ability to regulate water loss (Palumbo, 2011). In terms of wind, insects may not be able to take off at very high wind speeds, although the threshold wind speed differs among insect species. To fly successfully in windy conditions, insects need to fly faster than the wind speed (Pasek, 1988). During periods of strong wind, insects may cling to vegetation or display other hiding behaviour to avoid being injured (Lewis, 1965).

Biotic factors affecting seasonality of insects

Biotic factors such as resource availability and host plant quality may also play a role in affecting the seasonal patterns of insects.

Resource availability influences insect seasonality in insects through the availability of flowers for food, which themselves are often highly dependent on seasonally varying climatic variables (Souza-Silva *et al.,* 2001; Sajjad *et al.,* 2010). The abundance of flower visitors may then vary with the flowering season (Barret & Helenurm, 1987; Sajjad *et al.*, 2010).

Host plant availability and quality are particularly important for herbivorous insects. Seasonality can cause changes in host plant quality, which in turn affects the quality of the floral resource’s insects consume (Awmack & Leather, 2002). Changes in host plant quality could result in insects changing their floral diet and feeding on different plant species, which could affect insect’s growth, developmental time and/or fecundity (Ojala *et al.,* 2005). The timing of sexual and asexual reproduction of some insects may also be affected by changes in the host plant's quality (Awmack & Leather, 2002).

Effect of environmental conditions on the abundance of hover flies

Hover flies (Diptera: Syrphidae) are a diverse group of insects and are nearly worldwide in distribution (only absent from the Antarctic Region). Like most insects, the seasonal patterns of hover flies are affected by abiotic and biotic environmental factors (Stubbs & Falk, 2002; Djellab *et al*., 2019). Hover flies have evolved in response to these factors by showing a wide range of adaptations *e.g*. body size and colour that might influence tolerance to environmental conditions ((Aguirre-Gutiérrez *et al*., 2016; Hassall *et al*., 2017; Badejo *et al*., 2020).

In the Palaearctic, Nearctic and Neotropic Regions, hover flies are suggested to be heliophilic and are found in abundance in summer or spring where many are hovering near or on flowers where they feed on pollen and nectar (Thompson & Rotheray, 1998; Ansari & Memon, 2017). Adult hover flies are often seen basking in sunlight to increase their body temperature (Thompson & Rotheray, 1998). They are less active on days with extremely high temperatures due to the associated risk of dehydration and heat stress (Terry & Nelson, 2018).

In winter or cold weather, hover flies are less active, sitting motionless on low plants in thick vegetation, under leaves, or in other protected places where they enter a state of dormancy (diapause) (Hondelmann & Poehling, 2007). Some hover fly populations migrate in response to decreasing temperature, rather than entering diapause (Ouin *et al*., 2011). Others, such as members of the genus *Eristalis,* hibernate in cold climates and are not active in the field (Kendall & Stradling, 1972).

Although patterns of seasonal variation of hover fly larvae have received relatively little attention, studies have suggested that the abundance of larvae in some species is generally affected by local changes in weather patterns. This is because both oviposition and larval development rate are affected by temperature changes (Hagen *et al*., 1999). For instance, Pineda & Marco-García (2008) assessed the seasonal abundance of aphidophagous hover flies in Mediterranean sweet pepper greenhouses. They found that the most abundant aphidophagous hover fly larvae were *Eupeodes corollae* (Fabricius, 1794), *Episyrphus balteatus* (De Geer, 1776) and *Sphaerophoria rueppellii* (Wiedemann, 1830). These hover fly larvae exhibited variation in abundance during different seasons due to seasonal fluctuations and drought.

Studies focusing on the seasonal patterns of hover flies have been conducted in various parts of the world. In Brazil, Souza-Silva *et al.* (2001) investigated the seasonal abundance of flower-visiting flies. The results of their study showed that, as expected, the total abundance of flower visitors was significantly higher in the rainy season when a higher number of plants were blooming. Hover flies were found to be most abundant in January and August when other flower visitors were rare or absent. Sajjad *et al*. (2010) investigated seasonal variation in species abundance of hover flies in a subtropical region of Pakistan. Their results revealed that hover fly abundance peaked in March and April when the maximum number of plant species was flowering. Terry & Nelson (2018) investigated seasonal abundance of hover flies in the Rocky Mountains of central Utah (USA) and found that hover fly abundance showed a bimodal distribution with peaks in June and September. They also noted that hover fly abundance decreased in the driest months (July and August) of the year, which were also the hottest months. They speculated that the bimodal distribution was due to hover flies being able to adapt to the productive vegetation of spring and fall. Finally, Djellab *et al*. (2019) conducted a study in the semi-arid forests of Algeria, focusing on the diversity and phenology of hover flies in pine plantations. They found that hover fly abundance varied from one season to another and that hover flies were most abundant in spring which coincided with the flowering period of most plant species in the area. The above studies show that adult hover flies can be observed all year round even though their activity is not equal throughout the year. The studies also indicate that hover flies are abundant in hot months and are characteristic elements of spring and summer. Moreover, high hover fly abundance seems to coincide with the flowering period of most plant species.

Phenological patterns of the diversity of flying insects in an environment can be studied using different approaches, comprising direct field-based observations or collections as well as the study of historical museum collections. Collecting insects in the field can be done using different collecting techniques of which Malaise trapping, sweep/hand netting and pan trapping are the more commonly used (for a more complete overview see Kirk-Spriggs, 2017). Malaise traps are widely used due to their efficiency and ability to capture great numbers of insects with minimum effort (Matthew & Matthew, 1970; Darling & Packer, 1988; Campbell & Hanula, 2007). A Malaise trap is a passive insect collecting device made of a fine mesh tent-like structure. They mostly trap flying insects (Malaise, 1937). Sweep netting involves the collection of insects using a sweep net which one sweeps through low-lying vegetation, while hand netting is used to collect active insects from leaves or flowers (Southwood, 1978; Spafford & Lortie, 2013). Pan trapping involves setting up coloured pans filled with water and an additive such as soap to break the surface tension whereby insects are attracted to the colour, land on the water and sink to the bottom of the pan (Leong & Thorp, 1999).

Museum collections represent an important source of historical data records that provide valuable information for researchers, scholars and educators. They provide data records that can be used to assess occurrence, distribution and shifts in species ranges, changing species assemblages, the effects of global climate change, and patterns of biological invasion amongst others (McCarthy, 1998; Suarez & Tsutsui, 2004; LaDuc & Bell, 2010; Lister *et al*., 2011). Hover fly diversity has not been extensively studied using museum collections. Yet, Olsen *et al.* (2020) used museum collections to explore the phenological response by hover flies to continually raising annual temperatures. Both historical and direct field-based are important data sources as they can reveal differences, and probably provide complementary information on insect diversity patterns. The field data may provide detailed diversity patterns, but is generally often limited in time and space, whereas, museum collections do not consider fine-scale fluctuations in abundance.

Unlike other regions, seasonal patterns in Afrotropical hover flies have received relatively little attention. Research is still needed in southern Africa to cover gaps in our knowledge, including seasonal patterns in hover fly populations and the drivers of these patterns. Before these drivers can be investigated, seasonal patterns need to be identified. This chapter aimed to investigate monthly patterns in hover fly diversity in the KwaZulu-Natal province (South Africa), with a specific focus on the comparison of the museum and field-collection data. I specifically predict that there will be high numbers of hover flies recorded in hot months because previous studies suggest that adult hover flies prefer hot months that are associated with an abundance of flowering plants.

Materials and methods

Datasets

GBIF occurrence data from KwaZulu-Natal and the Karkloof

Hover fly occurrence data from the province of KwaZulu-Natal (South Africa) were extracted from GBIF (https://www.gbif.org) and were aggregated and sorted in Microsoft Excel by month as the principle unit of comparison (KZN dataset) (see Williams & Ranwashe, 2016; de Moor & Ranwashe, 2017; Gess & Ranwashe, 2017; Muller & Ranwashe, 2017; van Noort & Ranwashe, 2020; Zamisa *et al.*, 2020; Natural History Museum, 2021). From the resulting dataset, hover flies that were recorded in localities that had “Shawswood” and/or “Karkloof” in their description were filtered, extracted and then aggregated in Microsoft Excel (Karkloof dataset).

Field-collected data from the Karkloof using Malaise traps

To obtain a representative estimate of hover fly diversity and abundance in the Karkloof region, three Malaise traps were set up in each of three habitats: forest, grassland and plantation. Hover flies were sampled in each habitat from October 2020 – September 2021. A total of nine Malaise traps were set up, with three in each habitat to obtain a representative sample of each habitat. Each collecting bottle contained a killing agent in the form of a 3 g dichlorvos tablet, which was refreshed every six weeks. A dry killing agent was used rather than a wet killing agent to preserve pollen grains on hover flies in Malaise traps for potential future analyses. Malaise traps were generally serviced on a weekly basis unless this was impossible due to bad weather conditions or civil unrest, in which case the interval was longer. During the servicing, the dichlorvos tablet was removed from the collecting bottle and placed in a new empty collecting bottle that was then used for the next period of collection. The collecting bottles with the insects were tightly sealed and transported to the KwaZulu-Natal Museum (KZNM) where the Diptera were sorted. Hover flies were identified to genus level using the identification key in Ssymank *et al.* (2021) and further to species level using various identification keys and the Syrphidae reference collection at the KZNM. The data was aggregated and sorted in Microsoft Excel by month, which were determined by the last date of the collection month (field collection dataset).

Quantification of selected weather variables

To test whether changes in weather variables correlate with hover fly abundance and diversity patterns, the relationship between temperature and rainfall, and the abundance of hover flies were analysed. Monthly temperature data (°C) were taken from the AccuWeather's website (https://www.accuweather.com/). Temperatures from Howick (South Africa) (situated approximately 24km to nearest Malaise trap) were used, as it was the closest place to the Karkloof region that had temperature information recorded on the AccuWeather's website. Temperature was further categorized into five variables; minimum-minimum, average minimum, maximum-maximum, average maximum and average temperature (Table S2). Minimum-minimum was the lowest minimum temperature of each month whereas the average minimum was the average of the daily minimum temperatures in each month. Maximum-maximum was the maximum temperature of each month whereas the average maximum was the average of the daily maximum temperatures in each month. Average temperature was the average of the minimum and maximum temperature of each month. Rainfall (mm) data was measured at the Shawswood residence in the Karkloof, using a rain gauge. The total for each month was recorded.

Data analysis

Monthly patterns of occurrence data (GBIF) and abundance data (field collection) were visualized for each tribe using circular histograms, produced in Excel (as in Godoy *et al.*, 2009; Carnegie *et al.*, 2011; Staggemeier *et al.*, 2019). Hover flies were grouped to tribe level as the sample sizes for both the Karkloof datasets (GBIF and field collection) were not adequate to split by genus. Tribes that exhibited similar monthly peak occurrence/abundance based on visual inspection of the circular histogram were grouped together and their patterns were represented with the same colour.

The monthly abundance patterns of hover flies collected in the Karkloof region were visualized using a non-metric multidimensional scaling (NMDS) analysis. Bray-Curtis similarity of species abundance was calculated and used to implement NMDS in the Paleontological Statistics Software Package (PAST) ver. 4.03 (Hammer *et al*., 2001). NMDS calculates metric coordinates of species in samples, estimates their non-metric distances based on Bray-Curtis distances, displays species in a dimensional plot and quantifies goodness of fit (R^2) between the non-metric distances with a stress statistic (S) (Bray & Curtis, 1957).

The linear relationship between temperature and rainfall and the abundance of hover flies collected in the Karkloof region were analysed using the Pearson's correlation coefficient using PAST ver. 4.03. Additionally, the relationship between temperature and rainfall was also analysed. Pearson's correlation coefficient measures the linear relationship or association between two continuous variables. Pearson's correlation coefficient also gives information about the strength of the association, or correlation, as well as the direction of the relationship (Schober *et al*., 2018).

Results

The KZN dataset extracted from GBIF contained 6711 hover fly records from KwaZulu-Natal, of which 5617 records were identified to at least genus level. The records belonged to eleven tribes and three subfamilies: Eristalinae (N = 2516) (Brachyopini N = 50, Cerioidini N = 19, Eristalini N = 1519, Eumerini N = 387, Milesiini N = 410, Rhingiini N = 64, and Volucellini N = 67); Microdontinae (N = 256) (Microdontini N = 228 and Spheginobacchini N = 28), and Syrphinae (N = 2845) (Syrphini N = 2393 and Paragini N = 452) (Table 2.1).

The Karkloof dataset extracted from GBIF contained 266 hover fly records belonging to seven tribes of the three subfamilies: Eristalinae (N = 102) (Eristalini N = 58, Eumerini N = 28, and Milesiini N = 14); Microdontinae (N = 29) (Microdontini N = 10 and Spheginobacchini N = 19), and Syrphinae (N = 137) (Syrphini N = 133 and Paragini N = 4) (Table 2.1).

The field collection dataset included 280 hover flies belonging to eight tribes of the three subfamilies: Eristalinae (N = 56) (Brachyopini N = 8, Eristalini N = 14, Eumerini N = 21, Milesiini N = 9, and Volucellini N = 4); Microdontinae (N = 5) (Microdontini N = 5) and Syrphinae (N = 219) (Syrphini N = 177 and Paragini N = 42) (Table 2.1).

Table 2.1: Hover fly occurrence records sorted by tribe and genera extracted from GBIF database. Two databases were considered: one with data from the KwaZulu-Natal Museum (KZN) and one with data from the Karkloof region only (Karkloof). A third data set comprised data collected from Malaise traps in the Karkloof (field collection). The table lists the subfamily and tribe to which each hover fly genus belongs, both ordered alphabetically.

Subfamily	Hover fly tribe	Hover fly genera	Total recorded		
			KZN (GBIF)	Karkloof (GBIF)	Karkloof (field collection)
Eristalinae	Brachyopini	*Chrysogaster*	46	0	8
		Orthonevra	4	0	0
	Cerioidini	*Ceriana*	2	0	0
		Monoceromyia	1	0	0
		Sphiximorpha	16	0	0
	Eristalini	*Chasmomma*	2	0	0
		Eristalinus	723	24	13
		Eristalis	210	7	0
		Mallota	11	4	0
		Mesembrius	147	0	0
		Phytomia	248	13	1
		Senaspis	69	0	0
		Simoides	109	10	0
	Eumerini	*Amphoterus*	12	6	7
		Eumerus	356	22	5
		Megatrigon	1	0	0
		Merodon	18	0	9
	Milesiini	*Syritta*	404	14	4
		Syrittosyrphus	6	0	5
	Rhingiini	*Rhingia*	64	0	0
	Volucellinin	*Graptomyza*	63	0	4
		Ornidia	4	0	0
Microdontinae	Microdontini	**Archimicrodon* *Metadon*	223	10	5
		Paramixogaster	5	0	0
	Spheginobacchini	*Spheginobaccha*	28	19	0
Syrphidae	Syrphini	*Allobaccha*	198	5	0
		Allograpta	281	43	43
		Asarkina	367	3	13
		Betasyrphus	513	53	50
		Episyrphus	175	4	3
		Eupeodes	73	0	6
		Ischiodon	125	0	0
		Melanostoma	647	25	61
		Sphaerophoria	14	0	1
	Paragini	*Paragus*	452	4	42

*Taxonomy of these tribes require further study, we henceforth treat them as a single taxon

Most occurrence records in the KZN GBIF dataset were from September, December, and January and fewer records were from May, June, and July (Figure 2.1). Other months were intermediate in terms of hover fly occurrence. The tribes Eumerini, Milesiini, Eristalini and Syrphini showed a similar monthly occurrence pattern, henceforth referred to as “pattern A” which is characterized by taxa that have multimodal peaks and are recorded all year round, but are mostly present in early spring, late spring, throughout summer, late summer, and sometimes into early autumn. These taxa have relatively constant high numbers in four or five months with peaks between September and March (Figure 2.1). Brachyopini, Rhingiini, Spheginobacchini, Microdontini and Cerioidini illustrated similar monthly occurrence patterns, henceforth referred to as “pattern B” which is characterized by taxa that have bimodal peaks (except Spheginobacchini, which has unimodal peak) present from late spring, throughout summer and sometimes into late autumn and differs from pattern A in having high numbers in one or two months, with the majority peaking in January. Finally, the tribes Volucellini and Paragini illustrated similar monthly occurrence patterns, henceforth referred to as “pattern C” with taxa that have multimodal peaks and are present all year round, but which are typically highest in transition months, when it is neither very hot nor very cold. Volucellini peak in September, January, and April, whereas Paragini peak in December, March and April.

