Modelling the functional dynamics of carabid assemblages as indicators of agroecosystem stability

by

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PREFACE

The data described in this thesis were collected in the Bethlehem and Reitz regions of the eastern Free State, Republic of South Africa, from October 2020 to July 2021. The study was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, campus under the supervision of Dr Caswell Munyai and co-supervision of Professor Rob Slotow.

This doctoral thesis, presented for the attainment of a Doctor of Philosophy degree in the discipline of Entomology within the College of Agriculture, Engineering, and Science at the University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, is the result of the author's original research efforts and has not been previously submitted in any format for any other academic qualification at any University. Whenever the work of other researchers is incorporated due credit is given within the text.

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DECLARATION 1: PLAGIARISM

I, Maria Mammolawa Makwela, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

(iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a) their words have been re-written but the general information attributed to them has been referenced;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

(vii) this dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

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DECLARATION 2: PUBLICATION

<u>Makwela, MM</u>., Slotow, R., Munyai, T.C. 2023. Carabid Beetles (Coleoptera) as Indicators of Sustainability in Agroecosystems: A Systematic Review. Sustainability, 15, 3936. https://doi.org/10.3390/su15053936.

Author contribution:

Conceptualization of the study was done by M.M.M., R.S. and T.C.M. methodology, M.M.M.; data collection, M.M.M.; writing—original draft preparation, M.M.M.; writing—review and editing, R.S., T.C.M., and M.M.M.; supervision, R.S. and T.C.M.; funding acquisition, R.S., and T.C.M.

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DECLARATION 3: COVID IMPACT

This PhD project's progress was impacted by the Covid-19 outbreak. Laboratory access was restricted, and in-person meetings with farmers were unfeasible. The initial project plan involved selecting farms for sampling and conducting laboratory-based sample processing. Due to these constraints, the project commencement was delayed from June 2020 to mid-October 2020. Consequently, this delay had cascading effects on the selection, sorting, and identification of samples, requiring additional time and effort to coordinate and implement. The absence of laboratory access at the outset of the outbreak further hampered the sample processing timeline, exacerbating the project's setbacks.

ABSTRACT

Carabid beetles (Coleoptera: Carabidae) are ubiquitous and critically important in agroecosystems. Their rapid response to anthropogenic disturbances has been proposed as a practical and realistic tool for monitoring the sustainability of agricultural management practices. Carabid beetles significantly control pest populations, thereby aiding the regulation of harmful insects in agroecosystems. Recognizing their significance in this context highlights the potential of natural pest control strategies that can decrease reliance on chemical pesticides. Despite their potential importance, the impact of agricultural management practices on the diversity patterns and functionality of carabid beetles, specifically in South Africa, remains largely unexplored. Addressing this research gap is imperative to understand the complex association between agroecosystem management practices and carabid beetle populations in this region. This study aimed to advance knowledge about the ecological stability of diversely managed agroecosystems under conventional tillage, semi-natural grassland, conservation grazing, and semi-conservation agriculture by documenting and assessing the status of carabid beetle biodiversity and utilizing their functionality. This was done by (1) systematically reviewing literature on carabids as indicators of sustainability in agroecosystems, (2) assessing the diversity and community structure of carabid beetles in response to contrasting agroecosystem management, (3) investigating carabid beetle concordance with the selected epigeic arthropod taxa (ground spiders, ants, and rove beetles), and (4) characterizing carabid functional diversity (body size, feeding preference/guilds, and wing morphology). I achieved the aims by sampling over a two-year period, from 2020 to 2021, in the Free State province of South Africa using pitfall traps and active search methods. Carabid beetles were classified into morphospecies, and their functional diversity was determined using existing literature on carabid beetles. Data were analyzed with a sequence of multivariate and spatial statistical methods using the R software version 3.4.2. Carabid taxonomic and functional diversity patterns were significantly supported in conservation grazing compared with conventional tillage, semi-natural grassland, and semi-conservation agroecosystems. Notably, the conservation grazing-associated species included large flightless predators from the genera *Calosoma* and *Scarites*. Large, immobile, and specialized carabid beetles are sensitive indicators of management intensity in agricultural landscapes. However, not all carabid species are vulnerable to disturbances; some are eurytopic, occurring across all agroecosystems, such as the carabid genus *Pterostichus*, which are generalists and exhibit tolerance to disturbances. There was a high degree of congruence between the species richness and composition of carabid beetles and the overall epigeic arthropod taxa, indicating the efficacy of using carabid beetles as proxies for predicting the arthropod diversity patterns of epigeic taxa and identifying farms with conservation significance. The use of carabid beetles as model organisms in agroecosystems serves as a reliable proxy for assessing the impact of management practices on agroecosystems, enabling the ranking of disturbance, recovery, and stability levels. This knowledge will facilitate informed decision making and the implementation of effective conservation and sustainable management practices.

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DEDICATION

I dedicate this thesis to my beautiful, loving daughter (**Nolwazi Aria Nkalanga**), who is a ray of sunshine and a source of unwavering strength in my life. Because of you, I have learned to push myself through the limitations of fear, dissappointment, and failure. Every bit of effort in this work is for you, and my love for you knows no bounds.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Background information

The global agricultural industry faces significant challenges in meeting the ever-increasing demand for food caused by the projected population growth (Tilman et al. 2011). By 2050, the world's population is expected to reach 12.3 billion, putting immense pressure on agricultural production systems (Gerland et al. 2014; Ortiz et al. 2021). Various stakeholders, including scientists, farmers, industry players, and policymakers, have acknowledged this challenge (Tscharntke et al. 2021). However, meeting this demand for food often comes at a cost to the environment, as natural resources are depleted (Landis 2017). In Sub-Saharan Africa, where rapid population growth and heavy reliance on natural resources coincide, there is growing concern about biodiversity loss due to habitat degradation and climate change (Vink & Kirsten 2003; Hlahla et al. 2023). This biodiversity decline is particularly pertinent in the South African agricultural sector, which is characterized by the prevalence of monoculture practices in cultivating staple crops such as maize, soybean, sunflower, and groundnut (Midgley et al. 2015; DALRRD 2022). Although industrial farming may bring short-term economic benefits, it ultimately leads to habitat transformation, landscape alteration, and declining biodiversity and associated ecosystem services (Benton et al. 2003; Corcos et al. 2021).

In the face of these compelling challenges, a discernible shift in the agricultural production landscape of South African grain agroecosystems is evident, transitioning from conventional practices to more sustainable approaches (DAFF 2017; Malobane et al. 2020). This shift is driven by critical imperatives of food security and the preservation of biodiversity and ecosystem services. Consequently, an increasing number of farmers and stakeholders in South Africa are embracing regenerative agriculture to promote sustainability in farmlands (Blignaut et al. 2015; DAFF 2017). The implementation of conservation practices involves a range of strategies, including crop diversification, no-till practices, crop rotation, and the retention of cover crops and residues (Blignaut et al. 2015). However, a central concern surrounding the adoption of conservation farming is the assessment of its productivity, sustainability, and long-term stability, particularly when considering projected future food demands (Midgley et al. 2015). Despite the well-documented potential of conservation agriculture, particularly in grain agroecosystems, a significant research gap exists in the understanding of potential impact on, or role of, insect diversity, and impacts of different agricultural management on ecosystem functioning (Zulu et al. 2022).

1.2 Significance of the study

The efficacy of sustainable agroecosystems centers on a thorough understanding of the impacts of different management practices on species biodiversity (Bianchi et al. 2006). Existing research has underscored the importance of assessing environmental sustainability and changes within agroecosystems that encompass diverse farming practices, including organic (Eyre et al. 2013; Djoudi et al. 2018; Smith et al. 2020), mixed farming (Rusch et al. 2013; McKenzie et al. 2016; Boutaud et al. 2022; James et al. 2022), and conventional management (Menalled et al. 2007; Jonason et al. 2013; Njaimwe et al. 2016; Aldebron et al. 2020; Boinot et al. 2020). This rigorous assessment employs monitoring techniques capable of detecting ecological changes in their early stages and over an extended period, providing a basis for well-informed and cost-effective management decisions (Larsen et al. 2009). The concept of "biological indicator," commonly referred to as 'bioindicators,' has emerged as a well-established and effective approach for monitoring and detecting stability within agroecosystems (Koivula 2011). A bioindicator is defined as a species or assemblage which reflects the abiotic or biotic state of the environment and, functions as a representative measure of the effects of environmental changes on a habitat (McGeoch et al. 2002). Following the precise definition provided by Ochs et al. (2016), an "indicator" is an organism (taxa or group of taxa) whose characteristics, such as presence or absence, population density, dispersion, reproductive success, or functionality, are utilized as an index of attributes that are otherwise challenging, inconvenient, or costly to measure for other species or environmental conditions of interest. The term "indicator" is used in this context following this precise definition, unless explicitly stated otherwise.

Carabid beetles (Coleoptera:Carabidae), also known as ground beetles, were selected as model organisms in this study (Koivula 2011). Carabid beetles possess a myriad of characteristics that render them well suited as indicator species. These characteristics encompass their extensive geographic distribution, ability to serve as early warning indicators of change, diversity, functional and economic significance within ecosystems, and ease of sampling, sorting, and monitoring even by non-expects, including farmers (McGeoch et al. 2002; Cajaiba et al. 2018). Carabid beetles have been extensively and effectively used in studies related to urban ecology (Rainio & Niemela

2003), pesticides (Vician et al. 2018), habitat classification (Eyre et al. 2016), and agroecosystem health (Lemic et al. 2017; Ivanič et al. 2022). Thus, as bioindicators, they provide valuable insights into the repercussions of cultivation practices on agroecosystems over time and space (Horne 2007). Moreover, owing to their multifaceted ecosystem functions, including predation and decomposition, carabids are critical for promoting agricultural sustainability and productivity (De Heij & Willenborg 2020). However, while there is existing research on carabid beetles in forest ecosystems (Schoeman et al. 2018), and floristic landscapes (Gaigher 2008), their role as indicators in agricultural settings, particularly in the context of conservation and conventional farming methods, remains largely unexplored. Previous studies have identified distinct categories of indicators that correspond to different carabid beetle applications (Holland & Luff 2000; Rainio & Niemela 2003; Horne 2007). These categories provide valuable insights into the health and functioning of agroecosystems, and can aid in decision-making processes for conservation and management. An overview of the carabid indicator categories is as follows.

Ecological Indicators: Species that can be used to assess the impact of human activities on an ecosystem, particularly its biotic communities (Karyl 1999). Various insects, such as butterflies, ants, dung beetles, and dragonflies, have proven useful in evaluating the effects of anthropogenic activities on both terrestrial and aquatic ecosystems (Weibull et al. 2000; Andersen et al. 2002; Filgueiras et al. 2015; Kietzka 2019). Among these insects, carabid beetles have been extensively utilized as reliable ecological indicators due to their sensitivity to human-induced disturbances (Luff 1996; Holland & Luff 2000). This makes them particularly effective for assessing habitat quality and aiding in biodiversity and conservation studies. Carabid beetles are a diverse and widely distributed group found in agricultural landscapes worldwide, further highlighting their utility in ecological monitoring (Horne, 2007). Although their effectiveness has been well documented in developed countries, the potential of carabids as ecological indicators in South African agroecosystems remains largely unexplored (Kotze & Samways 1999; Kotze 2000; Botha 2017).

Biodiversity Indicators: A taxon or a functional group that reflects the diversity of other taxa, encompassing characteristics such as species richness and levels of endemism (Karyl 1999). In recent years, the quest for effective biodiversity indicators has gained momentum because of the practical constraints of time and resources, which often make it challenging to comprehensively survey species diversity within entire communities. However, the quest for reliable biodiversity indicators has proven to be a formidable challenge (Rainio & Niemela 2003). Although the effectiveness of carabid beetles as ecological indicators has been relatively well documented (Luff 1996; Schirmel et al. 2015), their potential as biodiversity indicators remains largely unexplored, especially within agricultural landscapes (Corcos et al. 2021).

Ecosystem Services Indicators: Species assemblages that play a pivotal role as keystone predators, primarily because of their predation on a wide range of pests and weed seeds (Shearin et al. 2008; Woodcock et al. 2010; Eo et al. 2016). As essential components of an agroecosystem, keystone species contribute significantly to their stability through their interactions with other species (Koivula 2011). Numerous studies have demonstrated the critical role of ground beetles as keystone species in various settings including agroecosystems, greenhouses, and laboratories (Diehl et al. 2012; Rusch et al. 2018; Deppe & Fischer 2023). Carabid beetles have shown remarkable efficiency in controlling pests and weed seeds, making them crucial contributors to biological pest and weed control (Diehl et al. 2012; Redhead et al. 2020). This is evident in their ability to prey on a wide range of pests, including corn earworms, stalk borers, and aphids (Rusch et al. 2013; Cardarelli & Bogliani 2014), as well as controlling weed seeds such as giant foxtail seeds, redroot pigweed and velvetleaf seeds (White et al. 2007). This dietary preference underscores their role in delivering essential ecosystem services to agroecosystems (Boinot et al. 2020)

1.3 Aim of research

The project aimed to advance knowledge about the ecological stability of diversely managed agroecosystems under conventional tillage, semi-conventional farming, conservation grazing, and semi-natural grasslands. I also documented and assessed the status and biodiversity of carabid beetles, and elaborated on their use as model organisms. The results obtained may be used to quantify and predict the ecological effects of production management practices in grain agroecosystems. The steps of the study layout are indicated in (Figure 1.1).

This thesis is comprises six chapters. Chapters two through five encompass the findings of the research questions outlined in Table 1.1 Each chapter is written as an independent paper for submission to peer-review journals, and comprises an abstract, introduction, materials and methods, results, discussion, conclusion, and references. The summarized contents and particular objectives of each chapter are as follows:

Chapter 1: The general introductory chapter provides background information on the study, motivation, aim, and specific objectives.

Chapter 2: Provides a systematic review of existing literature on Carabid beetles (Coleoptera: Coleoptera) as indicators of sustainability in agroecosystems. This chapter is published: Makwela, MM., Slotow, R. & Munyai, T.C. (2023). Carabid Beetles (Coleoptera) as Indicators of Sustainability in Agroecosystems: A Systematic Review. Sustainability, 15, 3936. https://doi.org/10.3390/su15053936.

Chapter 3: Ecological response of carabid beetle assemblages to agroecosystem management practices. The objective of this study was to assess the effects of several management practices employed in selected agroecosystems on carabid beetle abundance, richness, and composition.

Chapter 4: Carabid beetles (Coleoptera: Carabidae) are biodiversity indicators of epigeic arthropod taxa in agricultural landscapes. The objective of this study was to examine congruencies in the diversity patterns of carabids and other epigeic arthropods (*i.e.*, rove beetles, ground spiders, and ants) across different farm types.

Chapter 5: Characterization of the functional traits of carabid beetles in different farm systems. The objective of this study was to investigate carabid functional diversity (i.e., body size, wing status, and feeding type) in relation to vegetation cover in contrasting farm systems.

Chapter 6: Overall synthesis, recommendations, and concluding remarks.

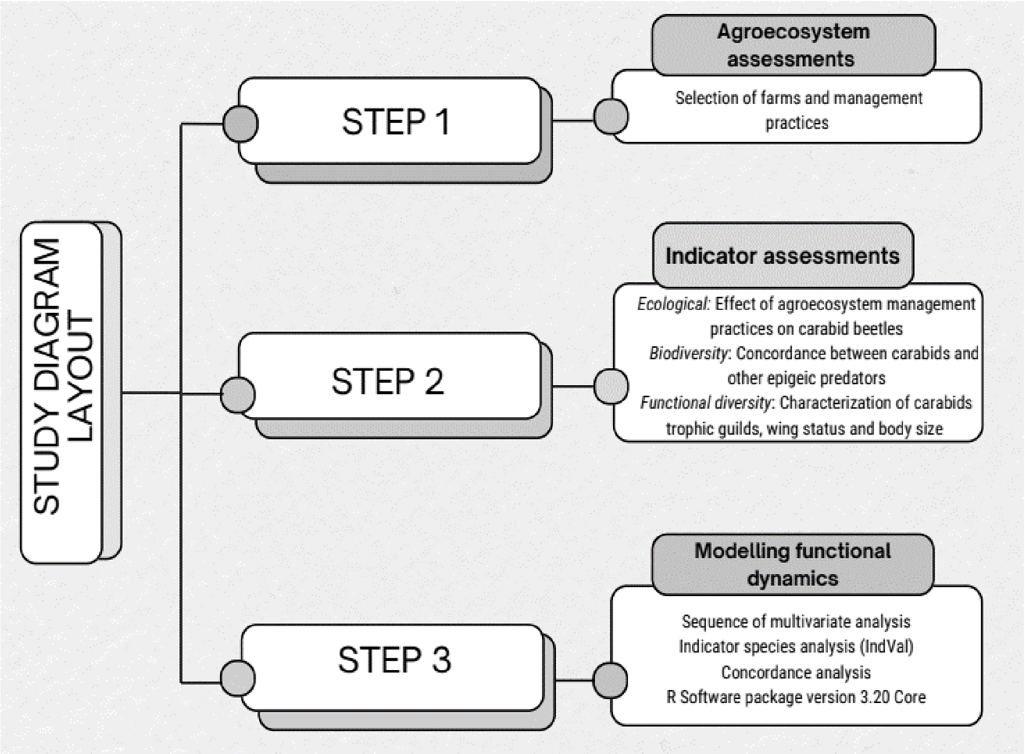

Figure 1.1. Diagram illustrating layout of steps summarizing the various elements considered in this study.

Table 1.1. Thesis research questions

Chapter (s)	**Research Question**
2	Can carabid beetles be used as indicators of agroecosystem stability?
3	How informative is the response of carabid beetle assemblages to contrasting management regimes in agricultural fields and semi-natural grasslands?
4	Is the diversity pattern of carabid beetles congruent with the diversity patterns of other selected epigeic arthropod taxa?
5	How do carabid functional traits (i.e., body size, feeding preference and wing morphology) differ in various farm types?

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CHAPTER 2: CARABID BEETLES COLEOPTERA) AS INDICATORS OF SUSTAINABILITY IN AGROECOSYSTEMS: A SYSTEMATIC REVIEW

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Abstract

The sustainability of agroecosystems is at risk owing to continuous anthropogenic disturbance. As such, there is a need to evaluate indicator taxa that may be used to monitor the health of agricultural management systems. Carabid beetles are ubiquitous and functionally crucial in agroecosystems while at the same time are sensitive to the changes caused by management practices. Their quick response to anthropogenic disturbances has been proposed as a practical and realistic tool for monitoring the sustainability of agricultural practices. However, there is still disagreement about carabids as possible indicators of agroecosystem sustainability. We conducted a systematic review of the responses of carabid beetles to agricultural systems in different biogeographical areas. We examined whether these beetles could serve as potential indicators of agroecosystem sustainability. The ISI Web of Science, Google Scholar, and Scopus were used to search for papers published from 2000-2019. In total, we included 69 studies indicating the use of carabids to monitor the impact of management practices in agroecosystems. Most studies were conducted in European countries (n = 37), while Southern Africa and East Asia countries were significantly under-represented (n = 10). Carabid beetle response to agroecosystems varied between management practices, with biodiversity indices (n = 41: positive 60%, negative 19%, and neutral 19%) being the most measured response variable, followed by functional diversity (n = 28: positive 67%, negative 25%, and neutral 7%). Overall, our findings highlight the need for more research in underdeveloped countries, to investigate the potential of overlooked carabids and include response variables measuring functional diversity in assessing the sustainability of agricultural management. This will assist policy makers and land managers in making active and informed decisions about agroecological disturbances and management.

Keywords: agricultural management type; biodiversity; ground beetles; ecological monitoring; functional diversity

2.1 Introduction

Agricultural intensification is one of the main causes of the biodiversity crisis (Sánchez-Bayo & Wyckhuys 2019), with repercussions for the functioning and sustainability of agroecosystems (Basedow 2002; Tscharntke et al. 2012). Agricultural management systems that involve the continuous use of pesticides result in habitat degradation, conversion of semi-natural habitats to cropland, and dominance of a few plant species in larger areas (Benton et al. 2003; Purtauf et al. 2005; Gallé et al. 2019). These significant challenges affect the ecological processes that provide the functions necessary for sustainable production (Rusch et al. 2018). Moreover, management practices are confronted with numerous challenges in multiple fronts, ranging from meeting the food demand of the growing population to dealing with climate change effects (El Chami et al. 2020; FAO 2020). Concerns about the negative effects of high-input industrially managed agriculture have prompted a call for sustainable management practices (Massaloux et al. 2020).

The implementation of sustainable agricultural practices should include cost-effective monitoring techniques that can be used to detect environmental changes, assess management performance, and provide early warning signals for imminent ecological transitions (Cajaiba et al. 2018). Ecological indicators are species or groups of species that are easily monitored, and whose status reflects or predicts the condition(s) of the environment in which they are found (Rainio & Niemela 2003). Indicator species may be a helpful tool for addressing agricultural intensification difficulties (Gerlach et al. 2013). For decades, changes in key indicator species have been used to underpin increasing concern about the necessity of biodiversity conservation and sustainability in the face of accelerated environmental change induced by human activities. Subsequently, the use of indicators has been extended to aquatic and terrestrial invertebrates used to detect environmental impacts in freshwater (Gioria et al. 2010; Backus-Freer & Pyron 2015; Govender & Willows-Munro 2019) and different ecosystems (Andersen et al. 2002; Rainio & Niemela 2003; Horne 2007; Work et al. 2008; Barriga et al. 2010; Koivula 2011; Joseph et al. 2018). Despite the extensive history of prospective indicator species, surprisingly, few studies have been conducted on indicators for sustainable agroecosystems (Karyl 1999; Niemelä 2000). Therefore, using taxonomic or functional groups that are sensitive to ecological change in agroecosystems might be a helpful tool to monitor the resilience and health of management practices.

Among edaphic arthropods, carabid beetles are regarded as excellent indicator species due to their abundance and diversity, well-known taxonomy, ease of sampling, and cost-effectiveness (Döring et al. 2003; Rainio & Niemela 2003). Carabids are particularly suitable for examining subtle effects of agroecosystem management practices such as pesticide use, depth of tillage, soil quality, moisture, and landscape heterogeneity, because certain species are stenotopic and thus intrinsically sensitive to environmental conditions (Holland et al. 2002; Döring & Kromp 2003; Horne 2007; Shearin et al. 2007). Other biodiversity assessments have reported carabid responses to grassland management practices (Botha 2017; Lemic et al. 2017; Rivers et al. 2017; Lyons et al. 2018). The importance of carabids in agroecosystems is critical due to their economic and functional value, acting as natural enemies of pests or components of trophic chains that support biodiversity (Trichard et al. 2014; Irmler 2018). Though carabids have been well studied taxonomically and ecologically in agroecosystems worldwide (Kotze & O'Hara 2003), most studies in Africa have documented the carabid beetle diversity in savanna biomes (Schoeman et al. 2018), forest–grassland mosaics (Yekwayo et al. 2017), vineyards (Gaigher 2008), and few in cereal agroecosystems (Botha 2017; Makwela 2019). Notably, their use as indicators of agroecosystem sustainability remains a challenge due to a lack of data on their ecological responses, particularly under different agricultural management scenarios (Kotze & O'Hara 2003; Taboada et al. 2011; Gailis & Turka 2014; Koivula 2014; Eyre et al. 2016; Jowett et al. 2019). A detailed knowledge of the response of carabids in various management practices can provide insight into the health of agroecosystems. This review aimed at providing a global and comprehensive overview of the use of carabid beetles in agroecosystems and assesses their inclusion as sustainability indicators. The focus is on conservation and biodiversity studies, with a geographical emphasis on agroecosystems where most research has been conducted, namely across semi-natural grasslands and field crops.