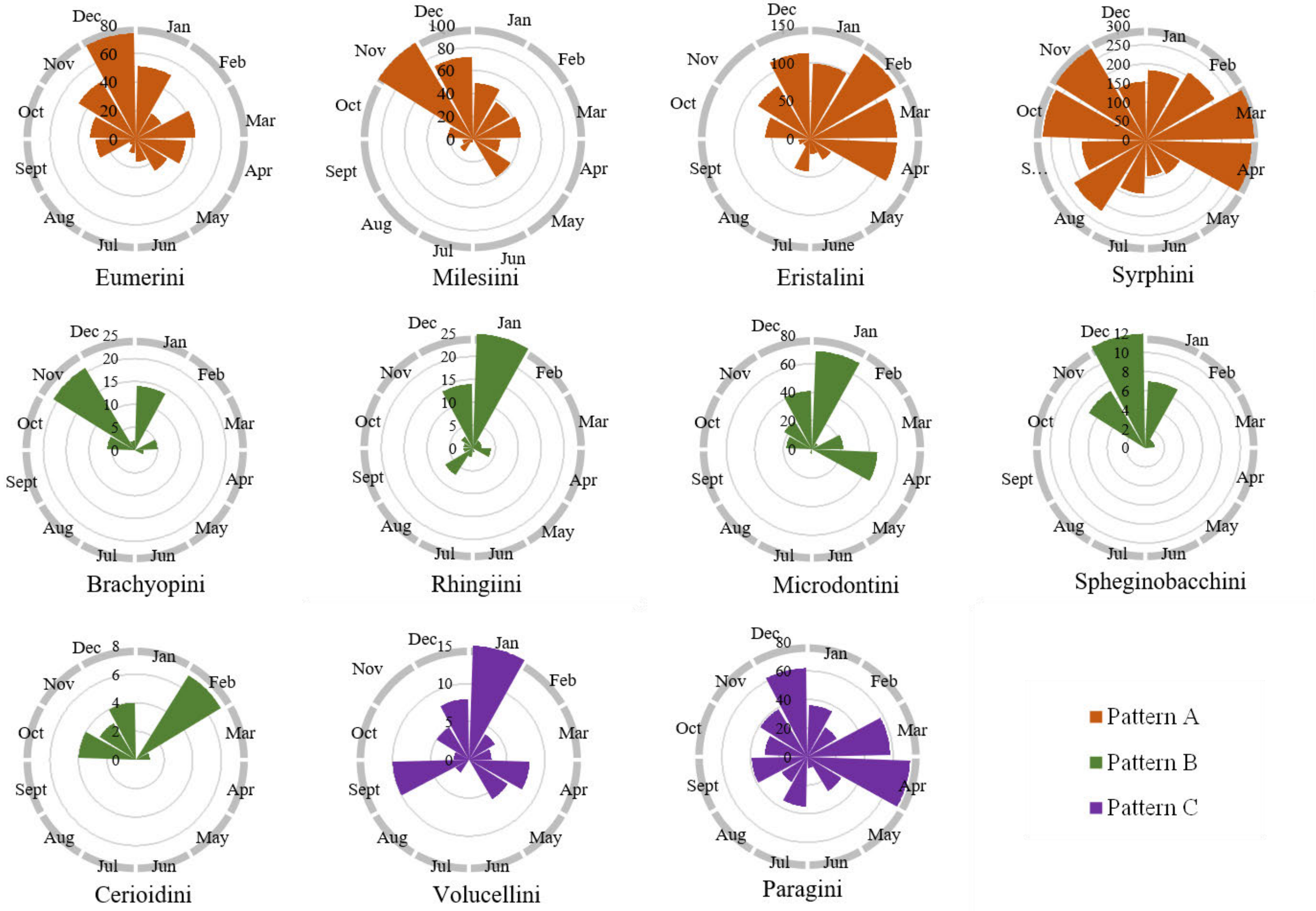

Figure 2.1: Circular histograms of monthly occurrence patterns of KwaZulu-Natal hover fly tribes extracted from GIBF. The height of the triangles represents the number of each hover fly tribe recorded in each month. The absolute number of individuals for each tribe is provided by the numbered inner circles (varies by tribe). Tribes with the same colour exhibit similar phenological patterns.

The Karkloof GBIF dataset (Figure 2.2) contained most records in December. There were no records for tribes Brachyopini, Rhingiini, Cerioidini and Volucellini. Eumerini, Milesiini, Eristalini, Spheginobacchini and Syrphini illustrated similar monthly occurrence patterns (pattern A), as some of the tribes in the KZN GBIF dataset (Figure 2.1). However, instead of peaking in January, as in the KZN GBIF dataset, the abundance peaked in December, except Eumerini that has a peak in October. Microdontini and Paragini illustrated similar monthly occurrence patterns, henceforth referred to as “pattern D”, which differed with the patterns in the KZN GBIF dataset (Figure 2.1). Pattern D is characterized by taxa that have bimodal peaks and are present throughout spring and early summer. There was variation in the peaks among taxa, with Microdontini peaking in October and December and Paragini peaking in August and November.

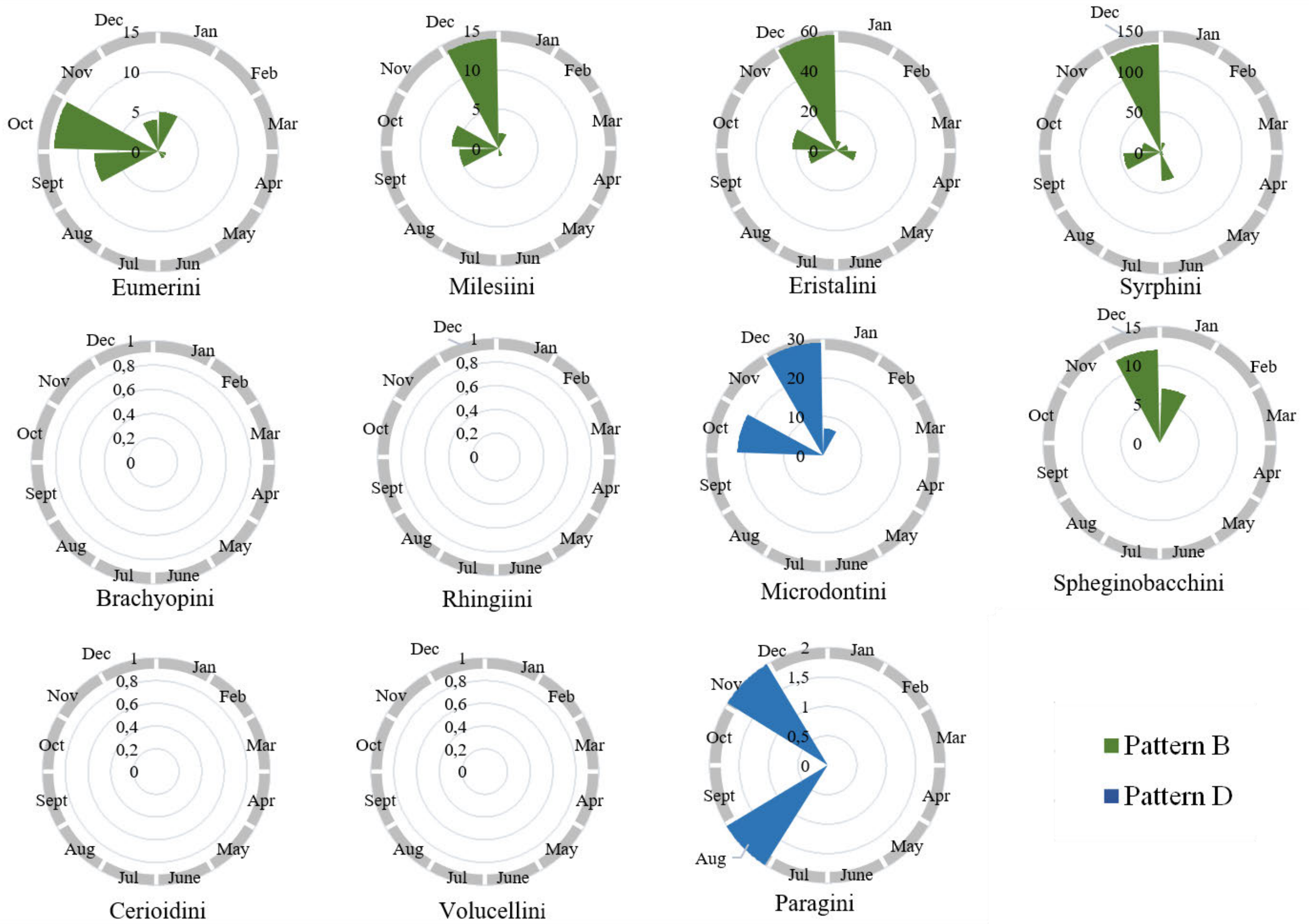

Figure 2.2: Circular histograms of monthly occurrence patterns of the Karkloof hover fly tribes extracted from GIBF. The height of the triangles represents the number of each hover fly tribe recorded in each month. The absolute number of individuals for each tribe is provided by the numbered inner circles (varies by tribe). Tribes with the same colour exhibit similar phenological patterns.

The field collection dataset (Figure 2.3) showed high numbers in October. There were no records for tribes Rhingiini, Spheginobacchini and Cerioidini. Eumerini, Milesiini, Eristalini, Syrphini, Brachyopini, Microdontini, and Volucellini showed similar monthly abundance pattern, pattern B, as some of the tribe in the KZN GBIF dataset (Figure 2.1) yet abundance peaks are between October to January. Paragini illustrated monthly abundance pattern C, similar to Paragini and Syrphini for the KZN GBIF data (Figure 2.1). As in the KZN GBIF, there are three monthly peaks, October, April and May.

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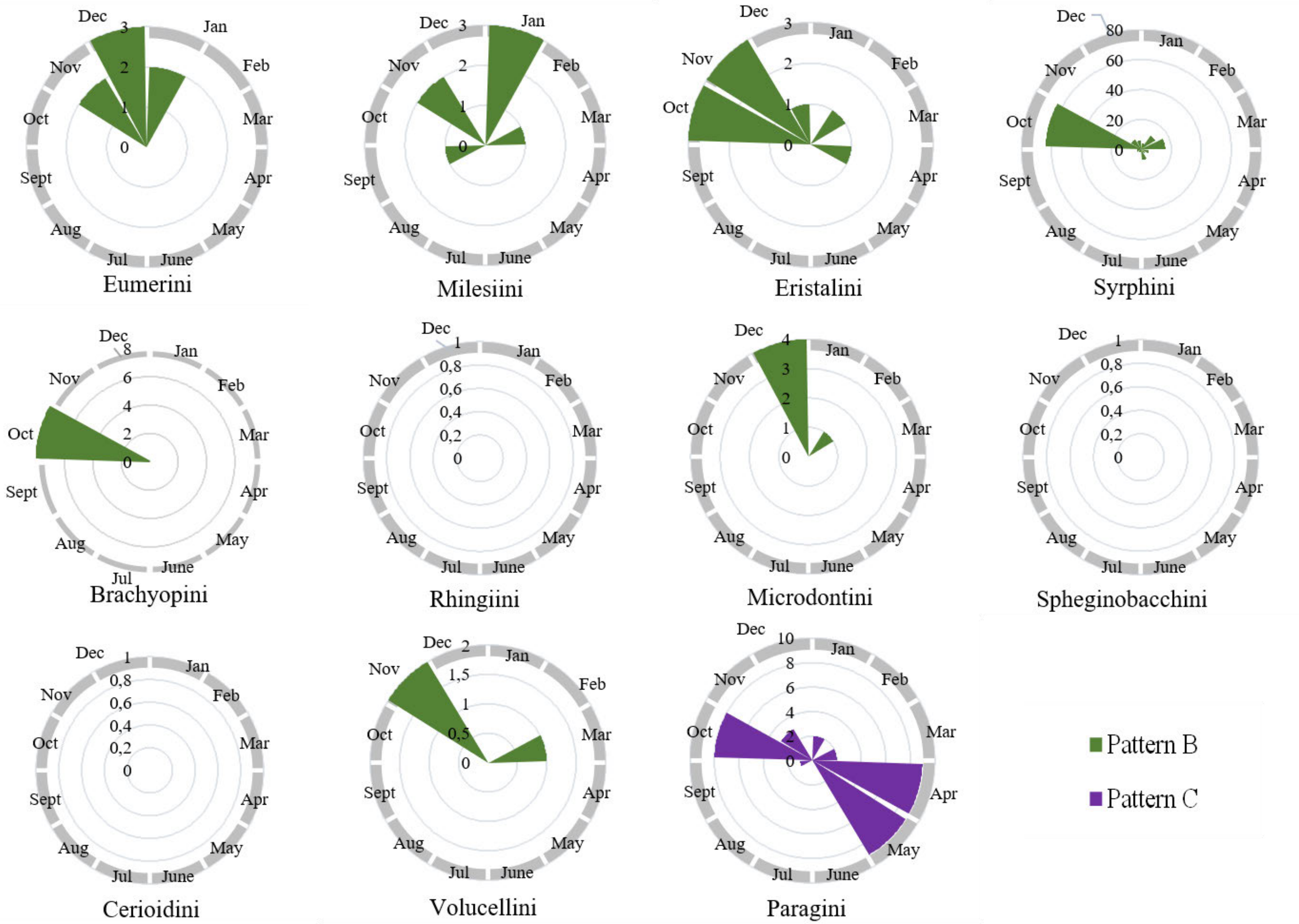

Figure 2.3: Circular histograms of monthly abundance patterns of the field collection dataset of hover fly tribes collected from the Karkloof. The height of the triangles represents the number of each hover fly tribe recorded in each month. The absolute number of individuals for each tribe is provided by the numbered inner circles (varies by tribe). Tribes with the same colour exhibit similar phenological pattern.

No clear groupings were observed in the NMDS plot, though the cooler months (June, July and August) were all on one side of the plot, whereas warmer months (November, December and January) were all on the opposite side (Figure 2.4). Transitional months (March, April and September), one cold month (May) and one warm month (February) all fell in an intermediate position.

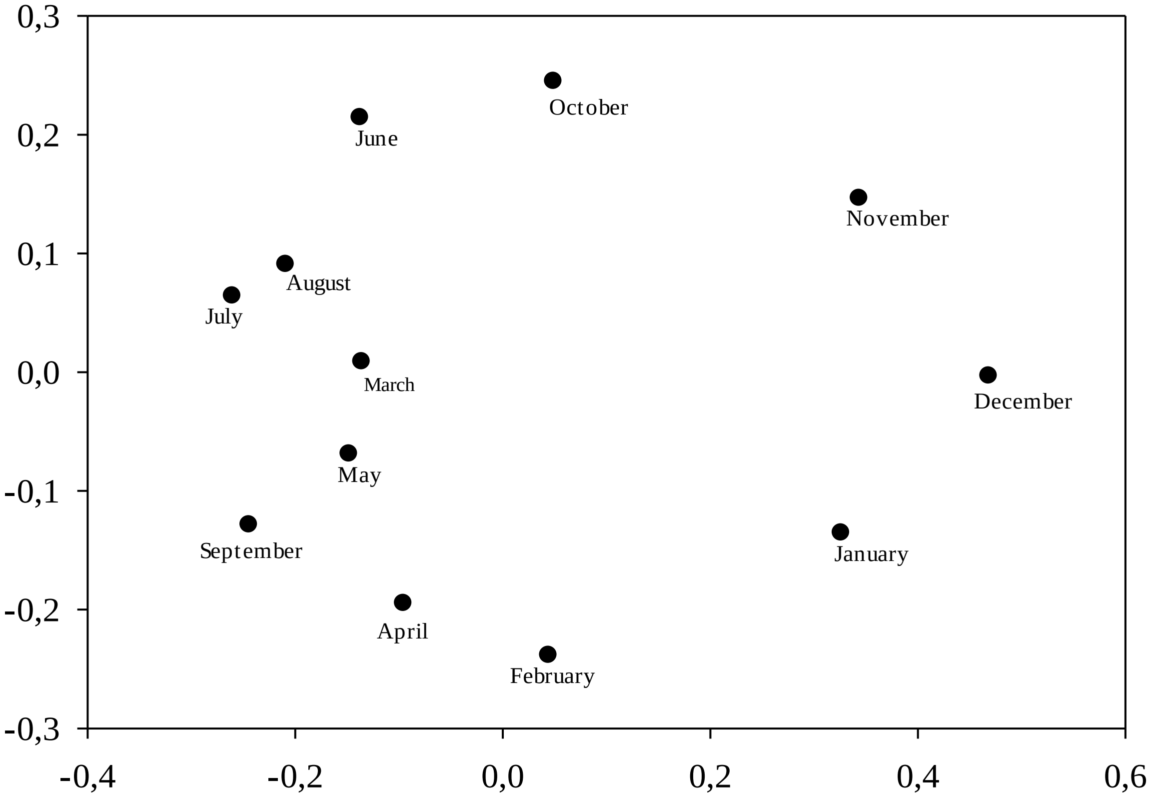

Figure 2.4: Non-metric multidimensional scaling (NMDS) ordination of the monthly abundance of hover fly assemblages in the Karkloof region collected using Malaise traps for 12 months.

Relationship between weather variables and abundance of hover flies:

No correlation was observed between hover fly abundance and the selected weather variables (five temperature and one rainfall variable) when the complete dataset was used. The p-value was > 0.05 for all six of the weather variables, which indicated that their correlations were not significant (Table S3). However, as the abundance in October was considerably higher than in the other months, the data was tested again without this outlier value. When October was removed, four of the variables showed a positive correlation. Maximum-maximum temperature and total rainfall were still not correlated with hover fly abundance but there was a correlation with the four other temperature variables (minimum-minimum: r = 0.71, p = 0.01 (Figure 2.5); average minimum: r = 0.65, p = 0.03 (Figure 2.6); average maximum: r = 0.75 and p = 0.01 (Figure 2.7); and average temperature: r = 0.694, p = 0.018 (Figure 2.8).

Correlation between rainfall and temperature was observed, the p-value was < 0.05 for all five temperature variables, which indicated that these weather variables are not independent (Table 2.2).

Table 2.2: Pearson's correlation coefficient for the relationship between rainfall and temperature in the Karkloof during October 2020 – September 2021. Bold values indicate weather variables with a positive correlation.

Temperature	r	p-value
Minimum-minimum	0.84	**0.00**
Average minimum	0.85	**0.00**
Average temperature	0.82	**0.00**
Maximum-maximum	0.72	**0.01**
Average maximum	0.75	**0.0**

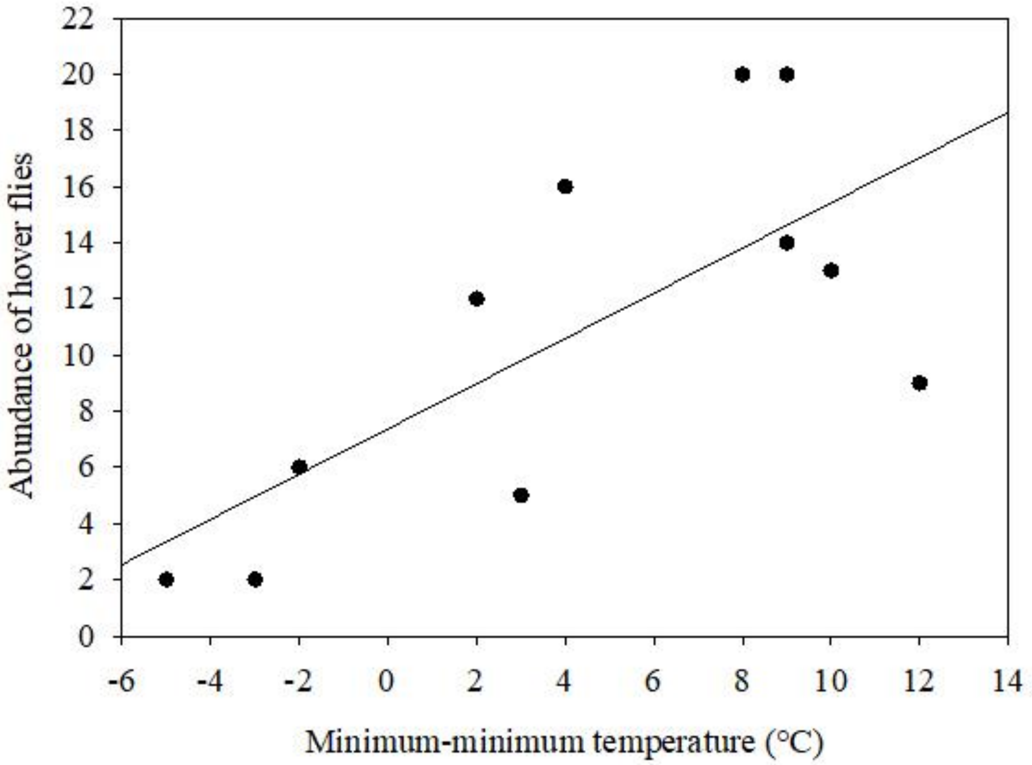

Figure 2.5: Relationship between minimum-minimum temperature and abundance of hover flies in the Karkloof from October 2020 to September 2021

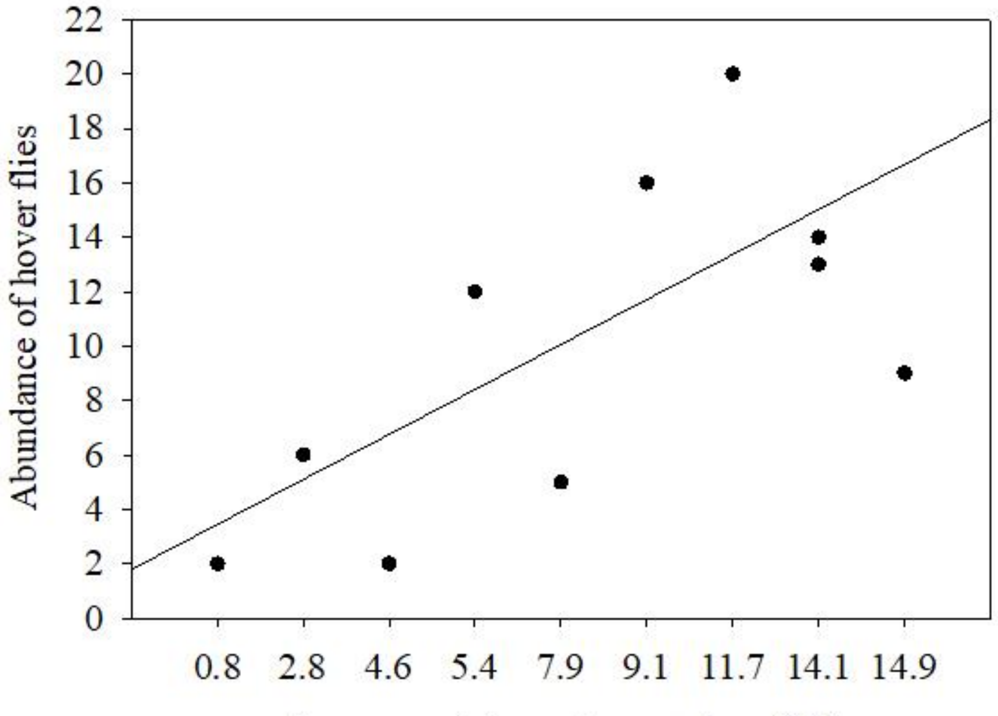

Figure 2.6: Relationship between average minimum temperature and abundance of hover flies in the Karkloof from October 2020 to September 2021

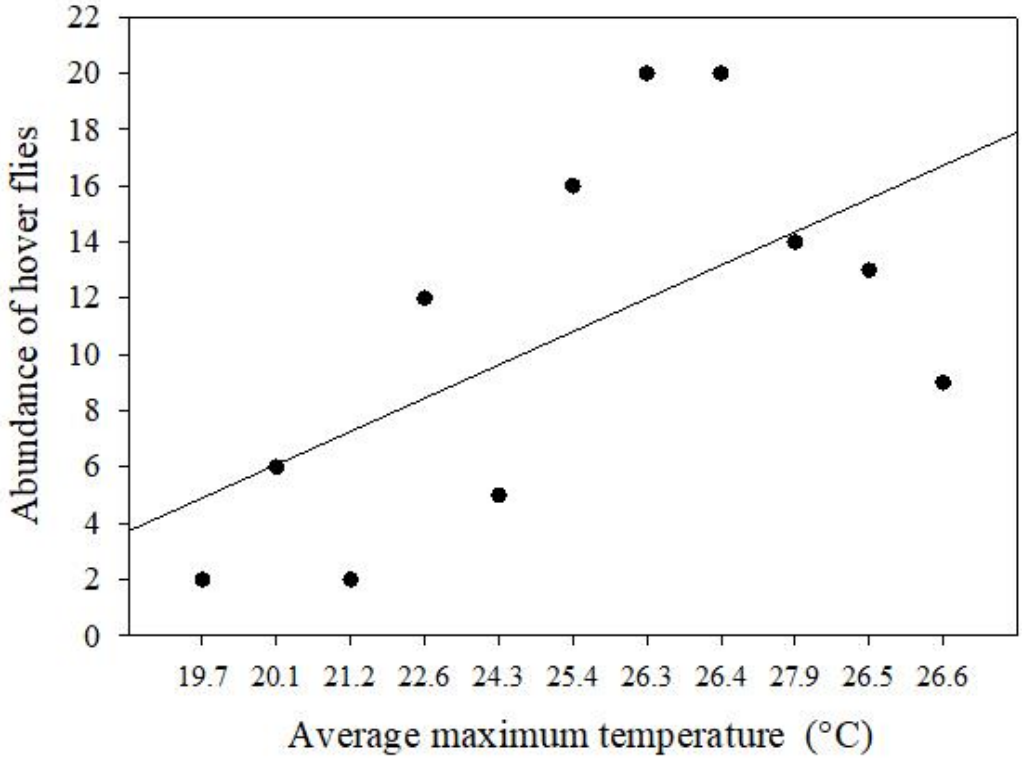

Figure 2.7: Relationship between average maximum temperature and abundance of hover flies in the Karkloof from October 2020 to September 2021

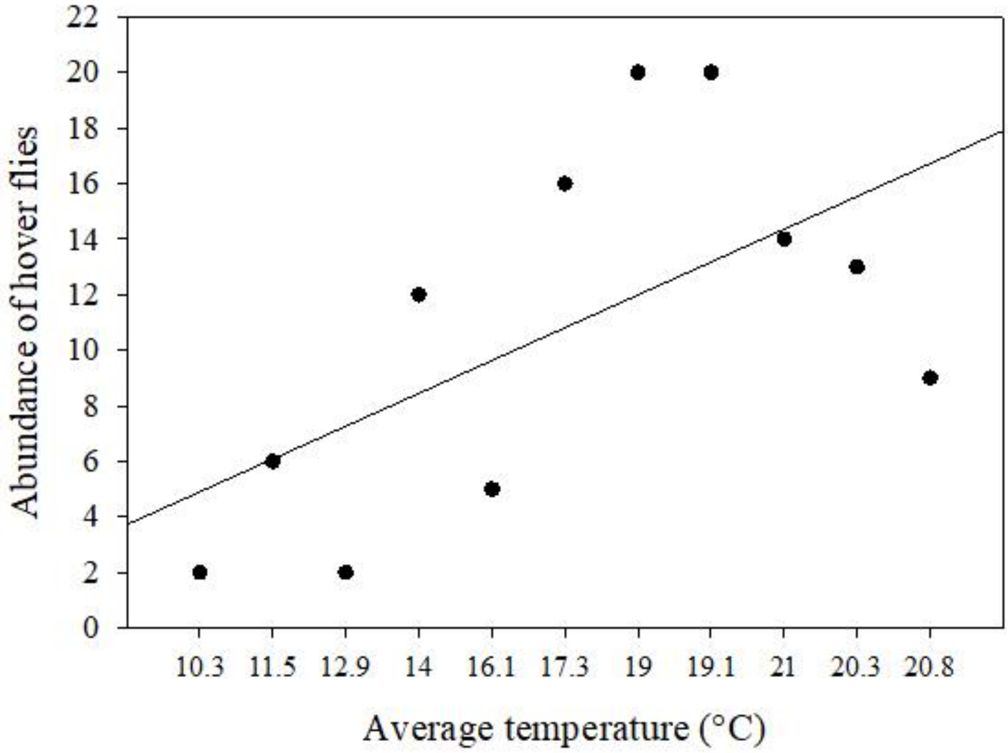

Figure 2.8: Relationship between average temperature and abundance of hover flies in the Karkloof from October 2020 to September 2021.

Discussion

The aim of the study was to investigate the monthly patterns of occurrence (GBIF) and abundance (field collection) data of hover flies in the KwaZulu-Natal province in South Africa. For the GBIF data, two separate data sets were considered, one with all records (KZN dataset) and one with records from the Karkloof region only (Karkloof dataset). The KZN GBIF dataset comprised of hover flies from 11 tribes and I recognized three different monthly occurrence patterns. The Karkloof GBIF and field collection dataset included species from seven and eight tribes, respectively, and both showed two different occurrence (Karkloof dataset) and abundance (field collection dataset) patterns. Pattern B, which was characterized by taxa that were present from late spring, throughout summer and sometimes late autumn, was the most common pattern illustrated by most hover fly tribes in all three datasets. Pattern D, which was characterized by taxa that were present throughout spring and early summer, was only represented in the Karkloof dataset by two tribes.

The occurrence and abundance patterns illustrated by the hover fly tribes from each dataset showed that hover flies can be found all year round, but with marked fluctuations in the numbers and the period recorded. Furthermore, the results also showed that tribes belonging to the same subfamily may exhibit different monthly patterns. The factors that drive variation in monthly occurrences of hover fly tribes are not fully understood, as the biology of many adult hover flies is still largely unknown (Ssymank *et al.,* 2021). One can speculate that the monthly occurrence and abundance patterns are driven by the larval behaviour, as the larvae of hover flies exhibit a wider variety of feeding modes than adults (see Table S4) (Dziock, 2006; D’Amen *et al*., 2013).

The KZN dataset represented eleven hover fly tribes that illustrated three distinct phenological patterns (A, B, and C). Eumerini, Milesiini, Eristalini, and Syrphini comprise pattern A and were found all year round, but mostly from early spring to late summer and sometimes into early autumn. Tribe Eumerini generally has taxa that have larvae that are phytophagous in plant bulbs and rhizomes. Tribes Milesiini and Eristalini have taxa that have larvae that are saprophagous in decaying organic matter whereas tribe Syrphini has taxa with predatory larvae that feed on aphids (Rotheray & Gilbert, 2011; Ssymank *et al.,* 2021). The presence of these hover fly tribes all year round might be explained by the fact that plant bulbs, rhizomes, decaying organic matter and aphids are generally present all year round even in the long cold months, providing food resources to the larvae. Moreover, Eristalini has some larvae that live in semi aquatic environments, which also provide a suitable larval habitat throughout the year. Brachyopini, Rhingiini, Spheginobacchini, Microdontini and Cerioidini illustrated similar monthly occurrence patterns and were found to be present from late spring until summer and, sometimes until late autumn (pattern A). Spheginobacchini and Microdontini have larvae that are associated with ants' nests whereas the other tribes that illustrated this pattern have larvae that are saprophagous, feeding on decaying plant matter. The quality of these resources is likely to change during the year, which could affect larval development. Volucellini and Paragini illustrated occurrence pattern C and were found to be constantly present all year round with several monthly peaks. Volucellini comprises taxa that are saprophagous in decaying fruits and roots (Ssymank *et al.*, 2021). Paragini comprises of taxa with predatory larvae that feed on aphids (Rotheray & Gilbert, 2011). Aphids generally have bimodal seasonal outbreaks, once in spring and again in late summer (McDonald *et al*., 2003; Nebreda *et al*., 2005; Dutcher *et al*., 2012). The availability of fruits and roots as well as aphids in different seasons might provide an explanation as to why these tribes have several monthly peaks.