2.2 Materials and Methods

To summarize the ecological response of carabid beetles to agricultural management practices in different geographical regions, we conducted a systematic review using the Preferred Reporting Items for Systematic Reviews (PRISMA) method and checklist (Moher et al. 2009; Page et al. 2021) (Figure 2.1, see Supplementary Information PRISMA checklists 2021). PRISMA is a standard protocol for conducting objective and reproducible systematic reviews to improve scientific transparency. We selected studies that examined cropland and semi-natural grassland because these agroecosystems are managed differently (from semi-natural habitats to homogeneous monocultures, crop rotations, pastures, organic farming, and diversified and conventional tillage), which affects carabid beetle biodiversity and functionality (Table 2.1, see Supplementary Information Figure S1 2.1).

Table 2.1. Categories used to classify studies found in the literature search.

Category items	Description
Agricultural management	Studies on organic and diversified farming, conventional tillage, conservation, grazing practices, and grassland effects on carabid beetles
Field crops	Soybean, wheat, peas, maize, clover, sunflower, oats, barley, alfalfa, rice, millet, and sorghum
Biodiversity indices	Studies including diversity: abundance, richness, evenness, and composition
Functional guilds	The trophic level of carabids: predators/carnivores, omnivores, and granivores and their functions in agroecosystems
Functional traits	Studies that recorded dispersal ability and morphometrics

Search and Selection of Publications

We searched the ISI Web of Science Core Collection (http://www.isiwebofknowledge.com), Scopus (https://www.scopus.com), and Google Scholar (https://scholar.google.ca) for peer-reviewed publications published on all continents. We used the following search term to find studies on the effects of agroecosystem management practices on carabid beetles: ("agri-environmental programmes" OR "organic farming" OR "sustainable farming" OR "diversified farming" OR "integrated farming" OR "conservation farming" OR "conventional tillage" OR "intensive farming" OR "semi-natural grassland AND *Beetles", AND *Carabidae", AND "ground beetles" AND *Indicator"). To find the response variables, we used the following search term: ("abundance" OR "richness" OR "diversity" OR "composition" OR "functional diversity" OR "weed predator" OR "generalist" OR "specialist" OR "morphological traits" OR "trophic guilds"). All journal citations and abstracts were imported into the Mendeley online importer reference management software (https://www.mendeley.com) and their titles, keywords, and abstracts were checked.

Data Extraction and Synthesis

We focused on extracting data on language (English), year of publication (March 2000 to April 2019), biogeographic region (country/continents), agricultural management type (conventional tillage, organic farming, diversified farming, conservation agriculture, and grazing), diversity (richness, evenness, composition, abundance, and active density), functional traits (body size and dispersal ability), and trophic guilds (predators, granivores, and omnivores) (Table 2.1). We also evaluated each publication according to whether the authors reported negative, positive, or neutral effects of different agroecosystem management practices on carabid beetles. Grey literature, books, conference proceedings, technical reports, and unpublished data were not considered in the review conducted here.

2.3 Results

General Overview

The initial search for relevant articles resulted in 1370 articles. After eliminating duplicates (919 articles), the search criteria yielded 451 articles across all databases. The titles, abstracts, and keywords of 451 articles were screened, with 217 excluded. Critical appraisal of the 234 studies that met the relevance criteria led to the exclusion of 165 studies due to low or unclear validity (see Supplementary Information, Figure S2 2.2). Consequently, 69 studies showing the response of carabid beetles to different management practices in agroecosystems were used for the qualitative synthesis. The search, screening, and inclusion of studies are schematically summarized in the flow chart below (Figure 2.1).

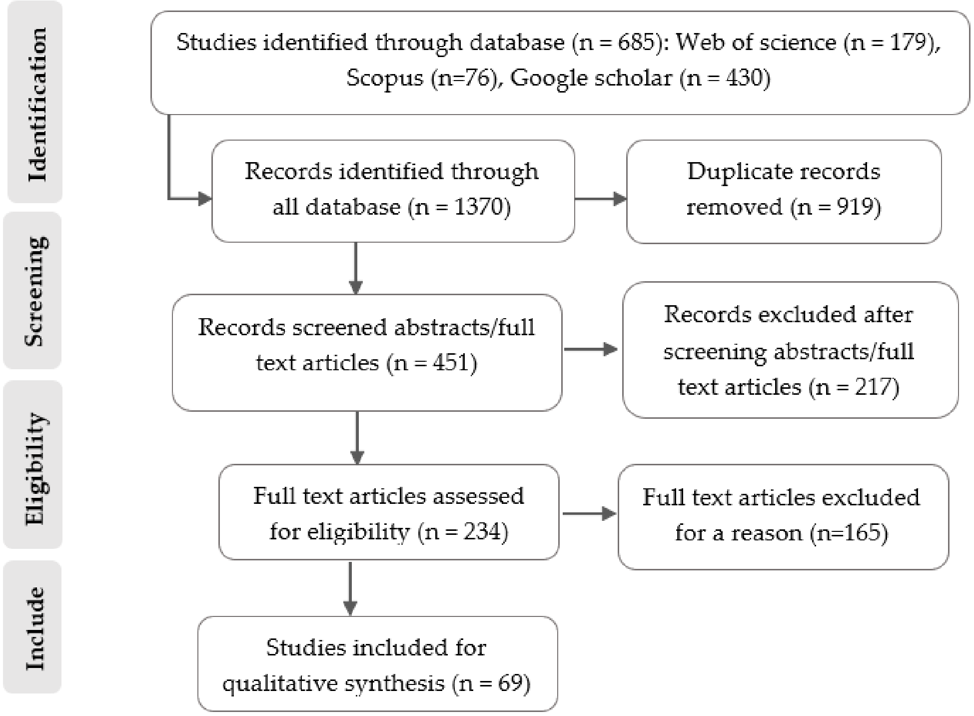


Figure 2.1. A flow diagram showing the systematic review process (adapted from PRISMA guidelines).

Trends in Carabid Beetle Studies and Status in Agricultural Management Systems

According to the systematic review, the first papers addressing the response of carabid beetles to agricultural management were published from 2000 to 2009, with no articles found in 2002. Since then, the temporal trend of studies dealing with this topic has shown a steadily increasing rate, indicating that it is an emerging field of research. This was found when 55 articles were published between 2010 and 2019, respectively (Figure 2.2). Overall, the selected papers show that most of the studies were conducted mainly in developed countries, particularly in Germany (n = 19), France (n = 11), the United Kingdom (n = 7), and the United States (n = 5), while few studies were conducted in developing countries in Southern Africa (n = 6) and East Asia (n = 4), (Figure 2.3). In terms of agricultural management systems, conventional farming predominated in 28% of studies, followed by diversified farming systems (17%), integrated agriculture (16%) and semi-natural habitats (16%). Only a few studies were conducted on organic farming (13%) and conservation agriculture (10%) (Table 2.2; Figure 2.4a).

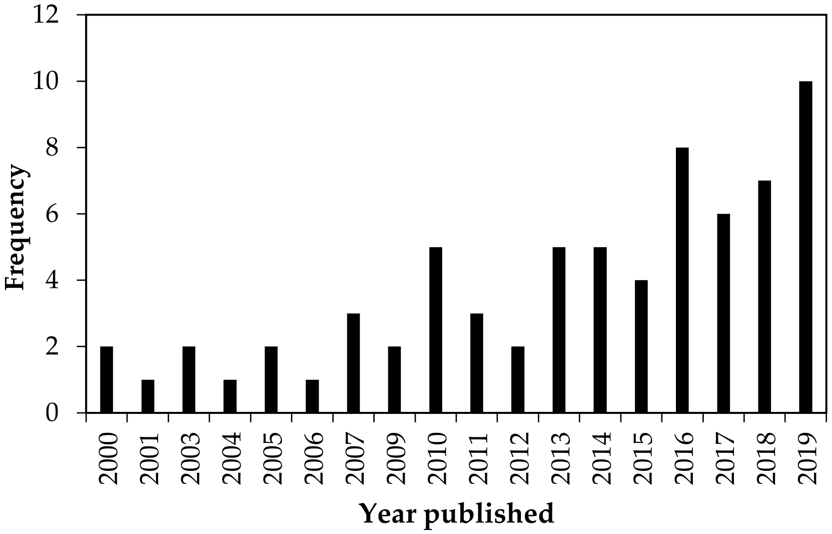


Figure 2.2. Publications (n = the total of 69 screened articles) that investigated the response of carabid beetles to agricultural management practices between 2000 and 2019.

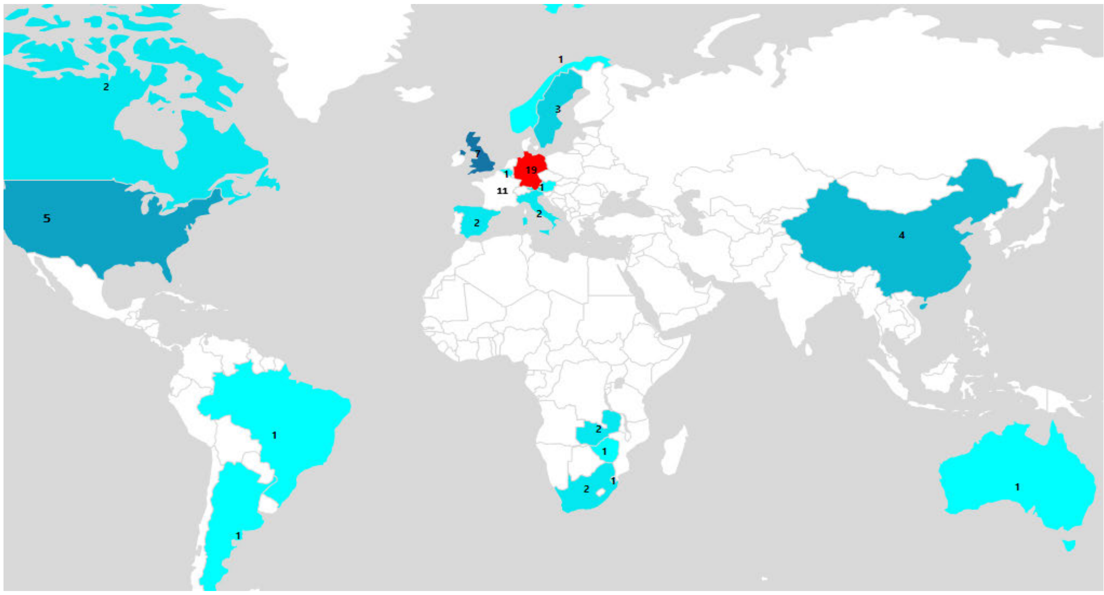


Figure 2.3. Geographic locations of the 69 included peer-reviewed studies on the world map.

Carabid Response Variables to Agricultural Systems

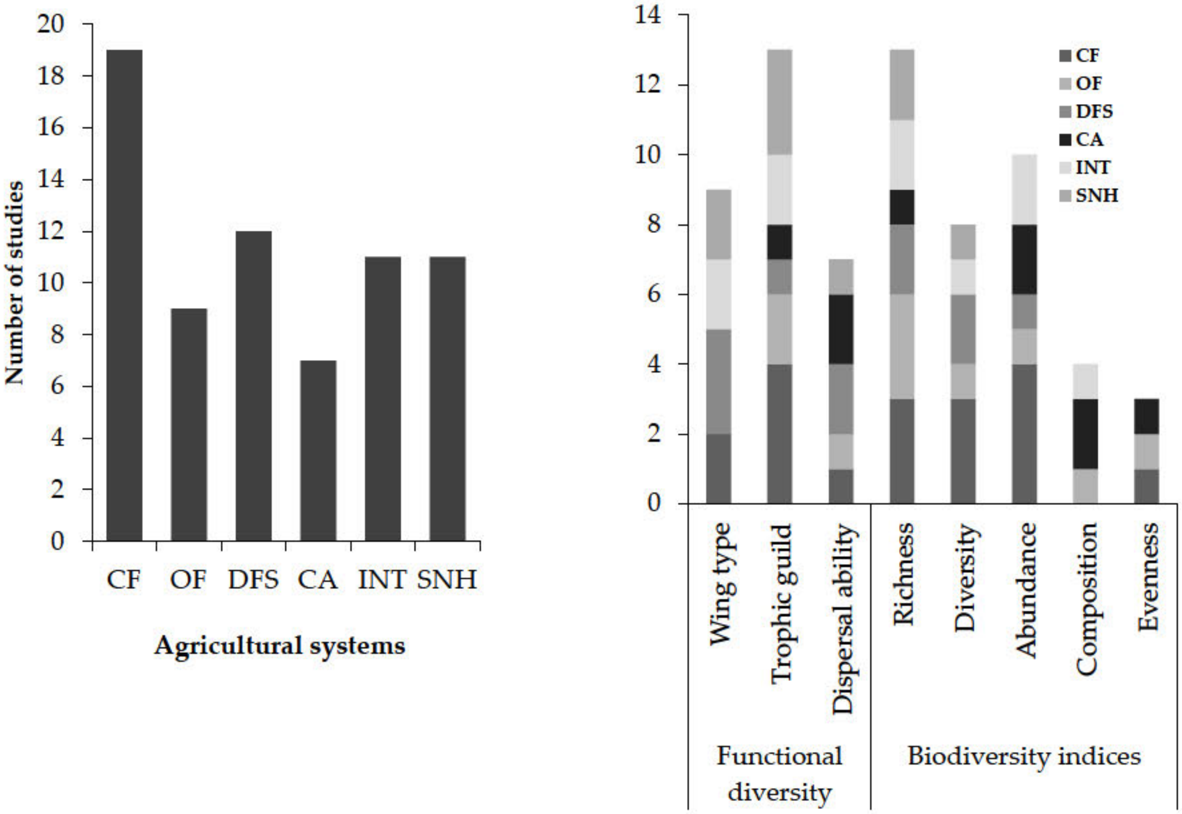
We recorded five carabid biodiversity indices (41 studies: 25 positive, 8 negative, and 8 neutral) used to assess the effects of agricultural management type. Richness (13 studies) and abundance

(10 studies), followed by diversity (9 studies), were the three most frequently assessed indices. The next frequently used measure was community composition (i.e., the assemblage of the different species comprising the studied community), followed by evenness. Functional diversity was measured in only a small proportion of papers (28 studies: 19 positive, 7 negative, and 2 neutral) and mainly concerned trophic guilds (13 studies), body size (9 studies), dispersal ability, and wing type (6 studies) across agricultural management type (Table 2.2, Figure 2.4b).

Table 2.2. Carabid functional diversity and biodiversity indices in different agricultural management types (CF–conventional farming; OF–organic farming; DFS–diversified farming system; CA–conservation agriculture; INT–integrated farming; SNH–semi-natural habitats).

Response variables		Agricultural Management Type							
	Effect	CF	OF	DFS	CA	INT	SNH	Total	% Total
Functional diversity									
Body size: small, medium, and large	Positive	1	-	2	-	1	2	6	8.7
	Negative	1	-	1	-	-	-	2	2.9
	Neutral	-	-	-	-	1	-	1	1.4
Trophic guilds: predators, omnivores, and granivores	Positive	2	2	-	1	2	1	8	11.6
	Negative	1	-	1	-	-	2	4	5.8
	Neutral	1	-	-	-	-	-	1	1.4
Dispersal ability (wing type): flightless, immobile, macropterous, brachypterous, wingless, and apterous	Positive	1	1	-	2	-	1	5	7.2
	Negative	1	-	-	-	-	-	1	1.4
	Neutral	-	-	-	-	-	-	-	-
Biodiversity indices									
Richness	Positive	1	3	1	1	2	1	9	13.0
	Negative	1	-	1	-	-	-	2	2.9
	Neutral	1	-	-	-	-	1	2	2.9
Diversity	Positive		- -	3	-	-	1	4	5.8
	Negative	2	-	1	-	1	-	4	5.8
	Neutral	1	-	-	-	-	-	1	1.4
Abundance/active density	Positive	2	1	1	2	1	-	7	10.1
	Negative	1	-	-	-	-	-	1	1.4
	Neutral	1	-	-	-	1	-	2	2.9
Composition	Positive	1	-	1	-	1	-	3	4.3
	Negative	1	-	-	-	-	-	1	1.4

	Neutral	-	-	1	-	-	1	2	2.9
Evenness	Positive	1	1	-	-	-	-	2	2.9
	Negative	-	-	-	-	-	-	-	0.0
	Neutral	-	-	-	1	-	-	1	1.4
Grand total		19	9	12	7	11	11	69	100



(a) **(b)**

Figure 2.4. Summary of number of papers published on (a) agricultural management type and (b) carabid functional diversity and biodiversity indices included in the systematic review (see Table 2 for abbreviations).

2.4 Discussion

This review highlights the need to increase our knowledge of the use of carabid beetles as indicators of agroecosystem sustainability. The use of monitoring techniques such as indicator species to assess environmental change in agroecosystems is an emerging topic in research (Eyre et al. 2013; Eyre et al. 2016; Lyons et al. 2018; Jowett et al. 2019). Because carabids clearly respond to agricultural management practices, they can play an important role in determining which practices in agroecosystems bring us closest to our goal of agroecosystem sustainability

(Kotze & O'Hara 2003). Despite the fact that the number of studies on carabids in agricultural systems is increasing globally, we have found that there is a clear geographical preponderance of studies from the most developed countries in Europe, with a large gap in the developing countries of Southern Africa and East Asia (Woodcock et al. 2010; Diehl et al. 2012; Schirmel et al. 2016; Gayer et al. 2019). This implies that indicator species are prioritized in developed countries for monitoring the status of management practices in agroecosystems (White et al. 2007; Petit et al. 2017).

Carabid beetles are ubiquitous, stenotopic, and influenced by different agroecosystem management practices (Marrec et al. 2015; Caro et al. 2016; Aviron et al. 2018; Djoudi et al. 2018). Conventional agricultural management has repeatedly been linked to negative effects on carabid diversity and functional traits (Andersen & Eltun 2000; Jonason et al. 2013; Melnychuk et al. 2013; Hussain et al. 2014; Chungu 2017). The detrimental effects of this management can be explained by the fact that the synchronization of tillage timing and agrochemical application reduces carabid diversity by causing direct mortality and disturbance of overwintering sites (Pfiffner & Luka 2003; Schröter & Irmler 2013; Ng et al. 2018). This disturbance indirectly eliminates food sources and alters the habitat by changing the density, distribution, and composition of weeds (Rouabah et al. 2015; Boetzl et al. 2019). According to Schröter & Irmler (2013), these provide foliage and seeds to different species, control microclimate and soil moisture, and determine the degree of physical protection from predators and freedom of movement. For example, species that breed in autumn and overwinter as larvae in the soil are vulnerable to having their abundance affected by conventional tillage (Liu et al. 2015; Labruyere et al. 2016; Li et al. 2018). However, not all species decline due to such disturbance; certain species from carabid genera *pterostichus* and *harpalus* may be resistant or sensitive (Bertrand et al. 2016; Hanson et al. 2016). Studies conducted in conventional systems have shown that carabids can be used as indicators for monitoring ecological changes caused by management practices such as pesticide use and tillage methods (Diekötter et al. 2010; Hof & Bright 2010; Mashavakure et al. 2019).

Furthermore, our results show some preferences in using biodiversity indices, i.e., species richness and abundance as indicators of agricultural management conditions (Cardarelli & Bogliani 2014; Pardon et al. 2019). Species richness is one of the simplest measures of species diversity, and along with species abundance, it provides useful information about the state of different management practices (Hummel et al. 2012). However, there is a significant gap in the use of carabid functional diversity metrics. Trait-based information should also be included when assessing the sustainability of agroecosystems because measures of species richness and abundance are clearly insufficient to explain ecosystem functioning (Hatten et al. 2007; Woodcock et al. 2010; Gayer et al. 2019). Dispersal ability, which is linked to functional traits such as body size, may be a key factor when assessing the health of agricultural management practices (Maisonhaute et al. 2010; Knapp & Řezáč 2015; Alignier & Aviron 2017; Barber et al. 2017). Body size has a greater influence on prey consumption (Makwela 2019). This shows that functional traits, rather than broad community descriptors such as species richness, can better indicate ecosystem services of pest control for agricultural systems (Shah et al. 2003; Woodcock et al. 2010; Eyre et al. 2016). The dominance of key indicator species with high feeding rates can be used to assess the efficiency of a predator community in controlling pests (Rouabah et al. 2015). For instance, larger carabids are a predictor of pest consumption, with larger species consuming large pests (Eyre et al. 2013; Koivula 2014; Chungu 2017). However, due to their limited dispersal ability, larger brachypterous predators are thought to be at greater risk of extinction than smaller macropterous species in severely disturbed and fragmented homogenized agroecosystems (Bertrand et al. 2016; Aviron et al. 2018). Smaller species thrive in open habitats because they can disperse when conditions are unfavorable (Shearin et al. 2007; Cardarelli & Bogliani 2014; Pardon et al. 2019), whereas species with restricted dispersal ability can only colonize new areas by running (Cole et al. 2002; Kotze & O'Hara 2003; Gobbi & Fontaneto 2008; Caro et al. 2016).

Carabid species that benefit from intact agroecosystems are considered indicators of sustainable management practices (Duflot et al. 2016). This implies that ecological, conservation, and integrated farming systems with a diverse crop mix and a diversity of field edges and strips are critical for the survival of carabid species (Weibull & Östman 2003; Kulkarni et al. 2017). Over time, these agroecosystems will provide shelter and more diverse food supplies, perhaps promoting carabid functioning and biodiversity (Ekroos et al. 2010; Hanson et al. 2016). Carabid species that occur in various habitats benefit from different management practices than specialists that occur in just one or a few habitats (Menalled et al. 2007). Each agroecosystem has its unique set of species, including both generalists and specialists, that can be used to track the effectiveness of management strategies (Duflot et al. 2016; Djoudi et al. 2018).

2.5 Conclusion

Given the constraints associated with implementing sustainable measures in agroecosystems, we suggest that carabid beetles can aid in monitoring the recovery and health of agricultural management practices. Continuous monitoring of indicator species in agroecosystems can reveal the pace and direction of change within management practices (Karyl 1999; Purtauf et al. 2005). Though carabids are receiving remarkably more attention as indicators of agroecosystem sustainability worldwide, there is still a need to quantify diversity or composition and the impact of species functioning on agroecosystems. Determining the functional diversity of carabid beetles in agroecosystems can help us better understand their ability to provide ecosystem services of pest control (Hanson et al. 2017). Therefore, selecting indices or descriptors that integrate functional diversity information is crucial for future sustainable agricultural efficiency.