When comparing the occurrence patterns of the two GBIF datasets (KZN and Karkloof), there is variation in the number of tribes represented as well as the patterns exhibited. The Karkloof dataset, which is nested inside KZN dataset, represented seven tribes instead of the eleven seen in the KZN dataset. In both GBIF datasets, pattern B was the most common pattern exhibited by the tribes. The differences in phenological patterns may be due to either seasonal or regional differences in the distribution and abundance of hover fly species in each tribe. The absence of tribes Brachyopini and Rhingiini, in the Karkloof dataset is likely due to the fact that both these tribes are habitat specific and are diverse in humid or wet habitats and in riverine forests with lush herbaceous vegetation (Ssymank *et al.*, 2021). Despite additional sampling efforts, no species of Rhingiini has been found in the Karkloof region so far (Midgley & Jordaens, pers. comm.). Brachyopini have been collected only once in the Karkloof region (see Chapter 3) when eight individuals were hand collected on a single day. The fact that repeated hand collecting during this study only recorded the tribe once suggests that they are present as adults for a short period and this could explain why they have not previously been collected. Cerioidini and Volucellini are represented by hover fly species that have very specific larval habitats which may be rare and/or unevenly distributed in the Afrotropics. Also, species of both tribes have been found recently in the Karkloof area (Midgley & Jordaens, pers. comm.) and I found one, probably undescribed, species of *Graptomyza* (tribe Volucellini) in the Malaise traps.

Although the data extracted from the GBIF produced extensive and potentially useful information on phenology patterns of hover flies, there are potential biases in the data. Firstly, there is no consistency in terms of temporal sampling. Secondly, the data was collected by several researchers with different research interests and without a specific focus on Syrphidae. Thirdly, different collection methods have been used (mostly hand-netting and Malaise trapping), meaning that differences in the number of hover flies in each dataset is partly explained by differences in collecting efforts of various researchers. The use of field-collection data using Malaise traps in comparison with GBIF data to infer monthly patterns helped to evaluate the accuracy and the reliability of data in the museum collections. This is because Malaise traps provide a standardized method and because the traps were generally serviced weekly, meaning sampling effort was consistent throughout the study period.

Nonetheless, one should consider potential biases of Malaise traps as well. Firstly, Malaise traps do not trap all insect species but collect insects flying through low vegetation. Secondly, Malaise traps tend to collect common species more than rare ones in a habitat (Hutcheson, 1999). Thirdly, certain insect taxa or groups are able to avoid Malaise traps. Lastly, Malaise traps are prone to disturbances and damage and may be torn by animals or strong winds (Skvarla *et al.*, 2020). Therefore, data gathered from Malaise traps should be complemented with data from other collecting methods to provide a full picture on the phenology of species. An effective complementary collecting method that could be considered in future work, is the use of yellow pan traps. These are effective for sampling a wide range of Diptera families (Leong & Thorp, 1999; Nuttman *et al.*, 2011). In this study, yellow pan traps were not used as they have a fluid preservative which is not ideal for the preservation of pollen grains on insects. Moreover, for practical reasons, Malaise traps were generally serviced on a weekly basis. If yellow pan traps would be left in the field for such long periods, they would be prone to flooding, liquid evaporation, and disturbance from wind or livestock (Bartholomew & Prowell, 2005). Malaise traps are particularly useful if they are operated for long periods of time as this data can be used to study meteorological factors that affect flight activity, diel activity and seasonal or phenological cycles (Murchie *et al.*, 2001; Witter *et al.*, 2012; Yuen & Dudgeon, 2016; Skvarla *et al.*, 2020), and therefore represented the most appropriate compromise for addressing the questions in this study.

There is substantial overlap in the patterns of the Karkloof GBIF and field collection datasets. The datasets recorded seven and eight tribes, respectively, with six being present in both datasets. There were no records for Brachyopini and Volucellini in the Karkloof GBIF dataset and no records for Spheginobacchini in the field collection dataset. Spheginobacchini is represented by the genus *Spheginobaccha* and Volucellini is represented by the genera *Graptomyza* and *Ornidia*. The absence of these tribes might be because *Spheginobaccha* and *Ornidia* are rare in South Africa, but *Graptomyza* is more common. Tribes present in both datasets also showed occurrence and abundance pattern B. Tribes Microdontini and Paragini (Figure 2.2) were an exception, as both tribes showed pattern D and Paragini (Figure 2.3) which showed pattern C. The similarities between the data collected using different methods suggests that the biases in the data do not materially affect the observed results.

The response of hover flies to weather variables is unclear in the literature but generally, their abundance seems to be affected by both abiotic and biotic factors (Souza-Silva *et al*., 2001; Shebl *et al*., 2008). The results of the NMDS show no clear groupings of the different months (Figure 2.4). However, warmer months seemed to be grouped together at a distance from the other months whereas cooler months and intermediate months seemed to be grouped closer together. There is no clear explanation regarding these observations, but one can speculate that they may be driven by one or more weather variables. To validate these observations, long-term sampling and monitoring of weather variables is suggested to pinpoint the drivers behind these observations. The weather variables (temperature and rain) that were recorded during the study period (Table S2) initially showed no correlation with hover fly abundance because these results were quite strongly influenced by the month of October, during which a large number of hover fly individuals were collected. It seems as though many individuals emerged in response to the start of the rainy season, as rain in the Karkloof region is likely to start in September (see Table S2). When the data from October was considered an outlier that was removed, minimum-minimum, average minimum, average maximum and average temperature where correlated to hover fly abundance whereas the two other weather variables still showed no correlation. The absence of correlation between hover fly abundance and maximum-maximum temperature might be because high temperature is often a major factor in limiting the activity of many insect species as it can lead to heat stress. Moreover, hover flies might be showing some form of heat avoidance behaviour to buffer them from short extreme events (Bowler & Terblanche, 2008; Kiritani, 2013). Sustained high temperatures (average maximum) can’t be avoided, nor can extreme cold (minimum-minimum) or sustained cold (average-minimum).

The composition and abundance of adult hover flies in a habitat at a particular time is, amongst other aspects, strongly dependent on the presence of flowering plants for food (Klecka *et al*., 2018). The months with high hover fly numbers can be associated with the hot rainy seasons, which may in turn be correlated with the flowering seasons (Struck, 1994; Heinsohn & Pammenter, 1988). The data presented in this chapter focused on temporal patterns. However, certain factors that likely influence hover fly diversity, such as flowering plant availability, not only vary in time but also in space. In chapter three of this thesis, I show that hover fly presence does differ among different habitats. This might be because hover flies prefer heterogeneous indigenous habitats (i.e. forests and grassland) that contain most of the factors required for survival, rather than a modified habitat (i.e. plantations) that lacks microhabitat diversity.

The trapping of hover flies using Malaise traps in this study took place over a period of 12 months. While this period covers a complete annual cycle, it is very short to study the phenology of insects as it does not consider potential inter-annual variation in occurrence and abundance due to temporal variation in environmental conditions. Therefore, increasing the scope to repeat annual cycles of Malaise trapping will allow testing of variation across multiple years.

This study is the first study that provides knowledge about the occurrence patterns (GBIF data) and abundance patterns (field collection data) of Syrphidae in the province of KwaZulu-Natal. The study showed that adult hover flies can be found all year round but with peaks in occurrence and abundance in September, December and/or January, depending on the taxa considered. Yet, there seems to be substantial variation in occurrence and abundance patterns among the three datasets. Hence, a comprehensive survey throughout KwaZulu-Natal and the rest of South Africa is required to obtain a more comprehensive picture of the phenology of hover flies. Such studies will not only be needed to pinpoint the biotic and abiotic factors that influence these monthly patterns, but will also provide useful insights for other fields of research such as the conservation of biodiversity and the relationship between plant communities and their pollinators.

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Supplementary material

Table S2.1. List of institutions containing occurrence data stored in the Global Biodiversity Information Facility database.

Institution code	Institution name	City	Country
AMGS	Albany Museum	Makhanda	South Africa
DMSA	Durban Natural Science Museum	Durban	South Africa
NHMUK	Natural History Museum	London	United Kingdoms
SAMC	Iziko South Africa Museum	Cape Town	South Africa
NMSA	KwaZulu-Natal Museum	Pietermaritzburg	South Africa

Table S2.2: Weather variables (temperature and rain) and hover fly abundance in Howick (South Africa) and Shawswood, Karkloof region, respectively, during October 2020 – September 2021

Month	Temperature (°C)					Total rainfall (mm)	Abundance of hover flies
	Min-min	Ave min	Max-Max	Ave max	Average temp		
October	5	10.3	33	26.2	18.3	78	74
November	8	11.7	34	26.4	19.1	211.5	20
December	9	14.1	33	27.9	21	170	14
January	12	14.9	33	26.6	20.8	285	9
February	10	14.1	31	26.5	20.3	188.5	13
March	9	11.7	31	26.3	19	77.5	20
April	4	9.1	31	25.4	17.3	108	16
May	2	5.4	28	22.6	14	26.5	12
June	-2	2.8	25	20.1	11.5	34	6
July	-5	0.8	29	19.7	10.3	5	2
August	-3	4.6	29	21.2	12.9	43	2
September	3	7.9	33	24.3	16.1	125	5

Table S2.3: Pearson's correlation coefficient for the relationship between hover fly abundance and weather variable (temperature and rainfall) in Howick (South Africa) and the Karkloof region during October 2020 – September 2021. Bold values indicate weather variables with a positive correlation.

Weather variables		With outlier		Without outlier	
		r	p-value	r	p-value
Temperature	minimum-minimum	0.27	0.4	**0.71**	**0.01**
	average minimum	0.29	0.35	**0.65**	**0.03**
	average temperature	0.35	0.27	**0.69**	**0.02**
	maximum-maximum	0.38	0.22	0.45	0.17
	average maximum	0.42	0.17	**0.75**	**0.01**
Total rainfall	rainfall	0.01	0.51	0.4	0.22

Table S2.4: List of the feeding behaviour of hover fly larvae of all the genera recorded in this study for both GBIF and field collection datasets, sorted by subfamily and tribe.

Subfamily	Hover fly tribe	Hover fly genera	Larval feeding behaviour
Eristalinae	Brachyopini	*Chrysogaster*	Aquatic detritus-feeders
		Orthonerva	Saprophagous in decaying vegetation
	Cerioidini	*Ceriana*	Saprophagous in decaying plant sap
		Monoceromyia	Saprophagous in decaying plant sap
		Sphiximorpha	Saprophagous in decaying wood and plant sap
	Eristalini	*Chasmomma*	Saprophagous in decaying organic matter
		Eristalinus	Saprophagous in decaying organic matter
		Eristalis	Saprophagous in decaying organic matter
		Mallota	Saprophagous in decaying organic matter
		Mesembrius	Saprophagous in decaying organic matter
		Phytomia	Semi-aquatic and saprophagous
		Senaspis	Aquatic detritophages
		Simoides	
	Eumerini	*Amphoterus*	Phytophagous in bulbs and plant rhizomes
		Eumerus	Phytophagous in bulbs and plant rhizomes
		Megatrigon	Phytophagous in bulbs
		Merodon	Endophytophagous in bulbs
	Milesiini	*Syritta*	Saprophagous in decaying organic matter
		Syrittosyrphus	Saprophagous in decaying organic matter
	Rhingiini	*Rhingia*	Saprophagous in animal dung

Subfamily	Hover fly tribe	Hover fly genera	Larval feeding behaviour
	Volucellini	*Graptomyza*	Saprophagous in decaying fruits and roots
		Ornidia	Saprophagous in decaying fruits and roots
Microdontinae	Microdontini	*Archimicrodon*	Predatory on ants
		Paramixogaster	Predatory on ants
	Spheginobacchini	*Spheginobaccha*	Predatory on ants
Syrphidae	Syrphini	*Allobaccha*	Predatory on aphids
		Allograpta	Predatory on aphids
		Asarkina	Predatory on aphids
		Betasyrphus	Predatory on aphids
		Episyrphus	Predatory on aphids
		Eupeodes	Predatory on aphids
		Ischiodon	Predatory on aphids
		Melanostoma	Predatory on aphids
		Sphaerophoria	Predatory on aphids
	Paragini	*Paragus*	Predatory on aphids

Chapter 3: Diversity of hover flies (Diptera: Syrphidae) in three adjacent habitat types in the Karkloof region, KwaZulu-Natal, South Africa

Abstract

Hover flies have a nearly global distribution, and are absent from the Antarctic Region and some remote oceanic islands. They occur in various habitat types including both open and those with closed canopies. Many species visit flowers and serve as pollinators of various agricultural and horticultural crops and wild plants. Hover fly abundance is generally expected to vary according to vegetation types, due to differences in the type and diversity of floral resources. However, most of what is known about hover fly diversity are based on studies done in the northern hemisphere. South Africa is characterized by tremendous plant diversity. This study uses this diversity to investigate patterns of hover fly abundance and diversity in three habitats (forest, grassland, and plantation) that are adjacent, but differ almost entirely in plant species composition, in the Karkloof, KwaZulu-Natal, South Africa. Hover flies were sampled using a combination of Malaise trapping and hand-netting for twelve consecutive months. A total of 195 hover fly individuals, belonging to 21 species and 15 genera of three subfamilies were collected using the Malaise traps. There was an overall effect of habitat type on both the mean number of species and the number of individuals per trap per week. In addition, Shannon's diversity index showed variation among the three different habitat types whereas Simpsons Evenness index showed no variation. Generally, the grassland contained the highest diversity and the plantation the lowest. Hover fly communities were distinct among the three habitats when abundance was considered. A total of 85 hover fly individuals belonging to 18 species and 15 genera of two subfamilies were collected with a hand-net. Four species, *Chrysogaster africana*, *Merodon* sp.1, *Phytomia incisa,* and *Episyrphus petilis,* were only caught with a hand-net but not with Malaise traps. The results confirm that heterogeneous, pristine habitats such as the grassland and forest yield high abundance, diversity, evenness, and richness of hover flies, potentially due to the diversity in available microhabitats, whereas the plantation has low hover fly diversity. Furthermore, the results suggest that a complementary collection strategy, including both Malaise trapping and sweep netting, provides a better representation of diversity than either method does on its own. Further studies should be undertaken in different regions of South Africa to assess the generality of findings from this study.

Keywords: *forest, grassland, plantation, flower fly, communities*

Introduction

Insects are one of the most abundant and diverse groups of organisms on earth, making up approximately 60% of all known species (Wilson, 1992; Stork, 2009). Many insect species perform key ecological functions (Kim, 1993). Insects are also good indicators of habitat quality because they respond quickly to environmental changes (Majer, 1987; de Sousa *et al.*, 2014). Of the known insect orders, four are dominant in terms of the number of described species: Coleoptera, Lepidoptera, Diptera, and Hymenoptera (Alder & Foottit, 2009; Stork, 2009).

The insect order Diptera, or 'true flies', is highly diverse and comprises approximately 125,000 species (Courtney *et al.*, 2009). Diptera have a wide distribution and can be found in nearly any environment (Courtney *et al.*, 2009). Adult Diptera are found in a variety of habitats, and some species can be found in highly polluted environments (Courtney *et al.*, 2009). Larval biology is highly diverse: various species occur in nearly every conceivable terrestrial and aquatic microhabitat and include browsers, fungivores, gall-formers, herbivores, leaf-miners, wood-miners and parasites, parasitoids and predators, as saprovores of decaying organic matter (Alder & Foottit, 2009; Courtney *et al.*, 2009; Borkent & Sinclair, 2017). Adults and larvae of Diptera exhibit a broad variety of diets including feeding on nectar or honeydew, pollen, vertebrate blood, insect haemolymph, and/or decaying matter, are also predators on invertebrates, plants and fungal tissue (Borkent & Sinclair, 2017; Marshal *et al.*, 2017).

Hover flies are one of the Diptera families that have a nearly worldwide distribution and are only absent from the Antarctic and some remote oceanic islands (Thompson & Rotheray, 1998). They occur in a various type of habitats including both those with open and closed canopies but they do not occur in deserts (Stubbs & Falk, 2002). In terms of their feeding behaviour, adult hover flies feed on pollen and nectar. Pollen is consumed by females for nutrients that are crucial for egg production. Males also feed on pollen, though less frequently. Nectar provides energy for flight in both males and females (Haslett, 1989; Sajjad *et al.*, 2010; Woodcock *et al.*, 2014; Moquet *et al.*, 2018). Hover fly larvae exhibit a variety of feeding modes: members of the Syrphinae are predators (usually on aphids but some also on other soft bodied arthropods) or occasionally pollinivorous, Eristalinae are saprophagous, phytophagous, and saproxylic and Microdontinae are predatory inquilines in ant nests (Knutson *et al.*, 1975; Ricarte *et al.*, 2008; Rotheray & Gilbert, 2011; Because hover fly larvae have more specialized feeding preferences than adults, they are potentially an important factor that determines adult hover fly diversity patterns (Dziock, 2006; D’Amen *et al*., 2013). Generally, hover flies are collected in microhabitats that provide the abiotic and biotic factors needed for survival, though large species can fly between habitats as needed for feeding, mating or oviposition. Adult hover flies can thus be collected when feeding on flowers, at oviposition sites, when hovering in sunny places, or when resting or basking on foliage (Stubbs & Falk, 2002; Naderloo & Rad, 2014).

Adult hover flies depend on flowers as food source. Areas with great diversity in terms of flowering plant species may therefore provide a larger number of hover fly feeding niches, potentially leading to an increased local hover fly species diversity (Naderloo & Rad, 2014). The abundance and diversity of hover flies in a particular area are generally expected to vary according to vegetation types, due to differences in the type and diversity of floral resources.). For instance, Ansari & Memon (2017) studied hover fly diversity in five different transformed agricultural habitats at many localities of central Sindh, Pakistan. They found that agriculture crops had the highest abundance, richness and diversity of hover flies, and suggested this was a result of the diversity of crops grown in different seasons on a large scale. Fields of fodder crops had the lowest abundance, richness, evenness, and diversity because these had fewer plant species with short flowering periods. Finally, Gaytán *et al.* (2020) surveyed hover fly diversity in ‘young’ and ‘mature’ woodland sites and two adjacent grassland sites in Central Western Spain. The woodland sites had a higher abundance and higher species richness of hover fly than the grassland sites. This suggests that woodland sites may act as hover fly reservoirs and sources. They also found that mature woodland had a higher species richness and abundance than young woodland. This is likely due to grassy clearings and decomposing materials in the mature woodland, which provided a wide range of resources for the hover fly community. The above studies show that adult hover flies are found in abundance in a heterogeneous habitat compared to a homogenous habitat, due to the diversity in microhabitats available for feeding, mating, and overwintering.

Although hover flies may be found in various of habitat types, several factors may limit their abundance and distribution, and their composition may differ among communities or habitats within the same geographical region (Petanidou *et al*., 2011). This may be caused by human activities such as habitat fragmentation and habitat loss, as these are the most influential factors, although other factors such as climate change also play a role (van Langevelde *et al.*, 2018; Forister *et al*., 2019; Sánchez-Bayo & Wyckhuys, 2019). Human modification of habitats may result in altered species interactions in fragmented habitats, which in the long term may reduce biodiversity and species abundance (Robinson *et al*., 1992). For instance, the transformation of pristine habitat for agriculture is one of the major factors that restricts the movement of hover flies between fields in Europe (Wratten *et al.,* 2003, Harwood *et al.*, 1994; Haenke *et al*., 2009). In general, hover fly communities are severely impacted by the transformation of landscapes for agricultural practices (Dormann *et al.,* 2007; Noel *et al.,* 2021). As an example, *Melanostoma fasciatum* (Macquart, 1850) prefers not to cross roads or bare ground such as ploughed fields (Lövei *et al.*, 1998).

In regions where hover fly community composition is relatively well-understood (*e.g.*, the Palaearctic, Nearctic and Neotropical Regions), research showed that hover fly abundance is generally expected to vary according to vegetation type, due to differences in the type and diversity of floral and other resources, but this has not yet been investigated in South Africa. South Africa is a biodiverse country, hosting three biodiversity hotspots comprising nine biomes (Mucina & Rutherford, 2006; Hrdina & Romportl, 2017). The richness of South Africa's biodiversity comes from the mix of tropical and temperate climates and habitats found in the country (Mazijk *et al*., 2021). The substantial heterogeneity of the South African landscape is likely to provide a useful system to investigate whether this diversity is associated with particular patterns of hover fly diversity that have been observed in other countries. The aim of this study is therefore to investigate the abundance and diversity of hover flies in three adjacent habitats (forest, grassland, and plantation) in the Karkloof region, KwaZulu-Natal province, South Africa. The Karkloof region is ideal for this study as it contains both homogenous and heterogenous habitats that might provide variation in available food resources as well as microhabitats. I hypothesize that there will be differences in hover fly abundance and diversity amongst the three habitats, due to the diversity in available microhabitats in each habitat. In particular, I expect the plantation to yield a low number of hover flies in comparison to the forest and grassland as it is a modified habitat that lacks microhabitat diversity.

Materials and methods

Study site

The study was conducted in the Karkloof region within the uMgungundlovu district in the province of KwaZulu-Natal of South Africa (Figure 3.1A). The region has a temperate summer-rainfall climate associated with large convectional thunderstorms as well as frontal conditions in summer and dry winters that have stable climatic conditions characterized by cold dry conditions and moderate frosts (Rambarath *et al*., 2017).

Habitats in the Karkloof region categorized as Southern Mist-belt Forest (FOz3) and Midlands Mist-belt Grassland (Gs9) (Mucina *et al*., 2006). The region is highly diverse and supports a range of flora species. The Southern Mist-belt Forest is multi-layered consisting of two layers of trees, a dense understorey, and an herb layer, and contains approximately 266 plant taxa such as *Podocarpus henkelii*, *Dryopteris inaequali*, *Streptocarpus daviesii*, *Isoglossa woodii*, etc (Wirminghaus, 1990; Mucina *et al*., 2006). The Midlands Mist-belt Grassland is dominated by forb-rich, tall, sour *Themeda triandra* grasslands and contains approximately 400 plant taxa including characteristic species such as *Andropogon appendiculatus, Vigna nervosa, Leonotis ocymifolia*, *Eriosema salignum,* etc (Mucina *et al*., 2006; Peter & Johnson, 2008).

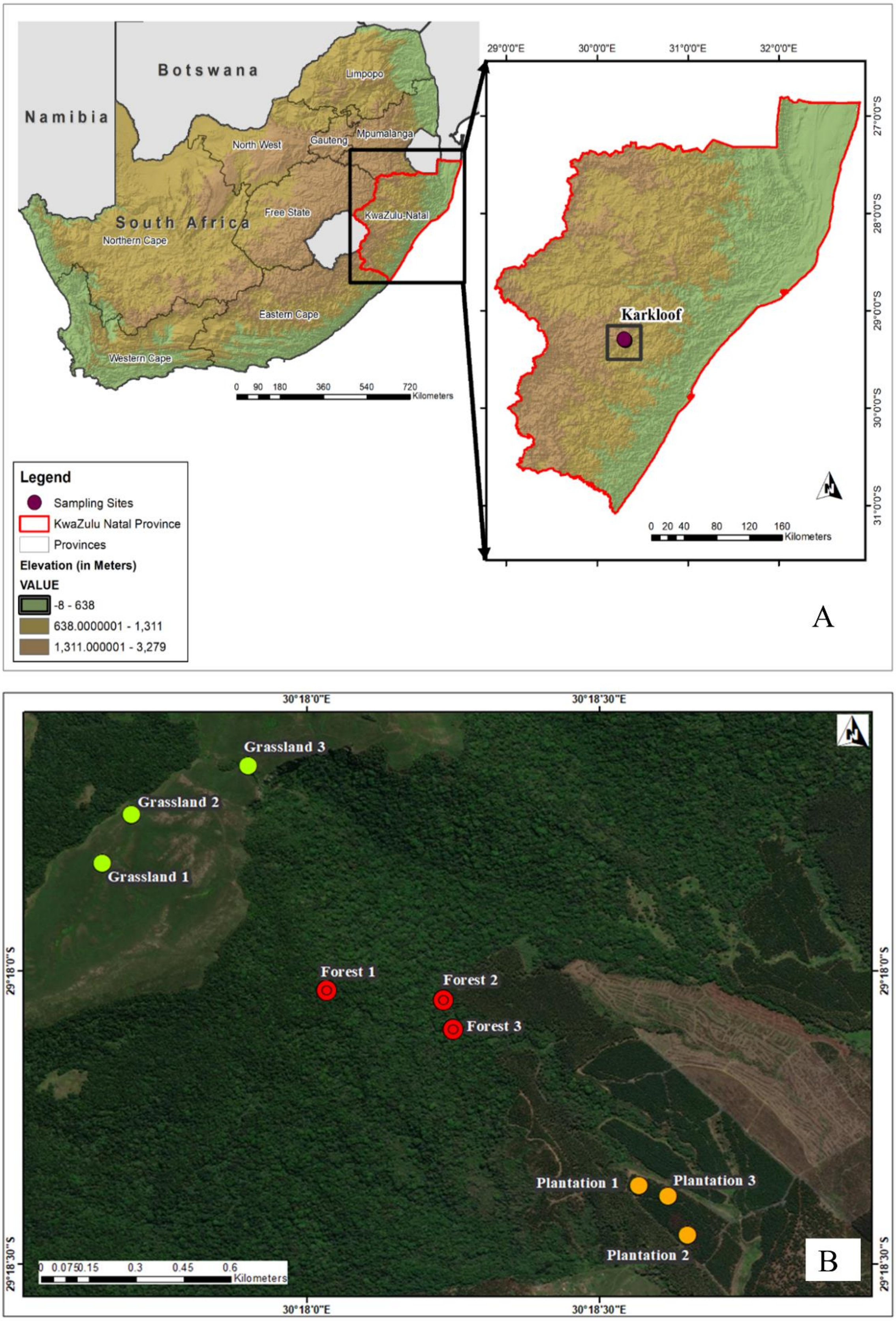

Figure 3.1: A) Map showing South Africa and the location of the Karkloof region within KwaZulu-Natal. B) Location of the nine Malaise traps in the forest, grassland, and plantation habitats in the Karkloof region (Photos: ArcGIS).

Collection of hover flies

To obtain a representative sample of the local hover fly diversity in the Karkloof region, I used a combination of Malaise trapping and hand netting. Malaise trap sampling was done by placing three replicate Malaise traps in each of the three habitats (Figure 3.1B, Table S3.1). Within each habitat type, Malaise traps were separated by a minimum of 95 m from each other to avoid pseudoreplication. Malaise traps were generally emptied weekly between October 2020 and September 2021, unless this was impossible due to bad weather conditions or civil unrest, in which case the interval was longer. Servicing of Malaise traps took place between 8:00 am and 12:00 noon and collecting bottles were tightly sealed before they were transported to the KwaZulu-Natal Museum (KZNM) for processing. Each collecting bottle contained a 3g dichlorvos tablet as a killing agent, which was refreshed every six weeks. A dry killing agent was used rather than a wet killing agent to preserve pollen grains on hover flies in Malaise traps for potential future analyses. During servicing, the dichlorvos tablet was removed from the collecting bottle and placed in a new empty collecting bottle.

In addition, hand-netting was used to collect hover flies along the walking route through the different habitats while servicing the Malaise traps between 8:00 am and 12:00 noon. The collected hover flies were kept in an aspirator and transported to the KZNM where they were killed by freezing. The main purpose of the hand-netting was to supplement the data with species that may be less likely to be caught in Malaise traps. Sampling was done haphazardly, instead of systematically (*e.g.*, timed intervals at fixed sites). As a result, the hand-netting data are analysed qualitatively and not quantitatively. Yellow pan traps were not used as a complementary collecting method in this study as they contain a fluid preservative.

Hover fly identification

At the KZNM hover flies were sorted from the Malaise samples, after which the bycatch was placed in 70% ethanol and not considered further for the purpose of this study. Hover flies were identified to genus level using the key in Ssymank *et al.* (2021) and further inspected for the presence of diagnostic characters using a binocular microscope to identify them further to species whenever possible using available keys (Curran, 1938a,b; Curran, 1939; Lyneborg & Barkemeyer, 2005; Tot *et al.*, 2020; Vujić *et al.*, 2008). After identification, hover fly specimens were relaxed, pinned, labelled, and added to the entomological collections of the KZNM.

Statistical analysis

To evaluate whether hover fly diversity differed among the three habitat types, the total number of species and individuals present in each sampling event (*i.e.*, week) was compared. The analysis implemented generalized estimating equations, using each trap as a subject variable, with the sampling event (week) as within the subject variable, using an autoregression matrix to correct for repeated sampling within subjects through time, and assuming a negative binomial distribution with a log-link function. The scale weight parameter was set to deviance to correct for overdispersion. Overall model significance was assessed with X^2 statistics, and pairwise comparisons were done with Šidák correction for multiple comparisons (van der Niet *et al.*, 2020). For graphing purposes, means and standard errors were back-transformed to the original scale. The analysis was performed in SPSS version 27.

To evaluate hover fly diversity among the three habitat types, the Shannon *H'* diversity index and Simpson's *D* evenness index were calculated for each habitat using Paleontological Statistics Software Package (PAST) ver. 4.03 (Hammer *et al.* 2001). The Shannon *H'* diversity index measures species diversity in the sample of hover flies collected from the three habitats and the Simpson's *D* evenness measures the abundance distribution of the species in the sample (Shannon & Weaver, 1949). To further test whether Shannon's *H'* diversity index and Simpson's *D* evenness index differed among the three different habitat types, a Kruskal-Wallis test was implemented in PAST ver. 4.03. A Kruskal-Wallis test is a non-parametric method that is used to determine whether the medians of three or more independent samples differ when the data is not normally distributed (Kruskal & Wallis, 1952).

To visualize and quantify whether hover fly communities differ among habitats, a series of multivariate approaches based on pooled samples for each trap was used. These analyses were based on two different similarity indices: the Bray-Curtis similarity index was used to evaluate whether hover fly abundance differs among habitats, whereas the Jaccard index was implemented to test whether habitats are characterized by the absolute presence and absence of species. A non-metric multidimensional scaling (NMDS) ordination plot was used to visualize hover fly assemblages among the habitat types for both Bray-Curtis and Jaccard indices. An NMDS is used to compare community data and produces a two-dimensional plot, positioning the sites according to similarities of the assemblages (Clarke & Warwick, 2001).

An Analysis of Similarity (ANOSIM) test was used to evaluate whether hover fly assemblages differ among the three habitat types for both Bray-Curtis and Jaccard indices. ANOSIM is a non-parametric test used to rank similarity matrices between two or more groups based on any distance measure (Clarke & Warwick, 2001). Additionally, a multivariate similarity percentage (SIMPER) test was performed to determine the contribution of each species to overall dissimilarity among the three habitats. Bray-Curtis, Jaccard index, NMDS, ANOSIM, and SIMPER were all performed using PAST ver. 4.03.

Results

A total of 195 hover fly individuals belonging to 21 species and 15 genera of three subfamilies were collected from the Malaise traps (Table 3.1). The total number of individuals of the subfamily Syrphinae (N=163) was higher than those of the subfamily Eristalinae (N=27) and Microdontinae (N=5). Grassland traps recorded 110 hover fly individuals from 17 species, with *Paragus* sp.1 (N=28) and *Allograpta fuscotibialis* (Macquart, 1842) (N=19) being the most abundant. Forest traps recorded 66 hover fly individuals from 12 species, with *Melanostoma annulipes* (Macquart, 1842) (N=19) and *Allograpta fuscotibialis* (N=14) being the most abundant. Plantation traps recorded 19 hover fly individuals from seven species, with *Melanostoma bituberculatum* (Loew, 1858) (N=10) being the most abundant.

Table 3.1: List of hover fly species found in the nine different Malaise traps set up in three habitats (plantation, forest and grassland) in the Karkloof region, Kwa-Zula Natal (South Africa). Within subfamilies, species are arranged alphabetically. Species only found in one habitat type are marked in light grey. The dark grey shading indicates species that were caught using Malaise traps but that were not caught with hand-nets.

Subfamily and species	Habitat type								
	Forest 1	Forest 2	Forest 3	Grassland 1	Grassland 2	Grassland 3	Plantation 1	Plantation 2	Plantation 3
Eristalinae									
Amphoterus braunsi (van Doesburg, 1956)	2	1	0	0	0	0	0	0	0
Eristalinus modestus (Wiedemann, 1818)	1	1	0	0	4	2	0	1	0
Eristalinus taeniops (Wiedemann, 1818)	0	0	1	0	0	0	0	0	0
Eumerus sp.1	0	0	0	0	0	4	0	0	0
Graptomyza sp.1	1	1	0	0	0	1	0	0	0
Syritta stigmatica (Loew, 1858)	0	0	0	0	2	0	0	0	0
Syrittosyrphus opacea (Hull, 1944)	2	3	0	0	0	0	0	0	0
Syrphinae									
Allograpta calopus (Loew, 1858)	0	0	0	0	1	0	0	0	0
Allograpta fuscotibialis	1	3	10	11	5	3	0	1	0
Asarkina sp.1	0	0	1	1	0	1	0	0	0
Betasyrphus adligatus (Wiedemann, 1824)	0	0	0	4	4	3	0	0	0
Betasyrphus intersectus (Wiedemann, 1824)	0	0	5	3	5	6	0	0	1
Betasyrphus saundersi (Goot, 1964)	0	0	0	0	1	0	0	0	0
Episyrphus trisectus (Loew,	0	0	0	0	0	0	0	2	0

	1858)									
	Eupeodes corollae (Fabricius, 1794)	0	0	0	0	3	3	0	0	0
	Melanostoma sp.1	2	0	8	1	0	1	1	0	0
	Melanostoma annulipes	4	0	15	2	1	0	0	0	0
	Melanostoma bituberculatum	0	0	1	0	3	1	1	2	7
	Paragus sp.1	0	1	2	16	6	6	2	0	1
	Sphaerophoria retrocurva (Hull, 1944)	0	0	0	0	1	0	0	0	0
Microdontinae										
	Archimicrodon sp.1	0	0	0	3	1	1	0	0	0

There was an overall effect of habitat type on both the number of species per trap per week (χ^2 =89.29, d.f. = 2, p<0.001; Figure 3.2A) as well as for the number of individuals per trap per week (χ^2 = 85.53, d.f. = 2, p <0.001; Figure 3.2B). Pairwise comparisons revealed that both the number of individuals and species are significantly lower in the plantation than in the forest and grassland (Figure 3.2).