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CHAPTER 3: ECOLOGICAL RESPONSE OF CARABID BEETLES TO AGROECOSYSTEM MANAGEMENT PRACTICES

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Abstract

Carabid beetles play vital roles in agroecosystems and occupy a range of functional niches. Their ability to swiftly respond to environmental changes makes them ideal indicator species for monitoring the impacts of agroecosystem management practices, but this is understudied. Therefore, we investigated the ecological response of carabid beetle diversity and composition to agroecosystem management practices, including conservation grazing, semi-conservation farming, conventional tillage, and semi-natural grassland. Pitfall traps and active search methods were used to collect carabids between 2020–2021. Carabid abundance and richness were significantly higher under conservation and semi-conservation management than under semi-natural grassland and conventional tillage. There were significant differences in assemblages among agroecosystem types and management practices. There were five indicator species of agroecosystems that might be useful for monitoring the impacts of various management approaches more broadly. The insights gained from this study can potentially guide future management strategies for conserving carabid diversity and fostering ecological balance in agroecosystems and grasslands.

Keywords: agricultural landscapes, composition, diversity, ground beetles, IndVal, sustainability

3.1 Introduction

The increasing food demand due to global population expansion has put agroecosystem and natural resource management under pressure (Licker et al. 2010; Tilman et al. 2011). The currently adopted conventional agricultural models, which rely heavily on agrochemical inputs, large monocultures, and habitat modifications, have undeniably boosted yields (Flohre et al. 2011). However, this intensification and expansion of agriculture has come at a significant ecological cost, causing severe declines in arthropod biodiversity and vital ecosystem services such as decomposition, nutrient cycling, pollination, and biocontrol (Tscharntke et al. 2012). These services are crucial for sustaining crop productivity and the overall agricultural sustainability (El Chami et al. 2020). Therefore, there is an urgent need to address the decline in insects (Redhead et al. 2020) because of their pivotal role in the structure and functioning of agroecosystems (Samways et al. 2020). Extensive research has demonstrated that adopting sustainable management approaches (Foley et al. 2011; Sattler et al. 2020; Ortiz et al. 2021) that strike a balance between production, ecosystem resilience, biodiversity support, and reduced chemical inputs can prevent the loss and extinction of arthropods (Branco & Cardoso 2020). Understanding the ecological significance of arthropod communities in agroecosystems holds great potential for informing decision-making and facilitating robust management and restoration efforts in endangered ecosystems (Tscharntke et al. 2021). For instance, ground-dwelling arthropods such as spiders (Batáry et al. 2012; Birkhofer et al. 2015), ants (Andersen et al. 2002; Braschler & Baur 2016; Munyai et al. 2021), and ground beetles (Horne 2007; Hummel et al. 2012; Schirmel et al. 2015) have emerged as valuable proxies for evaluating the impact of environmental changes on agroecosystems, generating increasing interest across various disciplines (Ochs et al. 2016).

Carabids (Carabidae:Coleoptera), also known as ground beetles, have several characteristics that make them highly suitable for ecological studies (Luff 1996; Pihlaja et al. 2006; De Heij et al. 2022). Rainio and Niemela (2003) identified several key attributes of carabids, including their ubiquity in all agroecosystems and their diverse functional roles in trophic food webs. They are also sensitive to landscape and habitat changes and their measurements are cost-effective and straightforward when standardized methodologies are employed (Rainio & Niemela 2003; Horne 2007; Martel et al. 2019). The diversity of carabid beetles is closely linked to habitat structure (Kang et al. 2012), and most species exhibit high sensitivity to management practices, such as soil cultivation patterns, burning, harvesting, grazing regimes, and pesticide use in agroecosystems (Pfiffner & Luka 2000; Hatten et al. 2007; Hummel et al. 2012). While previous research has extensively investigated the effects of ecosystem management on carabid beetles in forestry settings (Heyborne et al. 2003; Taboada et al. 2008; Magura & Lövei 2020), there has been a notable lack of emphasis on diverse agronomic practices, as highlighted in our previous review (Makwela et al. 2023). Only a limited number of studies have explored the influence of agroecosystem management practices on carabid diversity, with most comparing organic and conservation management systems (Menalled et al. 2007; Shearin et al. 2007; Gailis et al. 2017). Despite the critical role of carabid beetles in agricultural productivity, agriculture poses a significant threat to carabid beetle assemblages and their ecological function in agroecosystems. Previous evidence has suggested that intensive agroecosystem management, including tillage and agrochemical exposure, can have lethal effects on edaphic arthropods (Cole et al. 2005; Redhead et al. 2020).

Carabid beetles are sensitive to intensive management practices and thrive under conservation tillage conditions characterized by reduced soil disturbance, increased surface residues, and greater weeds diversity (Lessard-Therrien et al. 2018; Triquet et al. 2023). Numerous studies have demonstrated that such management practices benefit carabid populations by providing shelter, food resources, and a range of microhabitats that accommodate the preferences of various carabid species (Diehl et al. 2012; Melnychuk et al. 2013; Jowett et al. 2022). Therefore, understanding how agricultural management practices influence carabid beetle diversity patterns is crucial not only for conservation purposes but also for determining the disturbance, recovery, and stability levels of agroecosystems (Ochs et al. 2016; Cajaiba et al. 2018; Pozsgai et al. 2022). Therefore, it is critical to investigate how carabid beetle assemblages respond to various agricultural management practices. This study is the first to provide evidence of the effects of differently managed grain agroecosystems on carabid beetle assemblages in South Africa. This study aimed to assess the effects of several management methods employed in selected agroecosystems on carabid beetle abundance, richness, and composition. New insights into how carabid beetles interact with various managed agroecosystems may help establish guidelines for effective conservation management strategies. As mentioned by DAFF (2017), this could assist in evaluating the status of adopting conservation agriculture practices within South African grain agroecosystems.

Previous studies have shown that intensive agriculture and expansion have detrimental effects on soil-dwelling arthropods, including carabid beetles (Cole et al. 2005; Lessard-Therrien et al. 2018). Therefore, we predicted that: (1) there would be no difference in carabid abundance and richness between conventional tillage management and semi-natural grasslands (with an intermediate level of disturbance). The latter follows that crop diversification, via cover crops and conserving crop residues following rotations, can improve habitat quality for carabid beetles (Bengtsson et al. 2005; DuPre et al. 2021). (2) Semi-conservation farming, characterized by simplified crop rotation and cover crop mixtures, would support carabid beetle abundance and richness. (3) Conserved natural grasslands (i.e., beetle banks with grass species and forbs) and less intensive grazing regimes under conservation grazing agroecosystems would significantly increase the abundance and richness of carabid beetles by providing microclimatic refuges, overwintering sites, and food resources (Macleod et al. 2004; McKenzie et al. 2016). (4) There would be distinct differences in carabid species composition among the four agroecosystem types, primarily because of varying management practices. As detailed by Horne (2007) and Ivanič et al. (2022), these differences could serve as indicators of agroecosystem management practices.

3.2 Materials and Methods

Study area

The study sites were in Bethlehem (28°09'S; 28°18'E) and Reitz (27°52'S; 28°32'E) in the eastern Free State province of South Africa. Most of the Bethlehem-Reitz Basin is composed of mudstone and sandstone from the Tarkastad Formation of the Beaufort Group. The soil is mostly sandy loam or sandy clay loam, which is gray or yellow in colour. The Avalon, Westleigh, and Longland formations have mottled grey basement soils. Mispah soils are shallow, rocky, duplex soils (Knot 2014). The climate is typically semi-arid. It rains more in summer than winter, with an average annual rainfall of 709 mm. In the summer, the average temperature in January is 20.1 °C, whereas in the winter, the average temperature in July is 6.8 °C. Temperatures fluctuate around 13.3 °C during the year, and monthly 105 mm of precipitation falls (Sosibo 2016). Four grain agroecosystems were selected for sampling: (1) conventional tillage, (2) conservation grazing, (3) semi-conservation farming, and (4) semi-natural grasslands. These agroecosystems were located at least 5 km apart. To ensure the precision and comparability of diverse agricultural systems, nine distinctive management practices were replicated and evenly distributed at intervals of 500 m within each agroecosystem (Figure 3.1). The selected farm systems and management practices are detailed in Appendix 4.1.

Characterization of management types in the four sampled agroecosystems

1. **Conventional tillage:** This is a cultivar and seed multiplication trials defined by intensive management practices, including the cultivation of homogenous monocultures (MN), the burning of crop residues, commonly referred to as slush burn (SB), following harvest, and the presence of fallow land (FL), which has undergone tillage and harrowing but remains unsown with crops. Predominantly, small grain crops such as wheat, barley, oats, triticale, and rye are cultivated within this system.
2. **Conservation grazing:** These systems are characterized by the cultivation of ryegrass, maize, and rye, managed with minimal tillage and absence of agrochemical inputs. Rotational grazing practices are employed, whereby the range is subdivided into multiple pastures, each sequentially grazed throughout the grazing period. Pastures within this system are not permanently planted but instead alternate between fodder and arable crops. In the long-term (LG) continuous grazing approach, pastures are rested for approximately five years, whereas in short-term (SG) grazing, a rotation occurs between residual pastures and conserved natural grassland (NG).
3. **Semi-conservation farming** (5 years of conversion): The farm is transitioning from conventional farming to conservation agriculture. Crop rotation (CR) entails the sequential planting of diverse crops on the same plot of land. Cover crops (CC) are sown primarily to protect and enrich the soil rather than for direct harvest. Herbicides and reduced tillage methods are utilized in this transitional phase. The farm emphasizes the primary cultivation of cereals and perennial crops, including soybeans, maize, sunflowers, and potatoes, alongside secondary activities such as cattle and sheep husbandry for meat production.
4. **Semi-natural grassland** (3 years of conversion): This system is undergoing a transition from intensive to conservation grazing practices and is characterized by the presence of recovering grassland (RG), predominantly dominated by grass species such as Smuts' finger grass (*Digitaria eriantha*).

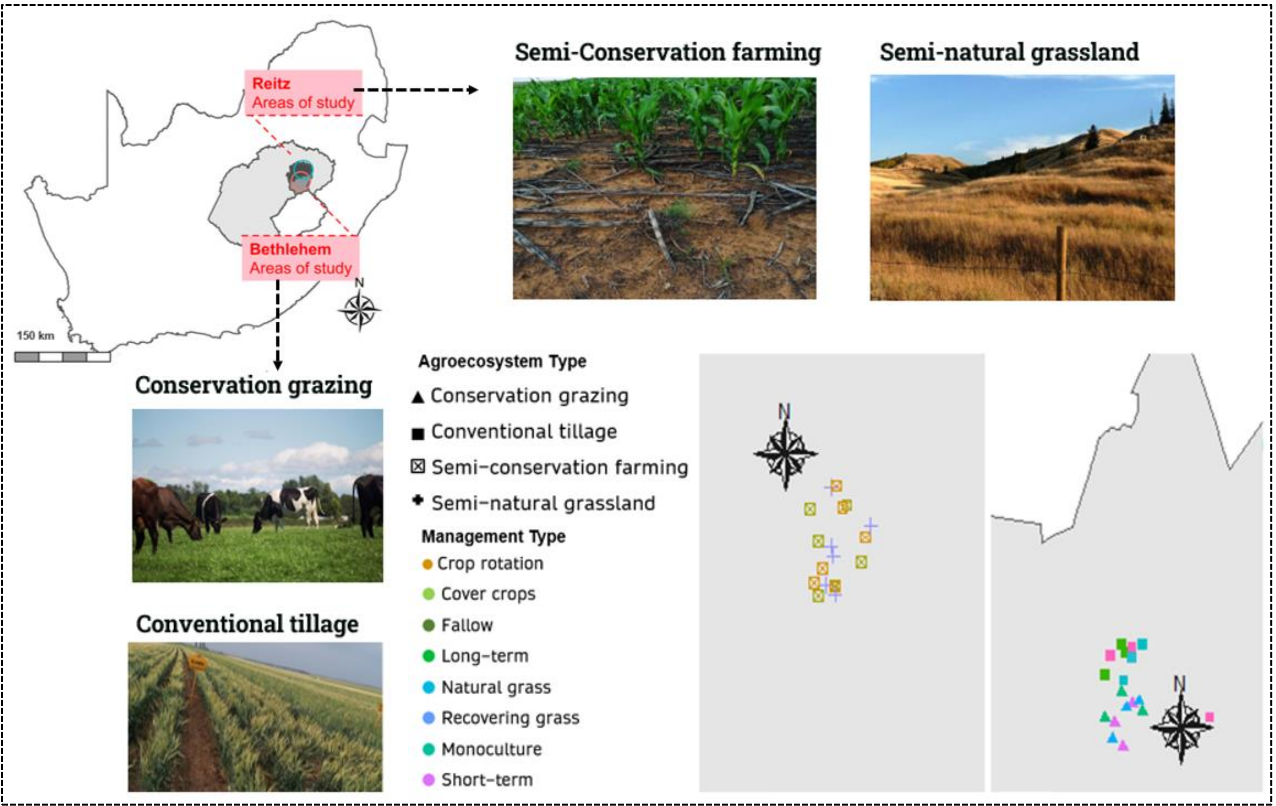

Figure 3.1. Location of the study areas in the Free State province of South Africa, including agroecosystem and management type.

Carabid beetle sampling and processing

Carabid beetles were collected over the course of two years, in 2020 (September-December) and 2021 (July-August). Two parallel transects (5 m apart) of four pitfall traps were set up at the center of each sampling site, 10 m from the bordering grass margins. This resulted in eight traps. The distance between each pair of traps along the transect was adjusted to 30 m to decrease spatial autocorrelation. Each trap consisted of a plastic cup with a depth of 9 cm and a diameter of 7 cm. The traps were filled with a 70% propylene glycol preservative solution and left for seven days to avoid digging-in effects (Schirmel et al. 2010). Pitfall traps are often used in agroecosystems and grasslands to capture active invertebrates that reside in the ground (Haysom et al. 2004). Although pitfall traps are the standard method for sampling ground-dwelling arthropods, we mitigated their limitations by incorporating active search sampling technique. Both methods were used to minimize the taxonomic bias that can arise from using a single sampling method (Lauchande et al. 2024). An active search method was also used, in which adult carabid beetles were hand-picked using forceps, and two people spent 10 minutes actively searching within eight 5 × 5 m quadrats (spaced 2 m apart) 10 m from pitfall traps. Samples were taken back to the laboratory for sorting and preservation in 70% ethanol. Carabid beetles were identified mostly to genus, some to family and then assigned to morphospecies by Dr Colin Schoeman (University of Venda)

3.3 Statistical analyses

Carabid beetle data from the two sampling methods and seasons were pooled, and only the identified morphospecies were included in the analyses. Prior to analysis, all response variables (total abundance and species richness) and covariates were tested for normal distribution using the Shapiro-Wilk test. The number of species was calculated as a proxy for species richness, and the number of individuals was calculated as a proxy for abundance. Furthermore, the rarefied morphospecies richness was calculated to account for incomplete sampling with a sample coverage of 90% in R 4.0.3 (R Core Team 2020) with the iNEXT package (Chao et al. 2015). To test the hypothesis, generalized linear mixed-effects models (GLMMs) with Laplace approximation were used to examine the effects of management types across the selected agroecosystems on carabid morphospecies richness and abundance. The R-package lme4 and generalized linear mixed effect models (GLMM) with a Poisson distribution account for overdispersion using a negative binomial distribution when necessary. Statistics for the tests were computed with 999 permutations using the "PIT-trap" resampling method (Wang et al. 2012).

To analyze carabid community composition, that is, variation in morphospecies assemblages, non-metric multidimensional scaling (NMDS) was performed based on Bray–Curtis's indices, which were also calculated based on morphospecies abundances. Permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations using the "Adonis" function of the vegan package was used to test for differences across agroecosystems and management types. Statistical analyses were performed with R 3.4.0 using the 'vegan' package. The number of dimensions (k) was set to two in the NMDS analysis, where the stress was < 0.2, to ensure a reliable interpretation of the graphical projections. Carabid morphospecies that were strongly associated with each agroecosystem type were identified using the IndVal values. Indicator species were analyzed using the "multipatt" command in the R package Indicspecies (Cáceres 2013). The significance of the indicator values (IndVal) was determined using a 999-permutation test and Sidak multiple testing correction. Only species that were significantly associated ($p < 0.05$) with the agroecosystem and management type were listed in the results of the multilevel pattern analysis. Microsoft Excel 2010 was used for data management and control, and R version 3.4.2 was used for all analyses (Powell 2018; R Core Team 2020).

3.4 Results

A total of 2078 carabid individuals represented by 14 morphospecies of five genera were recorded during the two years of the study. There were 1316 individuals collected in conservation grazing (ConsG), while 339 individuals were collected in semi-conservation farming (SemiC). A total of 195 individuals were collected in semi-natural grassland (SemiG), and 166 individuals collected in conventional tillage (ConvT). The most abundant carabid morphospecies were: *Calosoma* sp1 (248 individuals), *Scarites* sp1 (207 individuals), *Calosoma* sp2 (172 individuals), *Pterostichus* sp2 (170 individuals), *Pterostichus* sp1 (160 individuals) *Harpalus* sp1 (157 individuals) and *Amara* sp1 (154 individuals), together representing approximately 61% of total abundance (Appendix 1.1). All sampled agroecosystems had high observed coverage (ConvT, ConsG, SemiC, SemiN: 0.943, 0.986, 0.981, and 0.988, respectively) (Appendix 1.2).

Carabid abundance and richness

Carabid abundance and morphospecies richness were significantly higher in ConsG and SemiC than in SemiN and ConvT (Table 3.1; Figure 3.2). Carabid beetle abundance in ConsG was significantly different among LG, SG, and NG management ($p < 0.05$, Table 3.1; Figure 3.2a), followed by CC management under SemiC. Carabid morphospecies richness differed significantly among CC, LG, and NG management in the SemiC and ConsG farming systems ($p < 0.05$; Table 3.1; Figure 3.2b).

Carabid community composition

NMDS ordination showed a significant effect across carabid assemblages in the four agroecosystem types (stress 0.0165). There was a significant difference in carabid beetle composition among agroecosystems (PERMANOVA: F = 7.07, R2 = 0.39, $p = 0.001$) and management types (PERMANOVA: F = 3.37, R2 = 0.49, $p = 0.001$) (Table 3.2). The ordination plot (Figure 3.3) indicated a clear separation of carabid morphospecies from the genera *Calosoma* and *Scarites*, which were exclusively associated with ConsG. One morphospecies of the genus *Harpalus* was significantly associated with SemiC. The carabid genera, *Amara* and *Pterostichus*, were significantly associated with both ConsG and ConvT.

IndVal results

Five of the 14 morphospecies recorded throughout the study were identified as agroecosystem indicators. The carabid genera *Calosoma* and *Scarites* had the largest representation of indicator morphospecies from intact agroecosystems, while *Amara*, *Harpalus*, and *Pterostichus* showed significant indicative values in disturbed agroecosystems. No carabid species were indicators of grassland recovery in the semi-natural grasslands (Table 3.3).

Table 3.1. Summary results of Generalized linear mixed models (GLMMs) across the agroecosystem type; ConvT-Conventional tillage; ConsG-Conservation grazing; SemiC-Semi-conservation farming and SemiN-Semi-natural grassland) on carabid beetle richness, and abundance.

Response variables	Agroecosystem type	Explanatory variables	Estimate	Std.error	*z*-value	*p*-value
Abundance		(Intercept)	3.15	0.21	14.77	<0.001
	ConvT	Monoculture	-0.3	0.31	-0.96	0.34
		Slush burn	-0.26	0.31	-0.84	0.40
	ConsG	Long-term grazing	1.46	0.28	5.17	<0.001
		Short term grazing	1.13	0.29	3.97	<0.001
		Natural grassland	1.92	0.28	6.84	<0.001
	SemiC	Crop rotation	0.4	0.26	1.56	0.12
		Cover crops	1.3	0.25	5.2	<0.001
	SemiN	Recovering grassland	-0.02	0.26	-0.08	0.93
Species richness		(Intercept)	1.3	0.34	3.77	<0.001
	ConvT	Monoculture	-0.61	0.56	-1.08	0.28
		Slush burn	-0.32	0.52	-0.61	0.54
	ConsG	Long-term grazing	0.97	0.43	2.28	0.02
		Short term grazing	0.37	0.46	0.82	0.41
		Natural grassland	1.73	0.4	4.28	<0.001
	SemiC	Crop rotation	0.57	0.4	1.44	0.15
		Cover crops	1.1	0.38	2.86	0.01
	SemiN	Recovering grassland	-0.38	0.45	-0.86	0.39

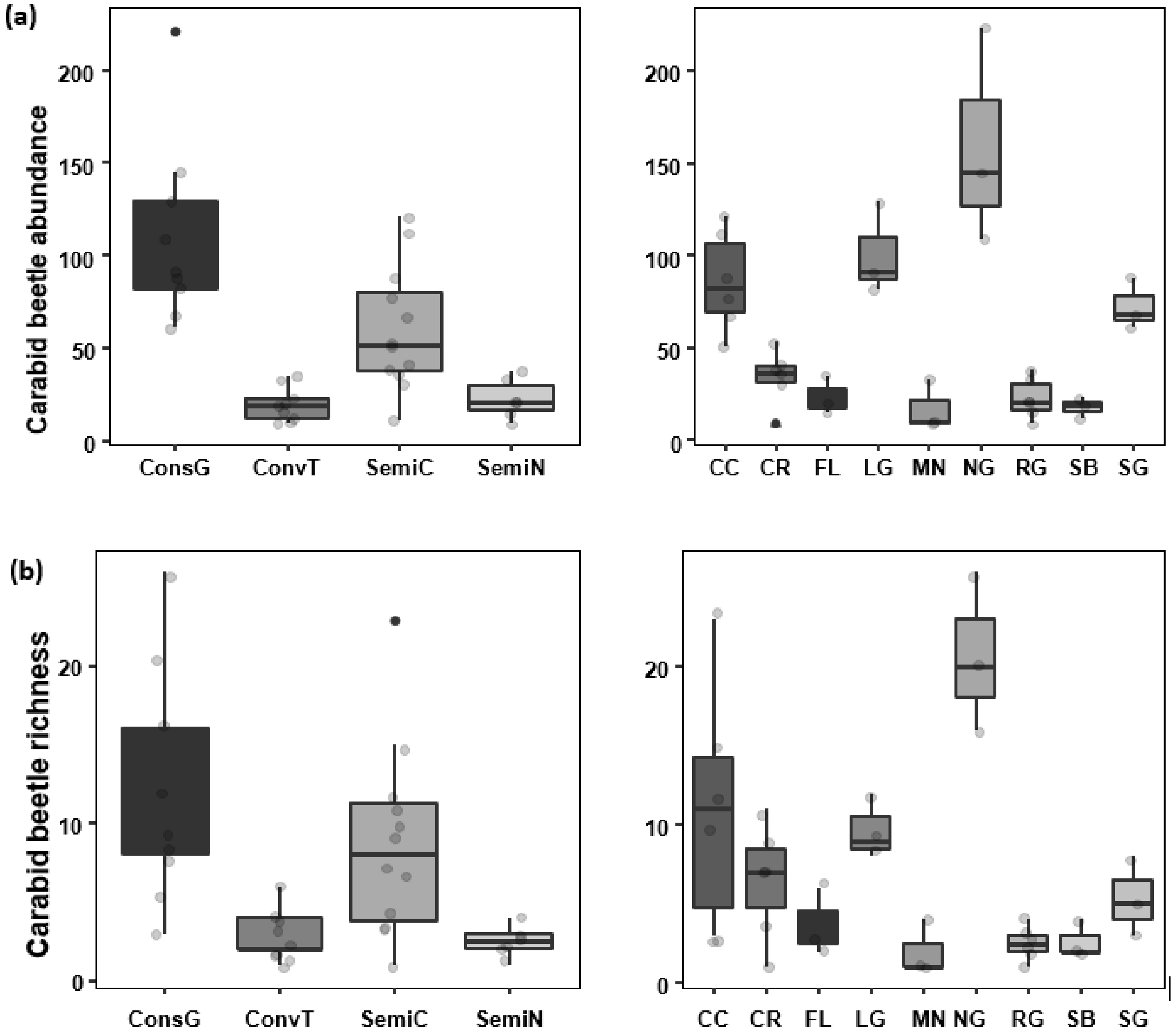

Figure 3.2. Box plot of (a) total abundance and (b) species richness for agroecosystem across management type. CC-Cover crops, CR-crop rotational, FL-Fallow Land, LG-Long-term grazing, MN-Monoculture, NG-Natural grass, RG-Recovering grass, SB-Slush burn, SG-Short term grazing. ($p < 0.05$) significant effect identified in GLMMs (see Table 3.1).