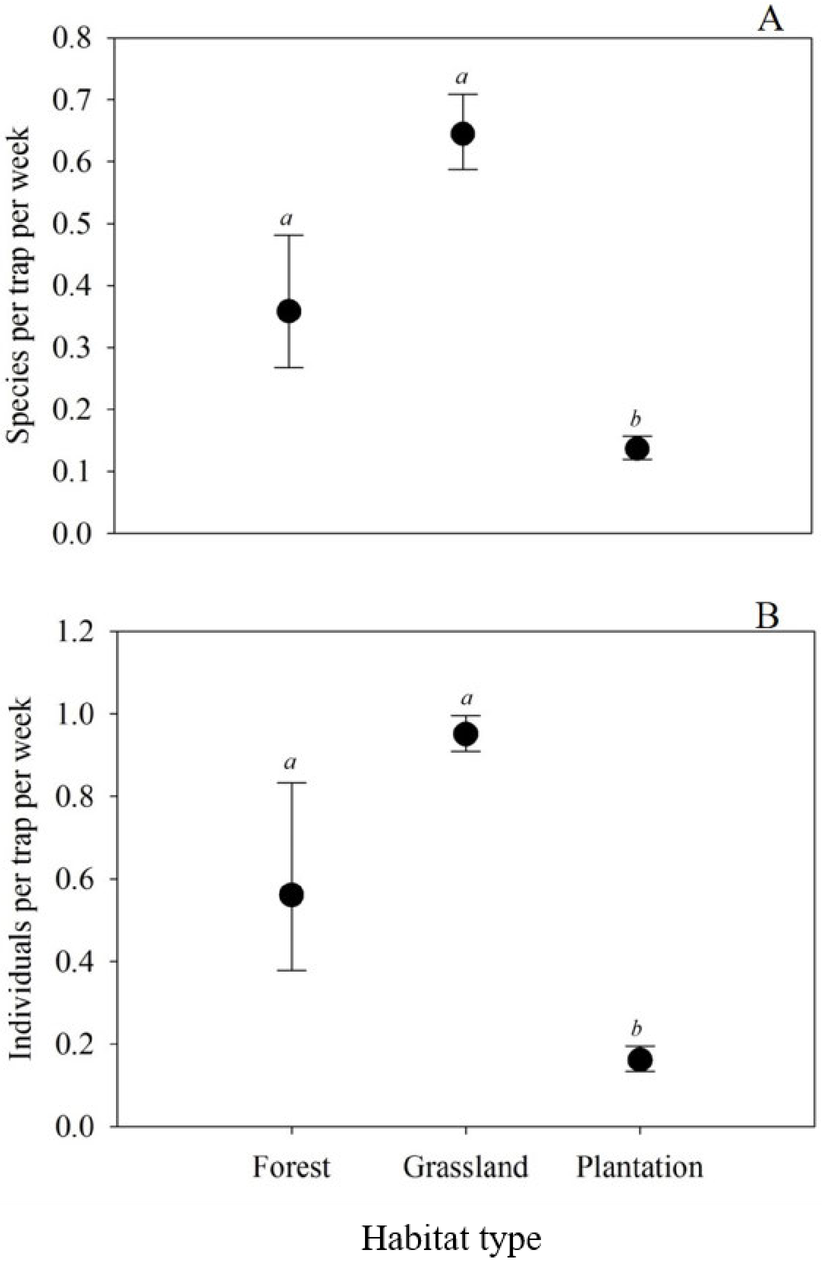

Figure 3.2: The effect of habitat type on A) the mean number of species per trap per week and B) the number of individuals per trap per week collected using nine Malaise traps in the Karkloof region, Kwa-Zulu Natal (South Africa). Letters indicate significant differences ($p < 0.05$) based on pairwise comparisons

The Kruskal-Wallis test revealed a significant difference for Shannon *H’* diversity index among the three habitat types (p = 0.02; Figure 3.3) whereas there was no significant difference for Simpsons *D*’ evenness index among the three habitat types (p = 0.06; Figure 3.4).

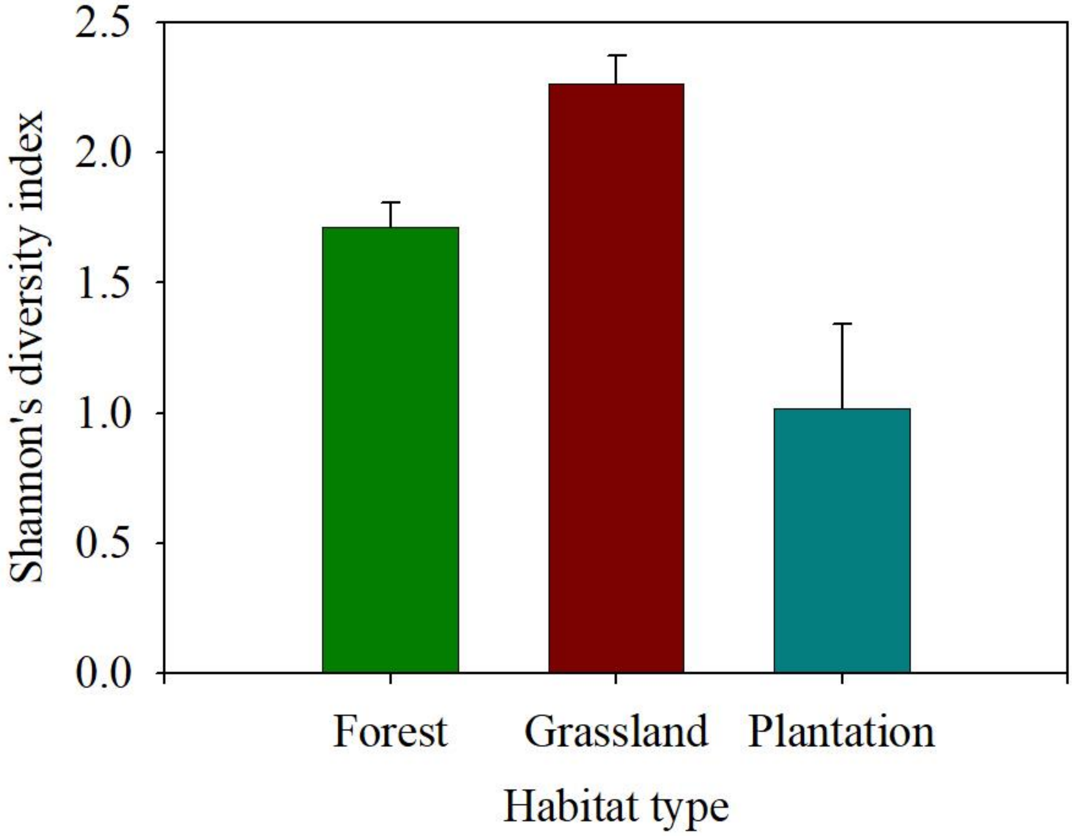

Figure 3.3: Shannon *H’* diversity index of hover flies collected in each Malaise trap in the three habitat types in the Karkloof region, KwaZulu-Natal (South Africa). Error bars represent the standard deviation of the mean.

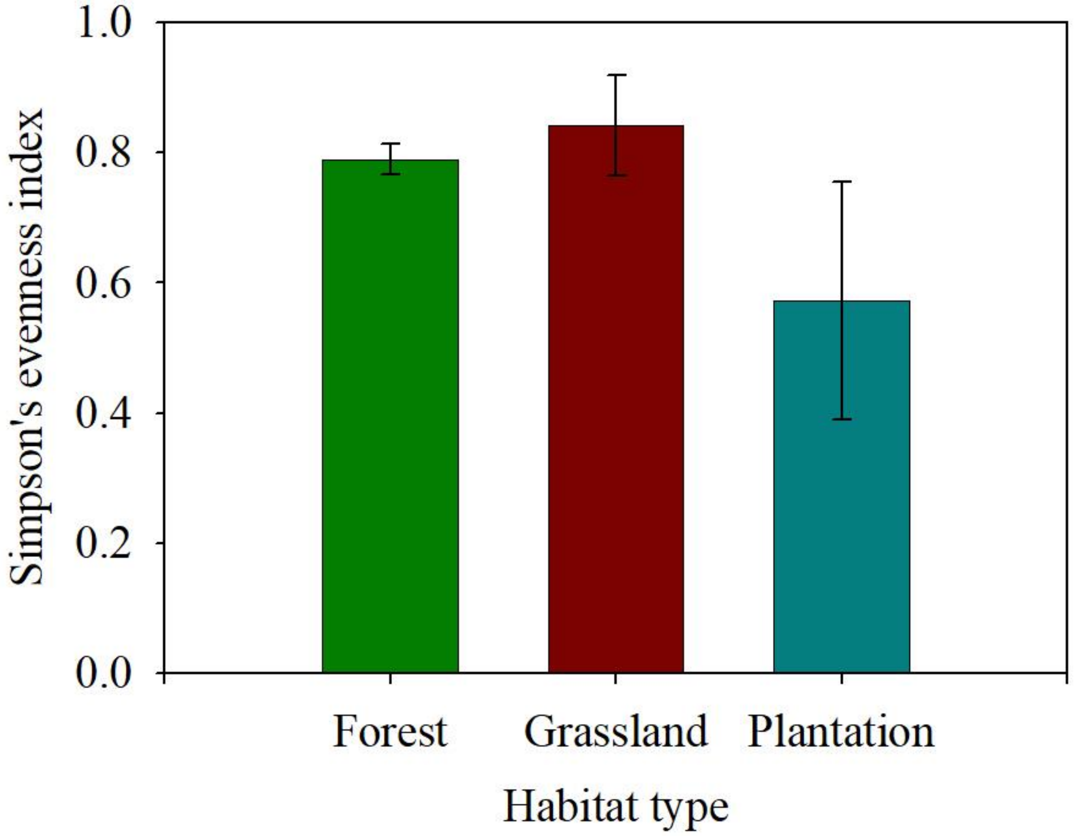

Figure 3.4: Simpson *D* evenness index of hover flies collected in each Malaise trap in the three habitat types in the Karkloof region, KwaZulu-Natal (South Africa). Error bars represent the standard deviation of the mean.

There was an overall effect of habitat type on both the number of species per trap per week (χ^2 =89.29, d.f. = 2, p<0.001; Figure 3.2A) as well as for the number of individuals per trap per week (χ^2 = 85.53, d.f. = 2, p <0.001; Figure 3.2B). Pairwise comparisons revealed that both the number of individuals and species are significantly lower in the plantation than in the forest and grassland (Figure 3.2). The Kruskal-Wallis test revealed a significant difference for Shannon *H'* diversity index among the three habitat types (p = 0.02; Figure 3.3) whereas there was no significant difference for Simpsons *D*' evenness index among the three habitat types (p = 0.06; Figure 3.4).

The ANOSIM for the NMDS ordination revealed that there was a significant difference between hover fly assemblages among the three habitats, if abundance was considered using the Bray-Curtis similarity (Global R = 0.605, p = 0.013; Figure 3.5), and if only species presence was evaluated using Jaccard similarity (Global R = 0.379, p = 0.048; Figure 3.6). However, visual inspection reveals that data from separate traps from the same habitat only cluster together marginally using Bray-Curtis similarity that takes abundance into account (Figure 3.5), and not when Jaccard similarity is used (Figure 3.6).

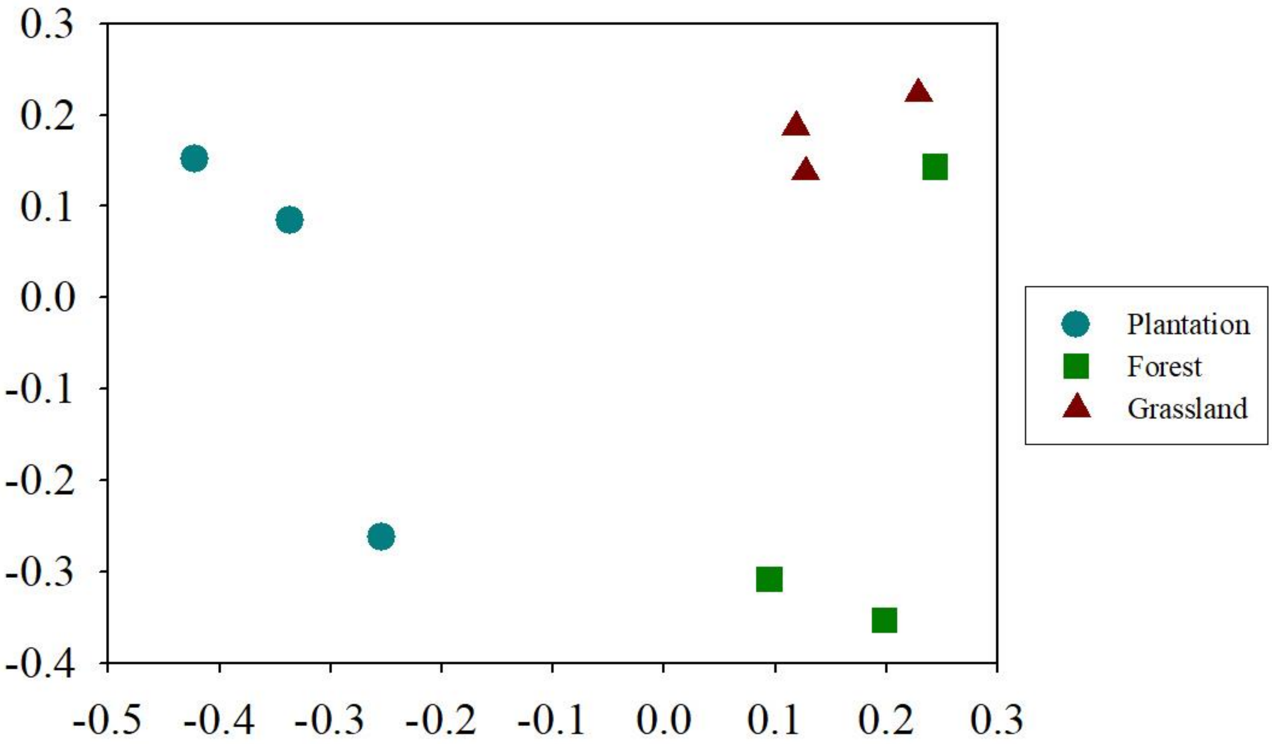

Figure 3.5: Non-metric multidimensional scaling ordination of hover fly abundance in the three habitat types collected using Malaise trap in the Karkloof region, Kwa-Zulu Natal (South Africa) using Bray-Curtis similarity.

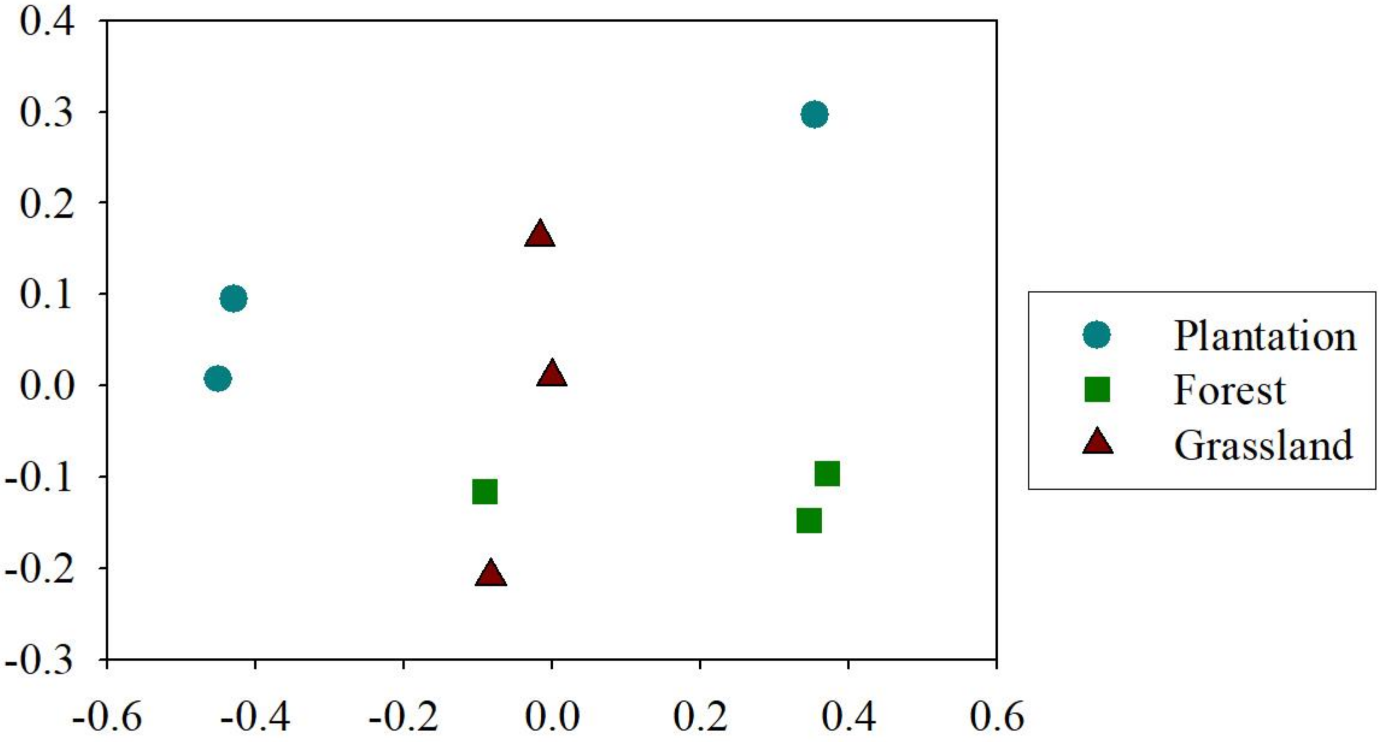

Figure 3.6: Non-metric multidimensional scaling ordination of hover fly species presence in the three habitats collected using Malaise traps in the Karkloof region, Kwa-Zulu Natal (South Africa) using Jaccard similarity.

The SIMPER analysis revealed that *Paragus* sp.1 was highly characteristic of grassland, whereas *Allograpta fuscotibialis* was present in both forest and grassland habitats but was mostly absent from the plantations (Table 3.2). *Melanostoma annulipes* were highly characteristic of the forest habitat while *Melanostoma bituberculatum* was highly characteristic of the plantations (Table 3.2).

Table 3.2: Similarity percentage analysis displaying the % contribution (contri. %) and cumulative % contribution (cumulative %) of each hover fly species (in decreasing order of % contribution) in the three habitat types (forest, grassland, plantation) in the Karkloof region, KwaZulu-Natal (South Africa).

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean forest	Mean grassland	Mean plantation
Paragus sp.1	12.54	15.23	15.23	1	9.33	1
Allograpta fuscotibialis	11.4	13.85	29.07	4.67	6.33	0.333
Melanostoma annulipes	9.311	11.31	40.39	6.33	1	0
Betasyrphus intersectus	7.258	8.818	49.2	1.67	4.67	0.333
Melanostoma bituberculatum	7.134	8.667	57.87	0.333	1.33	3.33
Betasyrphus adligatus	5.038	6.121	63.99	0	3.67	0
Melanostoma sp.1	4.851	5.893	69.89	3.33	0.667	0.333
Syrittosyrphus opacea	4.404	5.35	75.24	1.67	0	0
Eristalinus modestus	3.48	4.228	79.46	0.667	2	0.333
Eupeodes corollae	2.9	3.523	82.99	0	2	0
Amphoterus braunsi	2.543	3.089	86.08	1	0	0
Archimicrodon sp.1	2.228	2.707	88.78	0	1.67	0
Eumerus sp.1	2.042	2.481	91.26	0	1.33	0
Graptomyza sp1	1.906	2.316	93.58	0.667	0.333	0
Episyrphus trisectus	1.529	1.857	95.44	0	0	0.667
Asarkina sp.1	1.109	1.348	96.79	0.333	0.667	0
Syritta stigmatica	0.9123	1.108	97.89	0	0.667	0
Betasyrphus saundersi	0.4562	0.5542	98.45	0	0.333	0
Sphaerophoria retrocurva	0.4562	0.5542	99	0	0.333	0
Allograpta calopus	0.4562	0.5542	99.56	0	0.333	0
Eristalinus taeniops	0.3654	0.4439	100	0.333	0	0

A total of 85 hover fly individuals belonging to 18 species and 15 genera of two subfamilies were collected using hand-netting (Table 3.3). The species *Chrysogaster Africana* (Hull, 1944), *Merodon* sp.1, *Phytomia incisa* (Wiedemann, 1830), and *Episyrphus petilis* (Vockeroth, 1973*)* were only caught using hand-nets whereas *Syrittosyrphus opacea, Allograpta calopus, Episyrphus trisectus, Eupeodes corollae, Melanostoma bituberculatum, Sphaerophoria retrocurva, Archimicrodon* sp.1 were only caught using Malaise traps. In general, more hover fly species were collected with Malaise traps (Figure 3.7). Some species, such as *Asarkina* sp.1, were more regularly collected with hand-netting (N=10) than Malaise traps (N=3) (Table 3.1 and 3.2).

Table 3.3: List of hover fly species collected using hand-netting in three habitats in the Karkloof region, KwaZulu-Natal (South Africa). The light grey shading indicates species that were unique to a particular habitat. The dark grey shading indicates species that were caught using hand-netting but that were absent in the Malaise traps.

Subfamily and species	Habitat type		
	Forest	Grassland	Plantation
Eristalinae			
Amphoterus braunsi	4	0	0
Chrysogaster africana	0	8	0
Eristalinus modestus	0	2	0
Eristalinus taeniops	1	0	0
Eumerus sp.1	1	0	0
Graptomyza sp.1	1	0	0
Merodon sp.1	0	9	0
Phytomia incisa	0	1	0
Syritta stigmatica	2	0	0
Syrphinae			
Allograpta fuscotibialis	7	1	0
Asarkina sp.1	9	0	1
Betasyrphus adligatus	2	3	0
Betasyrphus intersectus	0	11	0
Betasyrphus saundersi	1	1	0
Episyrphus petilis	1	0	0
Melanostoma sp.1	6	0	0
Melanostoma annulipes	5	0	0
Paragus sp.1	0	8	0

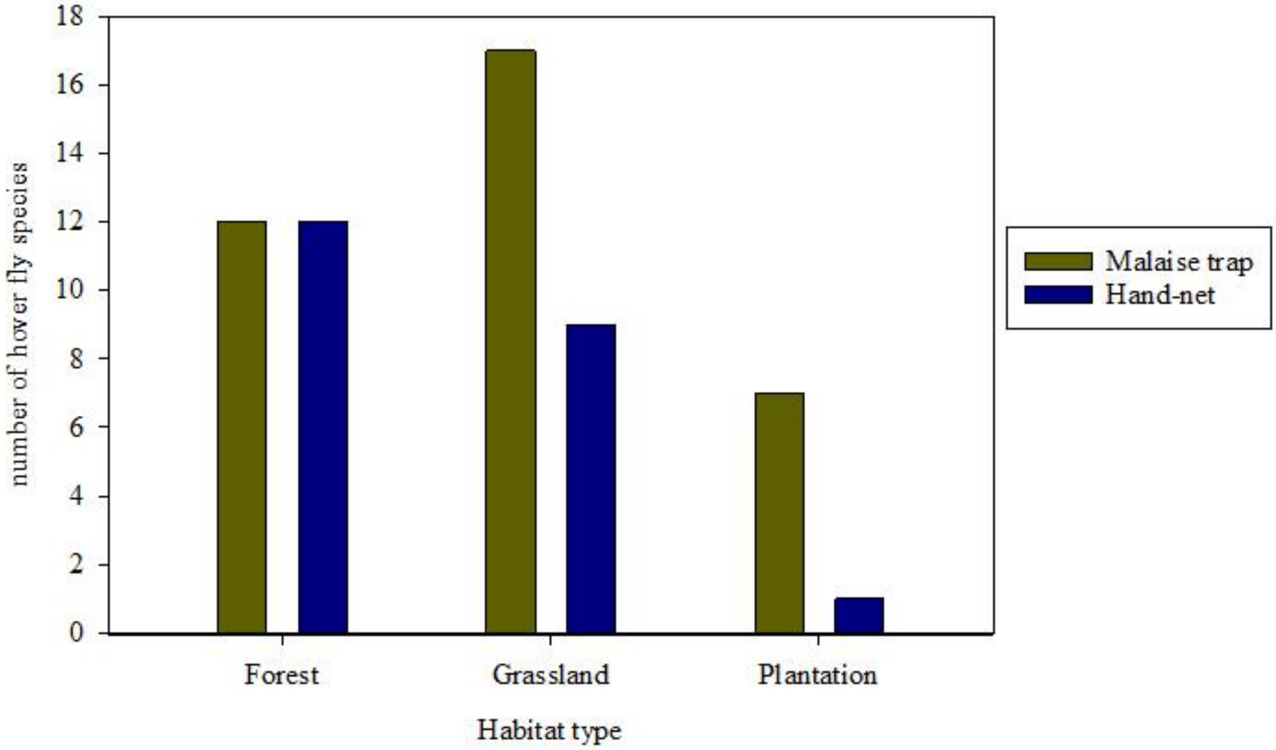

Figure 3.7: Total number of hover fly species collected in the Karkloof region, KwaZulu-Natal (South Africa) using Malaise traps and hand-nets in the three habitat types. The olive bar represents the number of species collected using Malaise traps and the blue bar represents the number of species using hand-nets.

Discussion

The main aim of this study was to investigate hover fly abundance and diversity in three adjacent habitats in the Karkloof region, KwaZulu-Natal (South Africa) using Malaise traps. Hover flies of the subfamily Syrphinae were the most abundant, followed by Eristalinae, whereas only a few Microdontinae were collected. There was an overall effect of habitat type on both the mean number of species and number of individuals per trap per week. In addition, there was clear variation in hover fly abundance and diversity among the three habitat types. The study showed that a heterogeneous indigenous habitat such as the grassland and forest yielded high abundance, diversity, and richness of hover flies, whereas plantations have a very low abundance, diversity, and species richness.

The variation in hover fly individuals, diversity, evenness, and richness among the three habitat types sampled may reflect diversity in available microhabitats as well as floristic diversity, which provides hover flies with nectar and/or pollen. The forest and grassland both provide a variety of environmental conditions that are suitable for hover flies, affecting factors such as food availability, temperature, sunlight, and oviposition sites (Naderloo & Rad, 2014; Gaytán *et al.*, 2020). One of the grassland Malaise traps was situated over a stream that may be favourable to hover flies that have aquatic and semi-aquatic larvae; these species are confined in water during their developmental stages (Thompson & Rotheray, 1998; Ghahari *et al.*, 2008). For example, this Malaise trap caught a number of *Eristalinus modestus*, this species belongs to a genus with semi-aquatic larvae that feed on bacteria in shallow water with rotting organic matter (Ssymank *et al.*, 2021).

The plantation was characterized by the lowest number of individuals and species of hover flies per week. This was expected, as it represents a transformed habitat with homogenous vegetation that was dominated by ground cover that contained dead pine needles. Consequently, this habitat may contain fewer food resources, as well as fewer environmental conditions to support a diversity of hover fly species (Naderloo & Rad, 2014; Moquet *et al.*, 2018). Moreover, the plantation experienced regular human disturbance such as logging. The presence of disturbance, fewer food resources, and shelter in the plantations could be the reason for the low abundance and diversity of hover fly species in this habitat. Hover flies collected in the plantation are likely specimens that move among the habitats. Yet, a high number of *Melanostoma bituberculatum* were recorded in the plantations. There is no documented explanation as to why *M. bituberculatum* is characteristic for plantations. One can only speculate that this species is more adapted to the conditions of the plantation than other syrphids. Furthermore, this species belongs to a genus that occurs in a wide variety of habitat types (Ssymank *et al*., 2021).

The response of hover flies to habitat type generally varies and is likely affected by vegetation type, floral diversity, and oviposition sites. The results of the NMDS using Bray-Curtis similarity showed clear groupings among the different habitat types where the forest and grassland were clearly separated from the plantations. However, there was a lot of variation among the Malaise traps of each habitat type. This suggests that within a habitat there is variation in plant diversity and habitat complexity that might affect the assemblage and abundance of hover flies within a habitat (Humphrey *et al*., 1999; Randlkofer *et al*., 2010; Aghadokht *et al*., 2020). For instance, one of the forest Malaise traps was closely grouped with those of the grassland. This suggests that the area of the forest where this Malaise trap was placed might have environmental conditions that are similar to those of the grassland. This emphasizes the importance of Malaise trap placement within a habitat in order to obtain a better representation of species in a particular habitat (Sheikh *et al*., 2016).

Based on the NMDS using Jaccard similarity, which is based only on the presence/absence of species, hover fly assemblages were significantly different among the different habitat types. This would mean that, although these habitat types may share similar hover fly species, those species may not be the most representative of these habitats. Moreover, the variation may be explained by three species: *Paragus* sp.1, *Allograpta fuscotibialis, Melanostoma annulipes,* all three species belong to genera that have predatory larvae that feed on aphids (Rotheray & Gilbert, 2011; Ssymank *et al*., 2021). Furthermore, genera of these species are common in the Afrotropical Region and are found in a wide variety of habitat types (Ssymank *et al*., 2021). *Allograpta fuscotibialis* was common in both forest and grassland, whereas *Paragus* sp.1 only dominated the grassland and *Melanostoma annulipes* dominated the forest respectively. Species of the genus *Allograpta* are widely distributed in the Afrotropics and adults are often found on flowers of a wide variety of trees, shrubs and herb species (Ssymank *et al*., 2021). Species of the genus *Paragus* are found in xeric to mesic open habitats such as grasslands or rocky areas, although some species also occur in forests or at forest margins (Ssymank *et al*., 2021). The adults visit a wide variety of flowers, mostly in the herb layer, and are generally encountered on Asteraceae (Ssymank *et al*., 2021). Species of the genus *Melanostoma* are found in a wide variety of habitat types ranging from forests to grasslands and wetlands, usually with a preference for moist to wet habitats (Thompson & Rotheray, 1998; Ssymank *et al.*, 2021). It is therefore not clear why this species was largely absent from the grassland.

Within a habitat, common species tend to be more abundant and widely distributed than rare species (Gaston, 2011). Indeed, the grassland and forest included a high number of hover fly species that constituted mostly common species with a wide distribution range. Rare hover fly species such as *Amphoterus braunsi*, and *Syrittosyrphus opacea*, were found in the forest; both these species are endemic to South Africa (Ssymank *et al.*, 2021). The presence of such rare species highlights the importance of conserving indigenous forest areas, of which relatively little remains in South Africa.