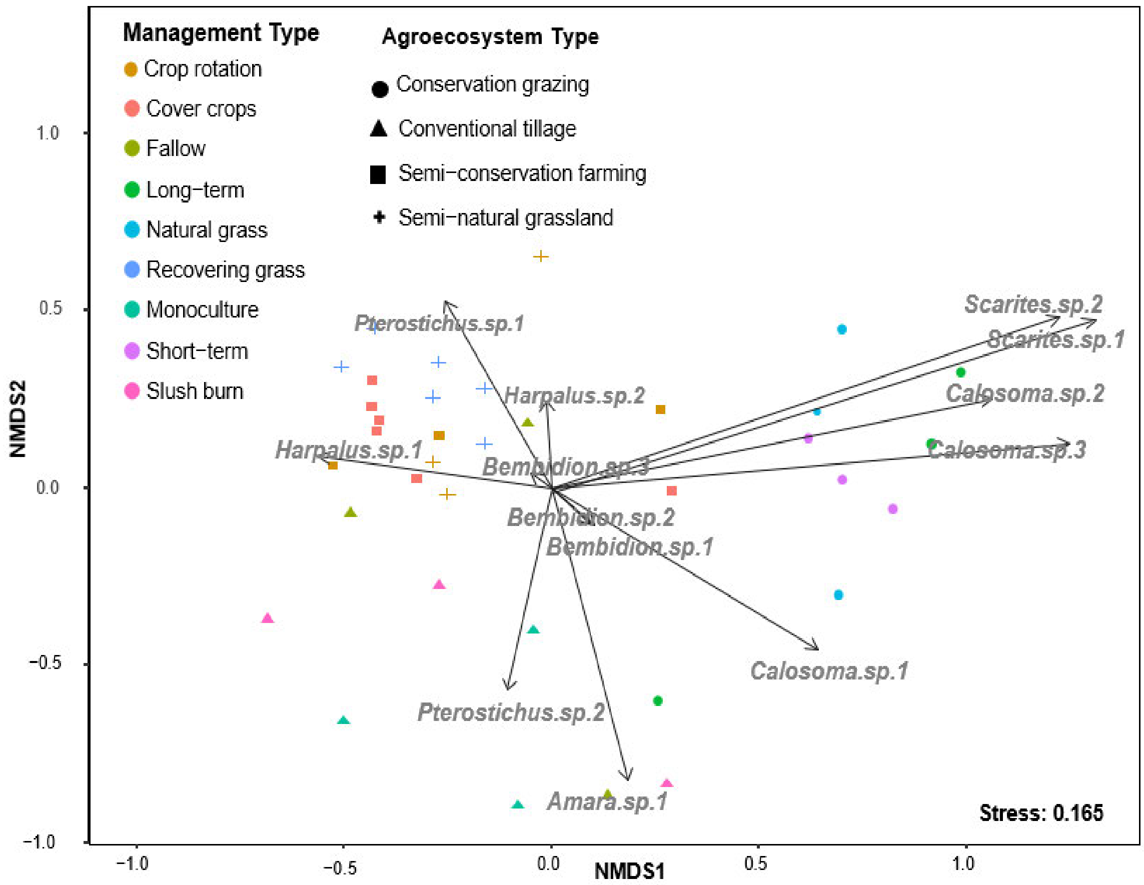

Figure 3.3. Results of the Non-metric multidimensional scaling (NMDS) ordination of carabid beetle assemblages based on morphospecies abundance sampled across (different colours) agroecosystems under contrasting management type. Arrow length indicates the strength of the predictors (genera) fitted to the ordination for $p \leq 0.001$.

Table 3.2. PERMANOVA results (through the 'Adonis' function, using a Bray-Curtis index as a dissimilarity measure and 999 permutations) between agroecosystem and management types on carabid community composition.

Effect	DF	SS	MS	F-Model	R^2
Among agroecosystem types	3	2.036	0.679	7.057***	0.398
Residuals	32	3.078	0.096		0.601
Total	35	5.114			1.000
Among Management within agroecosystem types	8	2.557	0.319	3.374***	0.499
Residuals	27	2.557	0.094		0.500
Total	35	5.114			1.000

*Significant results are printed in Asterisks (***$p < 0.001$). DF: degrees of freedom; SS: sums of squares; MS: Mean Square; F: F-statistic; R2: coefficient of determination

Table 3.3. Results of indicator value analysis (IndVal) showing carabid species associated significantly ($p < 0.05$) with (ConsG-Conservation grazing; SemiC-Semi - conservation farming; and ConvT-Conventional tillage).

Farm System	Species	IndVal Stat	IndVal p
ConsG	Scarites sp.1	0.765	<0.001
ConsG	Scarites sp.2	0.761	<0.001
ConsG	Calosoma sp.1	0.703	<0.001
ConsG	Calosoma sp.2	0.75	<0.001
ConsG	Calosoma sp.3	0.761	<0.001
ConsG	Harpalus sp.2	0.583	0.003
ConsG	Bembidion sp.1	0.52	0.004
SemiC	Harpalus sp.1	0.544	0.004
ConvT + ConsG	Pterostichus sp.2	0.606	0.037
	Amara sp.1	0.788	0.002
ConvT + ConsG + SemiC	Pterostichus sp.1	0.594	0.044

3.5 Discussion

Carabid abundance and species richness

The present study demonstrated that agricultural management practices, including soil cultivation, crop rotation, pesticide usage, burning, cover cropping, and the presence of semi-natural habitats such as grass and flower strips, significantly influence the diversity patterns of carabid beetles (Holland et al. 2002; Pfiffner & Luka 2000; Hanson et al. 2017; Torma et al. 2023). As expected, conventional tillage and recovering grassland practices were associated with lower carabid abundance and richness than other agroecosystems. These findings are consistent with previous research conducted in agricultural settings, which has consistently reported a decline in carabid diversity in conventional agroecosystems compared to organic and integrated agricultural systems (Menalled et al. 2007; Irmler 2018; Sutter et al. 2018). Disturbed agroecosystems subjected to frequent pesticide applications, fallowing of fields after soil cultivation, and burning of crop residues have negative consequences on the life cycle of carabid beetles from larvae to adults (Jowett et al. 2021). For instance, repeated tillage can lead to mortality of beetle pupae and diapausing larvae by exposing them to direct sunlight, consequently reducing the overall number of adult carabids (Kromp 1999; Shearin et al. 2007; Mashavakure et al. 2019). Additionally, intensive management reduces beetle activity by modifying the habitat structure and diminishing food resources, potentially resulting in the extinction of carabid species (Kotze & O'Hara 2003; Homburg et al. 2019).

However, our study yielded contrasting results, indicating that semi-conservation systems harbor a greater number and diversity of carabid beetles. This can be partly attributed to the management practices employed in these semi-conservation systems, such as the presence of cover crops (DuPre et al. 2021). A study conducted by Jackson and Harrison (2008) investigated the impact of conservation tillage with cover crop residues as mulch, compared with conventionally tilled plots, on populations of beneficial insects. They found that the cover crop mulching system resulted in a greater abundance of carabid beetles than treatments without cover crop residue. Cover crops and residues play crucial roles in fostering the accumulation of organic matter, enhancing the physical properties of the soil, and supplying a diverse range of food sources (Triquet et al. 2023). These characteristics are of utmost significance in cultivating favorable habitats for soil-dwelling insect populations. While previous studies have suggested that crop rotation could be a potential factor for increasing carabid diversity (Fahrig et al. 2015; Caro et al. 2016) the current study did not find a significant difference in carabid abundance and species richness under rotational crop management in semi-conservation systems. Despite this discrepancy with our current findings, a seven-year study conducted in Nafferton, northern England, indicated lower activity dynamics of ground beetles in crop rotation management (Eyre et al. 2016). Such results can be explained by the fact that simplified crop rotations deplete soils, promote pest infestations, and resistance from repeated pesticide applications (Le Provost et al. 2021). Furthermore, using herbicides in conjunction with tillage can indirectly influence carabid populations by altering surface residues and reducing weed diversity (Holland & Luff 2000). The complete eradication of weeds using mechanical methods will adversely affect the carabid beetle populations (Knapp & Řezáč 2015).

Furthermore, the results of this study suggest that transitioning from conventional tillage to conservation practices influences carabid survival and diversity (Schröter & Irmler 2013). Specifically, in the case of semi-conservation agroecosystems undergoing conversion to conservation agriculture, it is important to acknowledge that it may take time to observe a significant increase in species diversity (Pfiffner & Luka 2000; Boeraeve et al. 2022). This delay can be attributed to extensive management practices, such as deep tillage and herbicide application, which are often implemented in response to adverse conditions, such as drought or pest infestations. Previous studies have shown that the diversity of ground beetles did not exhibit significant changes even after seven years of transitioning from conventional to organic farming, while a remarkable increase was observed after 30 years (Andersen & Eltun 2000; Irmler 2018; Perner & Malt 2003; Purtauf et al. 2005). This aligns with our findings, which showed that the higher carabid abundance and species richness in conservation grazing may be linked to the fact that conservation management has been practiced for over 10 years (Rouabah et al. 2015). Furthermore, natural habitats, such as adjacent flower and grass strips and beetle banks, play a crucial role in providing shelter, sites for reproduction, and overwintering. These habitats also serve as initial sites for the cyclical recolonization of fields following mowing, grazing, and harvesting activities (McKenzie et al. 2016; Lyons et al. 2017; Boinot et al. 2020). The presence of these habitats can account for the observed higher species richness and abundance of carabid beetles within the conservation grazing agroecosystems. These findings highlight the critical role of preserving and incorporating these elements into agroecosystems to promote thriving carabid populations (Macleod et al. 2004).

Association of carabid beetle assemblages with agroecosystem managements

Notably, the conservation grazing-associated species included large flightless predators from the genera *Calosoma* and *Scarites* (Ball & Bousquet 2000; Larochelle & Larivière, 2003; Talarico et al. 2018). Similarly, a study by Cole et al. (2006) conducted in grazing habitats demonstrated that large flightless *Carabus* species exhibited a preference for extensive grazing regimes over intensive ones. The large, immobile carabid species depends on non-crop habitats at various stages of their life cycle, as highlighted by previous studies (Boetzl et al. 2019; Aguilera et al. 2020). They exhibit a preference for extensive permanent grasslands or habitats subjected to long-term grazing, providing year-round opportunities for both reproduction and overwintering (Grandchamp et al. 2005; McKenzie et al. 2016). In conservation grazing management, carabid species can move from arable fields to habitats characterized by high vegetation density and ample leaf litter. These habitats provide essential microhabitats through decaying plant material (Pozsgai et al. 2022). This observation aligns with the findings of Marrec et al. (2015) who investigated the impact of agricultural land spatial scale on carabid assemblages. They observed that larger species with limited spatial mobility often transition between different habitat types, particularly during agronomic interventions such as the harvesting period. The conservation of temporally permanent habitats is crucial for predatory beetles to overwinter, reproduce, and find refuge from detrimental agronomic practices, thus emphasizing their significance from a biocontrol perspective (Woodcock et al. 2010; González et al. 2020). Importantly, the ecological function of *Calosoma* and *Scarites* warrants attention because of their valuable contributions to the biological control of pasture pests such as fleas and ticks, which are of veterinary importance (Cividanes 2021).

Carabid species belonging to the genus *Harpalus* observed in semi-conservation management settings demonstrate intriguing associations with niche availability and food resources (Kosewska et al. 2016). These associations can be attributed to the specific characteristics of rotational and cover crop management, which creates a diverse and abundant weed flora providing additional habitats and food sources for carabids (Honek et al. 2003). Crop rotation plays a crucial role in providing a trophic resource, as seeds lost during harvest become palatable to certain granivorous and omnivorous carabids (Charalabidis et al. 2019; DuPre et al. 2021; De Heij et al. 2022). Notably, despite the implementation of tillage and herbicide application in semi-conservation agroecosystems, the genus *Harpalus* demonstrates persistence, highlighting its resilience in environments impacted by human activities (Holland et al. 2002). As shown in previous studies (Shearin et al. 2007; White et al. 2007; Davis et al. 2009), plots that were mechanically managed and treated with herbicides had a greater number of phytophagous *Harpalus* spp. adults. This was because there was greater weed growth in these plots.

It is important to note that not all carabid species are susceptible to disturbance. Some carabid species, known as eurytopic species, exhibit the ability to thrive in various agroecosystems (Hatten et al. 2007). These species may have a broad range of ecological preferences and demonstrate tolerance to disturbances (Kang et al. 2012). For example, the current study observed thriving populations of species of the genera *Pterostichus* and *Amara* in conventional agroecosystems. Several studies (Kromp 1999; Döring et al. 2003; Rouabah et al. 2015) have demostrated that both *Amara* and *Pterostichus* are frequently found in disturbed agricultural areas due to their strong dispersal abilities and opportunistic feeding behaviors of exploiting both plant materials and invertebrate prey. Notably, these carabids are among the initial colonizers of habitats following disturbance, showing their ability to quickly establish populations in altered environments (Cole et al. 2002; Perner & Malt 2003).

Value indicator – IndVal

Previous studies have repeatedly demonstrated that various carabid communities exhibit unique responses to agricultural practices, suggesting their potential as indicators of disturbance, recovery, and stability within agroecosystems (Rainio & Niemela 2003; Koivula 2011; Cajaiba et al. 2018). The application of indicator species analysis is diverse and encompasses areas such as conservation, land management, mapping, and habitat classification (Cáceres 2013; Bicknell et al. 2014). Although carabid beetles are predominantly generalists (Kotze & O'Hara 2003), there is increasing evidence that many species exhibit specialization and possess significant indicator values for specific ecosystems (Koivula 2011). As a result, carabid beetles have been extensively used as indicators to monitor ecological changes resulting from management practices such as grazing, tillage, and fertilization (Hummel et al. 2012; Schirmel et al. 2015; Cajaiba et al. 2018).

The diverse array of carabid species present in agroecosystems offers valuable insights into the detection of the ecological changes associated with different management practices (Batáry et al. 2012; Schirmel et al. 2016). In this study, carabid species of the genera *Calosoma* and *Scarites* appeared to be good indicators of agroecosystems, as depicted by IndVal values (Hatten et al. 2007; Davis et al. 2009; Hof & Bright 2010). Our findings suggest that these carabid species can serve as reliable indicators of undisturbed environments, as they were exclusively found in conservation grazing agroecosystems compared with other agroecosystem types (Cole et al. 2002). These findings can be explained by the fact that carabid species of these genera are large predators with limited dispersal ability and long life cycles (Kromp 1999; Martins da Silva et al. 2017). Consequently, they struggle to adapt to the significant ecological disturbances caused by pesticide use, cutting, burning, and tilling (Allema et al. 2019; Gayer et al. 2019). Because they are sensitive to such pressures, they can be used as ecological indicators of intact agroecosystems (Horne 2007).

3.6 Conclusion

Carabid beetles are widely distributed in agroecosystems and their presence and abundance are influenced by management practices (Holland & Luff 2000; Triquet et al. 2023). Our findings provide compelling evidence that conservation management practices have a substantial positive effect on the occurrence and diversity of carabid beetle assemblages. Furthermore, when implementing conservation measures in agricultural landscapes, it is crucial to consider grassland proximity and crop diversity (Duflot et al. 2017). We found that the carabid beetle community composition in agroecosystems is distinctive for each system and highly sensitive to anthropogenic activities. As a result, prioritizing not only higher biodiversity, but also indicator species that effectively monitor the health of production management practices is essential. This study underscores the significance of large carabid beetles as sensitive indicators of management intensity in agricultural landscapes (Fischer et al. 2021). These results support the prevailing consensus that carabid beetles serve as reliable proxies for assessing the impact of management practices in agroecosystems, enabling the ranking of disturbance, recovery, and stability levels (Solascasas et al. 2022).

Moreover, additional research is required to evaluate the influence of agricultural management methods on the functional diversity of carabids, enabling a more precise assessment of trophic guilds and morphometric traits. Conducting several replications of existing studies in various habitats across different geographical regions would enhance our understanding of how invertebrates respond to management interventions. Acquiring this knowledge will make it easier to make well-informed decisions and to adopt efficient conservation and sustainable management methods (Blignaut et al. 2015).

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CHAPTER 4: CARABID BEETLES (COLEOPTERA: CARABIDAE) AS BIODIVERSITY INDICATORS FOR EPIGEIC ARTHROPOD TAXA IN AGRICULTURAL LANDSCAPES

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Abstract

Epigeic taxa are integral in both agricultural systems and natural habitats, due to their critical roles in ecosystem processes, including nutrient recycling, pest and weed control, and soil enrichment. However, resources and taxonomic knowledge frequently limit the ability to conduct a thorough biodiversity assessment of these organisms within agricultural landscapes. As a result, there is a growing interest in identifying suitable surrogate-based biodiversity indicators to evaluate the overall diversity and health of ecosystems. Carabid beetles have emerged as a promising indicator due to their diverse representation, well-established taxonomic classification, cost-effective survey methods, and predictable responses to environmental changes. Therefore, it is important to assess the extent to which carabids reflect the general biodiversity of agricultural landscapes and serve as indicators for other soil-dwelling arthropods. This study aimed to assess the congruence between the species composition and richness of carabids and selected epigeic arthropod taxa. Additionally, this study aimed to determine whether the farm system with the highest carabid species richness also supports greater diversity among the selected epigeic taxa. To achieve our objective, pitfall traps and active search methods were used to capture the epigeic taxa. Our findings showed that the species richness of all epigeic taxa was significantly higher under conservation grazing. Both Pearson and Mantel correlation analyses further validated the robust congruence between carabids and overall epigeic predators ($r > 0.70$; $p < 0.001$). Among epigeic taxa, carabid species richness was strongly correlated with ground spiders and rove beetles. This study provides valuable insights into the potential of carabid beetles as a representative taxon for assessing the overall diversity of epigeic communities. This underscores the significance of conservation farming practices for fostering abundant arthropod diversity.

Keywords: ground-dwelling fauna, farm system, Mantel tests, Pearson correlation, surrogate taxa

4.1 Introduction

Biodiversity plays a pivotal role in upholding ecosystem functionality by offering a plethora of invaluable services (Tilman et al. 2011). Among the various biological groups, arthropods are prominent because of their contribution to biomass (Cardoso et al. 2020) and the provision of key ecological services (Sánchez-Bayo & Wyckhuys 2019). Epigeic taxa, such as carabid beetles, spiders, rove beetles, and ants, occupy pivotal niches in both environmental functioning and productivity (Sauberer et al. 2004; Buchholz & Buchholz 2010; Pardon et al. 2019; Jacobsen et al. 2022). These multifaceted organisms are vital in agroecosystems because of their diverse functions, including decomposition of organic material, soil aeration, and predation of pests and weed seed predators (Li et al. 2018; Boetzl & Krimmer 2019; Homburg et al. 2019; Deppe & Fischer 2023). Nonetheless, logistical and financial challenges constrain the comprehensive understanding and monitoring of ground-dwelling arthropod biodiversity (Kotze and Samways 1999; Cardoso et al. 2004; Sauberer et al. 2004; Chawaka et al. 2020). As such, a significant portion of this faunal group in agricultural ecosystems remains under-researched and inadequately documented (Kotze & O'Hara 2003). For instance, because of the paucity of taxonomic expertise, researchers often focus on higher taxonomic ranks; thus, investigating all epigeic arthropod taxa would require the collaboration of taxonomist experts (Lami et al. 2023). This highlights the need for reliable biodiversity proxies that can comprehensively reflect epigeic biodiversity (Koch et al. 2021).

An increasing body of research has suggested that exploring cross-taxonomic congruence can address the hurdles of vast resource requirements and financial limitations (Oertli et al. 2005; Leal et al. 2010; Hunter et al. 2016). This concept involves the use of surrogate taxa or biodiversity proxies to reflect broader biodiversity or specific taxonomic groups (Sauberer et al. 2004; Samways et al. 2020). For instance, cross-taxon congruence has been explored in different ecosystems among various groups, such as spiders (Cardoso et al. 2004; Foord et al. 2013), marine benthic: macro- and meiofaunal (Corte et al. 2017), phytoplankton and zooplankton (Allen et al. 1999), Odonata and aquatic taxa (Spigoloni et al. 2022), birds and macro-invertebrates (Chawaka et al. 2020), Herpetofauna (Yong et al. 2018), and ants (Lovell et al. 2007; Barton et al. 2019). However, few studies have focused on community congruence between carabids and other arthropods in agricultural landscapes (Cameron and Leather 2012; Tonkin et al. 2016; Oberprieler et al. 2020; Schoeman et al. 2020; Corcos et al. 2021; Zara et al. 2021). Furthermore, these investigations typically center around species richness, since taxonomic richness stands out as an efficient biodiversity metric, simplifying comparisons among diverse taxonomic assemblies (Allen et al. 1999; Hurlbert & Jetz 2007). Although community structures among taxa are often overlooked, evaluating both species richness patterns and compositional congruence across taxonomic groups is vital, particularly in agricultural contexts (Su et al. 2004). Such research may help conservationists and land managers develop effective strategies for preserving the overall biodiversity in the face of habitat degradation and rapid loss of species (Oberprieler et al. 2020).

Carabids (Carabidae: Coleoptera) play a pivotal trophic role in numerous terrestrial ecosystems, and are sensitive to environmental conditions (Niemelä 2000; Honek et al. 2003; Jowett et al. 2022). Like many epigeic organisms, they have adapted to diverse ecological niches. They are predatory, omnivorous, and even phytophagous, making them potential key agents for natural pest control in agroecosystems (Gayer et al. 2019; Redhead et al. 2020). Their sampling is straightforward, cost-effective, and requires relatively minimal effort (Döring et al. 2003). While the use of carabids as indicators of agroecosystem health has been frequently acknowledged, their significance as proxies for broader biodiversity remains relatively unexplored (Rainio & Niemela 2003; Oberprieler et al. 2020). Although there is evidence in developed countries that carabids are useful biodiversity indicators for other insect communities (Tonkin et al. 2016; Corcos et al. 2021; Zara et al. 2021), there appears to be a research gap regarding the congruence between carabids and epigeic insect groups in South Africa's cultivated lands (Lovell et al. 2007). Arthropod cross-taxon congruence studies in African terrestrial systems have mostly focused on wooded habitats in savannas and temperate grasslands (Kotze & Samways 1999; Foord et al. 2013; Schoeman et al. 2020), aquatic (Kietzka 2019) and wetland ecosystems (Slimani et al. 2019; Chawaka et al. 2020). Investigating congruency patterns in cultivated lands may significantly minimize the cost and time required for biodiversity assessments in agroecosystems. Using carabids as a representative taxon for epigeic fauna offers a promising avenue to bridge existing biodiversity data gaps, while simultaneously ensuring both time and economic efficiency (Hunter et al. 2016; Corcos et al. 2021).

In this study, we assessed carabid beetles as plausible biodiversity indicators within grain agroecosystems for the first time in South Africa. Specifically, the study (1) assessed whether diversity patterns of carabid beetles reflect the diversity patterns of epigeic arthropod taxa (namely, ground spiders, ants, and rove beetles) across divergent farming systems; and (2) determined whether the farm system exhibiting the highest carabid species richness ensures greater diversity among the selected epigeic arthropod taxa. The use of biodiversity indicators helps identify conservation areas that can effectively safeguard against species extinction (Lami et al. 2023). This study intends to shed light on the suitability of carabid beetles as effective biodiversity indicators of selected epigeic taxa in the grain agroecosystems of South Africa.

4.2 Materials and Methods

Study area and farming system classification

Fieldwork was conducted over the course of 2020 to 2021 in the areas of Bethlehem (28°09'S; 28°18'E) and Reitz (27°52'S; 28°32'E) within the eastern Free State province of South Africa. The climate in these areas is generally semi-arid. This is a summer rainfall area, with an average annual precipitation of 709 mm. During the summer season (November-February), the mean temperature averages 20.1 °C, while in winter (June-September), the mean temperature is around 6.8 °C. The landscape is characterized by an array of grain crops interspersed with semi-natural grasslands (Sosibo 2016).

The designated farm systems were delineated as follows. (1) Conventional Tillage (intensive): This system is marked by uniform grain crops and rigorous management practices involving activities such as burning, soil tillage, and pesticide application. This approach has been practiced consistently for more than ten years. (2) Conservation Grazing (less intensive): Characterized by a combination of livestock and prominent crops such as rye and maize, this farm embraces sustainable grazing management, encompassing long- and short-term grazing strategies. This approach has been used for more than 10 years. (3) Semi-Conservation Farming (intermediate): This system adopts practices such as crop rotation, use of cover crops, tillage, and judicious application of pesticides as needed. (4) Semi-Natural Grassland (intermediate): Currently undergoing a transition from intensive management (i.e., burning, deep tilling, and pesticide use) to conservation farming practices, this farm has pursued this transition for over four years. This was marked by the restoration of grasslands for grazing purposes. Detailed information is provided in Appendix 4.1.

Epigeic taxa sampling

Within each farm system, nine distinctive management practices were replicated and evenly distributed at regular intervals of 500 m (Figure 4.1). Two parallel transects (5 m apart) of four pitfall traps were set up at the center of each sampling site, 10 m from the bordering grass margins. This resulted in eight traps. The distance between each pair of traps along the transect was adjusted to 30 m to decrease spatial autocorrelation. Each trap consisted of a plastic cup with a depth of 9 cm and a diameter of 7 cm. The traps were filled with a 70% propylene glycol preservative solution and left for seven days to avoid digging-in effects (Schirmel et al. 2010). Pitfall traps are widely acknowledged and utilized for capturing active ground-dwelling invertebrates within agroecosystems and grasslands (Haysom et al. 2004; Birkhofer et al. 2015).

In addition, we used active search-hand collecting, whereby individual epigeic arthropods were collected using forceps. Two people undertook a dedicated 10-minutes period of diurnal active searching within eight 5 × 5 m quadrats (spaced 2 m apart) situated 10 m apart from the pitfall traps. The selected epigeic arthropod taxa were counted, sorted, and identified to the family or genus level, and then assigned to morphospecies. Ants were identified using an online database AntWeb (http://antweb.org/) following Munyai et al. (2021); Mthimunye and Munyai (2022). Ground spiders were identified using Dippenaar-Schoeman and Jocqué (1997); Mellet et al. (2006); Dippenaar-Schoeman et al. (2013); Dippenaar-Schoeman et al. (2018) and rove beetles Devine et al. (2022). Carabid beetles were identified mostly to genus and some to family, and then assigned to morphospecies by Dr. Colin Schoeman (University of Venda); see Appendix 2.1, which comprises a list of morphospecies.

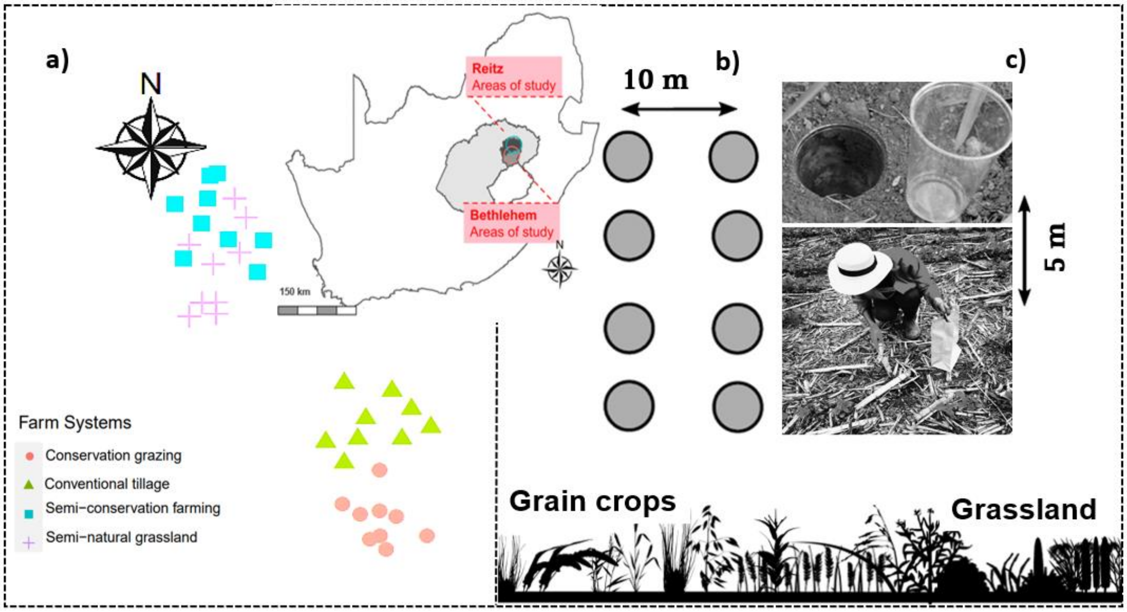

Figure 4.1. A South African map showing the position of the Free State Province and the study area (a), pitfall layout (b) and a picture of a pitfall trap (c). Colour and shapes indicate the replicated sites within the farm types.

4.3 Statistical analyses

Diversity Patterns

Data for all epigeic taxa (carabids, ants, rove beetles, and ground spiders), were analyzed independently for all the analyses below. We pooled specimens from each group collected using different sampling methods (i.e., active search and pitfalls) for each site. To evaluate the impact of different farm types (conventional tillage, semi-natural grassland, conservation grazing, and semi-conservation farming) on epigeic arthropod taxa, we examined abundance and species richness across these four farming systems. The lme4 package was used for linear mixed models (LMMs) to analyze species richness (Powell 2018). For abundance data, Generalized Linear Mixed Models (GLMMs) with Laplace approximation and negative binomial distribution were utilized (Powell 2018).

Congruence in species richness and community composition

Concordance analysis is a method used to assess the degree of similarity in species composition or diversity among sites across two or more taxonomic groups (Powell 2018). Species richness was determined using the Pearson correlation coefficient (*r*) to explore the congruency between carabid and epigeic taxa richness (Karyl 1999). Assessing the similarity of assemblages is often achieved through a statistical technique known as Mantel's correlation test (r_m). However, additional methods such as Procrustes analysis and co-correspondence analysis are also valid alternatives (Oksanen et al. 2022). We used the Mantel test for simplicity of interpretation, which is commonly used in ecology, and it allows the comparison of two matrices for similar covariation, but avoids independence issues of correlation analysis (Duan et al. 2016). All analyses were performed using R version 4.0.3 (R Core Team 2020).

4.4 Results

General patterns of arthropod epigeic taxa

The estimated rarefaction curves for all epigeic taxa indicated that most species were collected from the area sampled (Appendix 2.2). The analyzed data included 10612 identified epigeic taxa. Of these, the most abundant taxonomic groups were carabids (5994 individuals, 169 spp.), followed by ground spiders (2012 individuals, 61 spp.), rove beetles (1637 individuals, 57 spp.), and ants (969 individuals, 48 spp.) (Appendix 2.3).

Diversity patterns

Carabid beetle data, species richness, and abundance of epigeic taxa differed significantly across farm systems (Figure 4.2; Table 4.1), with ConsG being particularly individual-rich and SemiN showing the opposite trend. However, ants showed significant diversity in SemiN and ConsG compared to other farm systems (Figure 4.2a, Table 4.1).

Congruence in species richness and community composition

Carabid beetles consistently exhibited robust positive correlations with the overall richness of epigeic taxa (Pearson's correlation: $r > 0.70$, $p < 0.05$) (Table 4.2). A negative correlation emerged between the richness of ants and carabids ($r = -0.37$, $p = 0.02$). Conversely, a significant positive correlation was observed between carabid richness and ground spiders ($r = 0.68$, $p = 0.001$), followed by rove beetles ($r = 0.52$, $p = 0.001$) (Table 4.2).

There was significant covariation in species composition between carabids and combined epigeic taxa (Mantel: $r_m = 0.88$, $p = 0.001$) (Table 4.2), reflecting the pattern observed for species richness. There was significant positive covariation between the composition of carabid species and that of ground spiders and rove beetles, but no significant covariation between the composition of carabids and that of ants (Table 4.2).

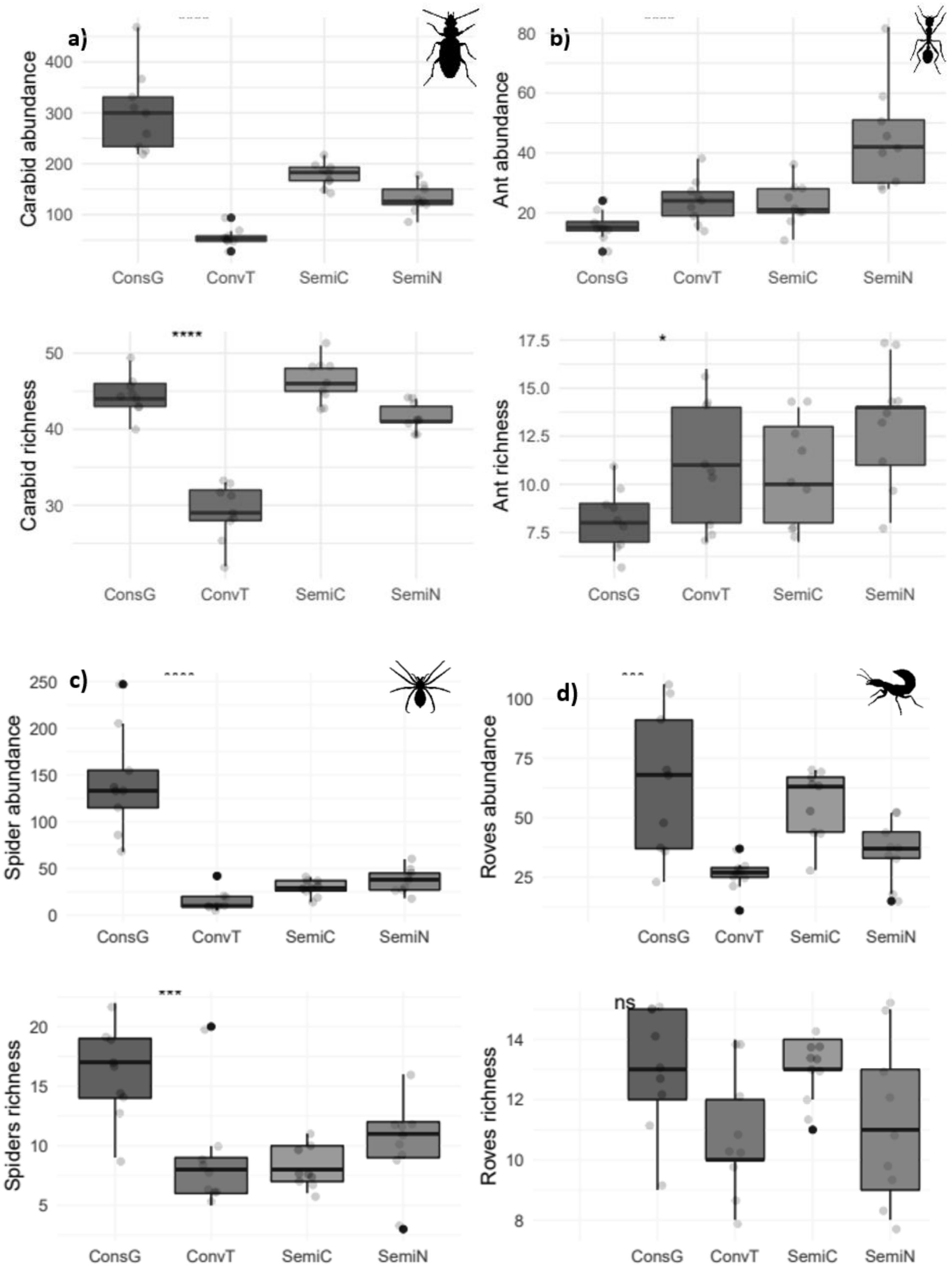

Figure 4.2. Box plot showing epigeic taxa (a) carabids, (b) ants, (c) ground spiders, (d) rove beetle diversity patterns (abundance and species richness) collected from the farm systems (ConsG - Conservation grazing; ConvT - Conventional tillage; SemiC-Semi conservation; SemiN-Semi natural grassland).

Table 4.1. Summary results of LMMs and GLMMs for the effects of farm systems on the abundance and species richness of the four epigeic taxa. Only the variables retained after the model selection procedure based on ΔAICc are shown.

Abundance		Estimate	Std. Error	z-value	Pr(>|z|)
Carabid beetles	Intercept (ConsG)	5.709	0.069	82.421	<0.001
	ConvT	-1.691	0.106	-15.962	<0.001
	SemiC	-0.526	0.099	-5.302	<0.001
	SemiN	-0.834	0.100	-8.311	<0.001
Rove beetles	Intercept (ConsG)	0.015	0.002	8.243	<0.001
	ConvT	0.023	0.005	4.598	<0.001
	SemiC	0.002	0.003	0.860	0.390
	SemiN	0.012	0.004	3.199	<0.001
Ants	Intercept (ConsG)	2.744	0.118	23.224	<0.001
	ConvT	0.434	0.159	2.720	0.007
	SemiC	0.386	0.160	2.412	0.016
	SemiN	1.067	0.153	7.000	<0.001
Ground spiders	Intercept (ConsG)	4.957	0.125	39.631	<0.001
	ConvT	-2.241	0.195	-11.519	<0.001
	SemiC	-1.586	0.185	-8.558	<0.001
	SemiN	-1.340	0.183	-7.321	<0.001
Species richness		**Estimate**	**Std. Error**	**z-value**	**Pr(>|z|)**
Carabid beetles	Intercept (ConsG)	3.794	0.050	75.885	<0.000
	ConvT	-0.427	0.080	-5.366	<0.000
	SemiC	0.042	0.070	0.595	0.552
	SemiN	-0.070	0.072	-0.971	0.332
Rove beetles	Intercept (ConsG)	2.565	0.092	27.744	<0.000
	ConvT	-0.177	0.137	-1.294	0.196
	SemiC	0.000	0.131	0.000	1.000
	SemiN	-0.147	0.136	-1.083	0.279
Ants	Intercept (ConsG)	2.120	0.116	18.362	< 0.001
	ConvT	0.268	0.153	1.743	0.081
	SemiC	0.247	0.154	1.602	0.109
	SemiN	0.453	0.148	3.069	0.002
Ground spiders	Intercept (ConsG)	2.773	0.083	33.271	<0.001
	ConvT	-0.613	0.141	-4.361	<0.001
	SemiC	-0.666	0.143	-4.655	<0.001
	SemiN	-0.427	0.133	-3.217	<0.001

Table 4.2. Mantel correlations (for community composition) and Pearson correlations (for species richness) showed congruence between the carabids and the selected epigeic taxa.

Epigeic Taxa	Community composition		Species richness	
	r_m	*p*	*r*	*p*
Carabids | All epigeic	0.880	0.001	0.9469	<0.001
Carabids | Ground spiders	0.411	0.001	0.676	<0.001
Carabids | Rove beetles	0.266	0.003	0.524	0.001
Carabids | Ants	0.015	0.369	-0.374	0.025

4.5 Discussion

Diversity patterns

Conducting extensive surveys of biological communities is crucial for safeguarding biodiversity in various ecosystems. However, conducting a thorough assessment of entire communities can be time-consuming and expensive (Heino 2010). Therefore, surrogate methods such as utilizing indicator species or groups present a more cost-effective approach for evaluating biodiversity (Kotze & Samways 1999; Heino et al. 2009). This study specifically investigated the potential of carabid beetles as indicators of epigeic arthropod diversity in different farming systems. Previous studies have recognized the advantages of using carabid beetles as indicators because of their prevalence, diversity, functional significance, and expected response to environmental fluctuations (Homburg et al. 2019; Oberprieler et al. 2020). Consequently, their diversity patterns can serve as valuable tools for examining the biodiversity of other epigeic arthropod groups (Uboni et al. 2019).

Our study found that conservation grazing farming had a significantly higher abundance and richness of carabid beetles than other farming systems. This can be attributed to the management practices used in conservation grazing, such as minimizing disturbances and maintaining higher levels of vegetation cover. These practices create a more suitable habitat for ground-dwelling and litter-residing arthropods, increasing their populations (Hummel et al. 2012; Lami et al. 2019). Our findings also showed a consistent and significant association between the diversity of carabids and other epigeic arthropods, such as ground spiders and rove beetles, in conservation grazing farming. This finding further supports the positive impact of conservation management practices on arthropod communities in agricultural landscapes. Similarly, Brévault et al. (2007) found that spiders, ground beetles, and rove beetles collectively play pivotal roles as broad-spectrum arthropod predators in non-tilled and covered landscapes, amplifying pest regulation. In contrast, ants were abundant in semi-natural grasslands and conventional tillage, possibly because of soil conditions and habitat maturity. This phenomenon is likely influenced by factors such as enhanced soil permeability, moisture retention, and increased bare ground (Vanolli et al. 2021; Zulu et al. 2022). Increased diversity of ants in disturbed grasslands have been reported by Yekwayo et al. (2017) and Hlongwane et al. (2019). Additionally, it has also been suggested that ants prefer to forage in mature grasslands and migrate from neighbouring environments to cereal fields rather than form new colonies within them (Magura et al. 2018). Thus, it can be argued that the observed higher ant abundance in semi-natural grasslands and conventional tillage is likely a consequence of favourable soil conditions and the migratory behaviour of ants from mature grasslands (Azcárate & Peco 2012).

Carabid beetles as biodiversity indicator for epigeic taxa

Although surrogates have become prevalent in terrestrial biodiversity studies spanning various taxa, there is a notable research gap concerning the interaction between carabids and epigeic invertebrate taxa in agricultural landscapes (Cameron & Leather 2012). We demonstrated the efficacy of using carabid beetles as indicators for assessing the richness of epigeic fauna. Although the correlation in community composition was statistically significant, its magnitude remains moderate. Taxonomic richness is a simple but revealing measure of biodiversity, compressing the dynamics affecting diverse species populations (Allen et al. 1999a). Similarly, Corcos et al. (2021) observed varying diversity within ground-dwelling predators, where correlations in species richness were more pronounced than those in the community composition. This observation is crucial given the pivotal function that epigeic taxa play in farming environments. Notably, the results showed a weak correlation between carabid abundance and ant richness and composition (Bazzato et al. 2022). Such disparities in congruence may stem from the distinct responses of carabids and ants to agricultural systems (Heino 2010; Guareschi et al. 2015). Additionally, Lövei and Sunderland (1996) suggested that competition for territory and resources may be intense, especially between ants and carabids, because carabids, spiders, and some ant species belong to a broad surface-active predatory group.

The noticeable congruence among carabids, ground spiders, and rove beetles could likely result from shared habitat preferences (Griffiths et al. 2007; Batáry et al. 2012; Gaspar et al. 2010; Báldi et al. 2013), and similar resource consumption patterns, such as prey predation (Pohl et al. 2007; García-Ruiz et al. 2018; Vleminckx et al. 2019; De Heij & Willenborg 2020). According to Larsen et al. (2009) concordance among these three assemblages can shed light on environmental patterns and interspecies interactions. Prior research on farmland spiders and carabid beetles has pinpointed farming practices as essential drivers of these community configurations (Mashavakure et al. 2019). Our results are further supported by Lami et al. (2023), who highlighted the advantages of carabid beetles as potential biodiversity indicators. Their findings emphasized the potential of these beetles to reflect the species richness and community dynamics of both rove beetles and spider communities, specifically in the maize-dominated landscapes of Northern Italy. Likewise, Corcos et al. (2021) argued that, irrespective of habitat nature (natural or cultivated), the richness of ground beetle species intrinsically provides insights into other beneficial terrestrial predatory communities. This observation strengthens the notion that trends in carabid beetle diversity may represent those in other epigeic organisms (Uboni et al. 2019).

However, it is critical to note that species richness and compositional congruencies may vary with scale (Heino et al. 2009), necessitating caution in their application. A standard for determining the efficacy of a surrogate group in predicting the presence of other groups as "adequate" is when it accounts for over 60% of the overall species richness (Leal et al. 2010). The results of the current study demonstrate that although there was significantly lower covariation between carabid community composition and individual epigeic taxa, there was a significant and positive correlation between carabid and overall epigeic taxa. It is vital to emphasize that community composition congruence is often less explored than species richness (Allen et al. 1999b; Gaspar et al. 2010). Future investigations on surrogate assessments should focus on this component to refine the use of biodiversity indicators in conservation strategies. Our results suggest that carabids are effective indicators of epigeic taxa in various farming systems (Billeter et al. 2008; Oberprieler et al. 2020). According to Flather et al. (1997), correlations ranging from less than 0.5 to more than 0.79 can still be regarded as evidence of covariation. Similarly, Karyl (1999) has also considered a correlation of 0.54 (with values between 0.36 and 0.73) to be indicative of carabid beetles' potential as biodiversity indicators of Coleopteran beetles. Other authors have demonstrated positive surrogacy values across diverse taxa (Kotze & Samways 1999; Lovell et al. 2007; Chawaka et al. 2020). For example, Beccaloni and Gaston (1995) found significant positive congruence between the richness of ithomiine species and the overall richness of other butterfly species. This suggests that ithomiine species can be useful biodiversity proxies for the overall richness of butterfly diversity. In line with these findings, the results of the present study revealed a strong, significant correlation between the species richness of carabids and epigeic arthropods across various agricultural landscapes. Under such circumstances, species richness of carabids can effectively act as a suitable proxy for the richness of epigeic arthropod taxa.