Obtaining a representative sample of hover fly species from an area can be done in several ways. Malaise traps are the most preferred sampling method for insects as they catch a wide variety of flying insects with minimal effort (Karlsson *et al.*, 2005), and passive sampling is independent of human effort. Nonetheless, Malaise trap sampling may underestimate the diversity of taxa with a low abundance. For instance, in this study *Chrysogaster africana, Merodon* sp.1, *Phytomia incisa* and *Episyrphus petilis* were only caught using hand-nets. It is not clear why these hover fly species were absent from the Malaise traps, as the biology of the adults of these hover fly species is still not fully known. However, some speculation on possible explanations is warranted. *Chrysogaster africana* belongs to a genus that is habitat-specific and prefers moist to wet habitat types that are suitable for larval development (Ssymank *et al.*, 2021). The placement of Malaise traps within each habitat type might not have been suitable for both adult *C. africana* and larval development, reducing the chances of them being caught in Malaise traps. *Merodon* sp.1 belongs to a genus that generally occurs in grasslands with adults that are rarely observed on flowers but are generally observed flying in low vegetation (Ačanski *et al.*, 2016). This may make it less likely to be caught in Malaise traps. *Episyrphus petilis* is rare in the Afrotropical Region and is confined to deeper forests in South Africa but generally prefer forests and vegetation at their margins, including mountain shrublands, and heathlands (Ssymank *et al.*, 2021). Their absence in the Malaise traps may be explained by the fact that rare species are generally underrepresented in a given area in comparison to common species that are generally collected in higher numbers (Hutcheson, 1999). Finally, *P. incisa* belongs to a genus that occurs in a wide range of moist to wet habitat types (Thompson & Rotheray, 1998). Adults generally have very large eyes which might mean that they can see and avoid the Malaise traps. Besides the complete absence from Malaise traps, certain species were also caught in lower abundance in Malaise traps, such as *Asarkina* sp.1. Inadequate sampling due to sample biases could lead to a poor understanding of both the diversity and biogeography of insects (Brown, 2005; Fraser *et al*., 2008). Despite the inconsistency in sampling effort with the hand-net, the results from the hand-netting showed that a complementary strategy of using both Malaise traps and hand-netting results in a better representation of diversity and species richness than either method does by itself (Fraser *et al.,* 2008; Missa, 2009; Petanidou *et al*., 2011).

This study done in the Karkloof provides the first effort in providing information regarding hover fly abundance and diversity in the region. The results show variation among the three habitats sampled, which may be due to factors such as food availability, microhabitat diversity, and oviposition sites. A total of 280 individual hover flies belonging to 25 species and 18 genera collected using Malaise traps and hand-nets during the study period suggests that the Karkloof region can be considered potentially diverse (Midgley & Jordaens, pers. Comm.). Irrespective of the sampling method used, biases should be limited as these would prevent obtaining reliable estimates of the diversity of natural populations (Magurran, 2004). In that context it is relevant to mention that the results of this study only provide baseline information regarding hover fly diversity in different habitat types in the Karkloof region of South Africa. Moreover, results of this study only come from one region, and therefore it is not clear how representative they are. Future studies should be undertaken in different regions of South Africa to validate the findings and to better understand the effect of habitat type in hover fly diversity as this is essential for species and habitat conservation.

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Supplementary material

Table S3.1: GPS coordinates (Longitude, Latitude and Elevation) of each Malaise trap set up in the Karkloof region, KwaZulu-Natal (South Africa).

Habitat type	Malaise trap number	Coordinates		
		Longitude	Latitude	Elevation (m)
Plantation	Plantation 1	29°18'22" S	30°18'34" E	1183
	Plantation 2	29°18'27" S	30°18'39" E	1164
	Plantation 3	29°18'23" S	30°18'37" E	1175
Forest	Forest 1	29°18'02" S	30°18'02" E	1447
	Forest 2	29°18'03" S	30°18'14" E	1318
	Forest 3	29°18'06" S	30°18'15" E	1312
Grassland	Grassland 1	29°17'49" S	30°17'39" E	1530
	Grassland 2	29°17'44" S	30°17'42" E	1520
	Grassland 3	29°17'39" S	30°17'54" E	1501

Figure S3.1**:** Photographs of the nine Malaise traps set up within the three habitats in the Karkloof region KwaZulu-Natal (South Africa).

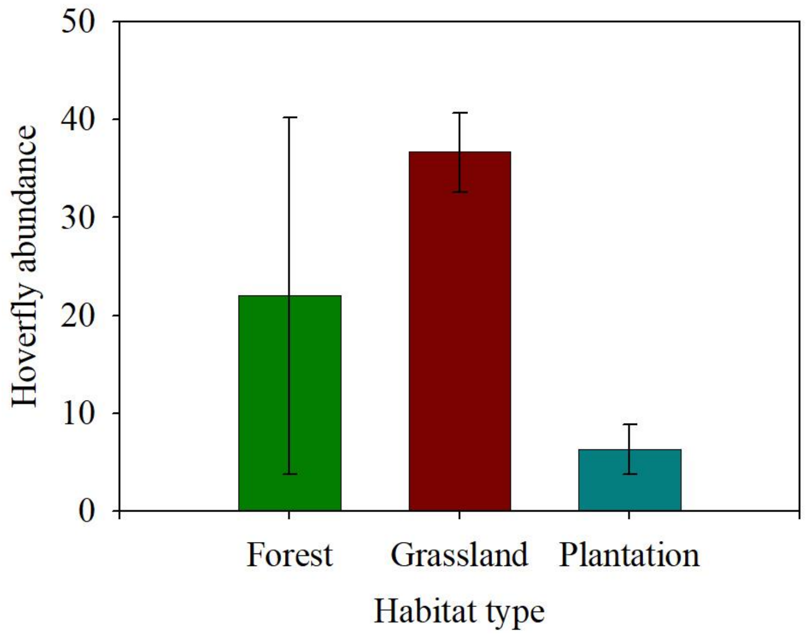

Figure S3.2: Total abundance of hover flies collected in each Malaise trap in the three habitats types in the Karkloof region, KwaZulu-Natal (South Africa). Error bars represent the standard deviation of the mean.

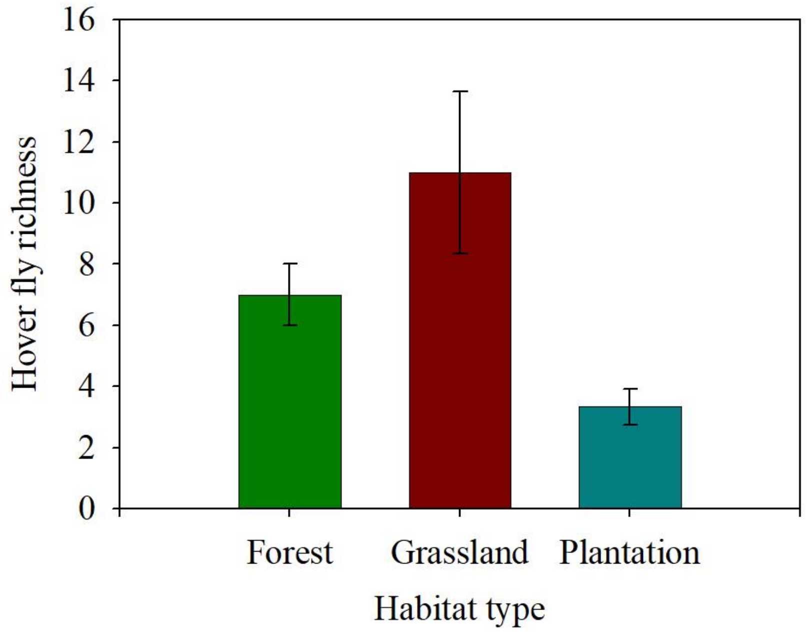

Figure S3.3: Total species richness of hover flies collected in each Malaise trap in the three habitat types in the Karkloof region, KwaZulu-Natal (South Africa). Error bars represent the standard deviation of the mean.

Chapter 4: General Discussion

I started my thesis with a summary of the ecology and life-history of a family of the order Diptera (true flies), viz. Syrphidae (hover flies or flower flies), which provide ecosystem services (pollination) to humans. It appeared that hover fly abundance and diversity may vary seasonally and among habitat types, but also that such knowledge is limited in the Afrotropical Region. My thesis, therefore, had two aims that I dealt with in two data chapters.

The aim of the first data chapter (Chapter 2) was to investigate monthly patterns of occurrence (mined from the GBIF database) and abundance (passive sampling using Malaise trap data) in hover fly diversity in the KwaZulu-Natal province (South Africa), with a specific focus on the comparison of the museum and field-collection data across months of the year. As such, I expected that seasons associated with hot months will record a higher number of hover flies. I also expected that the monthly occurrence patterns showed in the KZN GBIF dataset would vary compared to the two Karkloof datasets as they are both on the local scale whilst the KZN GBIF is province wide. I specifically compiled and analysed three datasets: all GBIF records for KwaZulu-Natal, GBIF records for the Karkloof region, and the Malaise collected dataset.

As expected, the three datasets showed distinct phenological patterns, of which the most common pattern was characterized by hover fly taxa with bimodal peaks that were present from late spring, throughout summer and, sometimes, late autumn and mainly comprised hover fly taxa with saprophagous larvae that exploit wet decaying wood and decaying plant sap (Ssymank *et al.*, 2021). The patterns in the different datasets were not perfectly aligned, but strong similarities were visible in the Karkloof GBIF and field collected datasets.

Grouping of genera into tribes may have affected the observed patterns. Grouping of species and genera to the tribe level was done to obtain taxonomic groups with a larger sample size to allow the recovery of general patterns and to create a manageable data set. As 35 adult hover fly genera are known from KwaZulu-Natal, generating phenological patterns for every genus was beyond the scope of an MSc. As a result, there may be relevant hidden genus- or species-specific occurrence or abundance patterns. For example, the monthly occurrence patterns of the tribe Eumerini illustrated in the KZN dataset may be driven by the genus *Eumerus* as this genus constituted 92% of the total records of this tribe. This leads to the following questions: is the visualized monthly occurrence pattern representative of the tribe Eumerini or is it of the taxa *Eumerus*? Moreover, would the visualized pattern be consistent should the rest of the genera in this tribe have a similar sample size as *Eumerus*? Investigating species- (or genus-) level phenology patterns is a natural future research path.

The results also show variation in the monthly patterns illustrated by different tribes belonging to the same subfamily, for example, the tribes Syrphini and Paragini. One might assume that both these tribes would have similar monthly patterns as they comprise taxa with predatory larvae that feed on aphids (Rotheray & Gilbert, 2011; Ssymank *et al.*, 2021), but they showed consistent variation in monthly occurrence and abundance patterns in all three datasets. Because the biology of many adult Afrotropical hover flies is still largely unknown, one could speculate that this variation may be due to the adult hover flies of these tribes feeding on pollen or nectar of plant species with different flowering seasons. Moreover, the larvae of the two tribes might feed on different aphid species with different seasonal outbreaks. To validate and better understand these assumptions, future studies focusing on the flower preference of hover fly taxa of tribes Syrphini and Paragini are required to determine whether there is variation in flower preference or not.

Museum collections provide a physical database of biodiversity and offer spatial and temporal data, which are potentially valuable in developing conservation strategies (Drinkrow *et al.*, 1994; Kress *et al.*, 1998). In this study, data from these collections have played an important role in providing baseline information on the monthly occurrence patterns of Syrphidae of the province of KwaZulu-Natal (South Africa). Regardless of their potential biases, the datasets have illustrated variations in the monthly occurrence patterns of hover fly tribes. Nonetheless, these monthly occurrence patterns give an indication as to whether the museum records accurately reflect the true monthly occurrence patterns of each hover fly tribe. It is important to interpret these patterns as relative abundance data instead of absolute abundance data. The accuracy of the patterns shown by museum records can be determined by long-term field collection of hover flies (Bradley *et al.*, 2014). The data collected in this study covered a complete annual cycle and showed similar patterns to museum data in many tribes. In the future, multi-year studies should be undertaken to further verify the value of museum collections.

In the second data chapter (Chapter 3), I compared hover fly abundance and diversity in three different but adjacent habitats (forest, grassland, and plantation) in the Karkloof region in the province of KwaZulu-Natal (South Africa). The forest and grassland were natural habitats, while the plantation was a human-modified monoculture. As such, I expected the plantation to yield a low number of hover flies (both in terms of abundance and species diversity) compared to the forest and grassland, as it is a modified habitat lacking microhabitat diversity.

The work presented here is relevant in the context of the habitat heterogeneity hypothesis, which suggests that species diversity increases with landscape diversity (MacArthur & MacArthur, 1961). Although habitat heterogeneity was not investigated in this study, the forest and grassland are generally considered heterogenous habitats due to the variety in resource composition and structural complexity that they provide (Tews *et al*., 2004). Indeed, the forest and grassland had the highest hover fly abundance, associated with high richness and diversity. This observation was also found in other studies comparing the diversity of hover flies in different habitat types (Naderloo & Rad, 2014; Ansari & Memon, 2017). Moreover, studies focusing on the diversity of other animals also support this hypothesis (Haslett, 1997; Tanabe *et al.,* 2001; Atauri & Lucio, 2001; Brose, 2003). For instance, in a study of leaf-litter invertebrate taxa in two plantation types and an indigenous forest, Ratsirarson *et al*. (2002) found that the indigenous forest had the highest species richness followed by the eucalypt and pine plantations. In another study comparing various arthropod groups in natural forests, grasslands, and pine blocks, Yekwayo *et al*. (2017) showed that natural forests had higher predator and detritivore diversity, while grassland had greater ant diversity. The above-mentioned studies both suggest that fewer arthropods occur in plantations than in indigenous forests and grasslands. This confirms the role of landscape diversity in the diversity of a variety of animals and the negative impact of monoculture plantations on biodiversity.

Shannon's *H'* diversity and Simpson's *D* evenness index where higher in the grassland than forest and plantation, and the lowest diversity values were recorded for the plantation. Markov *et al.* (2018) study observed an opposite pattern where forests had a higher hover fly abundance and diversity than grasslands. This variation suggests, structurally, South African grasslands to be different from those of Vojvodina, Serbia. South African grasslands are well-defined based on vegetation structure in combination with environmental factors (Mucina & Rutherford 2006). They are also high in plant diversity, housing approximately 3370 plant species. The richness of this biome is likely to provide microhabitats and environmental conditions that are preferred by hover flies and thus allow them to thrive. In terms of species composition, both forest, and grassland recorded 'forest' and 'grassland' species that were not recorded in the other habitat types, even though these vegetation types are adjacent. The forest recorded 10 'forest' species and the grassland 14 'grassland' species respectively. Additionally, the forest recorded two hover fly species that are rare and endemic to South Africa (Ssymank *et al.*, 2021). This observation suggests the importance of South African forests and grasslands as important habitats for hover flies, as they are biodiversity hubs with extremely high habitat complexity and diversity relative to their size (Carbutt *et al.* 2011).

While Malaise traps have the advantage of standardizing collection efforts, trap placement can affect the efficacy of these traps. In this study, one forest Malaise trap caught 65% of the total abundance and 67% of the total hover fly species from the forest during the study period. In the NMDs, this trap grouped with those set up in the grassland (Figure 3.5). This may suggest that the forest area where this Malaise trap was set up might have similar habitat characteristics as the grassland that are preferred by hover flies. Moreover, this also explains the imbalance among insects living in the same habitat, as there may be more insect activity in an open forest clearing compared to a closed forest clearing. Malaise traps are less effective in habitats with closed canopies as shading appears to reduce trap catch even when the insect communities are the same (Gitting *et al*., 2006; Irvin & Woods, 2007). This highlights the importance of Malaise trap placement within a habitat in order to maximize the number of insects caught. (Sheikh *et al.*, 2016).

Conclusion

Despite the intensive sampling over a long period, covering different habitat types and using a combination of two or more sampling methods, sampling strategies may be improved to provide a more realistic picture of the biodiversity and community structure of hover flies. Sampling in new localities will contribute towards a more accurate estimate of the diversity of Syrphidae in South Africa. Furthermore, the use of two or more sampling methods will help reduce biases and assist in collecting a high percentage of available taxa in a habitat (see also Fraser *et al*., 2008; Missa, 2009).

Since this study investigated hover fly diversity in three different habitats, it is advisable for future studies to determine the composition of the floral community of each habitat. Adult hover flies feed on pollen and nectar and are considered to be generalist flower visitors (Rotheray & Gilbert, 2011). However, they usually behave opportunistically and can be either pollen generalists or specialists (Branquart & Hemptinne, 2000; Lucas *et al.*, 2018). Generally, hover fly floral preferences may vary depending on flower colour, morphology, and inflorescence height (Colley & Luna, 2000; Lunau, 2014; de Manincor *et al*., 2020).

Understanding how, and to what extent the floral community of each habitat affects hover fly diversity is important, as several studies suggest that hover fly abundance and distribution is influenced by the diversity of plant species and flower presence (Barret & Helenurm, 1987; Ansari & Memon, 2017; Terry & Nelson, 2018; Djellab *et al.*, 2019).

The results of this study provide the first comprehensive temporal and spatial information on hover flies in South Africa. The results of this study showed that hover fly populations remain active throughout the year, but with distinct fluctuations in their abundance, and with differences among genera. Heterogeneous indigenous habitats harbour a larger and more diverse hover fly community in comparison to plantations that generally negatively influence diversity. This study contributes to the growing number of studies that provide knowledge on the biology and ecology of Afrotropical Syrphidae.

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