4.6 Conclusion

This study highlights the value of carabid beetles as reliable biodiversity indicators for other epigeic taxa, notably ground spiders and rove beetles. By assessing carabids as a representative taxon, we can extrapolate the broader biodiversity of epigeic fauna in different agricultural contexts. This offers a practical tool for assessing the conservation status of grain agroecosystems because the costs of field surveys are very high (Uboni et al. 2019; Yong et al. 2020). Furthermore, recognizing dependable biodiversity indicator species, such as carabid beetles, allows conservationists and land stewards to measure ecosystem health and biodiversity effectively.

The adoption of feasible and sustainable strategies to protect insect species and their communities within agricultural ecosystems is beneficial and indispensable (Samways et al. 2020). An enlightened understanding of the ramifications of farming activities on the intricate diversity of soil-dwelling arthropods, and their crucial ecosystem services and functions, may empower agriculturalists. We suggest that future studies focus on a multi-taxon or 'shopping basket' methodology (Lovell et al. 2007), to understand the effect of agricultural management regarding the idiosyncratic response of different ecological groups (Kotze & Samways 1999; Bazzato et al. 2023). This approach broadens and enhances biodiversity monitoring, and supports conservation evaluation efficiency (Filgueiras et al. 2019). Such strategies are particularly beneficial for resource-limited developing countries, which may struggle with comprehensive biodiversity assessments.

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CHAPTER 5: CHARACTERIZATION OF CARABID FUNCTIONAL TRAITS IN DIFFERENT FARM SYSTEMS

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Abstract

Assessment of agroecosystem sustainability has traditionally relied on parameters such as abundance, species richness, and community composition. However, to better understand the impact of agricultural practices, there is growing recognition of the importance of incorporating functional traits as a sensitive indicator of environmental changes. Therefore, to improve the assessment of agroecosystem sustainability, it is essential to gain a deeper understanding of how different farming practices affect functional diversity. In this study, we focused on the functional traits of selected carabid beetle genera and their relationship with vegetation cover in distinct farming systems. These traits were derived from species characteristics, such as body size, wing morphology, and feeding type. Our results revealed significant differences in the total abundance of carabid genera among farm types, which were closely associated with vegetation cover. A notable statistical interaction was observed between carnivorous and granivorous carabid groups and vegetation coverage. The functional traits of small-to medium-sized carabids, typically characterized as macropterous, were more abundant than those of larger brachypterous carabid species. Conservation grazing was distinctive for the prevalence of larger carabids of the genera *Calosoma* and *Scarites* when compared to semi-conservation farming and conventional tillage. These findings underscore the vulnerability of larger predatory carabids to intensive farming. Our results suggest that safeguarding carabid functional diversity within agricultural landscapes requires implementing conservation strategies that bolster ecosystem services.

Keywords: carabid beetles, body size, dispersal ability, functional diversity, Generalized Additive Models, vegetation cover

5.1 Introduction

Most biodiversity studies have primarily focused on measuring species richness, composition, and abundance to quantify the effects of agricultural practices (Boinot et al. 2020). Subsequently, there is a notable gap in our understanding of other critical aspects of biodiversity, particularly the loss of functional traits (Pedley & Dolman 2014). An essential dimension of biodiversity pertains to the functional traits exhibited by organisms, including attributes such as body size, dispersal capabilities, and trophic roles (Schirmel et al. 2016; Djoudi et al. 2018; Deppe & Fischer 2023). Accumulating evidence strongly suggests that agricultural management practices can significantly influence various functional traits in ecosystems (Barber et al. 2017; Baulechner et al. 2019; Torma et al. 2019). It is important to extend our focus beyond taxonomic diversity assessments and delve into the broader impact of farming systems on functional diversity (Rouabah et al. 2015). Functional diversity includes various traits such as morphology, physiology, behavior, and life history strategies, which determine how species interact with their environment and influence ecosystem processes (Barber et al. 2017; Gallé et al 2020). Functional diversity also reflects the complexity and stability of an ecosystem, making it a valuable measure for understanding and managing biodiversity (Birkhofer et al. 2015). Therefore, there is an urgent need to unravel the intricate connections between management practices and functional diversity of arthropods in agricultural landscapes. Carabid beetles are crucial components of agroecosystems, providing ecosystem services for the control of pests and weed seeds in arable fields (De Heij et al. 2022). For instance, maintaining vegetation cover through specific management practices such as cover crops and crop residues can favor granivorous and omnivorous carabid species that feed on weed seeds, thereby yielding tangible benefits for crop protection (Gaines & Gratton 2010)

The functional trait of body size is a key aspect of carabid beetles, often closely linked to their wing morphology, such that larger species have reduced flight capabilities (Kotze & O'Hara 2003). Extensive research has illustrated the dynamic relationship between agricultural management practices, carabid body size, and dispersal ability (Barber et al. 2017; Chungu 2017; Gayer et al. 2019). Notably, in more stable agroecosystems, brachypterous species with larger body sizes are prevalent and characterized by their limited flight mobility (Deppe & Fischer 2023). In agricultural landscapes, the dispersal ability of carabids is a critical functional trait that governs their survival (Ng et al. 2018). The capacity to disperse within highly disturbed agroecosystems is of paramount importance, as it facilitates access to essential resources, such as food and shelter (Nolte et al. 2019). An exemplary demonstration of this adaptation can be observed in macropterous carabid species, which rapidly move between habitats in response to deteriorating environmental conditions. This remarkable trait enables them to thrive in the face of environmental fluctuations (Hanson et al. 2017).

In contrast, brachypterous species, characterized by their limited dispersal ability, are particularly vulnerable to disturbances inherent in agroecosystems (Martins da Silva et al. 2017). Additionally, the challenges faced by larger carabid species extend beyond dispersal, as their longer larval development periods exacerbate their vulnerability to soil disturbances in agricultural environments (Boinot et al. 2020). Species with a larger body size may be advantageous in diverse environments, especially when alternative resources are readily available (Philpott et al. 2019). Furthermore, body size has emerged as a critical determinant of pest consumption, with larger carabid species demonstrating the ability to consume larger quantities of pests, particularly those of substantial size (Boinot et al. 2020). This emphasizes the pivotal role of beetle body size in the ecological dynamics of pest regulation in agricultural systems (Boetzl et al. 2019). Therefore, the effect of farming practices on farmland biodiversity extends beyond taxonomic measures of species richness, composition, and abundance. Understanding how these management practices affect functional traits, such as body size, trophic guilds, and dispersal abilities, is essential for a more comprehensive biodiversity assessment. This knowledge not only aids in uncovering the reasons behind species decline, but also helps us appreciate the intricate interplay between farming practices and the functional diversity of organisms within agroecosystems (Birkhofer et al. 2015; Homburg et al. 2019). In this context, the current study aimed to characterize carabid beetle functional traits, including body size, feeding type/guilds, and wing morphology to elucidate how farming practices influence the functional traits of carabids. By examining distinct farm types characterized by varying management practices, this study tests the hypothesis that carabid beetle assemblages within conventional tillage and semi-conservation farming will consist of lower abundance of (1) brachypterous species (2) larger species, and (3) carnivorous species compared with conservation grazing.

5.2 Materials and methods

Study area

The study was conducted in Bethlehem (28°09'S; 28°18'E) and Reitz (27°52'S; 28°32'E) in the eastern Free State province of South Africa. The prevailing weather conditions in these regions are typically mild, warm, or temperate. We selected different grain agroecosystems, each separated by a distance of 5 km. These included conventional tillage, conservation grazing, semi-conservation farming, and semi-natural grasslands. Nine representative management practices spaced 500 m apart were replicated within the designated sampling sites. For more comprehensive details on the selected farm systems and their respective management practices, please refer to (Chapter 3; Appendix 4.1).

Carabid beetle sampling

Carabid beetles were collected over the course of two years, in 2020 (September-December) and 2021 (July-August). Pitfall traps and active search methods were used to sample carabid beetles. Eight traps were set up at the center of each sampling site, 10 m from the bordering grass margins. The distance between each pair of traps along the transect was adjusted to 30 m to decrease spatial autocorrelation. The traps were filled with a 70% propylene glycol preservative solution (Haysom et al. 2004) and left for seven days to avoid digging-in effects (Schirmel et al. 2010). For active searching, adult carabid beetles were hand-picked using forceps: two people spent 10 min actively searching within eight 5 × 5 m quadrats (spaced 2 m apart) 10 m from pitfall traps. Samples were sorted, recorded, and stored in 70% ethanol. Carabid beetles were identified mostly to genus, some to family, and then these were confirmed and assigned to morphospecies by Dr Colin Schoeman (University of Venda)

Vegetation assessment

To assess local vegetation characteristics, we positioned eight 5 × 5 m quadrats 2 m from the trap. Within each quadrat, the coverage percentages of grain crops, weeds, and grass species (refer to Appendix 4 for a comprehensive list) were determined by capturing two parallel ground-level images, spaced at no less than 60 cm from the uppermost canopy. These visual data were subsequently subjected to accurate analysis utilizing specialized digital imaging software http://www.canopeoapp.com on a mobile device (Patrignani & Ochsner 2015). This software is specifically designed to measure the coverage of green canopies and is user-friendly and cost-effective. Canopeo utilizes a color-coding system to convert green cover into white pixels and bare land into black pixels, resulting in the percentage of white-colored pixels in the image (Govindasamy et al. 2022).

Functional traits

Carabid beetle functional traits were divided into three distinct groups: body size, feeding preference, and dispersal ability, as outlined in the Appendix 3.1. Carabid genera were assigned to body size classes ranging from small to medium (3 mm – 12 mm) and large (12.1 mm – 22 mm) according to (Cole et al. 2012; Schirmel et al. 2012). Dispersal ability was assessed through wing morphology, specifically distinguishing between brachypterous species with hind wings shorter than elytra or completely absent, and macropterous species with fully developed hind wings longer than elytra, drawing on data from Homburg et al. (2019) and Schirmel et al. (2012). Feeding preferences were classified as carnivorous/predators, granivorous, or omnivorous based on insights from several (Larochelle & Larivière 2003; Purtauf et al. 2005; Liu et al. 2015). For subsequent analyses, the data were standardized using the total abundance of the dominant carabid genera recorded across the selected study sites.

5.3 Statistical analysis

Data analyses were conducted on the total abundance of six carabid genera that occurred in the three-farm system (*i.e.,* conventional tillage, conservation grazing, and semi-conservation farming). Graphical representations were generated using ggplot2 (Wickham 2016). To ensure the integrity of the results, the data and residuals were tested for heterogeneity of variance and normality. This was achieved using the Shapiro-Wilk normality test using the package rstatix and residual graphs (Kassambara 2021). All analyses were conducted in R version 4.0.3 (R Core Team 2020).

To explore the potential influence of farm type on carabid total abundance and functional traits, Generalized Additive Models (GAM) with Poisson error distribution were used. Farm type was treated as a categorical explanatory factor, while vegetation cover percentage was incorporated as a smoothing factor using thin-plate splines (De Heij et al. 2022). Nonmetric Multidimensional Scaling (NMDS) was employed to visualize the similarities and differences among functional traits across different farm types. Additionally, we assessed the significance of clustering through ANOSIM analysis (Kędzior & Skalski 2019). These analyses were based on the total abundance of carabid genera, providing valuable insights into the functional diversity within farm types.

5.4 Results

Among the six recorded carabid genera, the majority (580 individuals), comprising four genera, were in the small-medium size category, measuring between 3 mm and 12 mm (Appendix 3.1). Notably, *Bembidion* spp. were highly dominant within this size category, with 256 individuals recorded. Additionally, three other genera, *Pterostichus*, *Harpalus*, and *Amara*, contributed substantially to this group. The remaining two carabid genera were larger, ranging between 13 mm and 22 mm (Appendix 3.1). A total of 318 individuals represented larger carabids. Among these, *Calosoma* emerged as the predominant genus, followed by *Scarites*.

Total abundance

The total carabid abundance of the most caught carabid genera differed significantly among farm types ($p < 0.001$, Table 5.1). The statistical model employed in our analysis explained 78.6% of the variance in total carabid abundance among the various farm types, as evidenced by an adjusted R-squared value of 0.768. Conservation grazing significantly supported the higher abundance of carabid genera compared with other farming systems.

Functional traits

Furthermore, larger-sized carabids exhibited significantly higher abundance in conservation grazing, whereas lower abundance was observed in semi-conservation and conventional tillage systems ($p < 0.05$). Within the small to medium-sized carabid group, *Bembidion*, *Amara*, and *Harpulas* showed significant differences across all farm types (Table 5.2). The analysis was extended to examine carabid functional traits and community composition, which revealed significant differences among the farm types. Non-Metric Multidimensional Scaling (NMDS) plots and Analysis of Similarities (ANOSIM) yielded an R-value of 0.652, indicating highly significant variation ($p = 0.001$) in carabid communities across different farm types. The carabid genera *Calosma* and *Scarites*, characterized as larger predatory species, played a pivotal role in shaping the observed community variations. Their prominent influence is evidenced by their centroids, which are notably distant from the center of the ordination graph (Figure 5.1).

There was a significant interaction between the functional traits, vegetation cover, and farm systems. Macropterous and brachypterous species and percentage of vegetation cover (smooth term) ($p < 0.001$) showed a strong statistical relationship. The high adjusted R-squared value of > 0.80 suggests that the model indicates variation in carabid wing morphology (Table 5.2; Appendix 3.2). The adjusted R-squared value of 0.575 showed moderate variation in granivorous carabids, while the adjusted R-squared value of 0.743 indicated significant variation in carnivorous/predaceous carabids. In contrast, omnivorous species did not show a significant relationship with the % vegetation cover (smooth term). The adjusted R-squared value of 0.274 indicated that the model explained no variation in omnivorous carabids (Table 5.2; Appendix 3.2).

Table 5.1. Effects of the farm type (Intercept - Conservation grazing; ConvT - Conventional tillage; SemiC - Semi-conservation farming) on the total carabid abundance of genera grouped according to their body size. Data were modeled (with GAMs).

	Farm type	Estimate	Std.error	t-value	Pr(>|t|)	R^2 adj	Deviance explained
Total abundance							
	(Intercept)	64.556	4.259	15.157	0.001		
	ConvT	-51.556	6.023	-8.559	0.001	0.768	78.60%
	SemiC	-45.889	6.023	-7.619	0.001		
Small-Medium (3mm-12mm)							
Harpalus							
	(Intercept)	1.674	0.1443	11.598	0.001		
	ConvT	-0.6131	0.2435	-2.518	0.012	0.154	0.21%
	SemiC	-0.47	0.2327	-2.019	0.043		
Pterostichus							
	(Intercept)	1.6529	0.1459	11.332	0.001		
	ConvT	-0.2392	0.2198	-1.088	0.276	-0.0418	0.0389%
	SemiC	-0.1613	0.2151	-0.75	0.453		
Amara							
	(Intercept)	2.0369	0.1204	16.92	0.001		
	ConvT	-2.2882	0.3967	-5.768	<0.001	0.483	0.516%
	SemiC	-1.2384	0.254	-4.876	<0.001		
Bembidion							
	(Intercept)	15.333	1.877	8.168	<0.001		
	ConvT	-10.444	2.655	-3.934	0.001	0.349	0.40%
	SemiC	-6.778	2.655	-2.553	0.017		
Large (12.1mm-22mm)							
Scarites							
	(Intercept)	1.914	0.128	14.946	0.001		
	ConvT	-21.216	3142.206	-0.007	0.995	0.688	0.891%

	SemiC	-21.216	3142.206	-0.007	0.995		
Calosoma							
	(Intercept)	3.18727	0.06773	47.059	0.001		
	ConvT	-21.4899	1905.844	-0.011	0.991	0.856	0.957%
	SemiC	-21.4899	1905.844	-0.011	0.991		

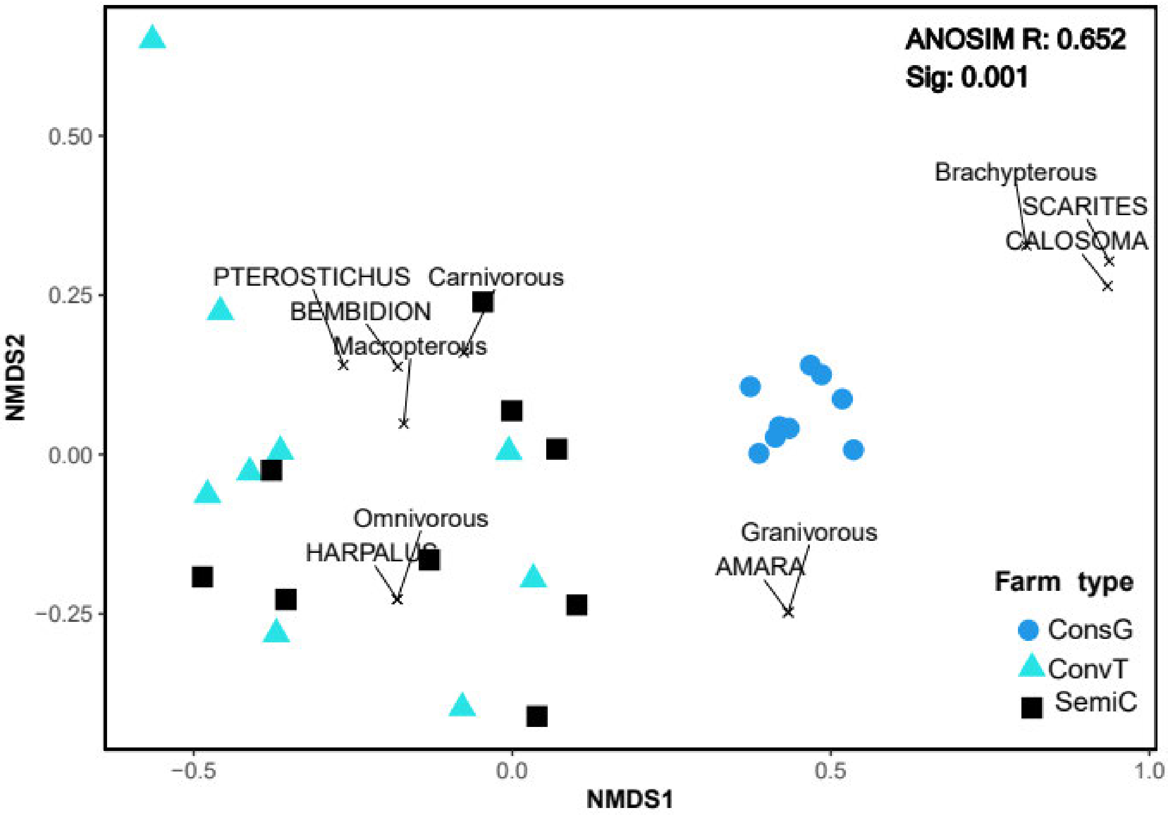

Figure 5.1. NMDS plots showing functional traits of carabid genera across the farm type ConG - Conservation grazing, ConvT - Conventional tillage, and SemiC - Semi-conservation farming. The shapes correspond to farm systems. ANOSIM indicates the significance of the separation between carabid functional traits and farm type based on species composition.

Table 5.2. ANOVA results for carabid functional traits: wing status and feeding type in relation to vegetation cover % across the farm systems modeled (with GAMs).

	Edf	Ref.df /df	χ^2	*p* value	R^2 adj
Wing Status					
Macropterous					
% VegCover (Smooth term)	8.781	8.98	45.7	< 0.001	0.866
*Farm.Sys * % VegC*		2	8.716	0.001	
Brachypterous					
% VegCover (Smooth term)	2.106	2.539	9.803	0.0147	0.88
*Farm.Sys * % VegC*		2	45.69	0.001	
Feeding type					
Granivorous					
% VegCover (Smooth term)	1.045	1.088	5.589	0.0197	0.575
*Farm.Syst * % VegC*		2	1.221	0.543	
Carnivorous					
% VegCover (Smooth term)	2.826	3.456	15.82	0.0021	0.743
*Farm.Syst * % VegC*		2	45.69	0.001	
Omnivorous					
% VegCover (Smooth term)	1.751	2.147	3.329	0.227	0.274
*Farm.Sys * % VegC*		2	7.58	0.0226	

*Significant effect at $p < 0.05$. Edf = effective degrees of freedom. Ref.df = reference degrees of freedom. $\chi2$ = Chi-square. R2 adj = adjusted R2; Farm.Sys: Farm System; % VegC: Vegetation Cover

5.5 Discussion

Carabid total abundance and functional traits differed significantly across various farm systems, and these can be explained by variations in management practices (as described in Chapter 3), also see Hatten et al. (2007). These results were driven by the higher abundance of smaller to medium-sized species compared to larger carabids (Hanson et al. 2016). This finding is noteworthy because body size plays a pivotal role in predicting pest control services (Chungu 2017; Rusch et al. 2018). Moreover, the body size distribution within carabid assemblages is crucial for effective pest control (Veres et al. 2013). Small-medium-sized carabids, including carnivorous species such as *Bembidion* and *Pterostichus*, are significantly more abundant in all farm types (Baguette & Hance 1997; Irmler 2003). Their abundance can be attributed to the availability of pest species, such as aphids, particularly in semi-conservation farming and conventional tillage, thereby contributing to biological pest control (Rusch et al. 2013). These carnivorous species may benefit from increased management intensity owing to their wing morphology, allowing them to move among habitats in unstable conditions and enabling survival in such environments (Winqvist et al. 2014).

Furthermore, granivorous and omnivorous carabid beetles, specifically *Amara* and *Harpalus*, show higher abundance in semi-conservation farm systems because of the availability of crop and weed species (Purtauf et al. 2005; Menalled et al. 2007). Semi-conservation farming practices, such as cover cropping and crop rotation, appear to foster a significant association between vegetation cover and omnivorous and granivorous taxa (White et al. 2007; Boinot et al. 2020). The high abundance of seed-eating ground beetles in semi-conservation farming may help reduce the weed seed bank (Lami et al. 2019), reducing competition with desirable planted crop species during their early establishment (Diehl et al. 2012; García-tejero et al. 2013). Vegetation cover plays a crucial role in providing shelter for ground-dwelling insects and suitable overwintering sites (de Pedro et al. 2020). In our study, the observed variations in wing status and feeding preferences or guilds within carabid populations were associated with the percentage of vegetation cover. Similarly, Meiss et al. (2010) noted a positive impact of vegetation cover in crop fields on carabid beetles, attributing it to several factors, such as establishment of favorable microclimates, provision of a substrate for reproduction, availability of alternative food sources, and a reduction in predation risk.

Conservation grazing is usually linked to increased food resources and microclimatic conditions, which could explain why carabid assemblages are dominated by larger species of *Calosoma* and *Scarites*, species known to hunt on the ground, and feeding on larger prey such as fall armyworms and slugs (Fusser et al. 2017; Mugala et al. 2023). Djoudi et al. (2018) found that carabid assemblages were characterized by medium to large species, feeding on a larger diversity of diets mainly due to an enhanced diversity of cultivated vegetation and weeds in organic farming. Soil cultivation significantly affects larger carabid species because of their reliance on stable conditions and limited ability to disperse under unfavorable circumstances, such as pesticide application, harvesting, and tilling (Griffin et al. 2017). This effect is observed in both conventional and semi-conservation farming practices, where the absence of the carabid genera *Calosoma* and *Scarites* is noted, as compared to conservation grazing. These findings support the notion that larger carabid species, particularly wingless ones, serve as sensitive indicators of less intensively managed habitats (Winqvist et al. 2014). Similarly, Cole et al. (2006) found that the large flightless carabid genus *Carabus* favoured an extensive grazing regime over intensive practice.

5.6 Conclusion

Our study revealed a significant interplay among carabid functional traits, farm systems, and vegetation cover. These findings support the prevailing consensus that large brachypterous and carnivorous carabid beetles serve as sensitive indicators of intensive management practices within agricultural landscapes (Cole et al. 2006). Consequently, it is evident that farm type, notably conservation grazing with less intensity, holds the potential to bolster the preservation of valuable large species, in contrast to intensive management practices that have detrimental effects on the functional diversity of insects (Cole et al. 2012). Additionally, our results underscore the importance of safeguarding vegetation cover on farms, as this has been demonstrated to support phytophagous carabid species. These carabids can offer valuable ecosystem services within croplands, particularly for weed seed suppression. By utilizing a functional trait-based approach, we can better understand the relationships among agricultural ecosystems, biodiversity, and ecosystem services. With this knowledge, informed decisions can be made to promote the preservation and sustainability of agricultural landscapes for the benefit of both humans and the environment.

5.7 References

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CHAPTER 6: GENERAL DISCUSSION AND CONCLUSIONS

The main goal of this thesis was to document and further elaborate on the use of carabid beetles (Coleoptera: Carabidae) as model organisms for evaluating the impact of grain agroecosystem management practices in South Africa. This evaluation encompassed a range of functional parameters such as taxonomic composition, abundance, diversity, and functional traits. The aim of this study was to validate the potential of carabids as robust indicators for ecological, biodiversity, and ecosystem service assessments.

In South Africa and other African countries, carabid beetles are widely distributed, occupy diverse habitats, and maintain stable populations throughout the year (Schoeman et al. 2018). They display strong ecological affinities to various environments and exhibit sensitive responses to changes in agricultural ecosystems (Botha 2017; Jowett et al. 2022). Furthermore, using well-established and standardized methods, carabids can be efficiently sampled with minimal effort and without specialized equipment (Schirmel et al. 2010). Their relatively uncomplicated identification also contributes to their status as one of the most extensively studied invertebrate taxa globally (Rainio & Niemela 2003).

Research Synthesis

Ecological Indicators: This study provides persuasive evidence that carabid beetles possess the attributes necessary to serve as reliable ecological indicators, given their consistent and readily observable responses to environmental shifts. Findings from conventional tillage and semi-conservation farming systems demonstrate the rapid responsiveness of carabids to ecological disturbances, owing to their sensitivity to factors such as pesticides, tillage practices, and post-harvest residue burning (Holland et al. 2002). However, the ecological requirements of different species vary, making them more susceptible or resistant to environmental change (Cole et al. 2006). This variability translates into distinct carabid species compositions among agroecosystems, reflecting the impact of various management practices (Koivula et al. 2004).

Biodiversity Indicators: Biodiversity serves as a fundamental cornerstone in maintaining ecosystem functionality and providing an array of invaluable services (Leal et al. 2010). Specifically, terrestrial ecosystems harbor substantial biodiversity beneath the soil (Munyai et al 2021; Solascasas et al 2022), yet comprehensive assessments of these communities using diverse sampling methods present significant economic challenges (Chiatante et al. 2021). Therefore, applying surrogate methods, such as indicators that accurately reflect the diversity patterns of other species, is essential for conservation initiatives within agricultural landscapes (Oertli et al. 2005). In this regard, this study demonstrated the efficacy of carabid beetles as biodiversity indicators for epigeic taxa, namely ants, ground spiders, and rove beetles. The current results revealed a robust and positive correlation between the diversity patterns observed in carabids and the overall diversity of the epigeic fauna. As such, preserving carabid populations ensures proportional protection of other epigeic organisms across diverse grain agroecosystem management practices in South Africa. Previous research by Beattie and Oliver (1995) identified carabid beetles as promising indicators of biodiversity for other epigeic families, including Scarabaeidae and Pselaphidae.

Ecosystem Services Indicators: Carabid beetles are economically important because of their role as substantial predators of agricultural pests and weeds. The provision of ecosystem services related to biological pest control is closely associated with various functional traits (Rusch et al. 2018). This study aimed to investigate the potential of these beetles as indicators of ecosystem services, focusing on three key functional traits: wing status, body size, and feeding preference/guilds. The underlying assumption was that the responses of the community in terms of these traits reflected the impact of farming practices and vegetation cover. The findings of the current study revealed that larger-bodied, predatory carabid species are sensitive to disturbances within agroecosystems (Fischer et al. 2021). This sensitivity is primarily attributed to wing morphology, as wingless or dimorphic carabid species face limitations in dispersal, hindering their ability to thrive in adverse conditions. The results of this study align with those of previous studies, notably Deppe and Fischer (2023), who also observed a decline in the population of specialized, large-bodied species in modern compared to traditional agricultural ecosystems in mid-western Germany. In contrast, smaller and versatile species with efficient dispersal capabilities tend to thrive under such conditions. The current study also suggests that "% vegetation cover" supports a substantial portion of the variance in functional traits, such as wing status, body size, and feeding preferences, among carabid beetles in diverse farm types (Frenzel & Fischer 2022).

Recommendation for Agroecosystem stability based on Carabid indicator species

Stability: Carabid beetles from the genera *Calosoma* and *Scarites* have demonstrated their potential as effective indicators of agroecosystem stability, as evidenced by their high IndVal values (Luff 1996; Horne 2007). These carabid species can be relied upon to signal undisturbed environments, as they were exclusively found in conservation grazing agroecosystems, in contrast to other farm types. In terms of their functional traits, these carabid species are characterized by their large body size and brachypterous nature, indicating limited dispersal ability (Kotze et al. 2011). This explains their absence in disturbed agroecosystems such as those subjected to conventional tillage. It should be acknowledged that body size is a pivotal factor in predicting pest control services, with larger carabids exhibiting higher rates of pest consumption (Chungu 2017). Farmers should recognize the presence of these species as indicators of stable habitat conditions, and effective predators of larger pest species known to affect crop yields, including fall armyworms, slugs, and snails (Mugala et al. 2023).

Disturbance: The results of this thesis underscore the fact that not all carabid species are susceptible to disturbances; some are eurytopic and can thrive in various agroecosystems (Hatten et al. 2007). The carabid genera *Pterostichus* and *Amara*, commonly observed in conventional agroecosystems, have been noted to thrive despite altered conditions (Holland & Luff 2000). This is further supported by their functional traits, characterized by their macropterous nature and strong dispersal abilities, which enable their persistence in unstable environments (Deppe & Fischer 2023). Despite their relatively small-medium body size these carabid species exhibit opportunistic feeding behaviors, allowing for the exploitation of both plant materials and invertebrate prey (Honek et al. 2003). With their occurrence in conventional tillage and semi-conservation farming settings, these carabids play an essential role in reducing pest species such as aphids and controlling weed seeds (De Heij et al. 2022). Furthermore, their rapid colonization in disturbed habitats highlights their resilience and ability to establish populations in altered environments (Cole et al. 2005). Considering these findings, it is crucial for farmers to recognize *Pterostichus* and *Amara* as indicators of disturbance and appreciate their contribution as generalist predators, providing valuable ecosystem services in terms of biological pest and weed control.

Conversion: The semi-conservation farming, which entails a progressive transition towards conservation agriculture, can be monitored through the occurrence of certain indicator species. I have found that carabid species of the genus *Harpalus* were significantly associated with semi-conservation farming. This correlation is likely attributed to the increased coverage of weeds and crop residues, which act as valuable food sources and provide shelter for these beetles (De Heij et al. 2022). Despite deep tilling and herbicide applications in semi-conservation agroecosystems, the *Harpalus* genus exhibits a significant response, indicating its ability to thrive in environments affected by human activity (Ivanicˇ Porhajašová & Babošová 2022). *Harpalus* beetles are characterized by their small body size and macropterous nature, which result in greater dispersal capabilities (Leslie et al. 2009; Deppe & Fischer 2023). Considering these findings, it is imperative for farmers, particularly those transitioning to conservation farming and implementing cropping strategies, to consider these carabids as omnivorous. They possess the capability to exploit a wide range of food sources to sustain their populations, including germinating weed seeds (De Heij & Willenborg 2020). It is crucial to recognize that these beetles thrive in anthropogenically altered environments, and can serve as indicators of stability and efficacy of transitioning to conservation agriculture.

Implication for agroecosystem conservation management

The intensification of agriculture within natural landscapes has primarily contributed to the biodiversity decline worldwide. In response to this pressing issue, South Africa has taken proactive measures to implement conservation agricultural practices (DAFF 2017). The primary goal of these initiatives is to promote biodiversity and ecosystem services in farmlands (Malobane et al. 2020). Furthermore, ongoing climate-smart agriculture initiatives are being pursued focusing on various indicator studies aimed at assessing the adoption and effectiveness of conservation agriculture (Blignaut et al. 2015; Midgley et al. 2015). Drawing from the findings of the current study, it is recommended that farmers adopting regenerative conservation agriculture employ the following practices to enhance biodiversity and ecosystem services in their farmlands:

Cropping management practices: This involves retaining mulch after harvest, employing crop rotation, and utilizing cover crops. These practices increase the diversity of vegetation cover, which in turn offers additional habitats and food sources for carabid beetles (Bengtsson et al.

2005). Crop rotation is crucial as it provides a trophic resource, with seeds lost during harvest becoming a palatable food source for granivorous carabid species. Diversifying crops, including non-harvested plants, promotes soil conservation and contributes to the survival of beneficial soil-dwelling arthropods, ultimately enhancing ecosystem services (Boetzl et al. 2019).

Semi-natural elements: Including neighboring strips of flowers, grass, and beetle banks, are pivotal in facilitating the provision of refugia, breeding grounds, and wintering habitats for carabid beetles (Purtauf et al. 2005). These habitats also serve as primary sites for re-colonization following mowing, grazing, and harvesting. The presence of a substantial amount of surrounding grasslands within agricultural landscapes enhances the functional dynamics of carabid beetle populations (Feng et al. 2021) .

Reducing soil cultivation: The implementation of reduced soil cultivation methods has been observed to results in higher plant density and greater weed diversity (Fanfarillo et al. 2022). As a result, this can create favorable microclimatic conditions, thereby promoting an increase in the population and diversity of ground-dwelling fauna. In addition, reducing reliance on chemical pesticides and promoting integrated pest management can foster a more balanced ecosystem.

Implementing these practices can significantly contribute to the success of conservation agriculture and the conservation of carabid beetles and other epigeic fauna, promoting biodiversity and enhancing ecosystem services in South African agricultural landscapes**.**

Limitations of the study and recommendation for future work

The use of carabid beetles as indicators of ecological conditions, biodiversity, and ecosystem services within the South African agroecosystem poses several significant challenges. A major difficulty is the limited attention these beetles have received, particularly in the African agricultural context, as evidenced by our recent review (Makwela et al. 2023). Consequently, our knowledge of the biology and distribution of most African carabid species remains limited because of a lack of accessible field guides and taxonomic keys. Insufficient funding for taxonomic research further compounded this issue, resulting in a lack of species-level invertebrate identification. The limited funding for biodiversity studies in agricultural landscapes has restricted our sampling to short-term periods, making it difficult to establish long-term biomonitoring for insects and their roles in ecosystem functioning in agricultural landscapes. As a result, expanding the sampling areas to encompass other regions within South African provinces has proven to be a daunting task, limiting the current study's ability to draw broader conclusions applicable to larger spatial scales and diverse grain agroecosystems.

The fact that I have provided evidence of the status of carabid beetles and their use as model organisms to evaluate their effectiveness as indicators of ecological conditions, biodiversity, and ecosystem services represents a significant step forward in advancing sustainable agricultural practices. Notably, larger *Scarites* and *Calosoma* carabids have been identified as key species because of their high sensitivity to disturbances, making them valuable indicators of ecological sustainability (Ball & Bousquet 2000; Talarico et al. 2018). Therefore, I recommend that future research endeavors to delve deeper into identifying carabid beetles to species level and quantifying their trophic networks using DNA barcoding, a molecular tool for species identification (Govender & Willows-Munro 2019). This approach can significantly contribute to the implementation of integrated pest management practices, ultimately diminishing reliance on agrochemicals, and fostering a more sustainable agricultural approach. By employing DNA barcoding to unravel the trophic interactions of these species, we can identify indicators of ecosystem services at species level, and further refine strategies for sustainable pest control in agriculture (Rusch et al. 2018).

Considering the lack of resources and the cost-intensive nature of measuring overall biodiversity within agricultural landscapes (Lovell et al. 2007), it is prudent to consider surrogate indicators that can effectively reflect the diversity of other arthropod species, particularly those inhabiting the soil (Solascasas et al. 2022). This approach would allow for a more efficient and cost-effective assessment of arthropod populations and their crucial roles in agroecosystems. It would be advantageous to undertake multi-taxon assessments across a variety of agroecosystems to accurately delineate and preserve biodiversity and the vital ecosystem services it provides (Boetzl et al. 2021). To facilitate such comparative surveys and support farmers in their efforts, systematic and rigorous observations must be conducted using standardized methodologies and measurements. Therefore, I encourage the implementation of regular monitoring protocols to effectively gauge the biodiversity present on farmlands and track the efficacy of conservation agriculture practices. Such a proactive approach has the potential to greatly inform and refine sustainable farming techniques while also providing valuable insights for effective biodiversity conservation and ecosystem service provision. This approach can serve as a valuable tool for farmers for long-term monitoring and conservation efforts. Given the ongoing decline in global arthropod populations and their essential contributions to agricultural productivity, it is imperative to employ innovative approaches for their conservation and management.

Conclusion

The findings of this thesis highlight the efficacy of carabid beetles as reliable indicators for evaluating environmental conditions within agricultural ecosystems in the studied region. This represents a significant advancement in facilitating decision-making processes and potentially promoting the robust management and restoration of agricultural ecosystems and semi-natural grasslands (Midgley et al. 2015). These results align with the growing recognition among policymakers that preserving biodiversity in agricultural landscapes plays a crucial role in upholding ecosystem functionality and stability and providing vital ecosystem services (Vink & Kirsten 2003; DAFF 2017). The knowledge derived from this thesis holds significant potential for supporting the adoption of regenerative conservation agriculture programs that aim to conserve biodiversity and ecosystem services (Knot 2014). These initiatives encompass a diverse range of indicator studies that assess the implementation and effectiveness of conservation agriculture in South Africa (Blignaut et al. 2015). This, in turn, raises awareness, enhances knowledge, and fosters collaboration between farmers and researchers in promoting sustainable production practices (DAFF 2017; DALRRD 2022).

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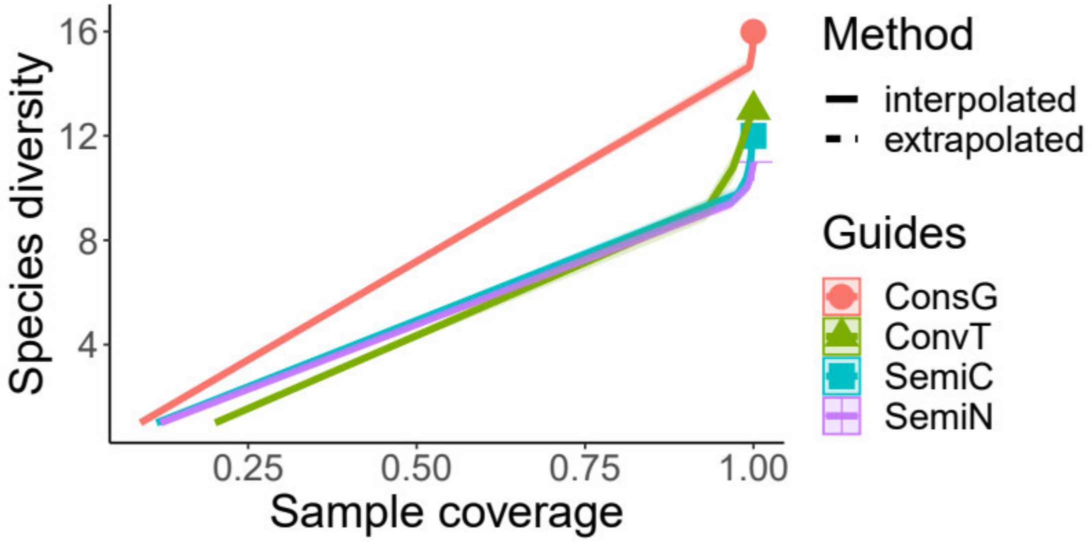
APPENDIX 1

Appendix 1.1. Abundance of carabid beetle morphospecies recorded in the sampled farm systems. ConvT = Conventional Tillage; ConsG = Conservation Grazing; SemiC = Semi-Conservation farming; SemiN = Semi-Natural grassland.

Code	Morphospecies	ConvT	ConsG	SemiC	SemiN	Total	%
Bsp1	Bembidion sp. 1	23	51	19	22	115	5.53
Hsp1	Harpulas sp.1	18	40	70	29	157	7.56
Csp1	Calosoma sp. 1	0	247	0	1	248	11.93
Hsp2	Harpulas sp.2	4	29	19	33	85	4.09
Bsp2	Bembidion sp. 2	19	34	15	9	79	3.80
Bsp3	Bembidion sp. 3	15	72	30	13	145	6.98
Psp1	Pterostichus sp. 1	27	49	49	35	160	7.70
Psp2	Pterostichus sp. 2	30	55	47	17	170	8.18
Csp2	Calosoma sp. 2	0	165	7	0	172	8.28
Csp3	Calosoma sp. 3	0	122	0	0	122	5.87
Hsp3	Harpalus sp. 2	11	53	43	13	120	5.77
Ssp1	Scarites sp. 1	0	207	0	0	207	9.96
Ssp2	Scarites sp. 2	0	144	0	0	144	6.93
Asp1	Amara sp. 1	19	59	40	23	154	7.41
	Abundance(N)	166	1316	339	195	-	-
	Richness(S)	25	107	61	17	-	-



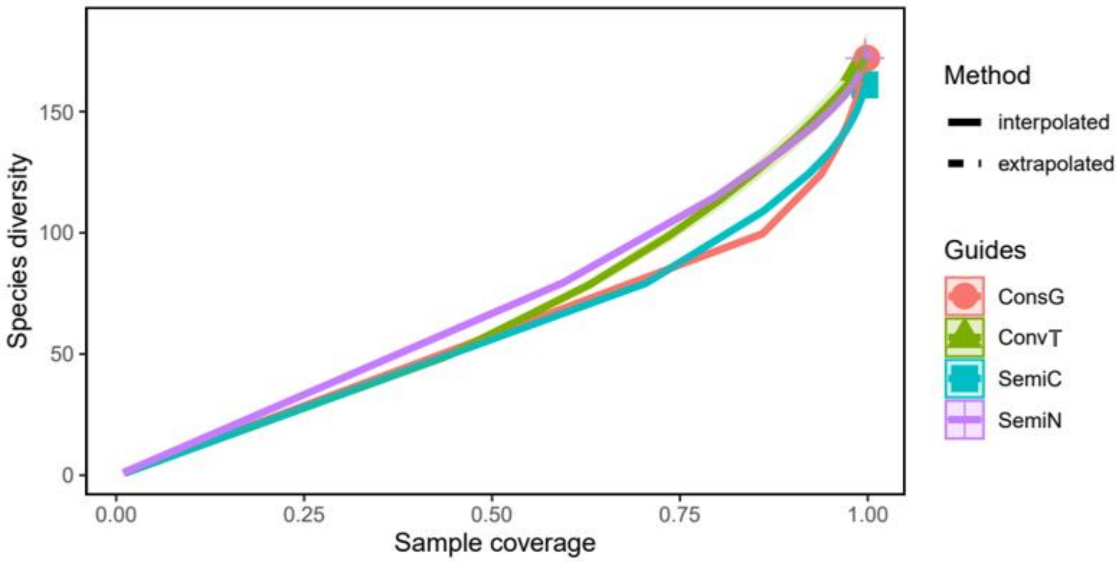
Appendix 1.2. Coverage-based rarefaction and extrapolation curves sampling curves with 95% confidence intervals (shaded areas, based on a bootstrap method with 200 replications) indicating carabid richness for data of the farm systems: ConvT-Conventional tillage; ConsG- Conservation grazing; SemiC-Semi-conservation farming and SemiN – Semi-natural grassland.

APPENDIX 2

Appendix 2.1. Epigeic arthropods taxa checklist of morphospecies collected across the study area) collected from the farm systems (ConsG - Conservation grazing; ConvT - Conventional tillage; SemiC - Semi conservation; SemiN - Semi natural grassland).

ORDER	Family	Morphospecies	ConsG	ConvT	SemiC	SemiN
Coleoptera	Carabidae	Bembidion sp. 1	x	x	x	x
	Carabidae	Harpulas sp.1	x	x	x	
	Carabidae	Calosoma sp. 1	x	x		
	Carabidae	Harpulas sp.2	x	x		
	Carabidae	Bembidion sp. 2	x	x	x	x
	Carabidae	Bembidion sp. 3	x	x	x	x
	Carabidae	Pterostichus sp. 1	x	x	x	
	Carabidae	Pterostichus sp. 2	x	x	x	
	Carabidae	Calosoma sp. 2		x	x	
	Carabidae	Calosoma sp. 3		x	x	
	Carabidae	Harpalus sp. 2	x	x	x	
	Carabidae	Scarites sp. 1		x		
	Carabidae	Scarites sp. 2		x		
	Carabidae	Amara sp. 1	x	x	x	x
	Carabidae	Carabidae sp.1	x			
	Carabidae	Carabidae sp.2	x		x	
	Carabidae	Carabidae sp.3	x		x	x
	Carabidae	Carabidae sp.4	x		x	
	Carabidae	Carabidae sp.5	x	x	x	
	Carabidae	Carabidae sp.6	x	x		x
	Carabidae	Carabidae sp.7		x		x
	Staphylinidae	Atheta sp.1	x			
	Staphylinidae	Atheta sp.2	x			
	Staphylinidae	Atheta sp.3	x			
	Staphylinidae	Atheta sp.4		x		x
	Staphylinidae	Atheta sp.5		x		x
	Staphylinidae	Atheta sp.6			x	
	Staphylinidae	Atheta sp.7			x	
	Staphylinidae	Staphylinidae sp.1	x	x		
	Staphylinidae	Staphylinidae sp.2	x	x		
	Staphylinidae	Staphylinidae sp.3	x	x		
	Staphylinidae	Staphylinidae sp.4	x		x	x
	Staphylinidae	Staphylinidae sp.5			x	
	Staphylinidae	Staphylinidae sp.6	x	x		
Araneae	Linyphiidae	Erigone sp.1	x			
	Linyphiidae	Erigone sp.2	x	x		
	Linyphiidae	Erigone sp.3	x			
	Linyphiidae	Meioneta sp.1		x		

	Linyphiidae	Meioneta sp.2	x			
	Licosidae	Pardosa sp.1			x	
	Licosidae	Pardosa sp.2	x		x	
	Licosidae	Pardosa sp.3			x	
	Licosidae	Pardosa sp.4			x	
	Gnaphosidae	Trephopoda sp.1	x	x		x
	Gnaphosidae	Trephopoda sp.2	x	x	x	x
	Gnaphosidae	Trephopoda sp.3	x		x	x
	Gnaphosidae	Trephopoda sp.4	x	x		
	Gnaphosidae	Nomisia sp.1				x
	Gnaphosidae	Nomisia sp.2			x	x
	Gnaphosidae	Nomisia sp.3				x
	Lycosidae	Lycosidae sp.1	x			
	Lycosidae	Lycosidae sp.2				
	Lycosidae	Lycosidae sp.3	x	x	x	x
	Lycosidae	Licosidae sp.1			x	x
	Lycosidae	Licosidae sp.2	x			x
	Lycosidae	Licosidae sp.3				x
	Lycosidae	Licosidae sp.4	x	x	x	x
	Lycosidae	Licosidae sp.5	x	x	x	
Hymenoptera	Formicidae	Tetramorium sp.1	x			x
	Formicidae	Tetramorium sp.2				x
	Formicidae	Tetramorium sp.3				x
	Formicidae	Dorylus sp.1	x			x
	Formicidae	Dorylus sp.2	x			x
	Formicidae	Pheidole sp.1		x	x	x
	Formicidae	Pheidole sp.2		x		x
	Formicidae	Pheidole sp.3		x		x
	Formicidae	Pheidole sp.4				
	Formicidae	Lepisiota sp.2		x		x
	Formicidae	Solenopsis sp.1		x		x
	Formicidae	Solenopsis sp.2		x		x
	Formicidae	Solenopsis sp.3		x		x



Appendix 2.2. Coverage-based rarefaction and extrapolation curves sampling curves with 95% confidence intervals (shaded areas, based on a bootstrap method with 200 replications) indicating epigeic taxa richness for data of four farm systems: ConvT – Conventional tillage; ConsG – Conservation grazing; SemiC – Semi-conservation farming and SemiN – Semi-natural grassland.

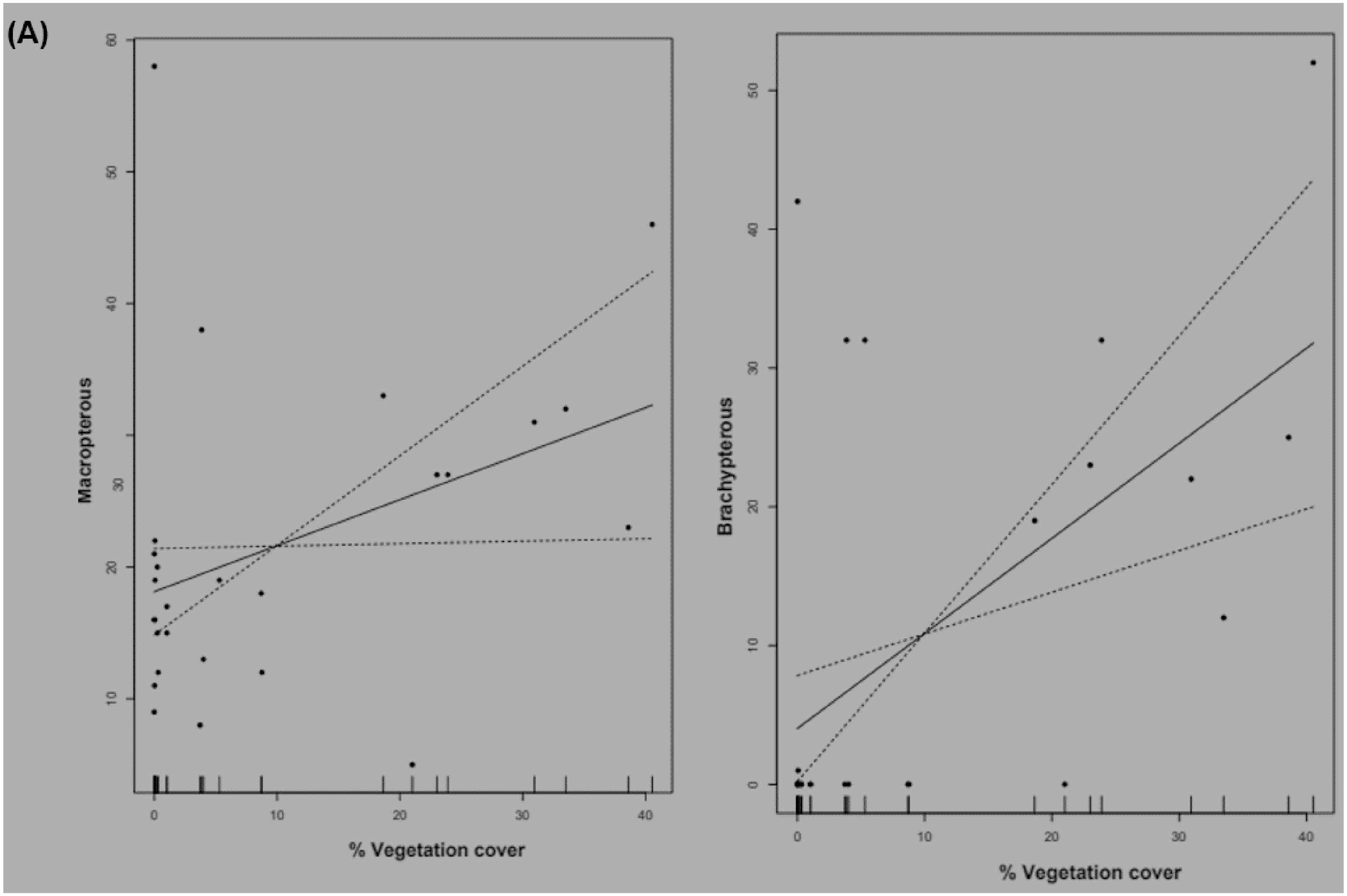
Appendix 2.3. Data indicating Ab (Abundance) and, SppR (Species richness); Car: Carabid beetles; G-Spid: Ground spiders; Rov: Rove beetles; Ant; across the four farm systems.

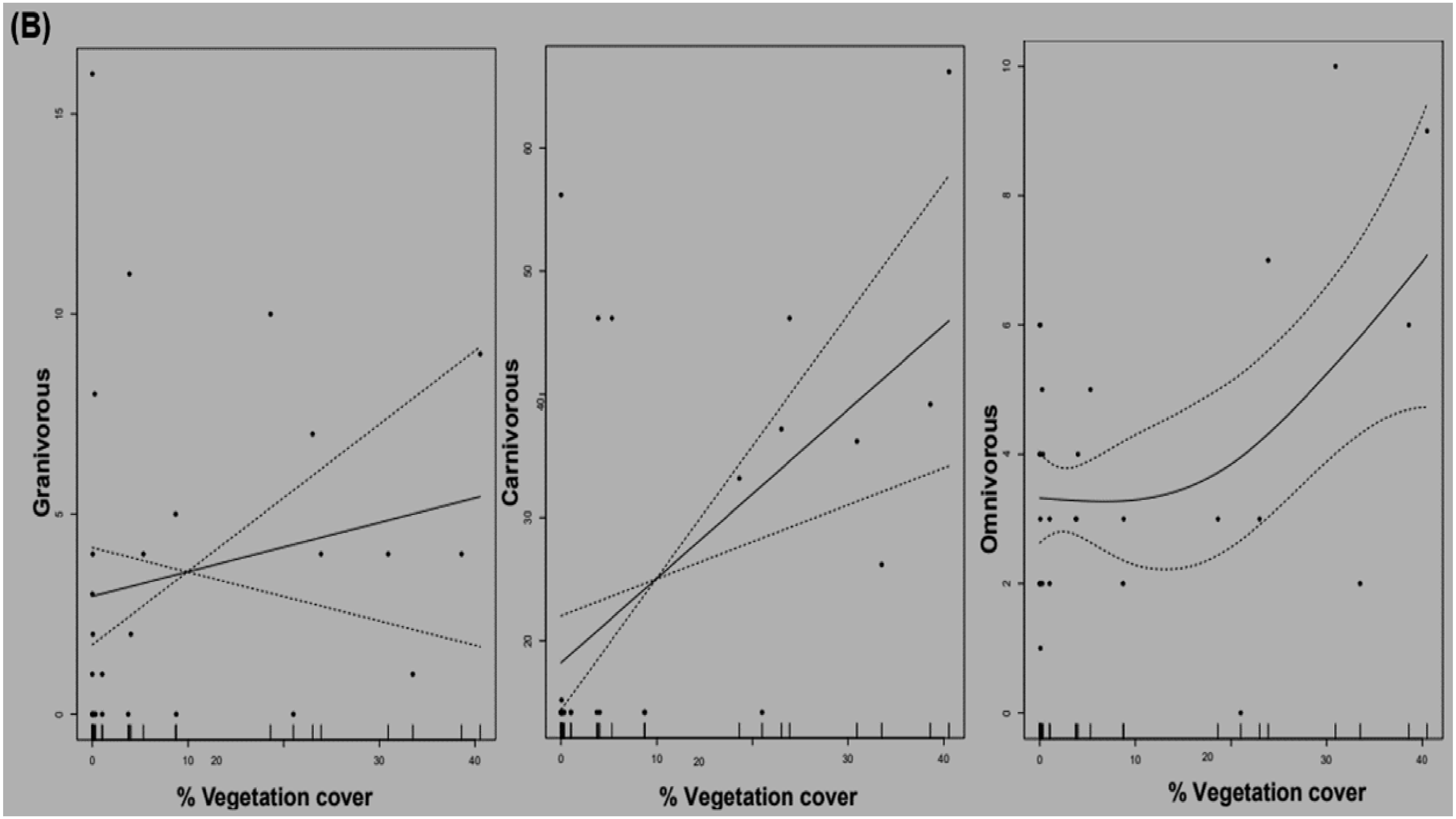
FarmID	Farm Systems	AbCar	SppR	AbSpid	SppR	AbRov	SppR	AbAnt	SppR
ConvT	Conventional tillage	23	4	27	30	41	0	32	0
ConvT	Conventional tillage	5	0	5	0	8	0	16	0
ConvT	Conventional tillage	15	3	18	0	5	0	4	0
ConvT	Conventional tillage	9	5	14	0	9	0	33	0
ConvT	Conventional tillage	12	2	14	0	15	0	51	0
ConvT	Conventional tillage	35	6	41	0	10	2	12	2
ConvT	Conventional tillage	44	1	11	0	4	0	32	0
ConvT	Conventional tillage	34	0	23	2	11	2	18	0
ConvT	Conventional tillage	20	0	20	0	19	0	6	0
ConsG	Conservation grazing	488	0	17	1	125	1	33	0
ConsG	Conservation grazing	44	9	49	0	23	1	6	0
ConsG	Conservation grazing	601	2	76	0	167	6	45	0
ConsG	Conservation grazing	356	8	117	0	13	2	10	0
ConsG	Conservation grazing	169	12	94	1	88	1	14	0
ConsG	Conservation grazing	564	4	41	0	9	9	38	1
ConsG	Conservation grazing	223	26	249	6	73	2	19	5
ConsG	Conservation grazing	129	8	137	4	37	4	31	1
ConsG	Conservation grazing	654	4	92	2	102	1	34	1
SemiC	Semi-conservation farming	251	11	56	7	76	6	21	0
SemiC	Semi-conservation farming	91	7	60	0	64	1	13	0
SemiN	Semi-natural grassland	38	2	40	0	41	0	39	0
SemiC	Semi-natural grassland	294	4	112	3	9	0	24	3
SemiC	Semi-conservation farming	103	0	44	1	55	0	55	1
SemiN	Semi-natural grassland	67	0	53	1	13	0	11	0
SemiC	Semi-conservation farming	334	5	93	0	3	3	16	0
SemiC	Semi-conservation farming	129	2	109	0	75	0	7	0
SemiN	Semi-natural grassland	32	0	12	0	34	0	5	0
SemiC	Semi-natural grassland	127	0	18	0	55	2	33	0
SemiC	Semi-conservation farming	76	5	77	0	37	1	25	2
SemiN	Semi-natural grassland	30	6	36	0	76	5	16	5
SemiC	Semi-conservation farming	450	7	51	0	61	2	20	3
SemiC	Semi-conservation farming	213	5	33	1	44	2	54	0
SemiN	Semi-natural grassland	69	3	72	2	22	3	35	7
SemiC	Semi-natural grassland	109	12	36	0	71	0	43	3
SemiC	Semi-conservation farming	112	2	23	0	59	0	47	9
SemiN	Semi-natural grassland	44	4	42	0	83	1	71	5
Total		5994	169	2012	61	1637	57	969	48

APPENDIX 3

Appendix 3.1. Carabid morphospecies functional traits information and their status +, presence; −, absence; in the sampled farm systems (ConvT – Conventional tillage, ConsG – Conservation Grazing, SemiC – Semi - Conservation farming, Semi- Semi - Natural grassland).

Morphospecies	Feeding type	Wing status	Body size (mm)	Grouping	CovT	ConsG	SemiC	SemiN
Bembidion sp. 1	Carnivorous	Macropterous	3.5	Small-Medium	+	+	_	_
Harpulas sp.1	Omnivorous	Macropterous	10.5	Small-Medium	+	+	+	_
Calosoma sp. 1	Carnivorous	Brachypterous	19.1	Large	_	+	_	_
Harpulas sp.2	Omnivorous	Macropterous	7	Small-Medium	+	+	+	_
Bembidion sp. 2	Carnivorous	Macropterous	4.5	Small-Medium	+	+	+	+
Bembidion sp. 3	Carnivorous	Macropterous	3.05	Small-Medium	+	+	+	+
Pterostichus sp. 1	Carnivorous	Macropterous	18	Large	+	+	+	_
Pterostichus sp. 2	Carnivorous	Macropterous	10.5	Small-Medium	+	+	+	_
Calosoma sp. 2	Carnivorous	Brachypterous	18.9	Large	_	+	_	_
Calosoma sp. 3	Carnivorous	Brachypterous	19.8	Large	_	+	_	_
Harpalus sp. 2	Omnivorous	Macropterous	11.5	Small-Medium	+	+	+	_
Scarites sp. 1	Carnivorous	Brachypterous	20.3	Large	_	+	_	_
Scarites sp. 2	Carnivorous	Brachypterous	21.4	Large	_	+	_	+
Amara sp. 1	Granivorous	Macropterous	6.5	Small-Medium	+	+	+	_


(A)
Macropterous
% Vegetation cover
Brachypterous
% Vegetation cover
0
10
20
30
40
50
60



Appendix 3.2. Smoothers (s) plots produced by the mgcv-package in R: showing the relationship (solid line) between functional traits (A) Wing status (B) Feeding type and % vegetation cover. The solid lines are the smooths fitted to the residuals to help highlight any strong trends that may be present. Plotted lines are based on model predictions (Tables 5.2).

APPENDIX 4

Appendix 4.1. Study Area (BHM – Bethlehem; RTZ – Reitz) information prior to sampling period indicating crop and weed species status, vegetation cover and pest status across the sampled farm systems (ConvT – Conventional tillage, ConsG – Conservation Grazing, SemiC – Semi - Conservation farming, Semi- Semi - Natural grassland) and ManID - management type (MN – Monoculture, SB – Slush Burn, FL – Fallow Land, LG – Long term Grazing, SG – Short term Grazing, NG – Natural grassland, CR – Crop Rotation, CC – Cover Crops, RG – Recovering grassland).

FarmID	ManID	Crop/Weeds type	Crop/Weed species	Farm status-2020	Avg/ % VegC	Farm status-2021	Pest status	Latitude	Longitude	Elevation	Area
ConvT	MN	Wheat	*Triticum aestivum*	Heading stage	34.32	Harvested	Aphids/Army worm	-28.1656	28.29247	1662	BHM
ConvT	SB	Wheat	*Triticum aestivum*	burned	0.6	Recovered slush burn	Aphids/Army worm	-28.1641	28.29726	1653	BHM
ConvT	FL	Bare soil	Bare soil	Tilled	4.34	Seedling stage/Barley (*Hordeum vulgare*)	Aphids/Army worm	-28.1748	28.33031	1647	BHM
ConvT	MN	Wheat/ Wild Buckwheat	*Triticum aestivum/ Polygonum convolvulus*	Heading stage	38.37	Harvested	Aphids/Army worm	-28.1558	28.2979	1654	BHM
ConvT	SB	Wheat/ Wild Buckwheat	*Triticum aestivum/ Polygonum convolvulus*	burned	83.61	Recovered slush burn	Aphids/Army worm	-28.1534	28.30459	1625	BHM
ConvT	FL	Bare soil	Bare soil	Tilled	59.89	Seedling stage/Wheat (*Triticum aestivum*)	Aphids/Army worm	-28.1543	28.30048	1646	BHM
ConvT	MN	Oats/ White Goosefoot	*Avena sativa/ Chenopodium album*	Heading stage	34.37	Harvested	Aphids/Army worm	-28.1535	28.29638	1653	BHM
ConvT	SB	Barley/ White Goosefoot	*Hordeum vulgare/ Chenopodium album*	burned	0.01	Recovered slush burn	Aphids	-28.0953	28.35226	1664	BHM

ConvT	FL	Bare soil	Bare soil	Tilled	0.41	Seedling stage/Oats (*Avena sativa*)	Aphids	-28.1569	28.29218	1655	BHM
ConsG	LG	Rye	*Secale cereale*	Full grown	25.16	Trimmed	Aphids	-28.1731	28.3045	1633	BHM
ConsG	SG	Maize	*Zea maize*	Leaves-cop D-stage	63.82	Maize residue	Slug/Aphids	-28.1708	28.30073	1653	BHM
ConsG	NG	Rye grass/ Fireweed	*Lolium perene/ Senecio madagascariensis*	Full grown	79.99	Trimmed	slug	-28.172	28.29823	1652	BHM
ConsG	LG	Rye	*Secale cereale*	Full grown	80.36	Trimmed	Slug/White grub	-28.1674	28.29648	1660	BHM
ConsG	SG	Maize	*Zea maize*	Leaves-cop D-stage	41.63	Maize residue	Slug/White grub	-28.1835	28.29693	1656	BHM
ConsG	NG	Rye grass/ Fireweed	*Lolium perene/ Senecio madagascariensis*	Full grown	56.42	Trimmed	Slug/White grub	-28.1813	28.29286	1669	BHM
ConsG	LG	Rye	*Secale cereale*	Full grown	47.89	Trimmed	White grub	-28.175	28.28996	1674	BHM
ConsG	SG	Maize	*Zea maize*	Leaves-cop D-stage	30.99	Maize residue	Weevil	-28.1763	28.29381	1669	BHM
ConsG	NG	Rye grass/ Fireweed	*Lolium perene/ Senecio madagascariensis*	Full grown	83.64	Trimmed	Weevil	-28.1701	28.30306	1648	BHM
SemiC	CR	Soybean-Maize	*Glycine max/Zea mays*	Seedling stage	68.2	Crop residue	Slug/White grub	-27.8954	28.54567	1729	RTZ
SemiC	CC	leguminous plant/Rye/Oats	*Vicia orobus/ Secale cereale/Hordeum vulgare*	Active growth	0.54	Active growth	Slug/Aphids	-27.8899	28.54679	1701	RTZ
SemiN	RG	Smut finger grass	*Digitaria eriantha*	Full grown	3.44	Trimmed	White grub	-27.894	28.5374	1695	RTZ

SemiC	CR	Soybean-Maize	*Glycine max/Zea mays*	Seedling stage	12.19	Crop residue	White grub	-27.8825	28.54135	1704	RTZ
SemiC	CC	leguminous plant/Rye/Oats	*Vicia orobus/ Secale cereale/Hordeum vulgare*	Active growth	13.68	Active growth	White grub	-27.8832	28.54018	1702	RTZ
SemiN	RG	Smut finger grass	*Digitaria eriantha*	Full grown	17.42	Trimmed	White grub	-27.9027	28.53793	1717	RTZ
SemiC	CR	Soybean-Maize	*Glycine max/Zea mays*	Seedling stage	26.2	Crop residue	Weevil	-27.8834	28.53042	1694	RTZ
SemiC	CC	leguminous plant/Rye/Oats	*Vicia orobus/ Secale cereale/Hordeum vulgare*	Active growth	20.26	Active growth	White grub/Aphids	-27.8782	28.5382	1713	RTZ
SemiN	RG	Smut finger grass	*Digitaria eriantha*	Full grown	23.36	Trimmed	Weevil	-27.9007	28.53535	1716	RTZ
SemiC	RG	Maize-Sunflower-Potatoes	*Zea maize-Harpalium-Solanaceae*	Leaves-cop D-stage	10.91	Crop residue	Weevil	-27.8906	28.53297	1686	RTZ
SemiC	CC	leguminous plant/Rye/Oats	*Vicia orobus/ Secale cereale/Hordeum vulgare*	Active growth	36.4	Active growth	Aphids/Army worm	-27.8929	28.53182	1680	RTZ
SemiN	RG	Smut finger grass	*Digitaria eriantha*	Full grown	22.7	Trimmed	Weevil	-27.9007	28.53535	1716	RTZ
SemiC	CR	Maize-Sunflower-Potatoes	*Zea maize-Harpalium-Solanaceae*	Leaves-cop D-stage	26.41	Crop residue	White grub	-27.8786	28.53686	1715	RTZ
SemiC	CC	leguminous plant/Rye/Oats	*Vicia orobus/ Secale cereale/Hordeum vulgare*	Active growth	20.9	Active growth	Aphids/Army worm	-27.8919	28.5367	1695	RTZ
SemiN	RG	Smut finger grass	*Digitaria eriantha*	Full grown	19.01	Trimmed	Weevil	-27.9006	28.5379	1709	RTZ

SemiC	RG	Maize-Sunflower-Potatoes	*Zea maize-Harpalium-Solanaceae*	Leaves-cop D-stage	15.56	Crop residue	White grub	-27.8899	28.54679	1701	RTZ
SemiC	CC	leguminous plant/Rye/Oats	*Vicia orobus/ Secale cereale/Hordeum vulgare*	Active growth	10.8	Active growth	Aphids/Army worm	-27.8908	28.53671	1692	RTZ
SemiN	RG	Smut finger grass	*Digitaria eriantha*	Full grown	23.16	Trimmed	Weevil	-27.9031	28.53298	1719	RTZ